Eggs development and fecundity of *Metanephrops rubellus* (Moreira 1903) (Crustacea: Nephropidae) and implications for fishery management in Brazil

EVANDRO SEVERINO-RODRIGUES, LIGIA GOMES FURQUIM, ROBERTO DA GRAÇA-LOPES & LUIS FELIPE DE ALMEIDA DUARTE[*]

Fisheries Institute: Av. Bartolomeu de Gusmão, 192 – Santos, São Paulo, Brasil – CEP: 11030-90.

* *Corresponding author: duarte.mepi@gmail.com*

Abstract: The Uruguayan lobster (*Metanephrops rubellus*, Moreira, 1093) is distributed in the Western Atlantic between 21º S and 42º S and is caught occasionally in the southeast and south of Brazil. There is no specific regulatory legislation for its exploitation and studies that can subsidize management measures are scarce. Reproductive biology contributes to the collection of valuable information aiming at strategic exploitation plans. This study gathered information on egg development and fecundity for this species. Between July 2011 and December 2012, 875 individuals were captured occasionally and collected from the fishery landings. Population structure of ovigerous specimens, egg development stages taking into account their gonad maturation, and relative fecundity were analyzed. This species has predominantly three egg development stages and two other less frequent stages. Throughout the year, females with gonads in a "mixed maturation state" and at all egg development stages were recorded, suggesting a continuous cycle of reproduction. Fecundity is low, the eggs are relatively large, their number increases with specimen size, and differences in fertility depend on egg development stage. Even if captured occasionally in Brazil, the results reveal a relative sensitivity of this species to fishing exploitation if no management measures are implemented to promote sustainability.

Key words: Uruguayan lobster, reproductive biology, Nephropidae, gonad maturation.

Desenvolvimento dos ovos e fecundidade de *Metanephrops rubellus* (Moreira 1903) (Crustacea: Nephropidae) e suas implicações para o manejo pesqueiro no Brasil. Resumo: O lagostim (*Metanephrops rubellus*) está distribuído no Atlântico Ocidental entre 21º S e 42º S e é capturado no sudeste e sul do Brasil. Não há legislação regulatória específica para sua explotação e estudos que possam subsidiar medidas de manejo são escassos. A biologia reprodutiva contribui para a coleta de informações valiosas visando planos estratégicos de explotação. Foram reunidas informações sobre o desenvolvimento e fecundidade dos ovos desta espécie. Entre julho de 2011 e dezembro de 2012, um total de 875 indivíduos foram coletados em desembarques pesqueiros. Foram analisadas a estrutura populacional das fêmeas ovígeras, estágios de desenvolvimento dos ovos considerando os estágios de maturação das gônadas dos exemplares e suas fecundidades relativas. Esta espécie tem predominantemente três estágios de desenvolvimento de ovos e dois outros estágios menos frequentes. Ao longo do ano, foram registradas fêmeas com gônadas em "estado de maturação mista" e em todos os estágios de desenvolvimento dos ovos, sugerindo um ciclo contínuo da reprodução. A fecundidade é baixa, os ovos são relativamente grandes, seu número aumenta com o tamanho do espécime e as diferenças na fertilidade dependem do estágio de desenvolvimento do ovo. Mesmo tratando-se de capturas consideradas ocasionais, os resultados obtidos revelam uma relativa sensibilidade

desta espécie à exploração pesqueira, caso não sejam implementadas medidas de gestão que promovam a sustentabilidade.

Palavras-chave: lagosta uruguaia, biologia reprodutiva, desenvolvimento de ovos, Nephropidae, maturação de gônadas.

Introduction

The Uruguayan lobster *Metanephrops rubellus* (Moreira 1903) is distributed in the Western Atlantic between 21ºS and 42ºS, in Brazil (from Espírito Santo to Rio Grande do Sul), Uruguay and Argentina (Melo 1999). It inhabits waters between 50 and 270 m deep, preferentially on sandy and sandy-muddy bottoms (Severino-Rodrigues *et al.* 2007).

Along the southeastern coast of Brazil, this species is caught by the trawling fleet targeting pink shrimps (*Penaeus brasiliensis* and *Penaeus paulensis*). Due to oscillations in the catches of these resources, the capture extended to other species found in deeper waters, including the Uruguayan lobster (Severino-Rodrigues *et al.* 2016, 2018). Such catches are discontinuous and focused mainly during the period when the shrimp fishery is banned, but fishing Uruguayan lobster is allowed (Brazil 2013). The landings of Uruguayan lobster fluctuate considerably both monthly and annually due to market reasons and operating costs (Severino-Rodrigues *et al.* 2007, 2016, 2018). There is no specific regulatory legislation for the capture of *M. rubellus* since there are few studies about its life cycle that could support management measures, as shown by the very limited bibliography available on to this the species (Severino-Rodrigues *et al.* 2007, 2016).

In the family Nephropidae have a great variability in periodicity of egg production, in egg number and size, reflecting its reproductive strategy (Sastry 1983, Yazicioglu *et al.* 2016). Species with very large eggs generally have low fertility (Wear 1976, Macdiarmid & Sainte-Marie 2006, Yazicioglu *et al.* 2016). Females of this family show external embryonic development, incubating their eggs under the abdomen inside burrows for a long period (Chapman 1980). During this period, the eggs undergo different stages, which change in size and color because of embryo development (Figueiredo & Barraca 1963, Fontaine & Warluzel 1969). To the Norway lobster (*Nephrops norvegicus*, Linnaeus, 1758), a European species of Nephropidae, there is a considerable number of studies on different aspects of its life cycle, which allows some comparisons with the Uruguayan lobster (*Metanephrops rubellus)*

since they have similar morphology and behavior (Aguzzi *et al*. 2004, Bell *et al*. 2006, Sabatini & Hill 2008, Eiriksson 2014, Nguyen *et al*. 2018). *M. rubellus* is oviparous with internal fertilization and external embryonic development. Females carry their eggs adhered to pleopods from externalization to hatching during the zoea phase (Severino-Rodrigues *et al*. 2016).

The reproductive biology of a fishery-exploited species provides valuable information for proposing strategic plans for the sustainable exploitation of the resource (Sparre & Venema 1998, Duarte *et al*. 2010, 2015, Yazicioglu *et al*. 2016). For example, the evaluation of the eggs development and fecundity is important to estimate reproductive potential and the size of future population stocks (Sparre & Venema 1998). Fecundity is, therefore, important tool to determine variations in the total number of individuals comprised in a population (Yazicioglu *et al*. 2016). Considering the lack of information on the biology and fisheries of *M. rubellus*, this study aims to gather information on reproductive biology of this species focusing on egg development and fecundity. In addition, baseline information on this species' life cycle is required for managing and promoting sustainability of the Uruguayan lobster fishery in Brazil.

Material and methods

Study area: The study area is an area locally called "Santos Basin". This area occupies approximately 350 thousand km^2 of the Brazilian southeast-south continental margin between the 23° and 28° S parallels. The northern limit is Cabo de São Tomé (22° S and 41° W), and the southern limit is Cabo de Santa Marta (28° S and 48° W) (Pereira & Feijó 1994). Bathymetry is strongly influenced by the geomorphological features that compose it. The continental shelf is relatively homogeneous in terms of width and slope, and the platform breaks between 50 and 180 m deep, more frequently between 140 and 160 m (Evain *et al*. 2015). The bottom`s composition is predominant muddy or sandy-muddy, and the surface temperature is around 20° C (Romero *et al*. 2013).

Sampling: Weekly monitoring (through visits to landing sites) and four sampling campaigns were

conducted during the year from July 2011 and December 2012 at all industrial landing sites in the State of São Paulo, Brazil. Data collected in 2012 were grouped by season. In occasionally fishing fleets targeting pink shrimps (*Penaeus brasiliensis* and *Penaeus paulensis*), 875 individuals of *M. rubellus* were collected. These fishing boats operate between 22° and 26° S on muddy or sandy-muddy bottoms at 60-140 m of depth (Fig. 1).

 The double-trawl that operates alone in the study area consists of vessels built with wood or steel whose lengths range from 18 to 24 m and whose engine power is between 267 and 320 HP. The fishing equipment used in Brazil is two identical conical nets (total length: from 15.00 to 20.00 m; mouth length: from 14.30 to 18.00 m; bagger: length from 4.40 to 5.30 m) with a similar mesh size (30 mm and bagger with 22 mm between nodes). Each net has a pair of trawl wood doors (40 to 50 kg each) that maintain the horizontal opening and a headline (steel cables: ½) with floats that maintain the vertical opening of net mouths (Duarte *et al*. 2010, Severino-Rodrigues *et al*. 2016).

Egg development and diameter, and Fecundity: Specimens sample was carried out from the boxes where there was no separation of the individuals by size and, therefore, we covered all sizes captured in the landings in this study. Specimens were separated by sex (gonopore in the 3rd pair of pereiopods in females and in the 5th pair in males, and presence of copulatory appendix) (Fig. 2).

 Total length (Tl), from the anterior end of the rostrum to the posterior end of the telson, was measured using a caliper (Severino-Rodrigues *et al*. 2016). By the macroscopic analysis of ovaries, four stages of female gonadal maturation were identified: I (immature), II (maturing), III (mature), and IV (spawned), according to the description of Severino-Rodrigues *et al.* (2016) (Fig. 3).

 Egg development stages were based on the macroscopic classification proposed by Severino-Rodrigues *et al.* (2016). Thus, eggs were classified by color (quantity of vitellus) and embryo development and assigned to the following stages: dark green (G) (post-laying), light green (Gl) (intermediate), and pinkish white (W) (close to hatching and with the embryo visible through the membrane) (Fig. 4) (Severino-Rodrigues *et al*. 2016). At this last stage, the membrane that
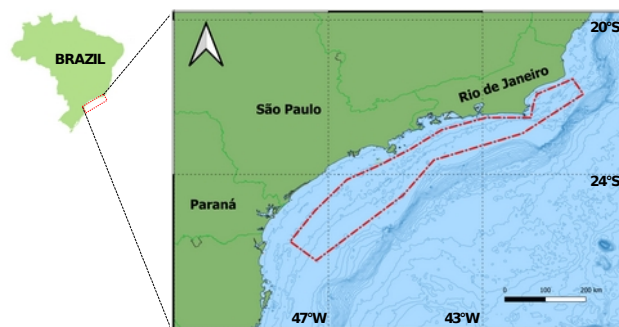

Figure 1. Map showing the area where *Metanephrops rubellus* were bycaught along the southeast and south coasts of Brazil

surrounds the embryo may already be broken, with free zoaeas, but still attached to pleopods.

 Individual fecundity and egg diameter were determined according to the adapted protocols of Corey & Reid (1991) and Heasman & Jeffs (2019). The entire exteriorized eggs (only from females that presented integral ovigerous mass) at different stages of development were separated from the pleopods using a brush, weighed on an electronic digital scale (0.001 g), and counted in checkered Petri dishes in a stereomicroscope (20x). Fecundity was estimated based on the number of laid eggs by each subsampled ovigerous female. A subsample of 21 eggs at different stages (seven at each development phase) were measured individually to estimate egg diameter with a micrometric ocular in an optical microscope (1000x).

Data analysis: We used the software R (version 1.2.1335) (Ihaka & Gentleman 1996) for statistical analysis. In cases of non-normality and heteroscedasticity of data, a non-parametric test (ANOVA by Kruskal-Wallis - KW) was performed, followed by *a posteriori* comparison of medians through multiple comparisons between treatments (Zar 1999).

 Regression analyses were performed through linear equations (y = a + bx) to establish empirical points for morphometric relationships between total length (Tl) and female fecundity (according to category of egg development: dark green, light green, and pinkish white). The coefficients of determination (R^2) were calculated in each equation to indicate how differences in female fecundity (by category) can be explained by total length (Zar 1999, Duarte *et al*. 2015). The possible differences between linear regressions obtained for each fecundity category were determined by analysis of covariance (ANCOVA), which compares the equations constants "*a*" (*intercept*, estimates the location where the linear fit crosses the axis) and "*b*"
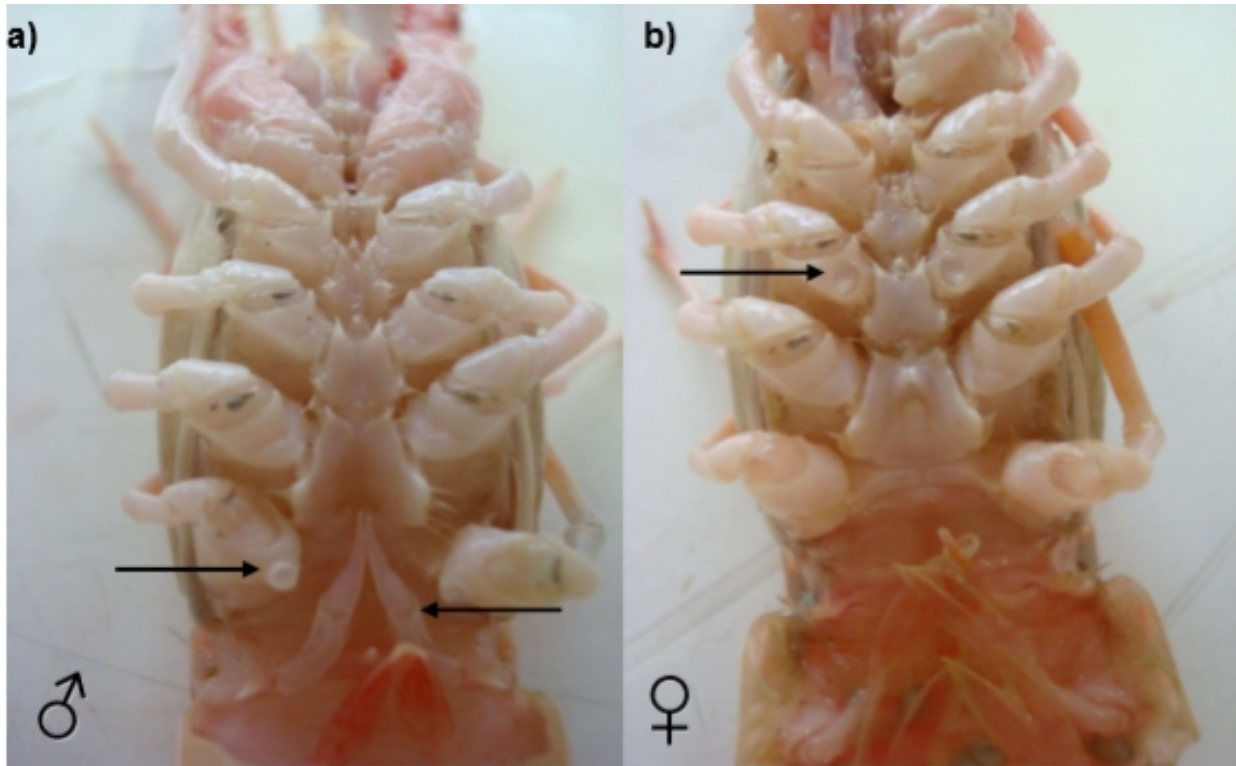
Figure 2. Gonopore position (detail of the copulatory appendix) in males (**a**) and females (**b**) of *Metanephrops rubellus*.
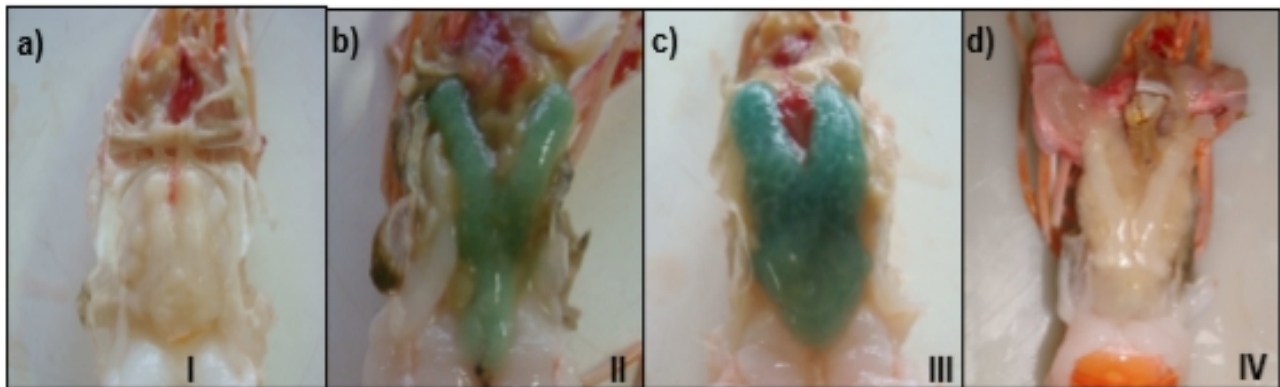

Figure 3. Maturation stages in ovaries of *Metanephrops rubellus*: a) I - immature, b) II - maturing, c) III - mature, d) IV - spawned (according to Severino-Rodrigues *et al*. 2016).

(*slope*, linear fit angle) between linear regressions (Zar 1999, Faraway 2002, Vargas *et al*. 2018).

Results
Egg development: A total of 875 individuals were identified, comprising 405 males (46.3%) and 470 females (53.7%). Overall 289 (61.5%) of females carried eggs at different egg development stages during the sampling period. Females with eggs adhered to pleopods ranged between 90.0 and 180.0 mm Tl, being concentrated mainly between 120.0 and 150.0 mm Tl. Eggs at the **G** stage (dark green) occurred in 118 females (40.8%), between 120.0 and 140 mm Tl; at stage **Gl** (light green) in 91 females

(31.4%), ranging from 130.0 to 150 mm Tl; and at stage **W** (white) in 80 females (27.8%), between 120.0 and 150 mm (Fig. 4).

There were no significant differences (K-W: $p > 0.05$) in female total length (Tl) as a function of the main categories of eggs development, despite the increasing trends between the stages G = 123.2 ± 22.2 mm Tl, Gl = 134.9 ± 23.8 mm Tl, and W = 140.7 ± 25.1 mm Tl (Fig. 5).

Females with eggs were observed throughout the analysis period at all development stages in the fall and winter. Eggs at the initial stage (**G**) and final stage (**W**) did not occur in the summer; eggs at the intermediate stage (**Gl**) occurred in all seasons,
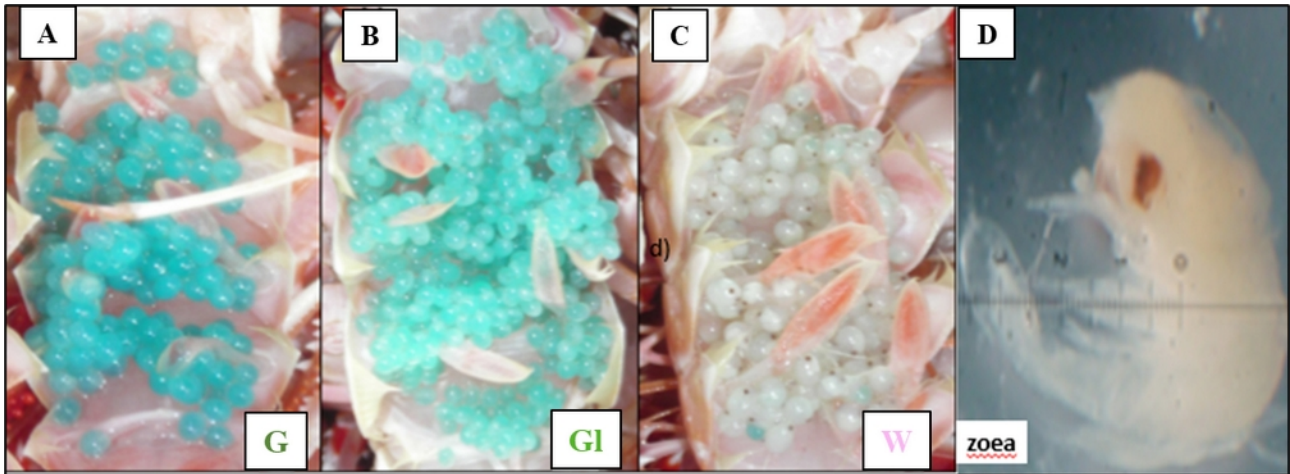
Figure 4. Egg development stages in *Metanephrops rubellus* based on the macroscopic classification proposed by Severino-Rodrigues et al. (2016): A) G - dark green (post-laying); B) Gl - light green (intermediate); C) W - pinkish white (close to hatching and with the embryo visible through the membrane); D) IV - zoea (recently hatched zoea still attached to pleopods).
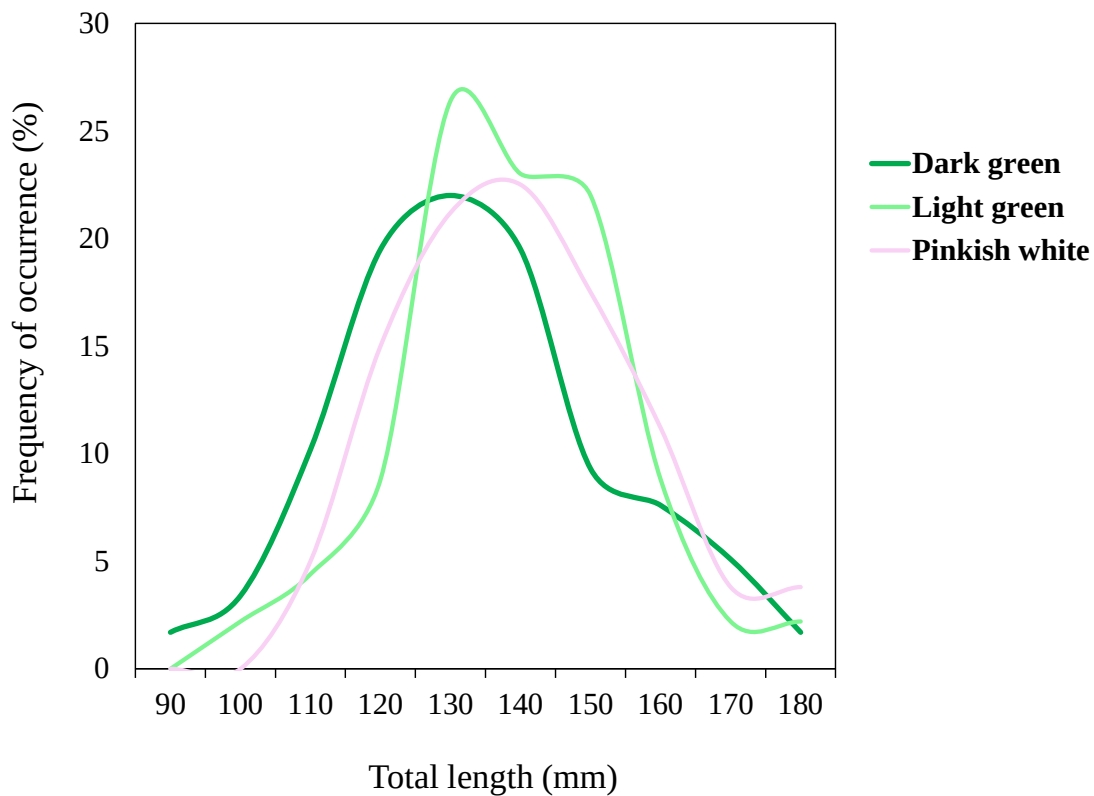

Figure 5. Distribution of ovigerous females of *Metanephrops rubellus* by size classes and categories of eggs development (dark green: post-laying; light green: intermediate; pinkish white: close to hatching and with the embryo visible through the membrane, see Severino-Rodrigues et al. 2016) captured in southeastern and southern Brazil.

mainly in the summer and spring; and eggs at the final stage (**W**) did not occur in the summer and spring, concentrating in the fall and winter (Fig. 6).

We report a result so far not reported in the literature on this species. Some females presented two additional categories of egg development, namely the simultaneous occurrence of eggs at different developmental stages in the same female (n = 39): dark green/light green (**G/Gl**) and light green/white (**Gl/W**) (Fig. 7). All stages of gonadal
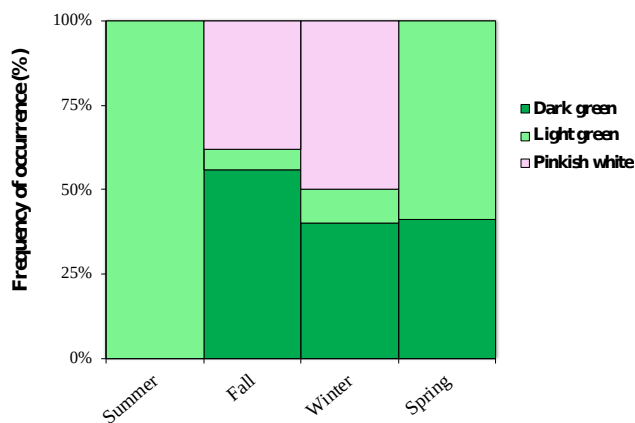
Figure 6 - Frequency (%) of egg development stages (dark green: post-laying; light green: intermediate; pinkish white: close to hatching and with the embryo visible through the membrane, see Severino-Rodrigues et al. 2016) of *Metanephrops rubellus* (from 875 females recorded) during the study period (by season, females with eggs [n], namely: summer = 218; fall = 230; winter = 214, and spring = 213) in southeastern and southern Brazil.

maturation, except for stage I (immature), occurred throughout the study period (Fig. 8).

Fecundity: Of 289 ovigerous females, 194 were selected for egg counting based on the criterion of the ovigerous mass integrity in order not to underestimate fecundity. The results presented a mean number of 401 eggs per female and ranging from 88 to 955 eggs depending on female size. Among these 194 females, 79 carried **green** eggs (425 ± 194 eggs), 62 **light green** eggs (397 ± 210 eggs), and 53 **pinkish white** eggs (370 ± 161 eggs).

Individual fecundity (number of eggs) of female *M. rubellus* females by category of eggs development (dark green, light green, and pinkish white), together with average egg diameter in those categories, are presented in Figure 9. Regardless of egg development stage, the individual number of eggs produced increased with female size (Tl). All linear regressions were significant (ANCOVA, p <0.05), allowing to perform interconversions between female total length and expected fecundity through the equations fitted with high determination coefficients (R2): green eggs (stage **G**: R^2= 0.97), light green eggs (stage **Gl**: R^2 = 0.92), and pinkish white eggs (stage **W**: R^2 = 0.94). The results of analysis of covariance (ANCOVA) performed to compare regressions between egg development stages, showed significant differences for the values of "a" (intercept) and "b" (slope) (p<0.01). The

average fecundity, reflecting the reproductive potential, was higher at the development stages green (**G**), followed by light green (**Gl**) and pinkish white (**W**).

Individually measured egg diameters (n = 37) varied between 3.50 and 5.60 mm, corresponding to a average egg diameter of 4.68 ± 0.54 mm. The average egg diameter was 4.62 ± 0.50 mm for green (**G**), 4.58 ± 0.62 mm for light green (**Gl**) and 4.88 ± 0.52 mm for pinkish white (**W**), without significant differences between categories (KW=1.79, p=0.40).

Discussion
We observed a slightly greater participation of females in laying, differently from that observed for population evaluations of *N. norvegicus*, in which the presence of ovigerous females was lower in most studies (Figueiredo & Barraca 1963, Symonds 1972, Farmer 1974, 1975). The smallest ovigerous female recorded had a total length of 90.5 mm, a value close to the L_{50} estimated for this species (82.5 mm) (Severino-Rodrigues *et al.* 2016). This indicates that copulation occurs just after maturity size, or just before it.

Females were observed at different stages of gonad maturation (except for the state I - immature). The eggs were adhered to pleopods during the gonad maturation cycle throughout the sampled period. Figueiredo & Barraca (1963) also identified in *N. norvergicus* several combinations of egg development: "gonads in a mixed maturation state" (part mature ovary, part in maturation, externalized eggs and embryos, close to hatching), which suggests a "continuous cycle of reproduction," without a resting state between two egg generations. In addition, throughout the sampling period, we also found females with eggs at all development stages (G, Gl and W) and at three gonad development stages (II, III and IV), confirming the uninterrupted reproductive process in the species studied.

Severino-Rodrigues *et al.* (2016) also found individuals of *M. rubellus* with empty gonads and without eggs. This may indicate a "split spawning," where the female, simultaneously with egg development, starts a new ripening of gonads and spawns a new batch of eggs, restarting the cycle until complete laying, as Jivoff & Hines (1998) and Jivoff *et al.* (2007) also observed for the blue crab *Callinectes sapidus*.

Ovigerous female sizes concentrated between 120.0 and 150.0 mm. However, there was no relation with animal size and egg development stage:
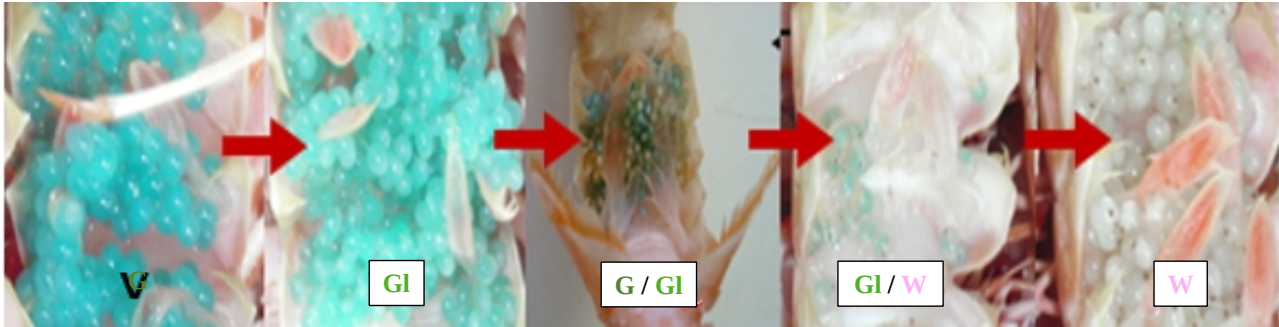
Figure 7. Variation in eggs development in pleopods of the same female of *Metanephrops rubellus*: G) dark green Gl) light green G/Gl) dark green/light green Gl/W) light green/white and W) white.
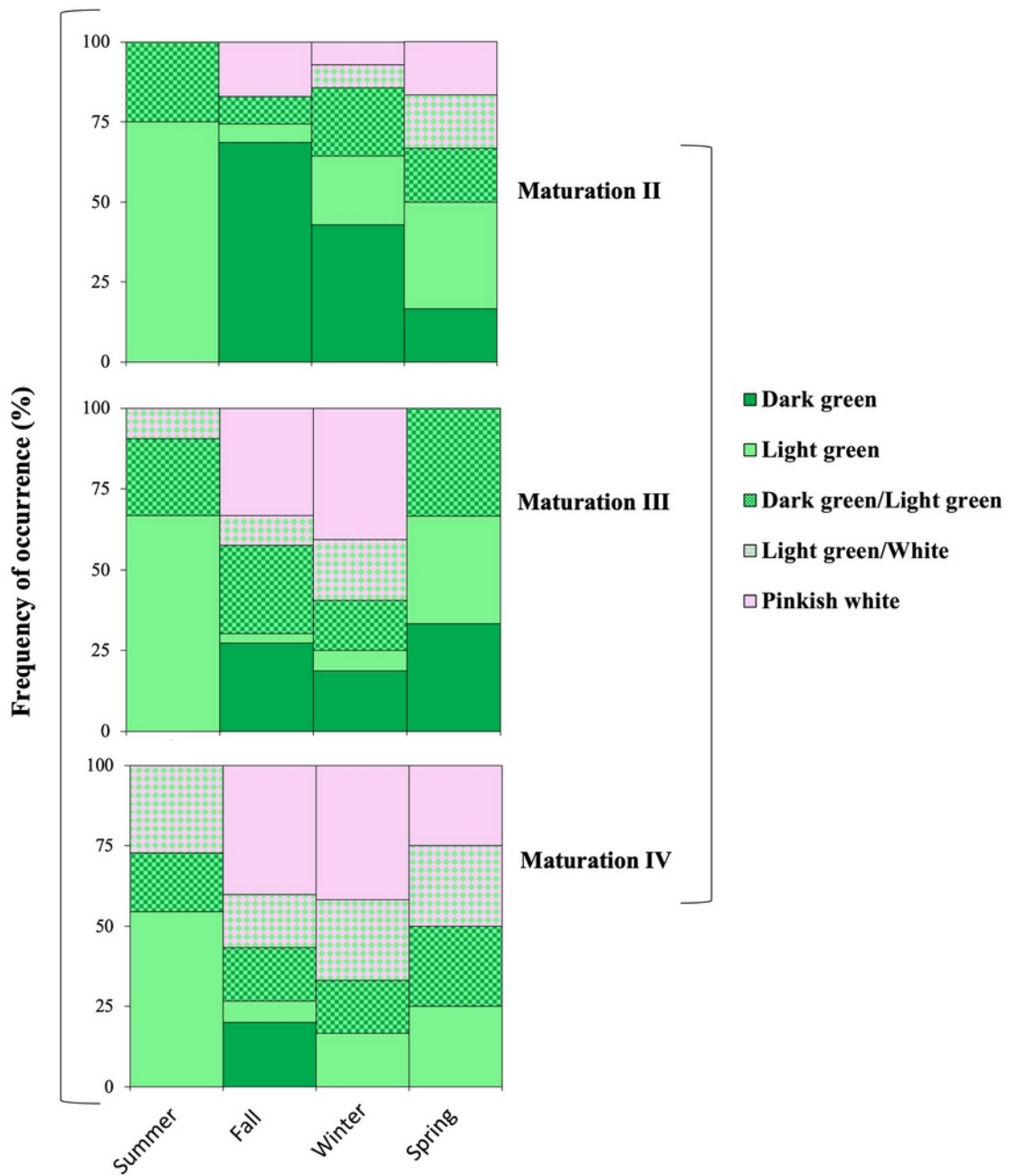
Figure 8 (previous page). Frequency of egg development stages (dark green: post-laying; light green: intermediate; Dark green/Light green: a mix of both stages; Light green/White: a mix of both stages; pinkish white: close to hatching and with the embryo visible through the membrane, see Severino-Rodrigues et al. 2016) of *Metanephrops rubellus* by gonadal maturation stage during the study period (by season, females with eggs [n], namely: summer = 218; fall = 230; winter = 214, and spring = 213) in southeastern and southern Brazil.
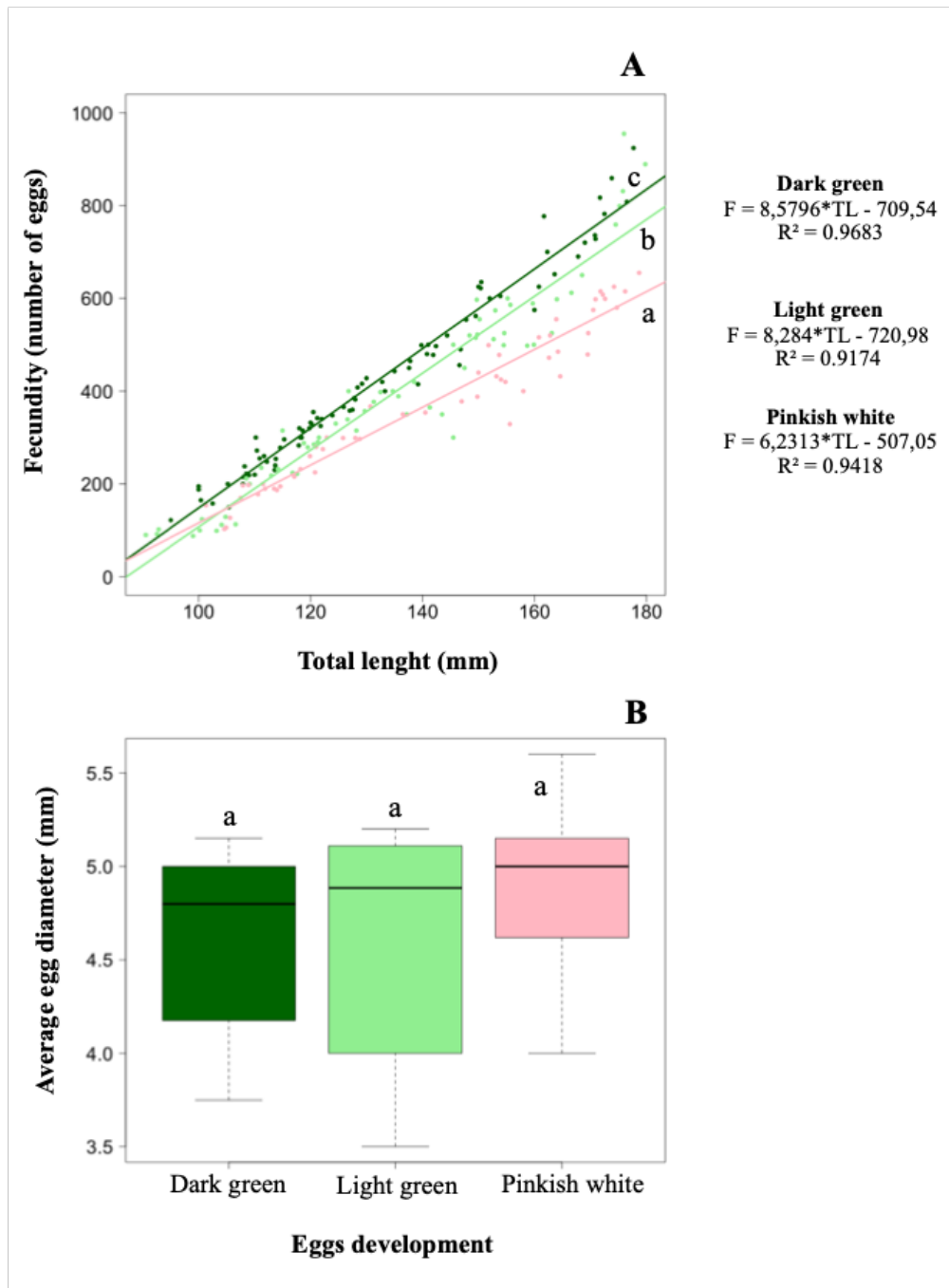

Figure 9 - Female fecundity and mean egg diameter of *Metanephrops rubellus* by category of egg development (dark green, light green, and pinkish white) captured in southeastern and southern Brazil. Adjusted lines containing different letters ("a," "b," and "c") indicate coefficients of linear regression (a = intercept and b = slope) with a statistically significant difference of 5% according to analysis of covariance (A). Average egg diameter (mm) in relation to these same categories. The medians associated with a same letter ("a") showed no statistically significant differences in average egg diameter at 5% according to Kruskal-Wallis test (KW) (B).

G (120.0 and 140 mm), Gl (130.0 and 150 mm), W (120.0 and 150 mm). This indicates, therefore, that although they occur within a certain size range, there are no changes in egg maturation.

Females also were observed with a mixed egg mass (G/Gl, Gl/G, Gl/W, W/Gl). However, their participation was not expressive, reason why we considered the predominant color of externalized eggs in the analyses (G, Gl and W). However, the presence of these mixed egg masses contributes to the hypothesis of a "continuous reproduction cycle" of *M. rubellus*.

The average number of females with post-laying eggs was slightly higher in relation to ovigerous mass, considered to be at the intermediate stage, followed by those in pre-hatch. This may be related to a progressive loss of eggs during incubation, as Mori *et al*. (1998, 2001) and Fariña *et al*. (1999) observed for *N. norvergicus*.

The egg diameter is the main factor responsible for variations in fecundity among crustaceans of equivalent size (Abellò & Sardá 1982). Species of the genus *Metanephrops* have much larger eggs compared to those of *Nephrops*, which directly reflects in the number of eggs laid and the reproductive strategy used (Hines 1982). In the present study, the egg diameter of *M. rubellus* did not show significant differences between different egg development stages, as well as in relation to female size, corroborating what Mori *et al*. (2001) and Mcquaid *et al*. (2009) observed for *N. norvegicus*. However, the average egg diameter of *M. rubellus* (4.68 mm) was greater than that observed for *N. Norvegicus (*1.63 mm) (Figueiredo & Barraca 1963, Mori *et al*. 1998), leading to a smaller number of eggs fixed to pleopods. Such a situation combined with losses during incubation results in low fertility but does not imply low reproductive potential. They mean different reproductive strategies, according to Hines (1982) and Yazicioglu *et al*. (2016), which in theory would guarantee a successful recruitment and population resilience, disregarding mortality due to fishing (Sparre & Venema 1998, Duarte *et al*. 2010, 2015). The presence of large and fewer eggs has been also observed for other species of the genus *Metanephrops* (Phillips 1992), such as *M. binghami* (Gomez *et al.* 2005), *M. Chalengeri* (Wear 1976, Macdiarmid & Sainte-Marie 2006, Wahle *et al*. 2011), *M. Thomsoni* (Choi *et al*. 2008), *M. Japonicus* (Okamoto 2005), and *M. velutinus* (Wallner & Phillips 1995). However, according to Raven (1961), egg size and volume besides

genetically determined, could also be influenced by temperature, available food, and other regional environmental conditions. Mori *et al*. (2001) mentioned the influence of depth (related directedly with these factors described above) on the egg volume of *N. norvegicus*. In the shallowest areas (200-450 m), there were statistically larger eggs than those in deeper waters (500-550m).

Estimates of fecundity of *N. norvegicus* differ in the literature available. The numbers vary between populations or even between different parts of a same population (Tuck *et al*. 2000). This is generally attributed to methodology, area, size at maturation, or even loss of eggs (Chapman & Bailey 1987, Chapman & Howard 1988, Tuck *et al*. 1997). Such variability in the Nephropidae family is often recorded for both egg number and size.

Species with very large eggs generally have a low fertility and vice-versa (Wear 1976, Corey & Reid 1991, Macdiarmid & Sainte-Marie 2006). In addition, environmental and regional factors (food, predation, natural loss of eggs) and anthropic factors, such as fishing (capturing ovigerous females), can also alter the population's reproductive potential (Chapman & Howard 1988, Tuck *et al*. 1997, Mori *et al*. 1998).

The ability to hold the number of eggs observed here is directly correlated with animal size. Larger and heavier females have a greater relative area to carry more eggs and, consequently, confirm the higher fecundity observed here. We also recorded this pattern for the species *M. rubellus*. The present study also provides equations with significant fittings resulting from linear models to apply interconversions between the total length of the female and the expected fecundity.

The average fecundity observed in our study for *M. rubellus* (491 eggs ranging between 88 and 955) is much lower than the estimate obtained for *N. norvegicus* (1475 to 2636 eggs, ranging between 800 and 5000), as Farmer (1974, 1975), Fariña *et al*. (1999) and Eiriksson (2014) reported, although both species reach relatively close maximum sizes: Tl = 19.2 cm for *M. rubellus* (Severino-Rodrigues *et al*. 2016) and 24.0 cm for *N. norvegicus* (Relini *et al*. 1999). Such evidence supports the hypothesis that the reproductive strategy is intrinsic to the evolutionary history of the species (Yazicioglu *et al*. 2016).

It should be noted that, as with other nephropids, the estimated fecundity obtained in the present study may be underestimated by the loss of eggs due to low adherence to pleopods, which

occurs naturally, and due to the long period of oviposition (Kuris 1991). Losses may also occur due to egg predation (Mori *et al*. 1998) and abrasion by trawls during capture (Chapman 1980, Leocádio *et al*. 2012, Severino-Rodrigues *et al*. 2016).

Depending on the intensity of egg loss in the natural environment, there may be a decrease in the production of larvae, hindering recruitment and consequently the replenishment of stocks (Froglia & Gramitto 1979, 1981, Chapman 1980, Morizur *et al*. 1981, Figueiredo *et al*. 1982, Mori *et al*. 1998, Dickey-Collas *et al*. 2000, Briggs *et al*. 2002). This changes the species population dynamics. Following this logic, analyses of catches of *Metanephrops velutinus* in Australia, whose fecundity is also relatively low, proved that trawl fishing can be an important factor in decreasing reproductive potential even if the female is returned to the sea. The interaction with fishing activity indirectly affects the larval and juvenile phases, which co-inhabit areas similar as those of adults, due to the loss of eggs and the destruction of burrows (Wallner & Phillips 1995).

In Brazil, there are no management measures for *M. rubellus*. As it is an undirected fishery, pink shrimp fleets adapt the fishing gear to catch Uruguayan lobster and, therefore, there is no specific legislation other than that for shrimp. On the other hand, for *N. norvegicus*, there are control measures: minimum landing, mesh size, and precautionary total capture (Briggs *et al*. 2002). Some studies have focused on measuring how replacing part of the fishing effort of trawlers for traps could be effective to promote biological and economic sustainability (Chapman 1980, Leocádio *et al*. 2012).

The relative low fertility estimated for *M. rubellus* in the present study, the evidence of egg loss during incubation, and the large participation of ovigerous females in catches are factors that trigger an alert for catches of this species and make it highly sensitive to exploitation, therefore requiring special care in its management. The exploitation of this species using trawl nets in the southeast and south of Brazil should be regarded with caution, considering the characteristic of this species of digging burrows, incubation of eggs for a long period, natural or provoked loss of eggs, combined with the observation that catches are preferably of females, most of them ovigerous. Another aggravating factor is that because Uruguayan lobster produces large eggs, fecundity is low, making the population more sensitive to wearing out and requiring a greater control of resource management bodies. On the other hand, we observed a low participation of immature individuals in the present study. It can be considered a positive factor for the restoration of stocks, while for *N. norvegicus* situations of overfishing of recruits were recorded in some regions of Europe (Orsi-Relini et al. 1989, 1998).

The species *M. rubellus* has predominantly three stages of egg development. Their color varies depending on the amount of vitellus and embryo development: dark green (close to posture), light green (intermediate), and pinkish white (close to hatching). However, the present study detected females in two more categories of development, that is, mixed eggs at different phases in a same animal (dark green/light green, and light green/white). Female size does not determine the stage of egg development, occurring proportionally in all adult animals. The species also has "gonads in mixed maturation state" and females at all stages of egg development occur at the three gonadal development stages throughout the year, suggesting a continuous cycle of reproduction.

The fecundity of this species is low. It has relatively large eggs and no differences in size between egg development stages. Regardless of egg development stage, the individual number of eggs produced by females increases the larger the animal is. The average fecundity is higher at the development stages green, followed by light green and pinkish white, which showed the lowest relative reproductive potential.

Because it has relatively large eggs (without differences in size between the stages of development), the fertility of *M. rubellus* is obviously low and, consequently, this species should be protected, as the IUCN recommended (Wahle *et al*. 2011). Regardless of the stage of development of the eggs, the number of them fixed on the pleopods increases the larger the specimen. In view of the reproductive fragility resulting from such low fertility, we recommend the planned and monitored capture of the resource *M. rubellus*, through the control of fishing effort, the definition of areas of exclusion from fishing and the adequacy of capture equipment. We also suggest that comparative studies be carried out between trawled and trapped catches in terms of the most vulnerable population strata, the quality of the fish and the financial return, in order to guarantee the biological and economic sustainability of the resource and the fishing activity.

References

Abellò P. & Sardá F. 1982. Morphometric characters of the sexual dimorphism in the chelae of *Goneplax rhomboides* (L.) (Decapoda: Brachyura). **Investigacion pesquera**, 46 (2): 163-170.

Aguzzi J., Sarda F. & Allue R. 2004. Seasonal dynamics in *Nephrops norvegicus* (Decapoda: Nephropidae) catches off the Catalan coasts (Western Mediterranean). **Fishery Research**, 9(2): 293-300.

Bell M.C., Redant F. & Tuck I. 2006. Nephrops species. In: Phillips B.F. (eds), **Lobsters: biology, management, aquaculture and fisheries**. Blackwell Publishing, Oxford, pp 412-461.

Brazil 2013. **Instrução Normativa nº 10, de 10 De Junho de 2011 Ministério da Pesca e Aquicultura**, DOU de 28/03/2013.

Briggs R.P., Armstrong M.J., Dickeycollas M., Allen M., Mcquaid N. & Whitmore J. 2002. The application of fecundity estimates to determine the spawning stock biomass of Irish Sea *Nephrops norvegicus* (L.) using the annual larval production method. **ICES Journal of Marine Science**, 59: 109-119.

Chapman C.J. 1980. Ecology of juvenile and adult Nephrops. Pp. 143-178. *In:* Cobb S, Phillips BF (Eds.). **The biology and management of lobsters 2**. Academic Press, London, 389 p.

Chapman C.J. & Bailey N. 1987. Biological research on fish and shellfish stocks. Recent progress in Norway lobster research. Pp. 99-111. *In:* Bailey RS, Parrish BB (Eds.). **Developments in fisheries research in Scotland**. Fishing News Books Ltd, Farnham, England, 111 p.

Chapman C.J. & Howard F.G. 1988. Environmental influences on Norway lobster (*Nephrops norvegicus*) populations and their implications for fishery management. **Symposium of the Zoological Society of London**, 59: 343-353.

Choi J.H., Jung N.K., Mi H.K. & Dae S. 2008. Population biology and feeding habits of the nephropid lobster *Metanephrops thomsoni* (Bate, 1888) in the East China Sea. **Journal Environmental Biology**, 29(4): 453-456.

Corey S & Reid D.M. 1991. Comparative Fecundity of Decapod Crustaceans: I. The Fecundity of Thirty-Three Species of Nine Families of Caridean Shrimp. **Crustaceana**, 60(3): 270-294.

Dickey-Collas M., Briggs R.P., Armstrong M.J. & Milligan S.P. 2000. Production of *Nephrops norvegicus* larvae in the Irish Sea. **Marine Biology**, 137: 973-981.

Duarte L.F.A., Severino-Rodrigues, E. & Gasalla, M.A. 2010. Slipper lobster (Crustacea, Decapoda, Scyllaridae) fisheries off the Southeastern coast of Brazil: I- exploitation patterns between 23° 00' and 29° 65'. **Fishery Research**, 102: 141-151.

Duarte L.F.A., Severino-Rodrigues, E., Pinheiro, M.A.A. & Gasalla, M.L.A. 2015. Slipper lobsters (Scyllaridae) off the southeastern coast of Brazil: relative growth, population structure, and reproductive biology. **Fishery Bulletin**, 113: 55-68.

Eiriksson H. 2014. Reproductive Biology of Female Norway Lobster, *Nephrops norvegicus* (Linnaeus, 1758) Leach, in Icelandic Waters During the Period 1960–2010: Comparative Overview of Distribution Areas in the Northeast Atlantic and the Mediterranean. **Advances in Marine Biology**, 68: 65-210.

Evain M., Afilhado A., Rigoti C., Loureiro A., Alves D., Klingelhoefer F., Schnurle P., Feld A., Fuck R., Soares J., Lima M.V., Corela C., Matias L., Benabdellouahed M., Baltzer A., Rabineau M., Viana A., Moulin M. & Aslanian D. 2015. Deep structure of the Santos Basin-São Paulo Plateau System, SE Brazil. **Journal of Geophysical Research: Solid Earth**, 120, 5401– 5431. doi:10.1002/2014JB011561.

Faraway J.J. 2002. Practical regression and Anova using R, 212 p. [Available from http://cran.r-project.org/doc/contrib/Faraway-PRA.pdf.].

Fariña A.C., Freire J. & Gonzalez-Gurriaran E. 1999. Fecundity of the Norway lobster *Nephrops norvegicus* in Galicia (NW Spain) and a review of geographical patterns. Ophelia, 50(3): 177-189.

Farmer A.S.D. 1974. Reproduction in *Nephrops norvegicus*. **Journal of Zoology**, 174: 161-183.

Farmer A.S.D. 1975. Synopsis of biological data on the Norway lobster *Nephrops norvegicus* (Linnaeus, 1758). FAO Fisheries Synopsis. 112:97 p.

Figueiredo M.J.E. & Barraca, I.F. 1963. Contribuição para o conhecimento da pesca e da biologia do lagostim (*Nephrops*

norvegicus). **Notas e Estudos, Instituto de Biologia Marítima**, 28: 1-31.

Figueiredo M.J., Margo O. & Franco M.G. 1982. The fecundity of *Nephrops norvegicus* (L.) in Portuguese Waters. **International Council for the Exploration of the Sea**. CM 1982/K, 29: 14p.

Fontaine B. & Warluzel N. 1969. Biologie de la langoustine du Golfe de Gascogne (*Nephrops norvegicus* L.). **Revue des Travaux de l'Institut des Peches Maritimes**, 33: 223-246.

Froglia C. & Gramitto M.E. 1979. An estimate of the fecundity of Norway lobster (*Nephrops norvegicus*) in the Adriatic Sea. **Rapp. Comm. Int. Mer Medit**, 25/26(4): 227-229.

Froglia C. & Gramitto M.E. 1981. Summary of biological parameters on the Norway lobster, *Nephrops norvegicus* (L.), in the Adriatic. **FAO Fisheries Reports**, 253: 165-178.

Gomez G.G., Marcano L.R., Guzmán R. & Ramirez T. 2005. *Aspectos biometricos y reproductivos de la cigala, Metanephrops binghami, en águas de Venezuela*. In: **Proceedings of the Gulf and Caribbean Fisheries Institute**, 47: 537-547.

Heasman K.G., & Jeffs A.G. 2019. Fecundity and potential juvenile production for aquaculture of the New Zealand Scampi, *Metanephrops challengeri* (Balss, 1914) (Decapoda: Nephropidae). **Aquaculture**. doi:10.1016/j.aquaculture.2019.05.069.

Hines A.H. 1992. Allometric constraints and variables of reproductive effort in Brachyyuran crabs. **Marine Biology**, 69: 309-320.

Ihaka R. & Gentleman R. 1996. R: A language for data analysis and graphics. **Journal of Computational and Graphical Statistics**, 5(3): 299-314.

Jivoff P. & Hines A.H. 1998. Female behavior, sexual competition and mate guarding in the blue crab, *Callinectes sapidus*. **Animal Behaviour**, 55(3): 589-603. doi: 10.1006/anbe.1997.0646.

Jivoff P., Hines A.H. & Quackenbush L.S. 2007. Reproduction biology and embryonic development. In: Kennedy, V.S. & Cronin, L.E. The blue crab *Callinectes sapidus*. **Maryland: Sea Grant.** p. 255-286.

Kuris A.M. 1991. A review of patterns and causes of crustacean brood mortality. Pp. 117-141.

In: Wenner A, Kuris A, Belkema, AA, Rotterdam (Eds.). **Crustacean Issues, 7: Crustacean Egg Production**. London, CRC Press, 438 p.

Leocádio A.M., Whitmarsh D. & Castro M. 2012. Comparing Trawl and Creel Fishing for Norway Lobster (*Nephrops norvegicus*): Biological and Economic Considerations. **PLoS ONE,** 7(7): e39567. doi:10.1371/journal.pone.0039567.

Macdiarmid A.B. & Sainte-Marie B. 2006. Reproduction. Pp. 45-77. *In:* Phillips, B.F. (Ed.) **Lobsters: Biology, Management, Aquaculture, and Fisheries**. Blackwell, Oxford 501 p.

Mcquaid N., Briggs R.P. & Roberts D. 2009. Fecundity of *Nephrops norvegicus* from the Irish Sea. **Journal of the Marine Biological Association of the United Kingdom**, 89(06): 1181-1188.

Melo G.A.S. 1999. **Manual de identificação dos Crustacea Decapoda do litoral brasileiro**: Anomura, Thalassinidea, Palinuridea, Astacidea. São Paulo, PLEIADE.

Mori M.F., Biagi F. & De Ranieri S. 1998. Fecundity and egg loss during incubation in Norway lobster (*Nephrops norvegicus*) in the North Tyrrhenian Sea. **Journal of Natural History**, 32(10/11): 1641-1650.

Mori M., Modena M. & Biagi F. 2001. Fecundity and egg volume in Norway lobster (*Nephrops norvegicus*) from different depths in the northern Tyrrhenian Sea. **Scientia Marina**, 65: 111-116.

Morizur Y., Conan G., Guenole A. & Omnes M.H. 1981. Fecondite de *Nephrops norvegicus* dans Ie golfe de Gascogne. **Marine Biology**, 63(3):319-324.

Nguyen T.V., Rotllant G.E., Cummins S.F., Elizur A. & Ventura T. 2018. Insights into sexual maturation and reproduction in the Norway lobster (*Nephrops norvegicus*) via in silico prediction and characterization of neuropeptides and g protein-coupled receptors. **Frontiers in Endocrinology**, 9: 430. doi: 10.3389/fendo.2018.00430.

Okamoto K. 2005. Survival, Egg loss, Hatcing larvae and Molting of Ovigerous Japanese Lobster, *Metanephrops japonicus* in Captivity. **Bulletin Shizuoka Prefectural Fisheries Experimental Station**, 40: 35-40.

Orsi-Relini L., Zamboni A., Fiorentino F. & Massi D. 1998. Reproductive patterns in Norway

lobster *Nephrops norvegicus* (L.), (Crustacea Decapoda Nephropidae) of different Mediterranean areas. **Scientia Marina**, 62 (Supl. 1): 25-41.

Orsi-Relini L. & G. Relini. 1989. Reproduction of *Nephrops norvegicus* L. in isothermal Mediterranean waters. **23rd European Marine Biology Symp**. (J.S. Ryland and P.A. Tyler eds): 153-160

Pereira M.J. & Feijo F.J. 1994. Santos Basin; Bacia De Santos. **Boletim de Geociências da Petrobras,** 1(8): 219-234.

Phillips B.F. 1992. Development of the trawl fishery for deep water Metanephropid lobsters of the Northwestern continental slope of Australia. Designing management strategy compatible with species life history. In: Rainer S.F. (ed) **The fisheries biology of deep water crustacea and finfish on the continental slope**. 308p.

Raven C.P. 1961. Oogenesis. The storage of development. **Information Pergamon Press**, Oxford: 273p.

Relini G., Bertrand J. & Zamboni A. 1999. Synthesis of the knowledge on bottom fishery resources in Central Mediterranean (Italy and Corsica). **Biology Marine Mediterranean**, 6 (suppl. 1): 868p.

Romero A.F., Abessa D.M.S., Fontes R.F.C. & Silva, G.H. 2013. Integrated assessment for establishing an oil environmental vulnerability map: Case study for the Santos Basin region, Brazil. **Marine Pollution Bulletin**, 74(1): 156-164. doi: 10.1016/j.marpolbul.2013.07.012.

Sardà, F. 1995. A review (1967-1990) of some aspects of the life history of *Nephrops norvegicus*. **ICES marine Science. Symposia**, 199: 78-88.

Sabatini M. & Hill J.M. 2008. *Nephrops norvegicus* Norway lobster. In Tyler-Walters H., Hiscock K. (eds). Marine Life Information Network: Biology and Sensitivity Key Information Reviews, [online]. Plymouth: **Journal of the Marine Biological Association of the United Kingdom**, https://www.marlin.ac.uk/species/detail/1672 .

Sastry A. 1983. Ecological aspects of reproduction. In: Bliss D.E. (ed). **The biology of Crustacea**. New York, Academic Press. p.179-269.

Severino-Rodrigues E., Hebling N.J. & Graça-Lopes R. 2007. Biodiversidade no produto da pesca de arrasto-de-fundo dirigida ao lagostim *Metanephrops rubellus* (Moreira, 1903) desembarcado no litoral do Estado de São Paulo, Brasil. **Boletim do Instituto de Pesca**, 33(2): 171-182.

Severino-Rodrigues E., Furquim L.G., Graça-Lopes R.G. & Alves P.M.F. 2016. Crescimento relativo e tamanho na maturidade sexual do Lagostim *Metanephrops rubellus* (Moreira, 1903) desembarcado no litoral do estado de São Paulo, Brasil. **Boletim do Instituto de Pesca**, 42 (2): 431-442.

Severino-Rodrigues E., Graça-Lopes R & Furquim L.G. 2018. Contributions to crustacean bycatch from urugavian lobster *Metanephrops rubellus* fisheries in southeastern coast of Brazil. **Boletim do Instituto de Pesca**, 41(3): 591-606.

Sparre P & Venema S.C. 1998 Introduction to tropical fish stock assessment. **Part 1 – Manual. FAO Fisheries Technical Paper 306/1**. Food and Agriculture Organization of the United Nations. p. 200-203.

Symonds D.J. 1972. The fishery for the Norway lobster, *Nephrops norvegicus* (L.), off the north-east coast of England. **Fishery Investigation (London)**, (2), 27(3):1-35.

Tuck I.D., Atkinson R.J.A. & Chapman C.J. 2000. Population biology of the Norway lobster, *Nephrops norvegicus* (L.) in the Firth of Clyde, Scotland II: fecundity and size at onset of sexual maturity. **ICES Journal of Marine Science**, 57: 1227–1239.

Tuck I.D., Chapman C.J. & Atkinson R.J.A. 1997. Population biology of the Norway lobster, Nephrops norvegicus (L.) in the Firth of Clyde, Scotland – I: growth and density. **ICES Journal of Marine Science**, 54: 125-135.

Vargas C., Alejandro M., Uriarte L., García-Guerrero E., Ulises M., Wehrtmann I. S., Ríos-Jara E. & Vega-Villasante F. 2018. Fecundity, egg volume and reproductive output of *Macrobrachium Tenellum* (Crustacea: Palaemonidae) from the Northern Coast of Jalisco, Mexico. **Latin American Journal of Aquatic Research**, 46(3), 502-511.

Wahle R., Macdiarmid A., Butler M., Chan T. Y. & Cockcroft A. 2011. *Metanephrops challengeri*. IUCN Red List of Threatened

Species. Version 2011.2. **International Union for Conservation of Nature**. Retrieved 1 January 2012.

Wallner B. G. & Phillips B.F. 1995. Development of a trawl fishery for deep water metanephropid lobsters off the northwest continental slope of Australia: designing a management strategy compatible with species life history. **ICES Journal of Marine Symposia**, 199: 379-390.

Wear R.G. 1976. Studies on the larval development of *Metanephrops challengeri* (Balss, 1914) (Decapoda, Nephropidae). **Crustaceana,** 30(2): 113–122.

Yazicioglu B., Reynolds J. & Kozák P. 2016. Different aspects of reproduction strategies in crayfish: A review. **Knowledge and Management of Aquatic Ecosystems**, 417(33), 15p. doi: 10.1051/kmae/2016020.

Zar J.H. 1999. **Biostatistical Analysis**. 4th Ed. Prentice Hall. 663p.