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Fisheries Research 129–130 (2012) 28–37

Contents lists available at SciVerse ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Annual brood number and breeding periodicity of squat lobsters (Decapoda: Anomura: Galatheidae) from the continental shelf of the SE Pacific—Implications for fisheries management

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ARTICLE INFO

Article history:
Received 3 January 2012
Received in revised form 17 April 2012
Accepted 6 June 2012

Keywords:
Squat lobsters
Trawl fishery
Fisheries management
Reproduction
Annual brood number
Mating synchrony

ABSTRACT

The reproductive potential of a population depends on the number of broods that individuals produce during the annual reproductive season. Determining the annual brood number is especially relevant for species that are actively fished. Herein we combined different approaches to estimate the annual brood number of two commercially exploited species of squat lobsters from the Chilean continental shelf and upper slope, *Cervimunida johni* and *Pleuroncodes monodon*. Long-term maintenance in the laboratory revealed that most females (>70%) produced 3 or more broods during the annual reproductive season. Incubation of individual broods required about 40 days, which would allow for 3 subsequent broods during the main reproductive period (June–September). The dynamics of brood release of ovigerous females that were collected from the field at approximately monthly intervals supported the estimate of 3–4 annual broods for adult females. Furthermore, these latter data also indicated a high degree of breeding synchrony among reproductive females. It is suggested that the production of successive broods might be an adaption to the variable oceanographic conditions during the reproductive period, ensuring that at least one larval cohort finds favorable conditions for development and settlement. Based on these results it is recommended that fishing effort is reduced during the main reproductive period of the two squat lobsters.

1. Introduction

Fisheries of crustaceans from the continental shelf and slope have been developed and intensified during the past decades. Some species, such as the Norway lobster *Nephrops norvegicus* (see Aguzzi et al., 2003) or the rose shrimp *Aristeus antennatus* (see Sardà et al., 2003) are exposed to intense trawl fisheries down to about 500 or 1000 m depth, respectively. Management of these fisheries is mainly based on information obtained from commercial catch data. While valuable, these data provide little information on feeding habits, ecological interactions or the behavior of the respective species. However, this biological information is of great importance for management decisions.

One of the least known components of the biology of crustaceans from the continental shelf is their reproductive behavior. Information that is commonly available (because it can be extracted from catch data) is the duration of the reproductive season, the proportion of the adult population that is reproductive, and fecundity and first sexual maturity of females. However, life history traits such as the number of broods produced during the annual reproductive period cannot be easily obtained from catch data.

Indirect measures such as the relationship between massive molting events and the seasonally changing proportion of ovigerous females have been used to infer the duration of embryo incubation and the frequency of brood production (e.g. in *Nephrops norvegicus* – Sardà, 1991). In species where mating occurs during the intermolt period, this inference is complicated, and direct observations are required to estimate the number of broods a female can produce during a given reproductive season. Reliable estimates of annual brood production (together with female fecundity) are important in order to (i) determine the population reproductive output, and (ii) identify sensitive periods during the reproductive season.

Various approaches have been used to estimate the annual brood number of females. Most studies used field-based samplings and seasonal estimates of the proportion of ovigerous females (e.g. Fukui and Wada, 1986; Števčić, 1988; Omori et al., 1997; Kyomo, 2002). Other studies examined the relationship between gonad maturation and appearance of ovigerous females (e.g. Minagawa,

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http://dx.doi.org/10.1016/j.fishres.2012.06.004

1997; Sardà, 1991; Orsi-Relini et al., 1998; Gelpi et al., 2009). In the deep-sea shrimp *Aristeus antennatus* the close relationship between molting, mating and brood production led to the inference that females produce at least three broods during the annual reproductive period (Demestre, 1995). For squat lobsters, Dellatorre and Barón (2008) elegantly showed that *Munida gregaria* females incubating advanced embryos also had ovaries in advanced developmental stages, indicating that these females produced two or three subsequent broods.

Individual females can also be maintained throughout the reproductive period in the laboratory to estimate the annual brood production. For example, several large decapod species that are commercially exploited were shown in laboratory experiments to produce two or more annual broods (Shields et al., 1991; González-Gurriarán et al., 1998; Hines et al., 2003). While providing valuable information, long-term maintenance of females in laboratory tanks might influence their brood production. Lack of reproductive males and/or sperm could suppress the female reproductive potential (Hines et al., 2003). On the other hand, ad libitum food supply might generate better feeding conditions for females maintained in laboratory environments than encountered by females in the natural environment, thereby possibly enhancing the brood production of laboratory females. This highlights the importance of comparing the reproductive potential of long-term laboratory inhabitants with that of females collected in the field (see also Hines et al., 2003).

One of the groups for which annual brood numbers are poorly known is squat lobsters (Thiel and Lovrich, 2011). This information, however, is especially relevant for those species that are commercially exploited or prospected for future exploitation. Two squat lobster species (*Cervimunida johni* and *Pleuroncodes monodon*) from the continental shelf and upper slope off Chile have been commercially exploited for about five decades. Dramatic declines of squat lobster stocks during the past decades had led to a diverse range of management measures, including complete or temporal closures of the fisheries (Bahamonde et al., 1986; Roa and Bahamonde, 1993; Acuña et al., 1998).

The fact that a large proportion (80–100%) of the adult females of *C. johni* and *P. monodon* are ovigerous from late fall until early spring (May–October) every year had led to the suggestion that each female produces only one annual brood (e.g. Wolff and Aroca, 1995; Palma, 1994; Palma and Arana, 1997). However, females with late-stage embryos are already found during the peak of the reproductive period and females with early-stage embryos are still observed toward the end of the annual reproductive periods (Wolff and Aroca, 1995; Palma and Arana, 1997). Similarly, late-stage larvae already appear in the plankton early during the reproductive season, while early-stage larvae are still found late in the annual reproductive period (Palma, 1994; Rivera and Santander, 2005; Mujica et al., 2011; Yannicelli et al., 2012). All this indirect evidence strongly suggests that females might produce more than one annual brood.

Herein we directly determined the number of annual broods and the duration of embryo development in two commercially exploited species of squat lobsters from the SE Pacific, *C. johni* and *P. monodon*. Specifically, we compared brood production in long-term laboratory residents with females collected on a monthly basis from the field. Based on the principal results we offer recommendations for an improved management of these exploited squat lobster stocks.

2. Materials and methods

2.1. Sampling, transport and maintenance of squat lobsters

Squat lobsters were captured with commercial trawlers at about monthly intervals during the reproductive period 2007 (between May and November). The fishing grounds were on the continental shelf and upper slope (100–250 m) off Coquimbo, Chile (30°S). Once the catch was on deck, adult individuals were sorted out, placed in large coolers with seawater, and transported to the seawater laboratory of Universidad Católica del Norte, where they were placed in large holding tanks with running seawater. Squat lobsters for the laboratory experiments were usually collected from the last hauls of the day, in order to reduce handling and transport time as much as possible.

Of each monthly sample we selected 60 ovigerous females (22–42 mm carapace length CL in both species) and up to 49 non-ovigerous females (21–37 mm CL in *C. johni* and 23–34 mm CL in *P. monodon*); during the peak of the reproductive season most females were ovigerous and consequently fewer than 60 non-ovigerous females (desired number) were available. Furthermore, we maintained large males for the mating experiments (25–46 mm CL in *C. johni*, $n = 334$ males; and 28–43 mm in *P. monodon*, $n = 79$ males). Squat lobsters were fed ad libitum with fish remains, clams, ascidians and other carrion. Food remains were cleaned and replaced with fresh food every 3 days.

During the study period, water temperature in the laboratory ranged between 11 °C and 13 °C, which is comparable to the temperatures on the main fishing grounds in the region (in July 2006 temperatures ranged between 11 °C and 12 °C on the continental shelf off Coquimbo at water depths of 100–200 m, J. Sellanes personal communication).

2.2. Estimating brood number of females in long-term laboratory experiments

Reproductive (=ovigerous) females from the field were held in the laboratory throughout the entire reproductive period to estimate the number of annual broods (Fig. 1). We maintained females as long as they produced new broods: a female was considered as having produced its last brood once it had been with males in pairing (or mating) tanks for a continuous period of 6 weeks without producing a new brood. Females were maintained in pairing tanks at a sex ratio of 1 large male per 3 females; this proportion was chosen in order not to overcrowd tanks and to avoid agonistic interactions between males (Espinoza-Fuenzalida et al., 2012). In *C. johni* most females were maintained in mating tanks with an individual male during the mate-guarding period (see below); these males were replaced with a new male in the pairing tanks (for further details see also Espinoza-Fuenzalida et al., 2012). Since most female *C. johni* had private males in the mating tanks and male *P. monodon* engaged in frequent mating interactions even late during the reproductive season (I. Vergara & M. Thiel, unpublished data), we consider it unlikely that sperm limitation influenced the outcome of these mating experiments.

Throughout the surveys we also registered female mortality. Since the mating behavior of *C. johni* and *P. monodon* differs substantially (I. Vergara & M. Thiel, unpublished data), in the following, we describe the procedures to estimate brood numbers separately for both species.

2.2.1. Cervimunida johni

In this species both ovigerous and non-ovigerous females reaching the laboratory at the start of the annual reproductive period (May, June) were used to estimate the annual brood number. The first brood of a female was assigned in two different ways. If a female came to the laboratory in May/June as an ovigerous female we considered her present brood as the first brood. Alternatively, if a female reached the laboratory as non-ovigerous but became ovigerous in the mating tanks during May or June, we considered that brood as her first brood. Females that had their first brood in May/June were monitored throughout the entire reproductive

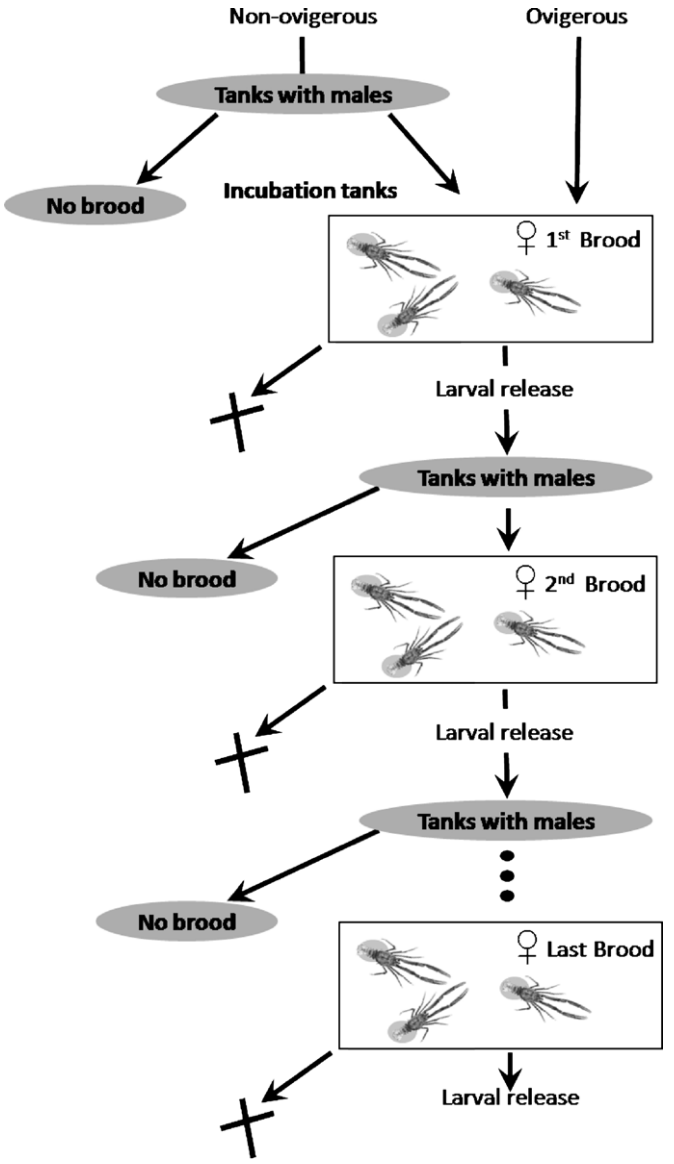

Fig. 1. Treatment schedule used to determine the number of broods produced by female squat lobsters *Cervimunida johni* and *Pleuroncodes monodon* that were maintained in the laboratory thoughout the reproductive season. † indicates removal of dead females.

period in order to determine the number of subsequent broods they produce during the annual reproductive period.

Females that arrived as ovigerous females were maintained together in 300 L holding tanks with flowing seawater; a maximum of 60 ovigerous females were held in each of these large tanks. In contrast, females that produced a new brood in the laboratory were grouped in incubation tanks of 12–100 L volume, depending on the number of females that became ovigerous within 2–8 day intervals (up to 29 females *C. johni* were maintained together). Females were checked every 3 days for their reproductive status (ovigerous or non-ovigerous). During these checks we also examined the developmental stage of the embryos according to Palma and Arana (1997) to verify that females had not aborted their broods prematurely.

Females that had released their larvae (i.e. which were identified as non-ovigerous during the 3-day checks) were placed in large pairing tanks together with large males (Fig. 1). Once females paired with a male they were placed in smaller mating tanks where they were monitored until they became ovigerous again (for details see Espinoza-Fuenzalida et al., 2012). In these mating tanks females were surveyed every 12 h. If a female had separated from the male, we examined whether it was ovigerous. Females that became ovigerous were then classified as females with their next brood and placed in incubation tanks together with other females that had produced a new brood during the same time period (Fig. 1). Occasionally a female mated with a male and became ovigerous in the pairing tanks. These females then were passed directly to the incubation tanks.

2.2.2. *Pleuroncodes monodon*

In this species we only used ovigerous females that were collected in June 2007. According to data reported by Palma and Arana (1997), these females reached the laboratory at the beginning of the annual reproductive period and most likely carried their first brood. Initially, all ovigerous females ($n = 64$) were maintained in large holding tanks where they were checked every 3 days for their reproductive status (ovigerous or non-ovigerous). Once they had released their brood, they were placed in pairing tanks and checked every 3 days for their reproductive status (for details see Espinoza-Fuenzalida et al., 2012). Once they were identified again as ovigerous they were placed in incubation tanks (Fig. 1) and monitored every 3 days for their reproductive status according to Palma and Arana (1997) to determine the duration of embryo incubation; up to 18 females *P. monodon* were maintained together in one incubation tank.

2.3. Duration of embryo incubation

In order to estimate the duration of embryo incubation we checked the females in the incubation tanks every 3 days for their reproductive status (see above). Females entered the incubation tanks within <3 days after turning ovigerous in the pairing or mating tanks. Due to logistic reasons (space availability in the seawater laboratory) females were pooled in incubation tanks for time periods of 1–8 days. In order to reduce handling stress as much as possible, we did not mark females individually. For the evaluation of the data, all females that were pooled over a period of 1–8 days in an incubation tank were counted as having become ovigerous at day 0 when the incubation tank was first established; thus all estimates of incubation time are conservative. We calculated the frequencies of females carrying their embryos for the respective time periods.

2.4. Reproductive activity of field-collected females

In order to determine the reproductive activity of females in the field, during the main reproductive period we regularly (every 4–6 weeks) collected adult females in the field (see above, Section 2.1), and examined whether they would produce a new brood in the laboratory. Ovigerous and non-ovigerous females were maintained in large tanks in the same way as outlined above for the estimates of annual brood numbers. Non-ovigerous females were immediately placed in pairing tanks with males where they were maintained for a maximum period of 6 weeks. Ovigerous females were first held in large holding tanks until they had released their brood, and then they were placed in pairing tanks for post-ovigerous females. Once being taken into the precopulatory embrace by males in the pairing tanks, female *C. johni* were placed in smaller mating tanks, where they were monitored every 12 h (see also above). Female *P. monodon* mated in the pairing tanks, and every 3 days we checked whether females had produced a new brood.

Based on the results from this experiment we calculated the monthly proportion of field-collected females that became

ovigerous in the laboratory, of females that did not produce a new brood, and of females that died during the survey period.

2.5. Reproductive periodicity of lab-held and field-collected females

In order to reveal whether females become receptive in synchrony, we examined the numbers of females that became ovigerous at 3-day intervals in the laboratory. We distinguished the long-term females, which were held throughout the entire reproductive season to determine the annual brood number of females, and the females that we collected at about monthly intervals. For each 3-day interval the total number of monitored females and the sum of females that produced a new brood was used to calculate the proportion of receptive females. In the case of the field-collected females, we combined the proportion estimated for different batches, simply averaging values for each date, in order to reconstruct a longer time-series.

Periodicities in the proportion of receptive females, for both species and lab/field experiments separately, were evaluated using a spectral analysis for unevenly spaced time series (Schulz and Mudelsee, 2002). Even though observations were carried out regularly, in some cases the total number of monitored females was too low ($n < 10$), potentially biasing our analyses. In order to reduce this problem, we only used values based on a minimum of 20 monitored females, which created gaps in the time series. Instead of interpolating the values for the missing dates, which may introduce severe bias in the analysis, we used a spectral analysis for uneven time series based on a Lomb–Scargle Fourier transformation (Schulz and Stattegger, 1997). In addition, because the power spectra of biological time series often show a 'red-noise' (i.e. increasing spectral power at lower frequencies), a first order autoregressive process is used as a null hypothesis. We tested whether the observed spectral peaks were significantly different than expected under a first-order autoregressive model. Analyses were carried out using the procedure REDFIT in the free software PAST v. 2.12 (Hammer et al., 2001).

3. Results

3.1. Number of broods per female

For *C. johni* we were able to obtain 158 females with their first brood. Of these, 92 females came to the laboratory at the beginning of the annual reproductive period with their first brood, and 66 females produced their first brood in the laboratory. Most of these females (70%) survived for long time periods in the laboratory (Fig. 2). Many females of *C. johni* produced 3 or 4 subsequent broods, and a few even produced >4 broods (Table 1A). After having been non-ovigerous for 6 weeks without producing a subsequent brood, females were eliminated from the pool of reproductive females (Fig. 2).

For *P. monodon* we obtained 64 females with their first brood at the beginning of the reproductive period. Most of these females produced 3 broods in the laboratory, but a few females produced even more broods (Fig. 3, Table 1B). A relatively high proportion (80%) of female *P. monodon* died after having produced 3 or more broods.

3.2. Duration of embryo development

Throughout the study we monitored the incubation times of 158 females *C. johni*, which produced a total of 318 successful broods in the laboratory. Most of these broods were incubated for 37–40 days, with an overall range of 28–52 days (Fig. 4). In *P. monodon* we followed 64 females, which produced 86 successful broods. The results show that in *P. monodon* embryonic development varies between 31 and 49 days with a peak at about 40 days (Fig. 4). Toward the end of embryonic development we frequently observed larvae in the incubation tanks, confirming that females of both species indeed produced viable larvae during the experiments.

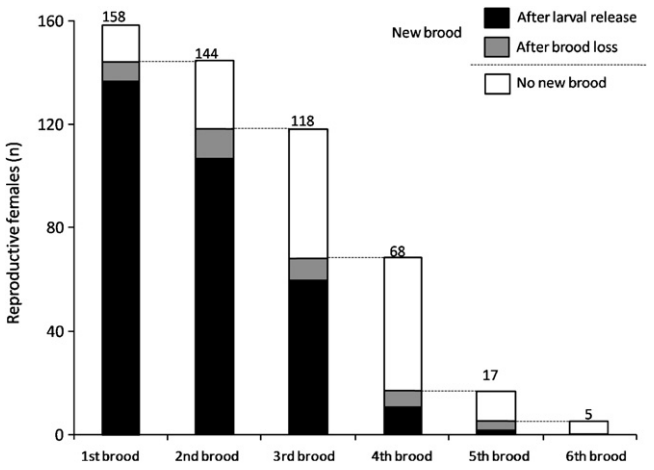

Fig. 2. Number of female *Cervimunida johni* maintained in the laboratory that produced successive broods during the reproductive season 2007. Each column represents the total number of females with the respective brood (number on top of column), indicating the number of females that successfully produced a subsequent brood after hatching of larvae (post-hatching) or after loss of embryos (post-loss), and those females that did not produce a subsequent brood due to various reasons (death during incubation, or 6 weeks in mating tanks without becoming ovigerous).

3.3. Reproductive activity of field-collected females

For *C. johni* we obtained many ovigerous females (270 out of a total of 416 females) during the main reproductive period (May–October 2007). No females could be maintained in November because all individuals reached the laboratory in poor condition due to intense molting activity in the field. The majority (92%) of the ovigerous females reaching the laboratory between May and September mated and produced a new brood in the laboratory (Fig. 5). In October, this proportion decreased substantially and only ~15% of all field-collected ovigerous females produced a new

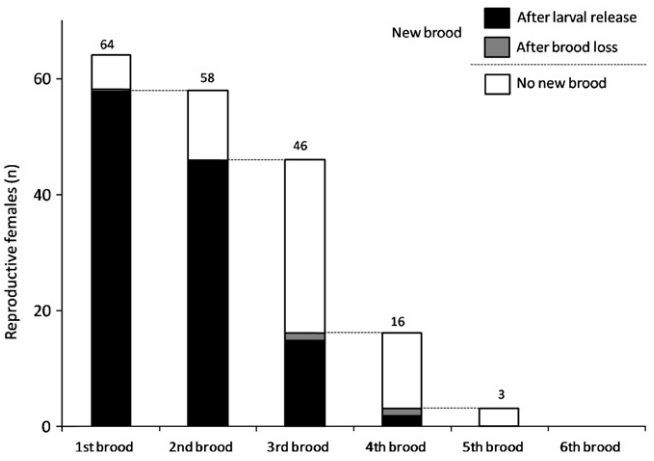

Fig. 3. Number of female *Pleuroncodes monodon* maintained in the laboratory that produced successive broods during the reproductive season 2007. Each column represents the total number of females with the respective brood (number on top of column), indicating the number of females that successfully produced a subsequent brood after hatching of larvae (post-hatching) or after loss of embryos (post-loss), and those females that did not produce a subsequent brood due to various reasons (death during incubation, or 6 weeks in mating tanks without becoming ovigerous).

Table 1
Annual brood production of female squat lobsters (A) *Cervimunida johni*, and (B) *Pleuroncodos monodon*. Table shows the number of females that produced the respective number of broods. Note: not all of the females successfully released larvae from their last brood.

Number of females with seasonal brood number		
N broods	*N* females	Percentage
(A) *Cervimunida johni*		
1	14	8.9
2	26	16.5
3	50	31.6
4	51	32.3
5	12	7.6
6	5	3.2

Number of females with seasonal brood number		
N broods	*N* females	Percentage
(B) *Pleuroncodes monodon*		
1	6	9.4
2	12	18.8
3	30	46.9
4	13	20.3
5	3	4.7
6	0	0.0

brood (Fig. 5a). Many of the non-ovigerous females (84.2%) that had been collected in May produced a brood in the laboratory, but starting in June that proportion steadily decreased and in September only ~10% of the field-collected non-ovigerous females produced a brood in the laboratory (Fig. 5b).

For *P. monodon*, we obtained 256 ovigerous females between June and November 2007 (in November only 16 females were taken into monitoring because most individuals arrived in poor condition). During the months of June and July most ovigerous females (92%) produced a new brood in the laboratory (Fig. 6a). In August, this proportion decreased to 53.3%, partly due to the increasing mortality of females (Fig. 6a). In October and November, the proportion of females that produced a new brood decreased drastically, to 11.7% and 1.7%, respectively (Fig. 6a). Only in November,

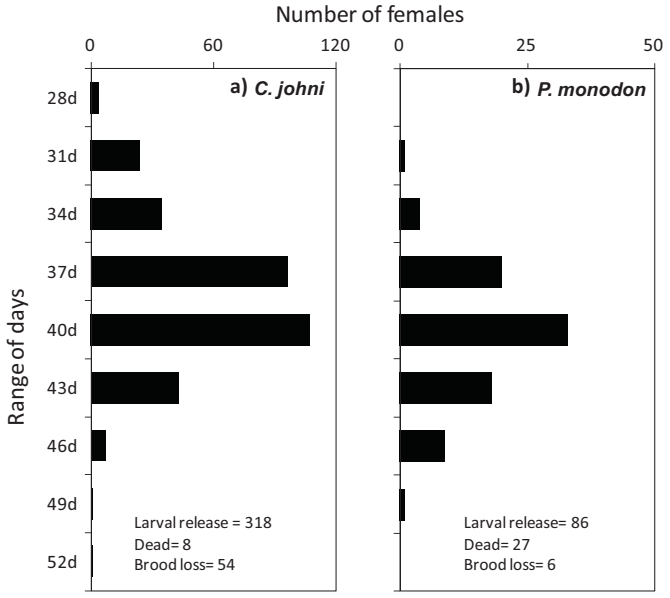

Fig. 4. Number of female *Pleuroncodes monodon* and *Cervimunida johni* that successfully released viable embryos after incubating them for 28–52 days under laboratory conditions. The number of females that had successfully released larvae, died during incubation or lost embryos prematurely during incubation are indicated in the lower part of the figure; figure only includes females that successfully released larvae.

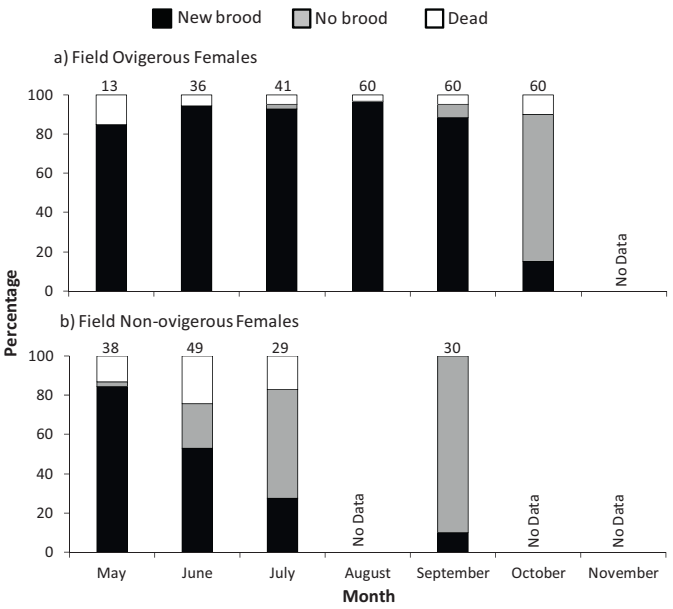

Fig. 5. Brood production of (a) ovigerous, and (b) non-ovigerous female *Cervimunida johni* reaching the laboratory during the respective months. Shown are the females which produced a new brood, which remained non-ovigerous after having been in mating tanks for at least 6 weeks, or which died during this experiment. Numbers on top of columns represent the number of females brought to the laboratory each month.

non-ovigerous females *P. monodon* reached the laboratory, but none of these females produced a new brood during the 6 weeks in the pairing tanks (Fig. 6b). In general, mortality was substantially higher in *P. monodon* compared to *C. johni* (Figs. 5 and 6).

3.4. Breeding periodicity

In both species we observed evidence of breeding synchrony (Figs. 7–9). The spectral analyses showed the existence of several

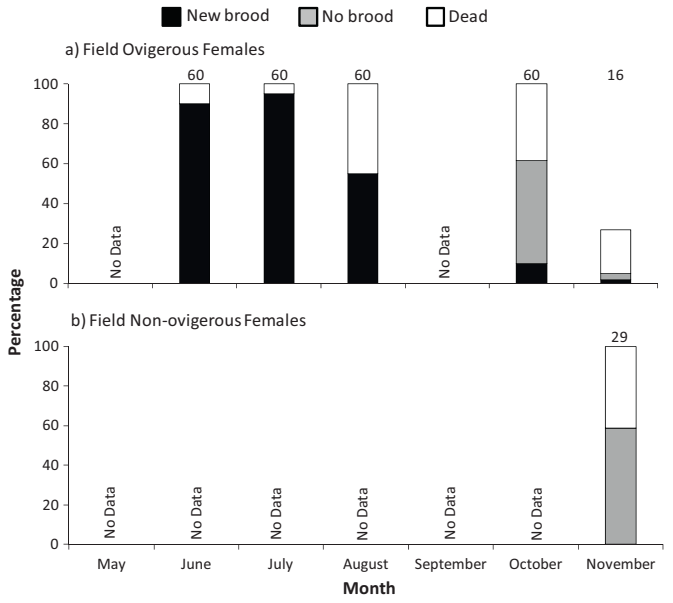

Fig. 6. Brood production of (a) ovigerous and (b) non-ovigerous female *Pleuroncodes monodon* reaching the laboratory during the respective months. Shown are the females which produced a new brood, which remained non-ovigerous after having been in mating tanks for at least 6 weeks, or which died during this experiment. Numbers on top of columns represent the number of females brought to the laboratory each month.

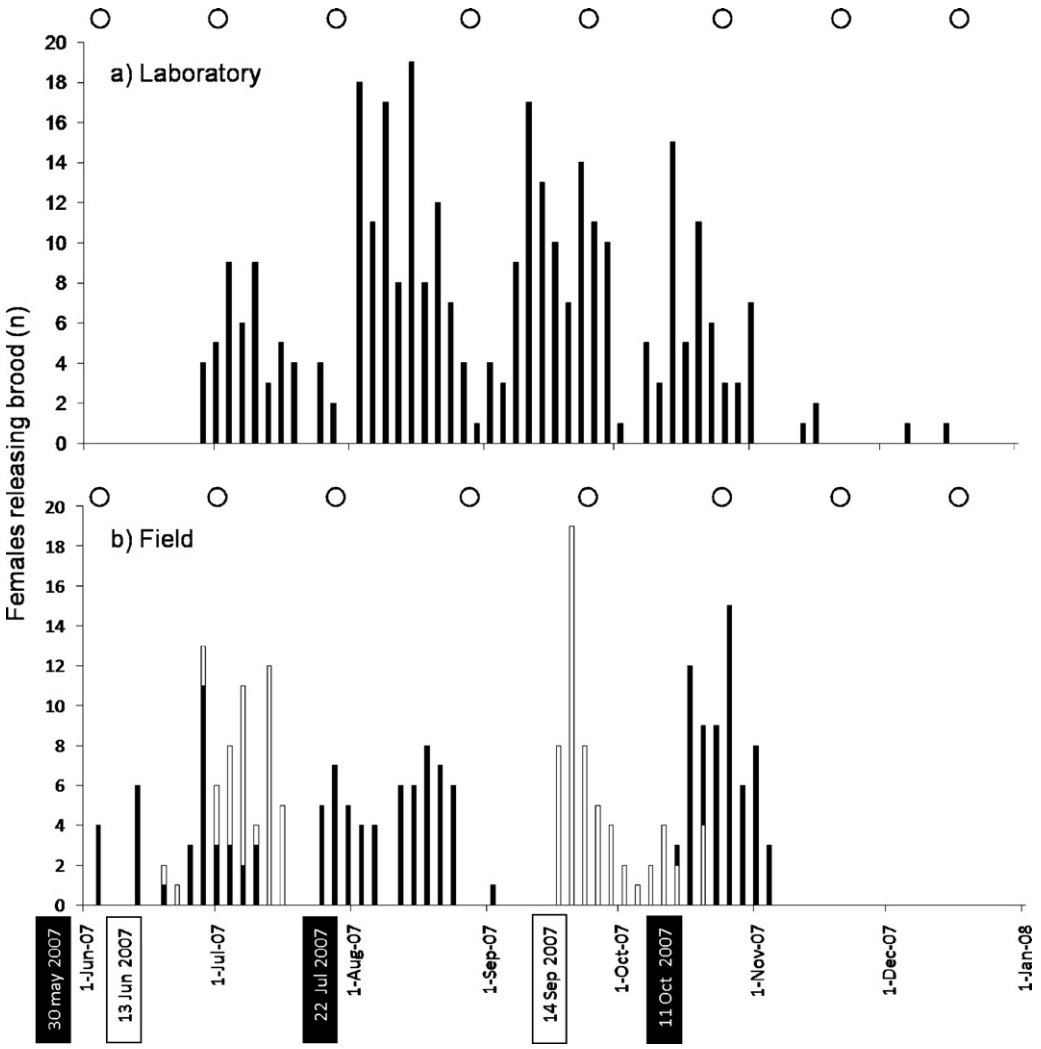

Fig. 7. Number of female *Cervimunida johni* releasing a brood (a) during the long-term laboratory experiments, or (b) after coming from the field. For the females collected from the field throughout the reproductive season, subsequent batches are indicated by different colors, indicating the date when these females arrived in the laboratory by the boxes on the *x*-axis; females were monitored every 3 days for brood release. The full moon is indicated by open dots.

cycles of brood production in both species as well as both field-collected and lab-maintained females (Fig. 9). The main spectral peaks were associated to 5–6 week cycles, not clearly coupled to lunar phases (Figs. 7 and 8). A secondary peak was associated to 11–18 day cycles, but this was not significant in most cases. Finally, a significant weekly signal was detected in all cases.

4. Discussion

4.1. Annual brood number

In both species of squat lobsters, most females (>70%) maintained throughout the reproductive season in the laboratory produced 3 or more successive broods. This number is substantially higher than previous estimates for both species (1–2 broods), which were based on indirect methods such as the proportion of ovigerous females, the developmental stages of incubated embryos, or the presence of larval stages in the plankton (Palma, 1994; Palma and Arana, 1997; Rivera and Santander, 2005). The high proportion of females from the field that readily produced a new brood in the laboratory environment confirms that female squat lobsters indeed produce more than one annual brood in the field. In particular, the similarity of peaks in brood production between long-term laboratory residents and field-collected females suggests that the laboratory data are a reasonable reflection of the situation in the natural environment.

The estimates of the incubation period for both species, the short interbrood intervals (Espinoza-Fuenzalida et al., 2012) and the continuously high proportion of ovigerous females observed throughout the main reproductive periods of both *C. johni* and *P. monodon* (Acuña et al., 2008) also suggest that females can produce 3 or more broods during each annual reproductive season. In *C. johni*, the proportion of ovigerous females remains high (>80%) between June and September (Wolff and Aroca, 1995). If indeed embryos develop as fast in the natural environment as observed herein under laboratory conditions (at about 40 days), then a female could easily produce 3 successive broods during the annual reproductive season. The analysis of embryo developmental stages of ovigerous *C. johni* from the field (Wolff and Aroca, 1995) suggests longer developmental rates (see also below), but the high proportion of females with early stage embryos late in the reproductive season clearly indicates that some females can produce 2 or even more broods in the field. Similar inferences can be drawn for *P. monodon*. A large proportion of females (generally $\gg$ 50%) are ovigerous between June and September (Palma and Arana, 1997), and with embryo development lasting ~40 days (this study) many adult females could produce 3 successive broods during the annual reproductive season. Indeed, in southern-central Chile (36–37°S)

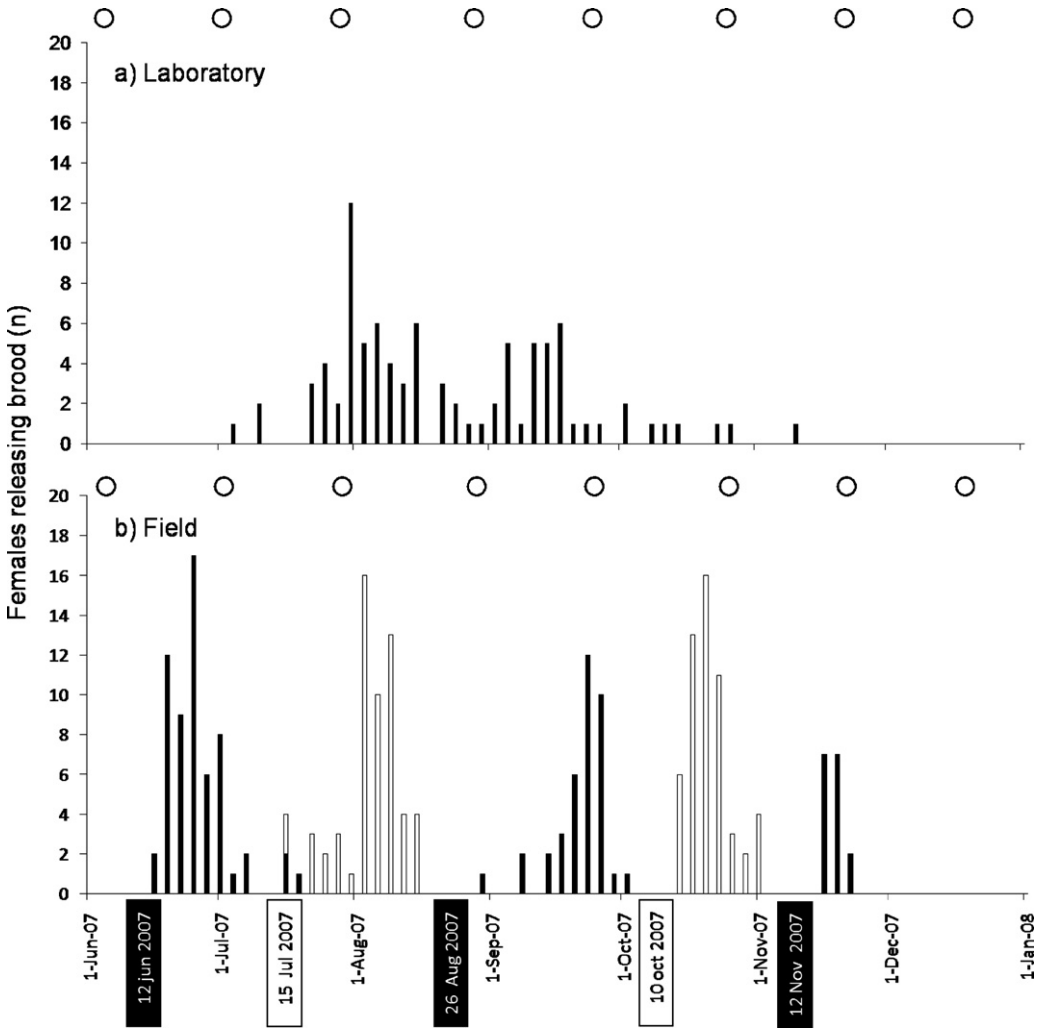

Fig. 8. Number of female *Pleuroncodes monodon* releasing a brood (a) during the long-term laboratory experiments, or (b) after coming from the field. For the females collected from the field throughout the reproductive season, subsequent batches are indicated by different colors, indicating the date when these females arrived in the laboratory by the boxes on the *x*-axis; females were monitored every 3 days for brood release. The full moon is indicated by open dots.

late stage embryos were already found in June and early stage embryos were still found in October (Palma and Arana, 1997), suggesting that in the natural environment many females produce more than one annual brood. Based on seasonally variable proportions of ovigerous females, Gutiérrez and Zúñiga (1977) also suggested several broods for *P. monodon* in northern Chile.

Numerous studies confirm that females of large decapods produce several successive broods during the annual reproductive season (e.g. Hartnoll, 2006). Littoral crabs produce two or more annual broods (Fukui and Wada, 1986; Števčić, 1988; Shields et al., 1991; Omori et al., 1997; Kyomo, 2002). Many other species, such as, e.g. the spiny lobsters *Panulirus japonicus* (Minagawa, 1997) and the deep-sea shrimp *Aristeus antennatus* (Demestre, 1995), also produce two or more annual broods. Some large decapods produce even more annual broods (Shields et al., 1991; González-Gurriarán et al., 1998; Hines et al., 2003; Gelpi et al., 2009). While some species of squat lobsters from the continental shelf are thought to produce only one annual brood (e.g. Brinkmann, 1936; Hartnoll et al., 1992), other species have been suggested (e.g. Bourdon, 1962; Boyd and Johnson, 1963) or shown to produce two or more broods per year (Dellatorre and Barón, 2008; this study). Thus, many commercially exploited decapod crustaceans, including squat lobsters, have a high potential to produce several successive broods during the annual reproductive season.

4.2. Incubation period

The incubation period revealed herein (~40 days) was substantially shorter than that reported in previous studies. Based on the proportion of field-collected females that were ovigerous, Palma and Arana (1997) had suggested an incubation period of 90–120 days for *P. monodon*. Using a comparable data set, Wolff and Aroca (1995) inferred a similar incubation period for *C. johni*. These previous estimates were based on indirect evidence from ovigerous females collected in the field; authors determined the embryo developmental stages to estimate the length of the entire incubation period. In particular, the final developmental stages of the embryos may be very short, thereby possibly obscuring indirect estimates.

In general, at temperatures ~10 °C the development of squat lobster embryos lasts between 30 and 40 days (Thiel and Lovrich, 2011). At temperatures of 11 °C embryo development was completed within 28 days in *M. gregaria* (Dellatorre and González-Pisani, 2011). Embryo development of *C. johni* and *P. monodon* proceeds within a similar temperature range. The bottom temperatures on the continental shelf off the Chilean coast (10–12 °C;

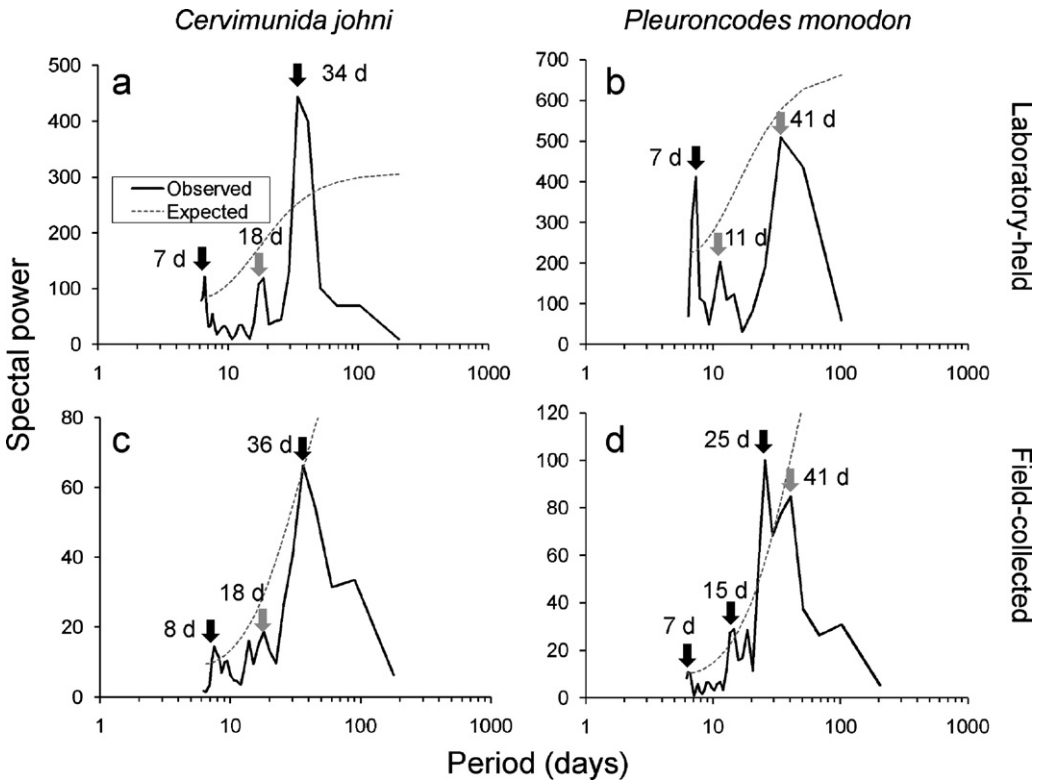

Fig. 9. Power spectral of the proportion of receptive females for *Cervimunida johni* (a and c) and *Pleuroncodes monodon* (b and d) from laboratory-held (a and b) and field-collected (c and d) females. The black arrows show the observed spectral peaks that are statistically significant ($p < 0.05$), and the associated periods (days). Non-signicant peaks ($p > 0.05$) indicated by grey arrows.

Mujica et al., 2011) are within a similar range as the temperatures prevailing in the laboratory tanks during the study period. Thus, within the observed temperature range, the estimates for the duration of embryo incubation obtained in our laboratory experiments appear reasonable.

Another factor that affects embryo development is oxygen supply (Anger, 2001). Both species of squat lobsters inhabit the oxygen minimum zone along the continental margin off the Chilean coast (e.g. Sellanes et al., 2010), where incubating females encounter hypoxic conditions, which could potentially delay embryo development in the natural environment (Anger, 2001). In our laboratory experiments, females were maintained in oxygen-rich surface waters. Consequently, the incubation periods estimated in this study might be shorter than that of females in the field. In brachyuran crabs, embryos that receive higher concentrations of oxygen develop faster than those maintained at low oxygen concentrations (Fernández et al., 2003). Female ventilation behavior of the embryo mass can partly offset the negative consequences of hypoxic conditions (e.g. Baeza and Fernández, 2002; Eriksson et al., 2006). Embryo survival and development can be affected by limited oxygen supply, but only under extreme hypoxia (Fernández et al., 2003; Eriksson et al., 2006). Thus, while low oxygen concentrations in the natural environment might delay embryo development, it should not severely affect the brood numbers of female squat lobsters estimated herein.

4.3. Breeding periodicity

The data obtained herein on brood production of the two studied species strongly indicate that larval release and subsequent production of new broods is strongly synchronized among females. Strong breeding synchrony is known for many species from coastal environments (e.g. McCurdy et al., 2000). For example, molting and brood production is synchronized in northern krill *Meganyctiphanes norvegica* (Tarling and Cuzin-Roudy, 2003). Gonad maturation also occurs synchronously in the penaeoid shrimp *Pleoticus muelleri*, and females become receptive for mating at the same time (Díaz et al., 2003). In many other species embryo development is synchronized (e.g. Omori et al., 1997; Johnston and Ritz, 2001), most likely because all reproductive females produced a new brood at the same time.

Brood production of the two squat lobster species occurred in well-defined 5–6 week cycles and less intense weekly cycles, not clearly coupled with the lunar cycle, as observed in other species. While reproductive activity of many littoral crustaceans is known to be synchronized with the lunar cycle (Reaka, 1976; Brown and Loveland, 1985; Kyomo, 2002), breeding periodicity is less well known for species from deeper waters. For Norway lobsters *N. norvegicus* from the continental shelf of the Mediterranean Sea, Gramitto (1998) confirmed that adult individuals molt synchronously within a relatively short time period, once or twice every year. In this species, molting and mating occur during the months immediately after release of the previous brood (Sardà, 1991). Given the observed patterns in *C. johni* and *P. monodon*, it should be expected that field-collected females show a high concordance between gonad maturation and embryo developmental stages, similar to what has been reported for *M. gregaria* (Dellatorre and Barón, 2008). The mechanisms and causes of reproductive synchrony in squat lobsters (and other species) from the continental shelf are not well known at present and require future investigation.

4.4. Implications for sustainable management

The results from this study suggest that female squat lobsters have a higher reproductive potential than previously assumed, and

that their breeding cycles are synchronized. These results have multiple implications for management measures. Females that produce several successive broods without molting will experience wear on their incubating structures (pleopods), and thus fecundity of subsequent broods might be expected to be lower than of first broods (but see Wada et al., 2007). Within the management context, this study confirmed that the present closures of the fishery during and right after the main molting period (January–March) does not actually protect the reproductive season (see also Palma and Arana, 1997; Acuña et al., 1998, 2008).

At the present state of knowledge about the reproductive biology of squat lobsters it is not clear whether an additional closure of the fishery during the annual reproductive period is recommendable. Possibly, it might be more effective to reduce the overall fishing pressure throughout the entire reproductive season in order to ensure larval input from all successive broods produced each year. The extended reproductive period with the production of multiple broods and thus several larval release events might respond to the high variability in environmental conditions (e.g. temperature, oxygen concentrations, food supply for adults and larvae) that planktonic larvae and early benthic stages encounter during their development. Future studies should examine whether broods released early during the reproductive period have a higher possibility of successful recruitment than those released late in the annual reproductive season.

Acknowledgments

Funding provided through the Fisheries Research Fund (FIP No. 2006-43) from the Chilean Ministry of Economy. Two anonymous reviewers and Beatriz Yannicelli provided many constructive comments on the initial draft of this manuscript. We are thankful to Lucas Eastman for revising the English of the final manuscript.

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