Reproductive strategies under different environmental conditions: total output *vs* investment per egg in the slipper lobster *Scyllarus arctus*

L. Fernández[1] (iD), C. García-Soler[2] and I. Alborés[1]

[1]Departamento de Biología, Facultad de Ciencias, Universidade da Coruña, Campus da Zapateira, 15071 A Coruña, Spain and [2]Aquarium Finisterrae, Paseo Alcalde Francisco Vázquez, 15002 A Coruña, Spain

Abstract

The slipper lobster *Scyllarus arctus* is an important fishery resource in Galicia (NW Iberian Peninsula), with a large reduction of its populations in recent decades in the North-east Atlantic and Mediterranean, but only limited information on its reproduction. This study provides an analysis of the reproductive potential of this scyllarid during two breeding cycles (2008 and 2009) in the NE Atlantic (43°20′N 8°50′W). We studied several reproductive traits (fecundity, brood weight, egg weight and volume) in broods with eggs both in an early and late embryonic stage, in relation to female size and temporal variations. Total output (fecundity and weight) and egg weight were closely linked to maternal size, and this relationship remained in broods with late-stage eggs. In relation to temporal variations, our data revealed an important seasonal variability in fecundity and egg weight, showing an inverse pattern in the reproductive strategy in the first two seasons of the reproductive period, with a maximum egg weight in winter (December–February) and a maximum number of eggs produced in spring (April–May). A predictive model for realized fecundity was developed: log (FE) = 0.064 + 2.907 log (length) − 0.018 Month^2 + 0.174 Month, which accounted for over 90% of variation in the total data.

Introduction

Scyllarids have been poorly studied, particularly in comparison to spiny and clawed lobsters (MacDiarmid & Sainte-Marie, 2006), and the existing information is limited to a few commercially relevant species in the genera *Ibacus* (Leach, 1815), *Scyllarides* (Gill, 1898) and *Thenus* (Leach, 1816) (Sekiguchi *et al.*, 2007). This is due to scyllarids traditionally having been regarded as secondary targets for fisheries. Nevertheless, since the 1990s, these lobsters have gained in commercial interest due to a decrease in the abundance of the main target species and, as a consequence, have suffered a sharp decrease in stock abundance at a local scale (Lavalli & Spanier, 2007). The main reason for the alleged overexploitation of many scyllarids is the lack of information about their life history parameters, which are essential in order to precisely assess population size and resilience to fishing pressure or to environmental changes (O'Malley, 2011).

In the particular case of *Scyllarus arctus* (Linnaeus, 1758), its increased commercial relevance can be confirmed by its high market values (€60 kg^{-1}, approximate average price at first sale, and maximum of €188 kg^{-1}, between 2001 and 2019 in Galicia, NW Iberian Peninsula), although the abundance of catches has not allowed for the development of a monospecific fishery. Captures of this scyllarid in Galicia are accessory and associated with coastal artisanal fisheries using octopus traps or trammel nets. In recent decades, despite some local regulation measures, the size of populations of this species on the Galician coast has been reduced (personal communication from fishermen), as has also been observed in the archipelago of the Azores (Santos *et al.*, 1995) as well as in some coastal areas in the Mediterranean (Lloret & Riera, 2008).

A better knowledge of the reproductive biology of *S. arctus* is essential for the sustainable management of populations (Alborés *et al.*, 2019). Moreover, the scarce information about the biology of this species is focused on studies of Mediterranean populations (Pessani & Mura, 2007) and is insufficient for developing appropriate measures for an effective management of populations across its broad geographic distribution. Within Crustacea, intraspecific differences in brood investment, number and size of produced eggs have been reported (Brante *et al.*, 2003; Verísimo *et al.*, 2011). Larger eggs contain more vitellum, which indicates substantial investment by the female in each embryo (Clarke, 1993), so that, after hatching, the larvae will have a greater chance of survival (Verísimo *et al.*, 2011; Alborés *et al.*, 2019).

Differences found in reproductive traits are attributed to environmental factors associated with habitat type along a latitudinal or bathymetric gradient (Brante *et al.*, 2003; Laptikhovsky, 2006; Fischer *et al.*, 2009; Alborés *et al.*, 2019), or to seasonal variability (Bas *et al.*, 2007; Verísimo *et al.*, 2011; Urzúa *et al.*, 2012). Furthermore, biological factors such as female size (Hines, 1982; Verísimo *et al.*, 2011), energetic condition (Bryant & Hartnoll, 1995;
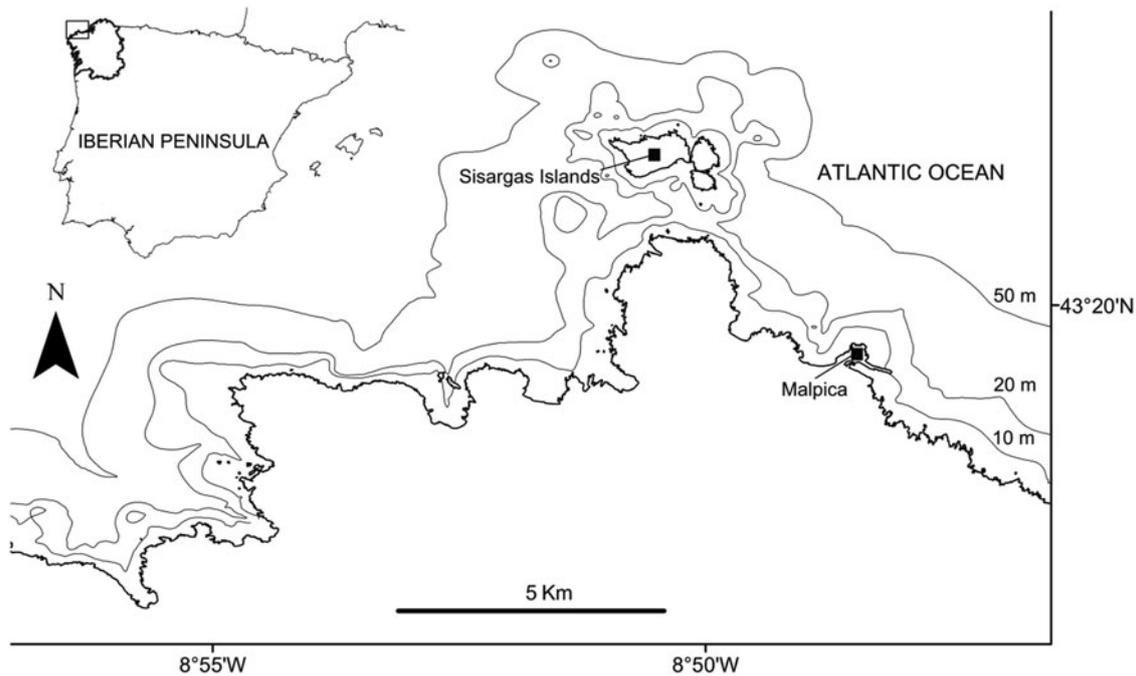
Fig. 1. Location of the regular fishing ground for *Scyllarus arctus* in Malpica in the Costa da Morte (Galicia, NW Iberian Peninsula).

Verísimo *et al.*, 2011), age of reproductive individuals (Groeneveld, 2005) or interactions with other species (Griffen *et al.*, 2011), have been identified as other important sources of variation.

The aim of the present study is the characterization of the reproductive strategy of *S. arctus* in the NE Atlantic. With this purpose, brood size (fecundity and weight) and individual egg traits (size and weight) in early and late egg stages, were analysed in relation to female size and temporal variations (both seasonal and interannual) in two breeding cycles (2008 and 2009). In addition, we propose a tool for the regulation of this resource: a predictive model for the fecundity of *S. arctus* which takes lobster size and temporal variability during the reproductive period into account.

Materials and methods

Sampling

This study was carried out in Malpica (43°20′N 8°50′W), one of the main exploitation sites for the small European locust lobster *Scyllarus arctus* in Galicia (NW Iberian Peninsula), during the years of 2008 and 2009 (Figure 1). Individuals of *S. arctus* were obtained monthly from catches by artisanal fishing vessels using octopus traps. Captured lobsters were kept in insulated tanks containing cooled water, in order to reduce stress and avoid egg loss during transport. Once in the laboratory, wet weight (precision ± 1 mg), and cephalothorax length (CL) of each female were determined, as well as the distance between the rostral sinus and the posterior margin (to the nearest 0.01 mm). Egg masses were carefully removed from pleopods and submerged for 3 min in an ammonium formate solution (31.5 g l^{-1}) in order to remove salts, being subsequently drained and weighed to obtain brood wet weight (BWW). Once brood colour was recorded, a sample of 30–40 eggs was taken from each brood and preserved in a 4% neutralized formaldehyde solution in order to determine embryonic developmental stage and measure egg size. Samples were then freeze-dried to constant weight for 48 h and brood dry weight (BDW) was determined with a precision of 0.1 mg.

For this study, according both to macroscopic (colour) and microscopic criteria (see González-Gurriarán *et al.*, 1996), two types of broods were used: broods in an early egg stage, constituted by yellow-coloured eggs with yolk occupying most of their volume (>80%) (from the blastula phase to an early differentiation of the naupliar mesoderm into an early gastrula), and broods in a late egg stage, characterized by brown-coloured eggs with well-developed larvae, where yolk occupied less than 10% or was absent.

The gravimetric method was used to estimate fecundity (FE) from three replicates of egg subsamples. Previously, a study was performed to determine if there was an optimal egg sample size that allowed for a better estimation of FE (Verísimo *et al.*, 2011). Subsamples of freeze-dried eggs of known weight were separated in a Petri dish containing a 70% alcohol solution for subsequent counting. This was carried out through image analysis with Nikon's Nis Elements software, using a Nikon DXM 1200 digital camera coupled to a Nikon SMZ 1500 stereomicroscope. Likewise, image analysis was used to determine average egg volume (V) by measuring the major and minor axis of 30 previously preserved eggs per brood. Egg V was obtained using the oblate ellipsoid volume equation,

$$V = \pi d_1^2 d_2/6,$$

where d_1 is the average minor axis and d_2 is the major axis.

Data analysis

For the study of FE, broods from 212 ovigerous females were analysed as a $V = \pi d_1^2 d_2/6$, function of size, brood period and egg developmental stage. Three periods were established due to the extended spawning period during a reproductive cycle, the presence of berried females with eggs in various developmental stages during most of the year, including multiparous females (Alborés *et al.*, 2019), and the different environmental conditions (temperature, available food, etc.) in each period or season. An early period of the reproductive cycle was established between December and February, characterized as 'winter brood', as well

as a second period between April and May, called 'spring brood', and a third period, the 'summer brood', comprised of broods of berried females obtained from July to September. Females captured in March and June were excluded from the analysis with the purpose of avoiding a possible overlap between periods. According to the stage of egg development in broods, FE estimates were divided as: realized FE, estimated as the number of eggs in broods with early stage eggs, and effective FE, estimated from broods with eggs close to hatching.

For the purpose of data analysis, it was necessary to transform FE, BDW, CL, egg dry weight (DWE) and egg V data using natural logarithms. Temporal differences within the two reproductive cycles studied, both for broods in early and late egg stages, were analysed through analysis of covariance (ANCOVA) using CL as covariable. Two-way ANCOVAs were performed to assess differences in reproductive traits among seasons and years (2008 and 2009) for early-stage broods. For late-stage broods, one-way ANCOVAs were performed to assess differences in reproductive traits among seasons during 2008. Furthermore, a two-way ANCOVA was performed between realized and effective FE with CL as covariable, to assess seasonal variability in egg loss during the spawning period. Interactions between categorical factors and the covariable were tested (CL × Season; CL × Stage). Since interactions were not significant, the interaction term was removed and models were refitted (homogeneity of slopes). Tukey's multiple comparison post-hoc test was performed when significant differences were found. For all the analyses performed, the obtained results were normal (Shapiro–Wilk test, $P > 0.05$) and homoscedasticity was met (Bartlett's test, $P > 0.05$). In order to determine temporal differences in the studied variables, data correction by size was performed on those for which it showed a significant effect. The effect of size was removed by standardizing data through linear regression between each dependent variable and size of *S. arctus*, calculated for the overall data set. Differences in average values of reproductive traits among broods for different developmental stages were assessed using Generalized Least Squares (GLS) to suitably model variance structure.

In a subsequent phase, generalized linear models (GLM) were used to analyse the variations of realized FE and the relative importance of the different variables, in order to develop a predictive model for FE during the reproductive cycle. The following predictive variables were considered: month of capture, CL and egg V. The study of residual distribution regarding the studied variables, previous to their insertion in the model, made it possible to determine a pattern for the variable Month, which was included in the model as a quadratic term. A first model was built where all the variables were included. In the process of variable selection (by backward elimination approach), Akaike's Information Criterion (AIC) and percentage of explained variation (deviance-D^2) were used to evaluate the relative importance of each variable and so determine which variables were to be included in the final model and in which order. Likewise, the analysis of deviance to assess the significance (test F) of the variables included in the final model was carried out as a step by step process. The selection of the model, the most suitable link function and error distribution were based on residual distribution. A gamma distribution with a log link function was found to be the most suitable (Green *et al.*, 2009), which implies that the explanatory variables have had a multiplicative effect on the response parameter.

$$\log\left(\mathbb{E}(\widehat{FE}_i)\right) = \eta_i$$
$$= \beta_0 + \beta_1 \log CL + \beta_2 Month^2 + \beta_3 Month$$

where the average FE $\mathbb{E}(\widehat{FE}_i) = \mu_i$ for an observation i is estimated as $\hat{\mu}_i = \exp(\hat{\eta}_i)$. All the analyses and model fitting have been performed using R.

Results

Optimal egg sample size

The previous study of optimal sample size (250, 500, 750 and 1000 eggs) did not yield significant differences in average DWE among the different sample sizes used (ANOVA, $F_{(3,333)} = 0.372$, $P > 0.05$). Nevertheless, for the purpose of this study, an optimal sample size of 750 eggs was selected, since samples of this size had a lower variability in the DWE obtained and, consequently, in the estimations of total number of eggs for each brood. The estimations carried out for the selected sample size showed coefficients of variation <3% in DWE determination (mean = 0.89%, 95% CI = 0.81–0.96%).

Reproductive effort

To estimate the realized FE of females of *Scyllarus arctus*, 149 individuals with a size range between 24.4 and 44.6 mm CL (34.5 ± 4.0 mm, mean $\pm$ SD) and a body wet weight between 11.8 and 71.9 g (35.2 ± 12.1 g) were used. The analysed broods showed a great variability both in weight, with a BWW between 0.76 and 7.03 g (2.74 ± 1.11 g) and a BDW between 0.32 and 2.50 g (1.05 ± 0.40 g), and in number of eggs, with 14,370–108,029 eggs ($45,292 \pm 16,265$ eggs). The investment in brood weight relative to body weight of this lobster during the reproductive cycle ranged between 4.9% and 12.1% ($7.7 \pm 1.1\%$). Egg production per gram of body weight also showed great variation, ranging from 924.6–1742.2 eggs g^{-1} (1293.5 ± 175.5 eggs g^{-1}).

Effective FE was determined for a size range similar to the one used for the determination of realized FE, between 28.5–44.6 mm (35.3 ± 4.4 mm, N = 65), and a body wet weight between 18.2–73.4 g (37.7 ± 13.4 g). The estimated number of eggs in broods in late egg stage ranged between 11,425 and 77,417 eggs ($37,141 \pm 16,587$ eggs) for a BWW between 1.04–9.58 g (3.89 ± 1.82 g) and a BDW from 0.23–1.80 g (0.85 ± 0.39 g). The average number of eggs per gram of body weight determined for late broods was 987.7 ± 212.3 eggs g^{-1} (range: 551.9–1418.7 eggs g^{-1}).

During embryogenesis, egg V increased by 22.2% on average, from 499 ± 62 mm^3 10^{-4} (early eggs) to 610 ± 67 mm^3 10^{-4} (late eggs). In regard to DWE, early eggs showed a great variation, ranging from 17.6–29.2 µg (23.2 ± 2.2 µg), while for eggs close to hatching, mean weight varied between 15.6–31.6 µg (22.4 ± 2.4 µg).

Influence of maternal size

Early-stage broods

Two-way ANCOVAs performed on brood size (FE and BDW) showed that female size, measured as CL, had a strong significant effect during the two years of study, accounting for >86% of the total variation (FE: $F_{(1,147)} = 1120.11$, $P < 0.001$; BDW: $F_{(1,147)} = 1477.89$, $P < 0.001$). The influence of CL on investment in brood size remained constant during the whole reproductive cycle (slope homogeneity). In general, the slopes of the adjusted allometric equations for brood size in each period ranged from 2.39–3.15, indicating the presence of a positive allometry (Figure 2). On the other hand, relative brood size (number of eggs per gram of body weight) did not show any relationship with lobster size (Pearson's $r = 0.05$, $P > 0.05$).

Regarding individual egg traits, maternal size had a significant effect on DWE (7.2% of variance explained; $F_{(1,147)} = 29.07$, $P < 0.001$). The relationship between DWE and CL exhibited positive
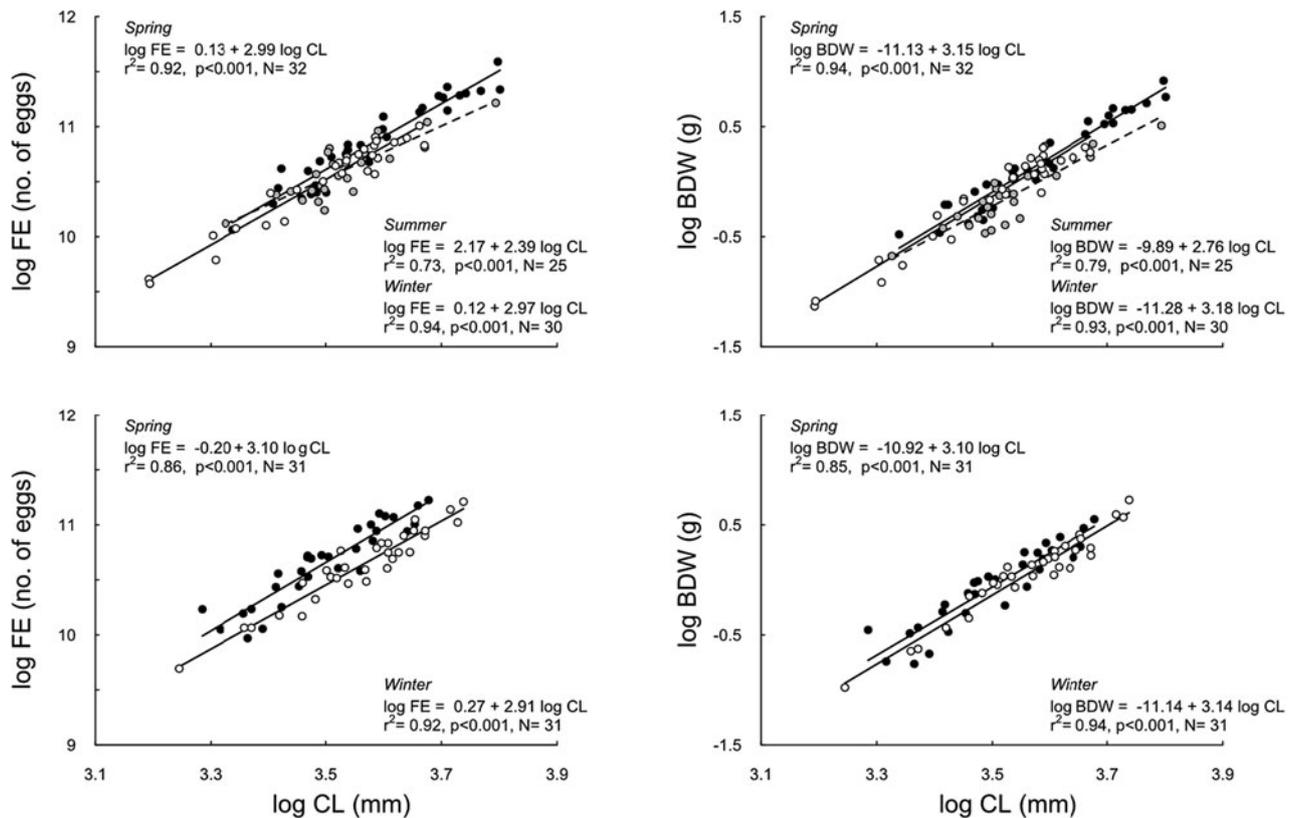
Fig. 2. Relationship between log realized fecundity (FE, number of eggs) and log brood dry weight (BDW, g) with body size (CL, mm) of a female *Scyllarus arctus* for winter samples (white dots, solid line), spring (black dots, solid line) and summer (grey dots, dashed line) for 2008 (top) and 2009 (bottom). Regression equation, coefficient of determination, significance and number of samples are indicated for each relationship corresponding to the season analysed.

allometry, determined by a mean estimated slope of 0.18 (95% CI = 0.08–0.29). On the other hand, egg V did not show any significant relationship with female size ($F_{(1,147)} = 2.06$, $P > 0.05$), although it showed a positive correlation with DWE (Pearson's $r = 0.55$, $P < 0.001$).

Late-stage broods

Brood size (FE and BDW) in late-egg broods also showed a significant positive relationship with lobster size (FE: $F_{(1,61)} = 204.70$, $P < 0.001$; BDW: $F_{(1,61)} = 279.74$, $P < 0.001$). Variation in brood size and CL between seasons showed that variation in the number of eggs is mainly explained by the size of females (>75.17%). Two-way ANCOVA performed to compare realized and effective FE revealed a significant brood loss in *S. arctus* during incubation in the different periods analysed in 2008 ($F_{(4,144)} = 98.75$, $P < 0.001$). Nevertheless, no differences were found between the slopes of the fitted lines ($F_{(4,144)} = 3.00$, $P > 0.05$), indicating that egg loss during incubation remains constant throughout the analysed size range (Figure 3).

On the other hand, the influence of maternal size on DWE remained for eggs with developed larvae (17.21%; $F_{(1,61)} = 20.87$, $P < 0.001$), with an average slope of 0.22 (95% CI = 0.07–0.37). For egg V, no significant relationship with size of individuals ($P > 0.05$) and DWE (Pearson's $r = 0.10$, $P > 0.05$) was found.

Temporal variations

Early-stage broods

The two-way ANCOVA analyses performed on FE ($F_{(4,144)} = 27.94$, $P < 0.01$), BDW ($F_{(4,144)} = 10.66$, $P < 0.001$), and DWE ($F_{(4,144)} = 60.89$, $P < 0.001$), with CL as the covariate, showed a temporal pattern in reproductive traits. Main differences were

found between the functions' intercepts for the different brood periods analysed ($P < 0.001$).

The average values of standardized realized FE in spring (48,116 ± 6314 eggs) were 18.0 ± 6.5% higher than FE of broods spawned in winter (40,815 ± 4428 eggs) in both years of the study, and 15.5 ± 0.8% higher than summer broods, with 41,660 ± 6163 eggs (Tukey's HSD, $P < 0.001$). The maximum differences in realized FE among broods were observed in 2009, when number of eggs in spring broods was 22.6% higher than in winter broods (Figure 4). On the other hand, standardized BDW decreased significantly at the end of the reproductive period by 10 ± 0.4% (mean summer BDW: 0.91 ± 0.14 g) with respect to broods spawned in winter (1.01 ± 0.11 g) and by 15.3 ± 0.1% with respect to spring (1.07 ± 0.12 g) in both years (Tukey's HSD, $P < 0.01$).

Investment in DWE was significantly higher in the first broods of the reproductive cycle, spawned during winter (24.7 ± 2.2 μg), than in broods spawned during spring and summer (Tukey's HSD, $P < 0.001$; Figure 4). However, this decrease in DWE was not significant between spring (22.4 ± 1.3 μg) and summer periods (21.8 ± 1.5 μg, Tukey's HSD, $P > 0.05$). DWE also showed significant differences between years of study with respect to season, DWE being higher in winter 2009 (25.5 ± 2.2 μg) than in 2008 (23.9 ± 1.9 μg; Tukey's HSD, $P < 0.01$). In contrast, average egg V was slightly higher in winter (514 ± 61 mm^3 10^{-4}) than in spring broods (503 ± 56 mm^3 10^{-4}) for the two years of study; however, this observed egg V was significantly reduced by 11.8 ± 0.7% in summer broods (451 ± 58 mm^3 10^{-4}, Tukey's HSD, $P < 0.01$).

Late-stage broods

Broods with eggs close to hatching also showed significant seasonal differences in FE ($F_{(2,58)} = 4.30$, $P < 0.05$), BDW ($F_{(2,58)} =$
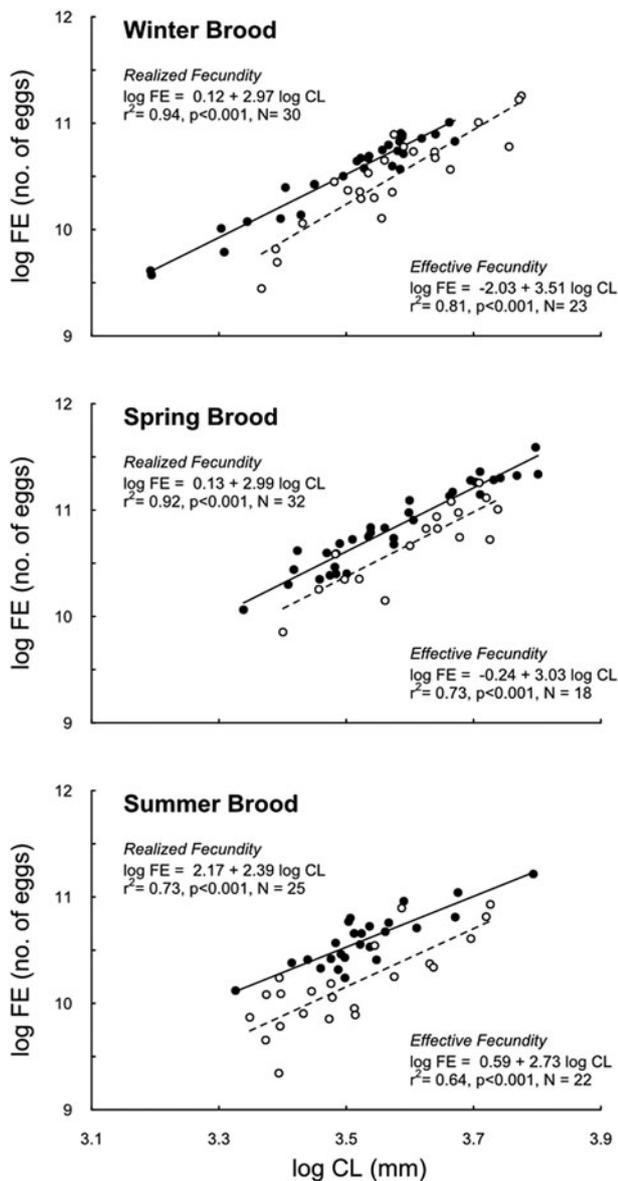
Fig. 3. Log-log relationship between realized fecundity (black dots, solid line) and effective fecundity (white dots, dashed line), and size of female *Scyllarus arctus* (CL, mm) for winter, spring and summer periods during 2008. Regression equation, coefficient of determination, significance and number of samples are indicated.

10.74, $P < 0.001$) and DWE ($F_{(2,58)} = 15.15$, $P < 0.001$), but not in egg V ($P > 0.05$). These reproductive traits showed a similar pattern to that observed in recent broods, although data showed a higher dispersion (Figure 4). Standardized effective FE in spring (36,889 ± 8901 eggs) was 21% higher than in summer broods (30,396 ± 8165 eggs; Tukey's HSD, $P < 0.05$); nevertheless, neither showed any difference with winter broods (33,454 ± 7662 eggs). Egg loss was evident in each season studied during 2008 (GLS, $P < 0.001$; Figure 4), showing an increase throughout the reproductive period, from 20.8% in winter broods to 23.0% in spring broods and 27.0% in summer broods (mean egg loss: 23.6 ± 3.2%). Effective investment in BDW showed a significant decrease in summer broods (0.63 ± 0.18 g) regarding winter and spring broods, with a mean BDW of 0.79 ± 0.14 g and 0.81 ± 0.18 g respectively (Tukey's HSD, $P < 0.01$; Figure 4).

DWE was also lower in summer broods (20.9 ± 1.3 µg) compared with winter (23.4 ± 1.7 µg; Tukey's HSD, $P < 0.001$) and spring broods (22.3 ± 1.2 µg; Tukey's HSD, $P < 0.05$). During the incubation period, eggs showed a significant increase in V, with

an average of 25.4 ± 9.5% in the three seasons (GLS, $P < 0.001$; Figure 4), reaching an average egg V of 605 ± 90 mm^3 10^{-4} for eggs in late stage.

Model for the estimation of realized FE

The variation in FE with female size and season demonstrates the importance of developing a model to predict FE during the reproductive period of *S. arctus*. For this analysis, data from years 2008 and 2009 were grouped since no significant differences in FE were found between years.

The model which only took female size into account explained 85.12% of variation in FE (Table 1), while the inclusion of month as a polynomial term accounted for an additional 5.87% of total deviance (90.98%). The model including all the variables showed the lowest AIC value, and all were found to be significant ($P < 0.01$). However, in spite of its significance ($F = 10.37$, $P < 0.01$, AIC = 2937), average egg V only accounted for an additional 0.60% of deviance (Table 1). In addition, even though AIC for this model was 7 units lower, Burnham & Anderson (2004) argue that there is no evidence of model improvement in cases like this. Therefore, based on these two criteria, a simpler model was selected, which did not include this variable. No evidence was either found of an interaction between female size and month of the reproductive cycle on the estimations of FE ($F = 3.10$, $P > 0.05$), thus the model proposed as the best one to assess realized FE was the one that included variables CL and Month (AIC = 2945), where all terms were significant ($P < 0.001$). Thus, the variable Month allowed an explanation of the relationship between FE and body size in this lobster, with a common slope of 2.91 (95% CI = 2.76–3.06) and a different intercept for each month during the annual reproductive cycle (Figure 5). Taking all this into account, the following expression is proposed for the prediction of FE in *S. arctus* during the reproductive period:

$$\log\left(\mathbb{E}(\widehat{FE}_i)\right) = \eta_i$$
$$= 0.064 + 2.907 \log CL - 0.018 \, \mathrm{Month}^2$$
$$+ 0.174 \, \mathrm{Month}$$

Discussion

The presence of females with broods showing eggs in early and late stages in all the seasons analysed in this study is in concordance with the extended spawning period shown by *Scyllarus arctus* in the Mediterranean, which practically encompasses the whole year, except for autumn, a season during which a peak moult could take place prior to the start of a new reproductive period (Vilotte, 1982; Mura *et al.*, 1984; Cau *et al.*, 1988).

Estimations of realized FE on the Galician coast (14,370–108,029 eggs, 24–45 mm CL, N = 149) were higher than previous estimations in the Mediterranean (30,000–70,000 eggs, 28–34 mm CL, N = 4; Vilotte, 1982). These geographic differences are partly due to methodological factors such as the narrow size range used and the number of females studied (Currie & Schneider, 2011). In this study, the smallest females used were close to the size of sexual maturity (25.7 mm CL, Alborés *et al.*, 2019), while the largest ones were over 45 mm CL (180 mm in total length), which is larger than the maximum length cited for this lobster (160 mm in total length; Relini *et al.*, 1999).

In general, the reproductive potential of female *S. arctus* has shown a strong positive correlation with the size of individuals (CL), which has also been described in other slipper lobsters (Oliveira *et al.*, 2008), and other crustaceans (Hines, 1982;
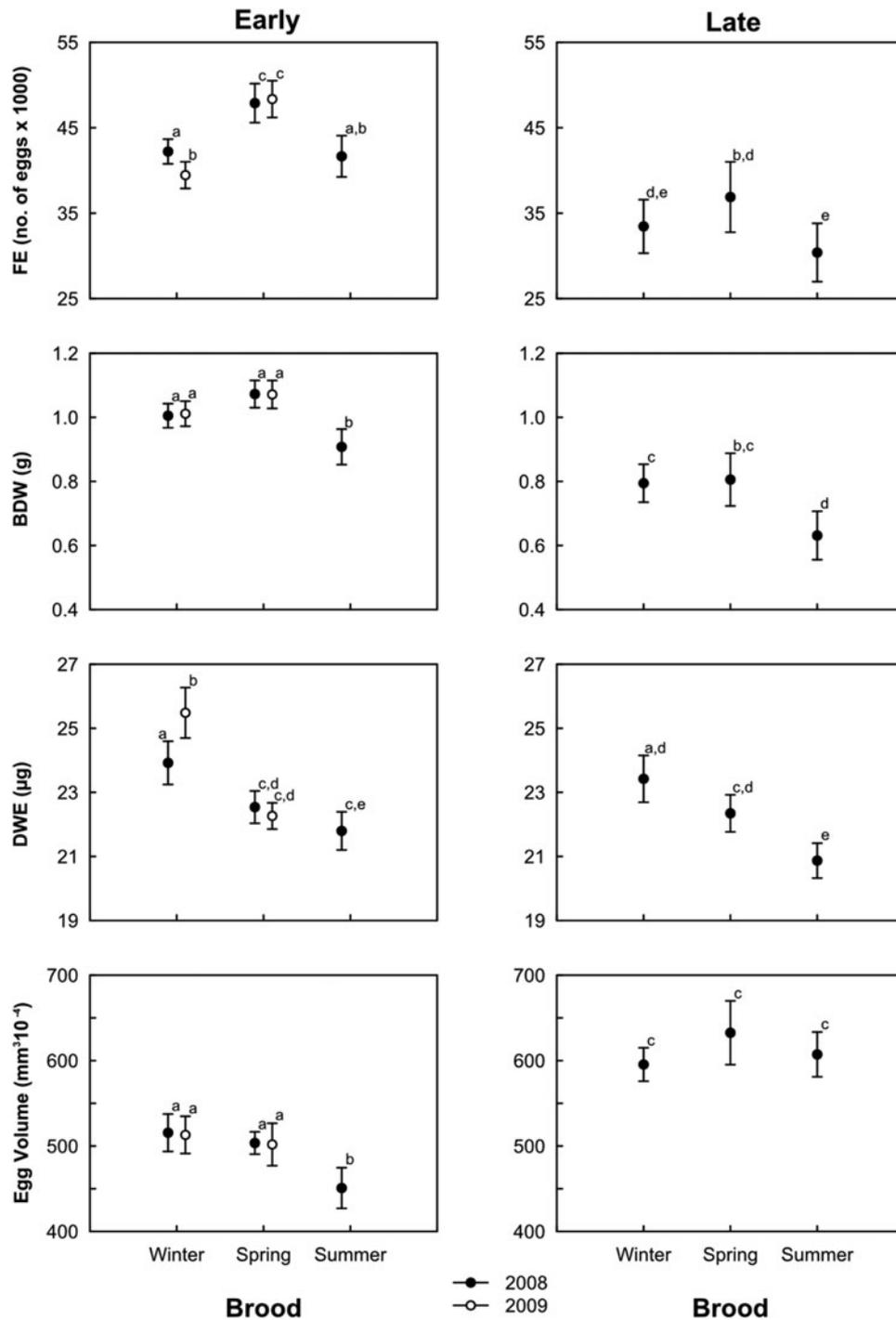
Fig. 4. Seasonal variations in brood and egg traits of *Scyllarus arctus* for both developmental stages in 2008 and 2009 (mean ± 95% CI). Mean values of fecundity (FE, number of eggs), brood dry weight (BDW, g), dry weight per egg (DWE, µg) standardized by size, and mean volume of eggs (mm^3 10^{-4}) are represented. Different letters indicate significant differences in brood traits (GLS, $P < 0.01$).

Attard & Hudon, 1987; Fischer *et al.*, 2009). Egg production in scyllarids is a power function of body size, although the type of function described can vary among populations and species of lobsters (DeMartini & Williams, 2001). In the specific relationships found between size-FE and size-brood weight in *S. arctus*, the observed slope for all relationships was not significantly different from a theoretical slope of 3 (*t*-test, $P > 0.05$), indicating a volumetric constraint to egg storage related to female size (Somers, 1991). Although female body size (CL) is the most important determinant of FE, other factors also contribute to the total variance. The influence of reproductive senescence (or reduced FE with age) was noted in large-sized females of

some spiny lobsters (Chubb, 2000). MacDiarmid & Kittaka (2000) suggest another reason: selective fishing of larger males. A male's capacity to fertilize the whole brood of a female mainly depends on its body size and, relatedly, on the amount of sperm it can produce. This limitation reaches a higher relevance in species with external fertilization and which do not accumulate spermatophores (MacDiarmid & Butler, 1999), as is the case of this slipper lobster. However, as relative brood size showed no relation to body size in *S. arctus*, there was no evidence that would support such an hypothesis. This is consistent with the fact that it is a highly exploited population, and larger (and older) individuals are quickly eliminated from the population.

Table 1. Results of sequential adjustment of model for realized fecundity of *Scyllarus arctus*

Model	Parameters (± SE)	Df	Res. Df	D^2	Res. D^2	Exp. D^2	F	P	AIC
Null			148		19.25				
Log CL	$\beta_0 = 0.445 \pm 0.346$, $\beta_1 = 2.891 \pm 0.096$	1	147	16.39	2.87	85.12	1466.3	<0.001	3016
+ Month^2 + Month	$\beta_0 = 0.065 \pm 0.271$, $\beta_1 = 2.907 \pm 0.076$, $\beta_2 = -0.018 \pm 0.002$, $\beta_3 = 0.174 \pm 0.018$	2	145	1.13	1.74	90.98	50.5	<0.001	2945
+ Egg Volume	$\beta_0 = 0.217 \pm 0.268$, $\beta_1 = 2.933 \pm 0.074$, $\beta_2 = -0.019 \pm 0.002$, $\beta_3 = 0.173 \pm 0.017$, $\beta_4 = -4.694 \pm 1.465$	1	144	0.12	1.62	91.59	10.4	<0.01	2937

Note: Columns represent degrees of freedom corresponding to the added term (Df), residual degrees of freedom for each model (Res. Df), deviance (D^2), residual deviance (Res. D^2), explained residual deviance (Exp. D^2, %), P-value when a F test is used as significance test and AIC value.
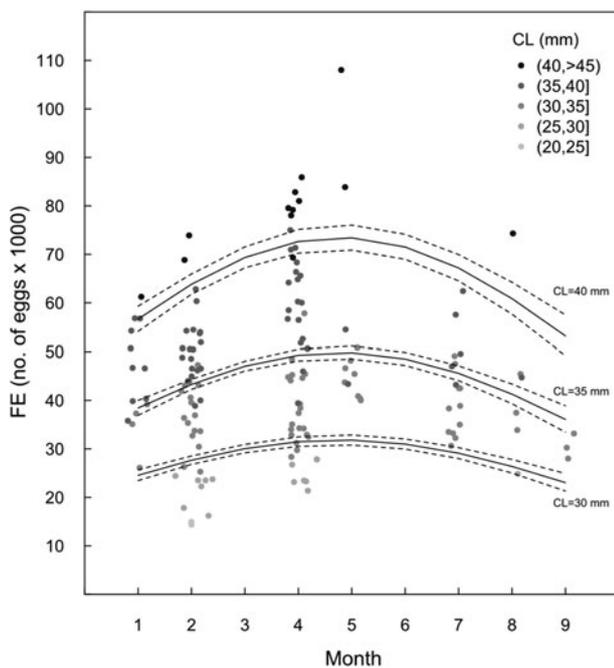

Fig. 5. Monthly realized fecundity (FE, number of eggs) during the reproductive cycle of *Scyllarus arctus* (January–September). Dots represent estimated FE for each individual, while the greyscale shows the size class they belong to. Solid lines show predicted FE for the corresponding size (30, 35 and 40 mm; CL) during the spawning period, while dashed lines indicate 95% CI.

The positive influence of maternal size on egg weight (DWE) has also been observed both in clawed lobsters such as *Homarus gammarus* (Linnaeus, 1758) (Tully *et al.*, 2001; Agnalt, 2008) and *H. americanus* (H. Milne Edwards, 1837) (Ouellet & Plante, 2004), and in spiny lobsters such as *Palinurus elephas* (Fabricius, 1787) (Goñi *et al.*, 2003) and *Jasus edwardsii* (Hutton, 1875) (Smith & Ritar, 2007), although this effect has not been previously described in scyllarid lobsters. There are several plausible explanations for this positive relationship in the life history theory: (i) density-dependent survival or competition due to an increase in brood size with female size (Parker & Begon, 1986); (ii) maternal phenotype-specific optimal egg sizes related to size-dependence in habitat selection (Hendry *et al.*, 2001); (iii) physiological or morphological constraints on egg size imposed by the size of the mother (Fox & Czesak, 2000); (iv) size- or age-dependence in female provision to their offspring (Sakai & Harada, 2001; Kindsvater *et al.*, 2011). However, there is no evidence to support these theories for marine decapods, and further research is needed to determine the source of this maternal effect.

In addition to the effect of size of individuals, seasonal variations observed in brood traits during the long spawning period in both years of study could reflect the existence of a reproductive strategy. Our data revealed that seasonal changes in reproductive traits follow a cyclical pattern, reflecting the inverse relationship between values of FE and DWE in the two first seasons of the cycle, with a maximum egg weight in winter and a maximum number of produced eggs in spring. The seasonality in brood traits observed in this scyllarid is in accordance with observations in other species of crustaceans with a long reproductive period, such as *Maja brachydactyla* (Balss, 1922) (Verísimo *et al.*, 2011), *Panulirus inflatus* (Bouvier, 1895) (Garcia, 1985), *P. argus* (Latreille, 1804) (Fonseca-Larios & Briones-Fourzan, 1998), *Crangon crangon* (Linnaeus, 1758) (Oh & Hartnoll, 2004; Urzúa *et al.*, 2012), and *Cancer setosus* (Molina, 1782) (Fischer *et al.*, 2009). Nevertheless, in *S. arctus* this pattern does not continue in summer, when a lower reproductive investment in broods is observed, both in terms of total energetic investment and in terms of individual characteristics of eggs within them (DWE and *V*). This decrease in investment in the final broods of the reproductive cycle, also observed in other lobsters, is related to the capacity to carry out successive spawnings (Chubb, 2000; Vijayakumaran *et al.*, 2005; Chang *et al.*, 2007). In this way, the capacity of *S. arctus* females to spawn several times during a reproductive period (up to three subsequent broods in captivity, Alborés *et al.*, 2019), in terms of energetic investment in broods, might be conditioned by their nutritional status (Wen *et al.*, 2002; Verísimo *et al.*, 2011). Furthermore, the balance of energy available for growth and reproduction (see Hartnoll, 1985), which bears more importance in species with indeterminate growth (which continue to grow after sexual maturity), as in *S. arctus*, might contribute to the decrease in reproductive investment in the last broods produced during summer.

In marine crustaceans, seasonal differences found regarding brood traits have also been related to environmental factors such as temperature, food availability and day length (Pond *et al.*, 1996; Fischer *et al.*, 2009; Urzúa *et al.*, 2012). On the Galician coast, seasonal variation in egg traits in *S. arctus* might be related to the variation in oceanographic conditions caused by the occurrence of upwelling of nutrient-rich deep waters (Alvarez *et al.*, 2011). Thus, broods showing a higher investment per egg are produced during winter (December–February), when water temperature is lower and plankton is less abundant; while the production of smaller eggs takes place during spring (April–May) and summer (July–September), when water temperature and plankton densities are either rising or show higher values (Álvarez *et al.*, 2012). Nevertheless, this explanation about an adaptive response to environmental changes is difficult to validate, since available data are limited to a two-year-long series.

The seasonal pattern and maternal size effect observed in DWE were similar to that of broods with eggs close to hatching, thus confirming the persistence of traits from early eggs to those in the final stages of their incubation period. Egg *V* and DWE are widely used to determine investment in offspring in marine invertebrates; nevertheless, variation in egg *V* within a species may not be related to variation in parental investment (see Clarke, 1993). In marine decapods, DWE is a good approximation of offspring size (Giménez & Anger, 2003; Moland *et al.*, 2010; Diez & Spivak, 2012; Urzúa & Anger, 2013) and predictor of the physiological condition of larvae, which affects the capacity of newly hatched larvae to survive in highly variable environmental conditions (Schuh & Diesel, 1995; Hancock *et al.*, 1998; Paschke *et al.*, 2004). Therefore, observed differences in average DWE in *S. arctus* could represent actual differences in larval size or energetic condition. However, further research is needed in order to determine how this variation in DWE translates to offspring in this slipper lobster.

The presence of this intraspecific variability in FE during the reproductive period, is evidence of the importance of the development of an optimal predictive relationship between number of eggs produced and body size. The advantage of using GLM with respect to classical linear models lies in the fact that it provides estimations in the original measuring scale, thus removing interpretive difficulties associated with subsequent transformations and generating a useful tool for stock assessment (Green *et al.*, 2009). In addition, the insertion of a variable with a higher temporal resolution (month) allowed the final model to account for more variation. The great percentage of variation explained by this model (>90%) indicates its potential use for the estimation of FE during the annual reproductive cycle (January to September).

The model obtained for the determination of FE in *S. arctus* suggests the need to protect larger females, with the highest FE, and which are not protected by current legislation. However, it is worth mentioning that the relative contribution to population egg production by any size class is a function both of frequency of spawning and of the proportion of the population it represents (Aiken & Waddy, 1980). The determination of these parameters and the constant egg loss rate (24%) shown by *S. arctus*, will allow for the calculation of more accurate annual egg production indices and an improvement in estimations of relative reproductive potential.

The results of this research have direct implications for fisheries management of *S. arctus* and other commercial crustacean species with similar reproductive strategies. The development of a fisheries management plan should take into account both seasonal and maternal size effects on investment per egg. Since variations in egg weight affect the initial larval stage, as well as later phases of life history of marine decapods (Jørstad *et al.*, 2005; Giménez, 2006; Bas *et al.*, 2008; Guay *et al.*, 2011), this trait could have implications both in future recruitment success and in population recovery of *S. arctus*.

References

Agnalt AL (2008) Fecundity of the European lobster (*Homarus gammarus*) off southwestern Norway after stock enhancement: do cultured females produce as many eggs as wild females? *ICES Journal of Marine Science* **65**, 164–170.

Aiken DE and Waddy SL (1980) Reproductive biology. In Cobb JS and Phillips BF (eds), *The Biology and Management of Lobsters*. London: Academic Press, pp. 215–276.

Alborés I, García-Soler C and Fernández L (2019) Reproductive biology of the slipper lobster *Scyllarus arctus* in Galicia (NW Spain): implications for fisheries management. *Fisheries Research* **212**, 1–11.

Alvarez I, Gomez-Gesteira M, DeCastro M, Lorenzo MN, Crespo AJC and Dias JM (2011) Comparative analysis of upwelling influence between the western and northern coast of the Iberian Peninsula. *Continental Shelf Research* **31**, 388–399.

Álvarez I, Lorenzo MN and DeCastro M (2012) Analysis of chlorophyll a concentration along the Galician coast: seasonal variability and trends. *ICES Journal of Marine Science* **69**, 728–738.

Attard J and Hudon C (1987) Embryonic development and energetic investment in egg production in relation to size of female lobster (*Homarus americanus*). *Canadian Journal of Fisheries and Aquatic Sciences* **44**, 1157–1164.

Bas CC, Spivak ED and Anger K (2007) Seasonal and interpopulational variability in fecundity, egg size, and elemental composition (CHN) of eggs and larvae in a grapsoid crab, *Chasmagnathus granulatus*. *Helgoland Marine Research* **61**, 225–237.

Bas CC, Spivak ED and Anger K (2008) Variation in early developmental stages in two populations of an intertidal crab, *Neohelice* (*Chasmagnathus*) *granulata*. *Helgoland Marine Research* **62**, 393–401.

Brante A, Fernández M, Eckerle L, Mark F, Pörtner HO and Arntz W (2003) Reproductive investment in the crab *Cancer setosus* along a latitudinal cline: egg production, embryo losses and embryo ventilation. *Marine Ecology Progress Series* **251**, 221–232.

Bryant AD and Hartnoll RG (1995) Reproductive investment in two spider crabs with different breeding strategies. *Journal of Experimental Marine Biology and Ecology* **188**, 261–275.

Burnham KP and Anderson D (2004) Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research* **33**, 261–304.

Cau A, Davini MA, Deiana AM and Salvadori S (1988) Gonadal structure and gametogenesis in *Scyllarus arctus* (L.) (Crustacea, Decapoda). *Italian Journal of Zoology* **55**, 299–306.

Chang YJ, Sun CL, Chen Y, Yeh SZ and Chiang WC (2007) Reproductive biology of the spiny lobster, *Panulirus penicillatus*, in the southeastern coastal waters off Taiwan. *Marine Biology* **151**, 553–564.

Chubb CF (2000) Reproductive biology: issues for management. In Phillips BF and Kittaka J (eds), *Spiny Lobster: Fisheries and Culture*. Oxford: Blackwell, pp. 245–275.

Clarke A (1993) Egg size and egg composition in polar shrimps (Caridea; Decapoda). *Journal of Experimental Marine Biology and Ecology* **168**, 189–203.

Currie J and Schneider D (2011) Spatial scaling from latitudinal gradients: size-specific fecundity in the American lobster *Homarus americanus*. *Marine Ecology Progress Series* **439**, 193–201.

DeMartini EE and Williams HA (2001) Fecundity and egg size of *Scyllarides squammosus* (Decapoda: Scyllaridae) at Maro Reef, Northwestern Hawaiian Islands. *Journal of Crustacean Biology* **21**, 891–896.

Diez MJ and Spivak ED (2012) Seasonal variations in size, biomass, and elemental composition (CHN) of *Halicarcinus planatus* (Brachyura: Hymenosomatidae) larvae from the Beagle Channel. *Journal of Crustacean Biology* **32**, 575–581.

Fischer S, Thatje S and Brey T (2009) Early egg traits in *Cancer setosus* (Decapoda, Brachyura): effects of temperature and female size. *Marine Ecology Progress Series* **377**, 193–202.

Fonseca-Larios ME and Briones-Fourzan P (1998) Fecundity of the spiny lobster *Panulirus argus* (Latreille, 1804) in the Caribbean coast of Mexico. *Bulletin of Marine Science* **63**, 21–32.

Fox CW and Czesak ME (2000) Evolutionary ecology of progeny size in arthropods. *Annual Review of Entomology* **45**, 341–369.

Garcia A (1985) Variación estacional en la fecundidad de la langosta *Panulirus inflatus* (Bouvier, 1895) (Crustacea: Decapoda: Palinuridae). *Ciencias Marinas* **11**, 7–27.

Giménez L (2006) Phenotypic links in complex life cycles: conclusions from studies with decapod crustaceans. *Integrative and Comparative Biology* **46**, 615–622.

Giménez L and Anger K (2003) Larval performance in an estuarine crab, *Chasmagnathus granulata*, is a consequence of both larval and embryonic experience. *Marine Ecology Progress Series* **249**, 251–264.

Goñi R, Quetglas A and Reñones O (2003) Size at maturity, fecundity and reproductive potential of a protected population of the spiny lobster *Palinurus elephas* (Fabricius, 1787) from the western Mediterranean. *Marine Biology* **143**, 583–592.

González-Gurriarán E, Fernández L, Freire J and Muiño R (1996) Reproductive biology of the spider crab *Maja squinado* (Decapoda, Majidae) based on the analysis of seminal receptacles. ICES, Shellfish Committee C.M., p. K:29:17.

Green BS, Gardner C and Kennedy RB (2009) Generalised linear modelling of fecundity at length in southern rock lobsters, *Jasus edwardsii*. *Marine Biology* **156**, 1941–1947.

Griffen BD, Altman I, Hurley J and Mosblack H (2011) Reduced fecundity by one invader in the presence of another: a potential mechanism leading to species replacement. *Journal of Experimental Marine Biology and Ecology* **406**, 6–13.

Groeneveld JC (2005) Fecundity of spiny lobster *Palinurus gilchristi* (Decapoda: Palinuridae) off South Africa. *African Journal of Marine Science* **27**, 231–238.

Guay C, Sainte-Marie B and Brêthes JC (2011) Strong maternal effects and extreme heterogeneity of progeny development in the caridean shrimp *Sclerocrangon boreas* (Crangonidae). *Marine Biology* **158**, 2835–2845.

Hancock MA, Hughes JM and Bunn SE (1998) Influence of genetic and environmental factors on egg and clutch sizes among populations of *Paratya australiensis* Kemp (Decapoda: Atyidae) in upland rainforest streams, south-east Queensland. *Oecologia* **115**, 483–491.

Hartnoll RG (1985) Growth, sexual maturity and reproductive output. In Wenner A (ed.), *Factors in Adult Growth*. Rotterdam: Balkema, pp. 101–128.

Hendry AP, Day T and Cooper AB (2001) Optimal size and number of propagules: allowance for discrete stages and effects of maternal size on reproductive output and offspring fitness. *American Naturalist* **157**, 387–407.

Hines AH (1982) Allometric constraints and variables of reproductive effort in brachyuran crabs. *Marine Biology* **69**, 309–320.

Jørstad KE, Prodöhl PA, Kristiansen TS, Hughes M, Farestveit E, Taggart JB, Agnalt AL and Ferguson A (2005) Communal larval rearing of European lobster (*Homarus gammarus*): family identification by microsatellite DNA profiling and offspring fitness comparisons. *Aquaculture* **247**, 275–285.

Kindsvater HK, Bonsall MB and Alonzo SH (2011) Survival costs of reproduction predict age-dependent variation in maternal investment. *Journal of Evolutionary Biology* **24**, 2230–2240.

Laptikhovsky V (2006) Latitudinal and bathymetric trends in egg size variation: a new look at Thorson's and Rass's rules. *Marine Ecology* **27**, 7–14.

Lavalli K and Spanier E (2007) Introduction to the biology and fisheries of slipper lobsters. In Lavalli K and Spanier E (eds), *The Biology and Fisheries of the Slipper Lobster*. Boca Raton, FL: CRC Press, pp. 3–21.

Lloret J and Riera V (2008) Evolution of a Mediterranean coastal zone: human impacts on the marine environment of Cape Creus. *Environmental Management* **42**, 977–988.

MacDiarmid AB and Butler MJI (1999) Sperm economy and limitation in spiny lobsters. *Behavioral Ecology and Sociobiology* **46**, 14–24.

MacDiarmid AB and Kittaka J (2000) Breeding. In Phillips BF and Kittaka J (eds), *Spiny Lobsters: Fisheries and Culture*. Oxford: Blackwell, pp. 485–507.

MacDiarmid AB and Sainte-Marie B (2006) Reproduction. In Phillips BF (ed.), *Lobsters: Biology, Management, Aquaculture and Fisheries*. Oxford: Blackwell, pp. 45–68.

Moland E, Moland Olsen E and Stenseth N (2010) Maternal influences on offspring size variation and viability in wild European lobster *Homarus gammarus*. *Marine Ecology Progress Series* **400**, 165–173.

Mura M, Cau A and Deiana AM (1984) Il genere Scyllarus Fabr., 1775 nel Mediterraneo centro-occidentale. *Rendiconti Seminario Facolta Scienze. Università Cagliari* **54**, 266–274.

Oh CW and Hartnoll RG (2004) Reproductive biology of the common shrimp *Crangon crangon* (Decapoda: Crangonidae) in the central Irish Sea. *Marine Biology* **144**, 303–316.

Oliveira G, Freire AS and Bertuol PRK (2008) Reproductive biology of the slipper lobster *Scyllarides deceptor* (Decapoda: Scyllaridae) along the southern Brazilian coast. *Journal of the Marine Biological Association of the United Kingdom* **88**, 1433–1440.

O'Malley JM (2011) Spatio temporal variation in the population ecology of scaly slipper lobsters *Scyllarides squammosus* in the Northwestern Hawaiian Islands. *Marine Biology* **158**, 1887–1901.

Ouellet P and Plante F (2004) An investigation of the sources of variability in American lobster (*Homarus americanus*) eggs and larvae: female size and reproductive status, and interannual and interpopulation comparisons. *Journal of Crustacean Biology* **24**, 481–495.

Parker GA and Begon M (1986) Optimal egg size and clutch size: effects of environment and maternal phenotype. *American Naturalist* **128**, 573–592.

Paschke KA, Gebauer P, Buchholz F and Anger K (2004) Seasonal variation in starvation resistance of early larval North Sea shrimp *Crangon crangon* (Decapoda: Crangonidae). *Marine Ecology Progress Series* **279**, 183–191.

Pessani D and Mura M (2007) The biology of the Mediterranean scyllarids. In Lavalli K and Spanier E (eds), *The Biology and Fisheries of the Slipper Lobster*. Boca Raton, FL: CRC Press, pp. 263–286.

Pond D, Harris R, Head R and Harbour D (1996) Environmental and nutritional factors determining seasonal variability in the fecundity and egg viability of *Calanus helgolandicus* in coastal waters off Plymouth, UK. *Marine Ecology Progress Series* **143**, 45–63.

Relini G, Bertrand J and Zamboni A (1999) Synthesis of the knowledge on bottom fishery resources in central Mediterranean (Italy and Corsica). *Biologia Marina Mediterranea* **6**, 593–600.

Sakai S and Harada Y (2001) Why do large mothers produce large offspring? Theory and a test. *American Naturalist* **157**, 348–359.

Santos RS, Hawkins S, Monteiro LR, Alves M and Isidro EJ (1995) Marine research, resources and conservation in the Azores. *Aquatic Conservation: Marine and Freshwater Ecosystems* **5**, 311–354.

Schuh M and Diesel R (1995) Effects of salinity and starvation on the larval development of *Sesarma curacaoense* de Man, 1892, a mangrove crab with abbreviated development (Decapoda: Grapsidae). *Journal of Crustacean Biology* **15**, 645–654.

Sekiguchi H, Booth J and Webber R (2007) Early life histories of slipper lobsters. In Lavalli K and Spanier E (eds), *The Biology and Fisheries of the Slipper Lobster*. Boca Raton, FL: CRC Press, pp. 69–90.

Smith GG and Ritar AJ (2007) Sexual maturation in captive spiny lobsters, *Jasus edwardsii*, and the relationship of fecundity and larval quality with maternal size. *Invertebrate Reproduction and Development* **50**, 47–55.

Somers K (1991) Characterizing size-specific fecundity in crustaceans. In Wenner A and Kuris A (eds), *Crustacean Egg Production*. Rotterdam: Balkema, pp. 357–378.

Tully O, Roantree V and Robinson M (2001) Maturity, fecundity and reproductive potential of the European lobster (*Homarus gammarus*) in Ireland. *Journal of the Marine Biological Association of the United Kingdom* **81**, 61–68.

Urzúa A and Anger K (2013) Seasonal variations in larval biomass and biochemical composition of brown shrimp, *Crangon crangon* (Decapoda, Caridea), at hatching. *Helgoland Marine Research* **67**, 267–277.

Urzúa A, Paschke U, Gebauer P and Anger K (2012) Seasonal and interannual variations in size, biomass and chemical composition of the eggs of North Sea shrimp, *Crangon crangon* (Decapoda: Caridea). *Marine Biology* **159**, 583–599.

Verísimo P, Bernárdez C, González-Gurriarán E, Freire J, Muiño R and Fernández L (2011) Changes between consecutive broods in the fecundity of the spider crab, *Maja brachydactyla*. *ICES Journal of Marine Science* **68**, 472–478.

Vijayakumaran M, Murugan TS, Remany MC, Leema TM, Kumar JD, Santhanakumar J, Venkatesan R and Ravindran M (2005) Captive breeding of the spiny lobster, *Panulirus homarus*. *New Zealand Journal of Marine and Freshwater Research* **39**, 325–334.

Vilotte O (1982) *Recherches sur la biologie et l'elevage de la cigale de mer Scyllarus arctus (L., 1758) (Crustacea, Decapoda, Scyllaridae)* (PhD thesis). Université des sciences et techniques du Languedoc, Montpellier, France.

Wen XB, Chen LQ, Zhou ZL, Ai CX and Deng GY (2002) Reproduction response of Chinese mitten-handed crab (*Eriocheir sinensis*) fed different sources of dietary lipid. *Comparative Biochemistry and Physiology Part A* **131**, 675–681.