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Modelling seasonal and annual variation in size at functional maturity in the European lobster (*Homarus gammarus*) from self-sampling data

Martial Laurans[1, *], Spyros Fifas[1], Sébastien Demaneche[1], Stéphane Brérette[1] and Olivier Debec[2]

[1] Technopole Pointe du Diable, Ifremer, 29280 Plouzané, France
[2] 14 rue Pierre Bouguer, 44490 Le Croisic, France

*: Corresponding author : M. Laurans: tel: +33 2 29 00 85 02; fax: +33 2 29 00 85 47; email address : martial.laurans@ifremer.fr

Abstract:

Fishers from Le Croisic (France) measure all the lobsters (*Homarus gammarus*) they capture, indicating their sex and whether the females are ovigerous or non-ovigerous. Between 2003 and 2006 and mainly between April and September, 16 884 lobsters were measured in this manner. These self-sampled data were used to study catchability and functional maturity of lobsters. The sex ratio was 50%, and catchability did not change if a female was ovigerous or non-ovigerous. With the help of a logistic function, a relationship was established between body size and the proportion of ovigerous females. For the study area, 100% of the females were mature upon reaching a carapace length (CL) of 115 mm, and the proportion of ovigerous females reached 70% each year. The L_{50} value evolved over a CL of 103–106 mm. From the size when 100% of the females matured (115 mm), there was a larger proportion of ovigerous females than in other studies carried out in more northern European areas.

Keywords: catchability, functional maturity, *Homarus gammarus*, self-sampling

1. Introduction

An annual activity calendar documents the two main fishing trips performed each month for each boat of the French fishing fleet. In 2007, 405 potters and 127 netters composed the fleet targeting crustaceans. The netters target only spider crab with special gear. Of the 405 potters, 190 targeted European lobster (*Homarus gammarus*) during at least one month, mainly along the Brittany and Normandy coasts. They were essentially represented by boats smaller than 12 m and with a maximum of 3 men on board. The other potters are less dependent on lobster, targeting both edible crab and spider cab. Currently, the French lobster landings represent approximately 400 t, of which the lobster potters catch 70%. Fishing effort is currently controlled by a number of licences and a maximum number of pots per fisherman on board.

The maintenance of the reproductive capacity of a stock is a constant concern in fisheries management. For many species, the L_{50} for maturity is used to establish the minimum legal size of catches. The reproductive biomass, and increasingly, the relative reproductive potential (Katsukawa, 1997) are being used in management to define the maximum threshold fishing mortality (F).

“Data on reproductive biology are important for modelling and the management of population egg production in lobster fisheries. It is also important to determine the geographic scales over which these biological characteristics vary in order to apply appropriate stock management measures to each region” (Tully *et al.*, 2001). In the case of lobster, the relationship between size and fecundity does not seem to vary significantly between areas (Tully *et al.*, 2001). On the other hand, some published results show wide variations for the maturity ogive and L_{50} (Table 1) according to the area considered [e.g. Latrouite *et al.* (1981, 1984), Free *et al.* (1992), Tully *et al.* (2001), and Lizarraga-Cubedo *et al.* (2003) for the European lobster, Aiken and Waddy (1980) for the American lobster (*Homarus americanus*), and (Hobday and Ryan, 1997) for the rock lobster (*Jasus edwardsii*)].

What is indicated by “maturity” varies according to authors. A distinction is made between physiological maturity and functional maturity, but different stages are reported depending on the study. For instance, Aiken and Waddy (1980) consider that physiological maturity is the size at which a lobster starts to produce spermatozoa or ovules, and functional maturity as the size at which lobsters are ready to copulate or to effectively spawn and which can be assessed by morphometry.

Morphometry has frequently been used to define the size at maturity of male or female lobsters. This is more obvious in males, where one can define maturity by direct observation (presence/absence) of a secondary sexual character (e.g. appendix masculaina) (Kulmiye *et al.*, 2006), than in females, where it is more difficult. In addition, it also provides little information on the real contribution of reproduction in terms of eggs. Conan *et al.* (1985, 2001) conclude that the appearance of maturity in American lobster cannot be effectively detected by morphometry for either males or females. Tully *et al.* (2001) come to a similar conclusion for European lobster. Other techniques can be used to determine physiological maturity, such as the observation of the colour of ovaries and the presence of gametes in testicles.

It might be preferable to use the terms “morphological maturity” and “physiological maturity” depending on circumstances and retain the expression “functional maturity” only when maturity is based on the observation of ovigerous females. One could also suggest another term such as, for example, “spawning size”. The functional maturity model quantifies the annual proportion of spawning females by class size, with the beginning of the asymptote defining the minimum size where 100% of the females are mature. In any event, the functional maturity ogive is the most relevant parameter to model the fecundity of a stock or the egg yield per recruit. The aim of the present research is to attempt to describe, with precision, factors affecting the construction of the model, such as time of year, size, year, area, and so on (Waddy and Aiken, 2005). The dataset used was the result of self-sampling data carried out by a fisherman of the Loire Atlantique in the southern part of the fishery.

2. Material and methods

Self-sampling data

A privileged relationship with a fisherman from Le Croisic harbour in the Loire Atlantique area (Figure 1) led him to offer to measure a sample of caught lobsters in 2003. This fisherman targets lobster part of the year and fishes for shrimp (*Palaemon serratus*) the remainder of the year. After a short trial period with his crew, he offered to measure all lobsters. After each string of pots, the fishermen measured all lobsters, indicating their sex regardless of size and whether the females were ovigerous; ovigerous lobsters were landed. The fishing area was off Le Croisic on banks (Figure 1) in close proximity to each other.

Catchability

A comparison of the catchability between ovigerous and non-ovigerous female lobsters was performed. The evolution of the sex ratio of the catch was analysed by developing an ANOVA test, where the effects of year, month, and proportion of ovigerous females (level from 1 to 10) were tested. Data consisted of 391 records, each representing the data for one fishing day, with the following information: year, month, total number of lobsters, number of females, and number of ovigerous females.

Model of functional maturity

In many studies, a logistic function enables the establishment of a relationship between body size and the proportion of ovigerous females. This method is sensitive to annual and seasonal factors (Tully *et al.*, 2001) and Wenner and Siegel, 1981). However, a logistic model was developed where the asymptote (*AS*), the L_{50}, and the slope (γ) were linear functions of year and month modality (we assumed that slope was not dependent on year):

$$\theta(l) = AS \Big/ 1 + \exp[-\gamma(L - L_{50})]$$

$$AS = 1 - \alpha_1 M - \beta_1 A_1 - \beta_2 A_2$$

$$\gamma = p - \alpha M$$

$$L_{50} = C - \alpha_2 M - \beta_{11} A_1 - \beta_{22} A_2$$

where M is month, A_1 = 1 for 2005 or 0 elsewhere, and A_2 = 1 for 2006 or 0 elsewhere. When the model was fitted, the following parameters were estimated: p, C, α, α_1, α_2, β_1, β_2, β_{11}, and β_{22}.

The model was fitted minimizing the sum of mean residual squares. In order to test the model sensitivity for the variables considered, the matrix of variances–covariances was calculated according to a parametric procedure (Fifas and Berthou, 1999). This calculation was possible considering, at the first analysis stage, limited developments of order 1 in Taylor's series (Laurec, 1987 and Fifas *et al.*, 2004). Our work aimed at deriving the above model relative to the nine estimated parameters. With the help of the estimation of each variable's variance, a Fisher–Snedecor test was used to evaluate whether they were significant.

In order to perform the analyses, the data were aggregated according to the following rules:
by size classes of 2 mm from 80 to 140 mm of carapace length, and
by month and size class, considering the proportion of ovigerous females as the total of ovigerous females divided by the total number of females.

3. Results

Self-sampling data
The data used in this study were measurements of the lobsters fished by a potter between June 2003 and October 2006. During that time, 16 884 lobsters were measured mainly between April and September of each year (Table 2, Figure 2). During this period, daily fishing effort remained constant at 400 pots. The crew typically fished every day except Sunday. In June 2005, no data were collected for 2 weeks. The catch of lobsters (number per month) increased yearly until July followed by a decrease. This situation characterises the high activity of lobsters during summer.

Sixty percent of the total catch had carapace lengths greater than 100 mm. With a legal size of 87 mm, this represents as much as 70% (Figure 3). The same structure was observed when only females were considered (Figure 3). This size structure suggested the catch came from several cohorts and indicates a moderate exploitation rate.

Catchability
After a first exploratory analysis, the year 2003 was excluded from our analysis as well as March and October of each year because of poor data (absence or few fishing days) (Figure 2). The ANOVA test indicated no significant differences in sex ratio between years, months, or the proportion of ovigerous females (Table 3, Figure 4). This result enabled us to assume that female catchability does not change throughout the year. Consequently, these catch data were considered as representative of the lobster population studied.

Model of functional maturity
An exploratory analysis suggested that the proportion of ovigerous females changed according to year and month (Figure 5). This observation led to the development of a logistic function describing the ovigerous curve, where the variables year and month were taken into account. Moreover, in order to express the asymptote, slope, and L_{50} as linear functions of the variables, the fitted function was realised for March–July 2004–2006, where a decrease or increase was observed for these parameters. The year 2003 was not taken into account because no data were provided for April and May.

After the calculation of the parameters and their variance, the Fisher–Snedecor test indicated that the coefficients associated with month were significant, and for the year variable, only the coefficients β_1, β_2, and β_{11} were significant (Table 4).

These results suggested several aspects of the functional maturity. The period July–August was characterized by a lower percentage of ovigerous females (Figure 5). Each year, the ovigerous curve varied between April and July, with an increase in the L_{50} (Figure 6). This situation could indicate that the biggest females keep their eggs externally for a longer time. Moreover, considering a single month, the year effect (β_{11} significant) suggested that the L_{50} value could change from year to year (Figure 7). Considering the months of April of 2006 and 2004, the L_{50} value was 103 mm; however, in 2005, it was 106 mm. The asymptote values (Figure 7) indicated that at least 70% of the females of carapace length greater than 115 mm were ovigerous each year. This value was clearly greater in 2005 and 2006 (β_1 *and* β_2 significant), approximately 80 and 90%, respectively.

Discussion

High quality of data

The high quality of the data collected by the fisherman must be emphasized. The fisherman indicated that every potter with a minimum of two crew members, including the skipper, could perform the same work. Indeed, a maximum of 2 min is necessary to measure lobsters and can be done in the sailing time between two strings of pots. In any given area, observers cannot achieve such a sampling intensity simply because of the high cost. This highlights the importance of encouraging fishermen to develop self-sampling schemes and the usefulness of having good contacts with the fishing industry.

The measurements of all caught lobsters provided a sample which was very representative of the population in this area. The daily information allowed continuity in monitoring several parameters of the population, including the proportion of ovigerous females.

Catchability

For the lobster, maturity studies suggest that results can be biased by a difference between catchability of ovigerous and non-ovigerous females (Latrouite *et al.*, 1981); Tully *et al.,* 2001; Branford, 1979; Agnalt *et al.*, 2007). However, in this study, the data available were sufficiently precise to suggest that catchability of females was the same whether they are ovigerous or non-ovigerous. This conclusion is important in order to validate the results on the proportion of spawning females, because it means there is little or no modification of the behaviour of the ovigerous female lobster. This result is equally reinforced by the fact that the fishing techniques were not modified during the fishing period.

Model of functional maturity

The results of this study indicate that a minimum of 70% of females were ovigerous each year at a carapace length greater than 115 mm. In France, Latouite *et al.* (1981, 1984) suggested a similar value for two different areas, one in Brittany and one south of the present area. Further north, no studies show such a high proportion of ovigerous females at the size where 100% are considered mature (Tully *et al.*, 2001; Free *et al.*, 1992; Agnalt *et al.*, 2007). However, differences can originate from the time of year considered. Here, the proportion of berried females was greater in April than in June. Latrouite *et al.* (1981) take this situation into account to propose a functional maturity curve. Conversely, Tully *et al.* (2001) consider all the data between April and October and Agnalt *et al.* (2007) propose a value of 58% for all sizes in spring. We assume that these studies underestimate the proportion of mature females that become ovigerous each year.

The year effect in the value of the asymptote (Table 4) can account for the lobster reproductive cycle in which lobsters may spawn annually, biannually, or pluriannually. Agnalt *et al.* (2007) or another study using few individuals (Bertran and Lorec, 1986) illustrate well this variability. Nevertheless, the absence of data in January and February means that it is impossible to conclude whether the year effect is the consequence of changes in environmental parameters (actual difference in the value of the peak of ovigerous females (Figures 5 and 7) or the consequence of a difference in the time the peak takes place. Latrouite *et al.* (1984) suggest that a lack of information in January and February can lead to an underestimation of the proportion of ovigerous females and an overestimation of the value of the L_{50}. With the present data (Figure 5), the peak of spawning females also seems to be in January and February. Moreover, continuity in lobster spawning, as seen by the presence of some berried females every month and their subsequent release of eggs throughout a large period of the year from March to July (i.e. the process is not synchronized to occur at any one time) is observed (Smith, pers. comm.) and confirmed by the increase of the L_{50} throughout the period from April to July. These elements and the high proportions of berried females in April suggest that almost all female lobsters of carapace length greater than 115 mm are spawning annually in the study area. This scheme differs from the 2-year reproductive cycle described by Agnalt *et al.* (2007), but is similar to the multiple fertilization pattern described by Waddy and Aiken (1986), in which the large American lobster (*Homarus americanus*) females of >120 mm carapace length consecutively spawn.

Several authors suggest that the variation in the L_{50} value for one area [interannual variation as seen in the present study or in Hobday and Ryan (1997)] or for distinctive areas [different latitudes as in Aiken and Waddy (1980), Hobday and Ryan (1997), Annala *et al.* (1980), or Free *et al.* (1992)] may be explained by the impact of environmental factors such as temperature or by other factors such as growth rate, age, metabolic rate, population density, or food availability. The present study confirms the high interannual variations in lobster maturity found in previous research. With a longer time-series, it will be possible to test the influence of some environmental factors (Landers *et al.*, 2001). Since January 2007, an instrument buoy, which measures temperature, salinity, oxygen, and chlorophyll at a fixed point on the ground and surface, has been positioned close to the fishing area. With the acquisition of this data, it will be possible to test those elements assumed to influence the L_{50}.

In the present study, it appears that the largest females retain their eggs externally for a longer time. To date, available data do not support the fact that this observation could result from later spawning of these large females. That could mean that most of them have more energy to carry their eggs for a longer period of time compared to young females. This situation can be linked to the increase in egg size and fecundity with the size of the female (Latrouite *et al.*, 1984; Tully *et al.*, 2001), which characterizes the higher spawning capacity of the bigger females.

One of the main applications of functional maturity is to estimate the relative reproductive potential (RRP) (Katsukawa, 1997; Tully *et al.*, 2001; Agnalt *et al.*, 2007; Linnane *et al.*, 2008). This enables the identification in a lobster population of the size classes which have the maximum potential to produce eggs. The value of the RRP is sensitive to the functional maturity curve used. Underestimating the proportion of ovigerous females (e.g. by using a curve fitted in a period when few females are ovigerous) leads to bias in the RRP and its evolution. We can assume that the estimation of the RRP in the study by Tully *et al.* (2001) or Agnalt *et al.* (2007) could be different if the calculation of the functional maturity introduced a seasonal effect. The proposed method for estimating the functional maturity curve provides a better understanding of the population dynamics of lobsters.

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Tables

Table 1. Estimation of the L_{50} for the physiological and functional maturity of the European lobster from different areas.

Authors	Areas	Physiological maturity, size (mm)	Functional maturity, size (mm)
Free *et al.* (1992)	Bridlington	82.5	90
	Dale	95	105
	Selsey		85
Tully *et al.* (2001)	Northwest Ireland	96	107
	West Ireland	92.5	116
	Southwest Ireland	94	122
	Southeast Ireland	95	140
Lizarraga *et al.* (2003)	Firth of Forth		95
	Hebrides		98
Latrouite *et al.* (1981, 1984)	Iroise, Guernesey, Yeu Island, Roches Douvres		$98<L_{50}<102$

Table 2. Presentation of the measurements performed by the fishermen and some of the mean characteristics.

Year	Total number of measurements	Number of fishing days	Number of lobsters under the MLS	Number of females	Number of males	Number of ovigerous females	Size (mm) of the smallest ovigerous

							females
2003	1354	69	101	618	736	70	100
2004	4510	146	548	2410	2100	437	96
2005	4878	131	556	2633	2245	409	94
2006	6142	164	760	3201	2941	624	91

Table 3. ANOVA test for seasonal and physiological effects on the sex ratio. The variable Ovi represents 10 classes that characterize the percentage of ovigerous female in the daily catch. The value 1 indicates a percentage of ovigerous females comprised between 10 and 19.99.

	Df	Deviance	Resid Df	Resid Dev	F	Pr(>F)
Null	391	3.55				
Year	2	3.55	389	0.955	0.3857	ns.
Month	5	3.47	384	1.572	0.1669	ns.
Ovi	9	3.39	375	1.023	0.4208	ns.

Table 4. Estimation of the parameters and testing the significance of associated variables.

Parameter	Estim	σ	CV	Test t	P(test t)	Ccl
p	0.407	0.016	0.644	0.039	0.000	***
α	0.043	0.002	0.009	0.051	0.000	***
C	81.582	4.556	37 168.001	0.056	0.000	***
α_1	0.077	0.004	0.034	0.058	0.000	***
β_1	–0.126	0.035	0.444	0.280	0.000	***
β_2	–0.198	0.037	0.733	0.187	0.000	***
α_2	–5.933	1.072	636.197	0.181	0.000	***
β_{11}	–3.493	1.234	430.979	0.353	0.005	**
β_{22}	1.325	1.377	182.476	1.039	0.337	ns.

Figures

Figure 1. Fishing area off Le Croisic.

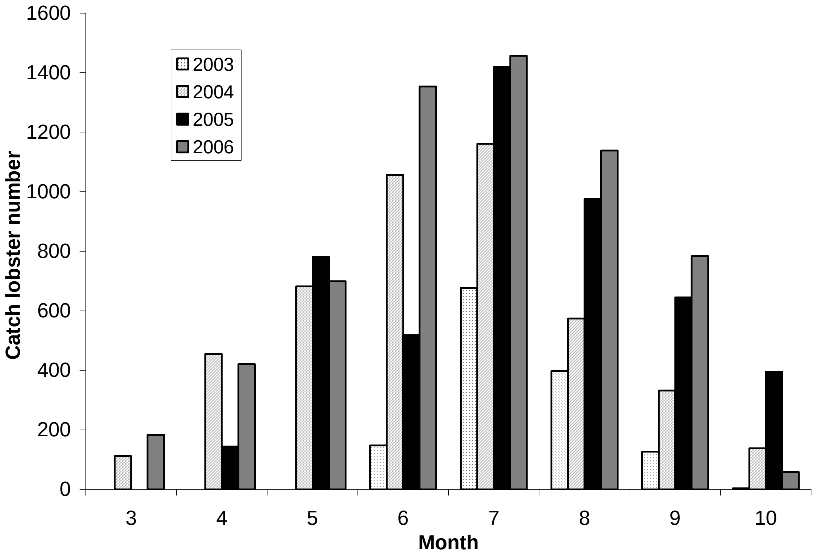


Figure 2. Number of measurements per month over the 4-year period.

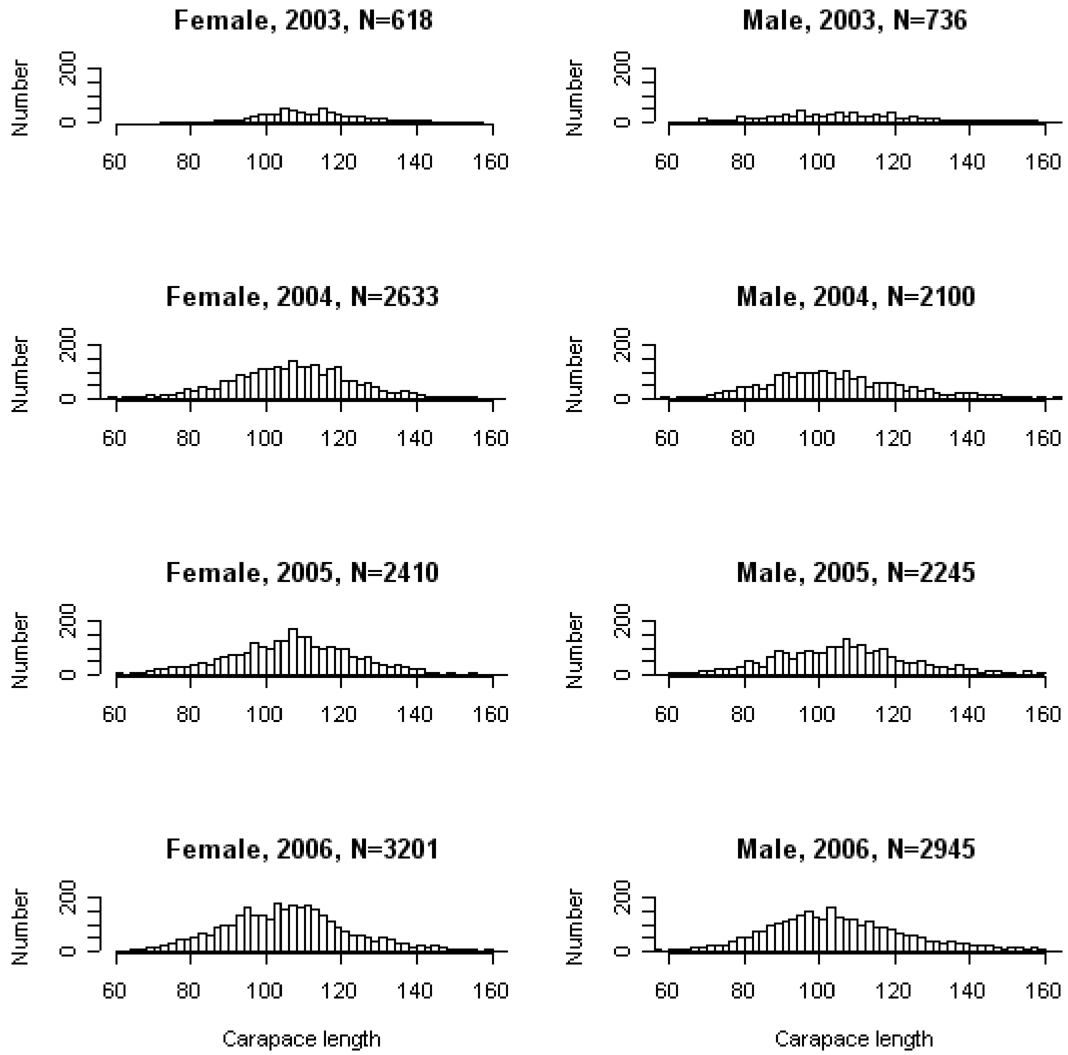


Figure 3. Size structure of the males and females.

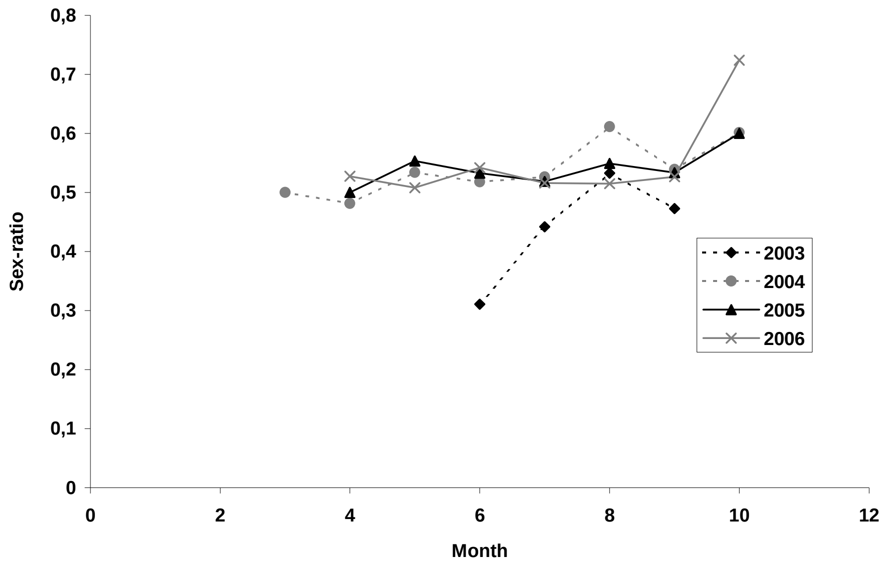


Figure 4. Sex ratio (proportion of females) of lobsters per month for each year.

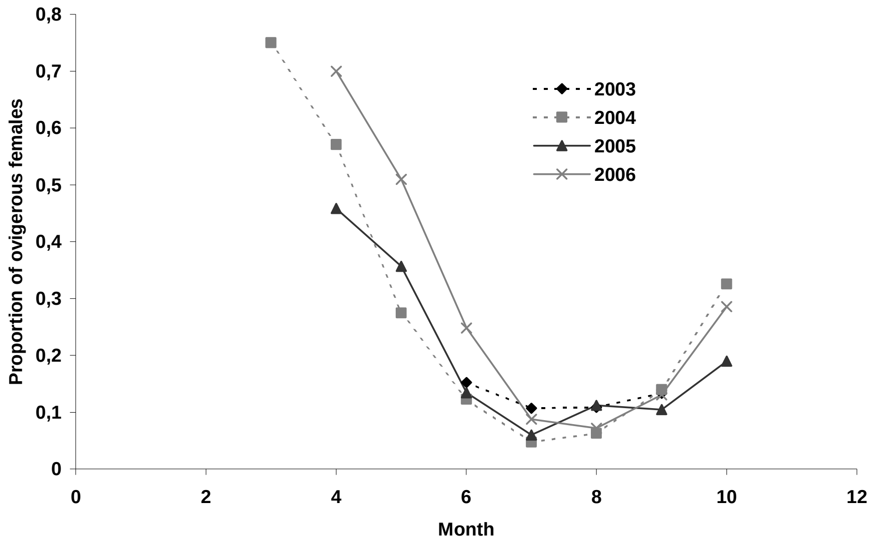
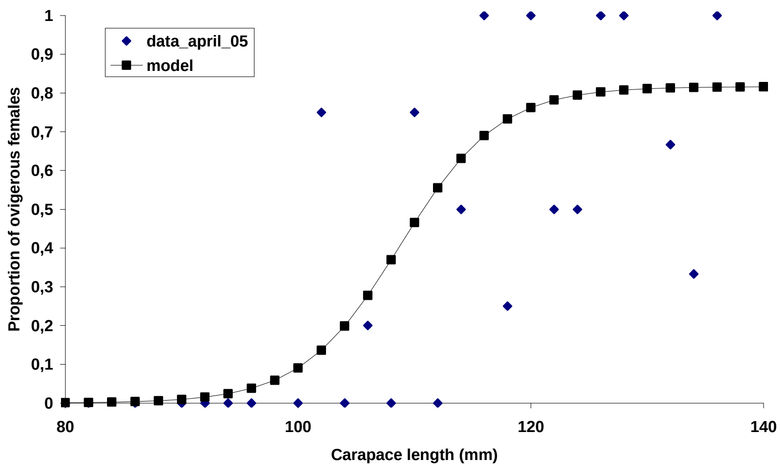
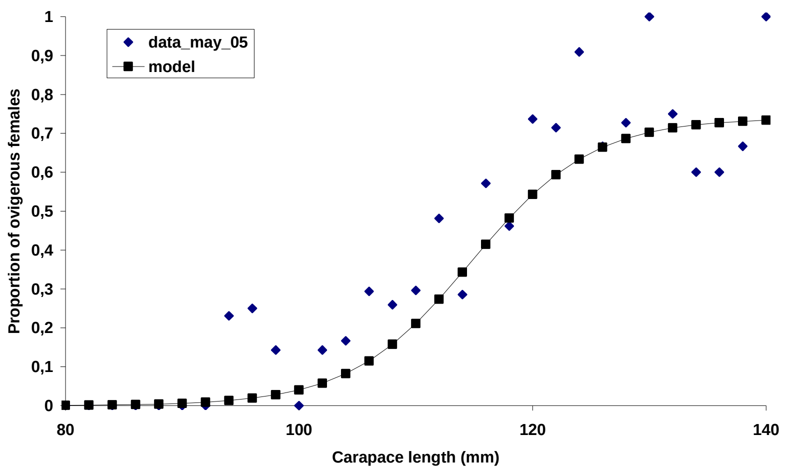


Figure 5. Proportion of ovigerous females in the catches for each year.



a



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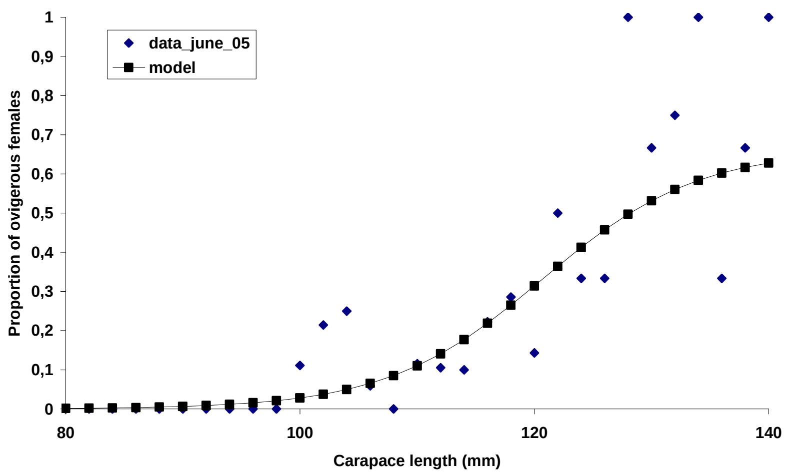

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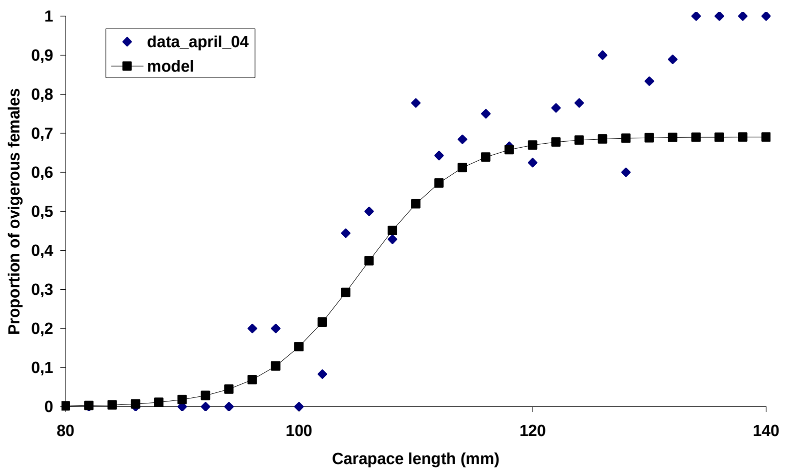
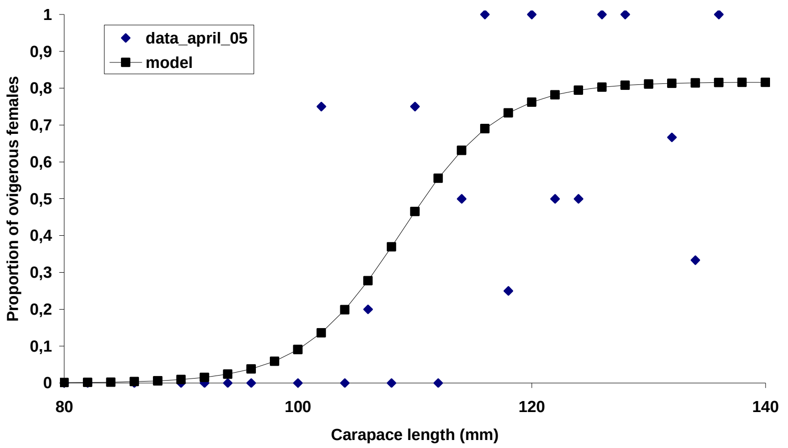
Figure 6. Functional maturity curve from April (a) to June (c) in 2005.



a



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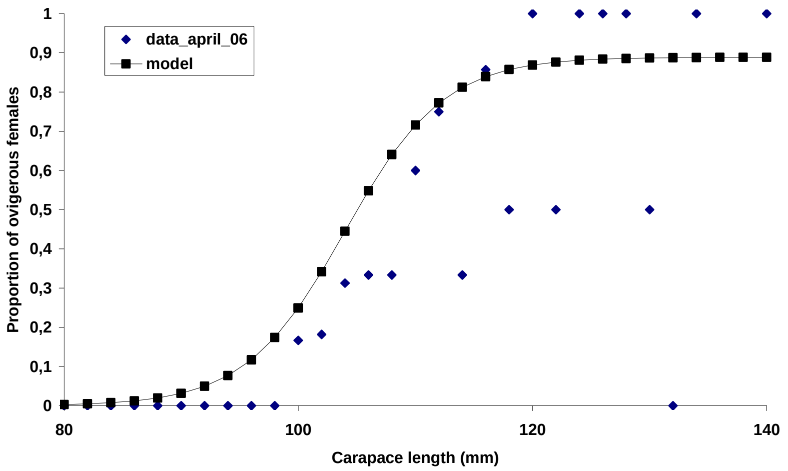

c

Figure 7. Functional maturity curve in April for the three years considered in the study: 2004 (a), 2005 (b), and 2006 (c).