

LIFE HISTORY OF *TANAIS DULONGII* (TANAIDACEA: TANAIDAE) IN AN INTERTIDAL FLAT IN THE SOUTHWESTERN ATLANTIC

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ABSTRACT

We studied the life history, reproductive biology and spatial distribution of *Tanais dulongii* on an intertidal flat near Mar del Plata, Argentina. The animals were obtained by systematic sampling in three intertidal zones (high, mid and low), from October 2008 to September 2009. The population density was low during most of spring and summer, increased during autumn and reached its maximum values at the end of this season (35 000 individuals/m²); a second, but lower, density peak occurred at the end of winter (15 000 individuals/m²). Male density remained below 1000 individuals/m² during most of the year in the three zones, although in September it was higher than 1800 individuals/m² in the high and mid intertidal zones. Female and juvenile density was below 5000 individuals/m² in spring and summer, with little variation between areas, but it differed among areas during autumn and winter, when both groups reached their maximum densities (20 000-40 000 individuals/m²) in the low and mid intertidal zones. Ovigerous females were always present; their maximum occurred in spring and summer but earlier in the low and later in the high intertidal zone. Recruitment was higher in autumn and early winter. The sex ratio was strongly female biased (0.08 ± 0.01). Individual life time was estimated to be 8-9 months and females developed through more instars than males. This study suggests that the different environmental conditions that *T. dulongii* faced in the 3 intertidal zones caused an important effect on the population dynamics.

KEY WORDS: intertidal, life history, reproduction, spatial and temporal variation, *Tanais dulongii*

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INTRODUCTION

Tanaids are small benthic peracarids that live from deep-water to coastal marine environments, such as estuaries and tidal flats, where they may reach densities up to 5000 individuals/m² (Lang, 1968; Mendoza, 1982; Kneib, 1992). In spite of their ecological importance in the marine benthos as food source for many organisms (Mayer, 1985; Nagelkerken and van der Velde, 2004; Ferreira et al., 2005), little is known about the population dynamics of many species (Schmidt et al., 2002). Ecological studies on tanaids in the Soutwestern Atlantic are particularly scarce (Masunari, 1983; Elías et al., 2001; Leite et al., 2003; Fonseca and D'Incao, 2006; Rosa and Bemvenuti, 2006; Pennafirme and Soares-Gomes, 2009).

Tanais dulongii (Audouin, 1826) is considered a cryptogenic species in Argentina (i.e.: a likely introduced organism), and was found in the rocky intertidal zone of several sites between Mar del Plata (37°58'S) and Puerto Madryn (42°46'S) (Orensanz et al., 2002; Adami, 2008). Like many other tanaid species, both males and females of *T. dulongii* build residential tubes that are used for protection, brood-nursery, and feeding (Bückle Ramírez, 1965; Johnson and Attramadal, 1982a). During the breeding period males migrate from tube to tube searching for ovigerous females, which carry their eggs in a ventral pouch, the marsupium (Johnson and Attramadal, 1982a; Borowsky, 1983). Once

fertilization occurs, offspring pass through two larval stages, manca I and II, inside the marsupium (Johnson and Attramadal, 1982a; Hamers and Franke, 2000). When mancae are released, they begin to build their tubes associated to the maternal tube and to develop independently (Johnson and Attramadal, 1982a).

Several studies carried out on *T. dulongii* in Norway and Spain showed that: 1) populations are present throughout the year with maximum densities in summer and minimum densities in winter, 2) sex ratios are female biased, and 3) reproduction is continuous albeit with strong recruitment in summer (Johnson and Attramadal, 1982b; Perez-Ruzafa and Sanz, 1993). Differences in environmental conditions affect the life history strategies of other tanaid species, causing marked changes in their population dynamics (Pennafirme and Soares-Gomes, 2009). The aim of this paper was to study the populational and reproductive biology of *Tanais dulongii* in the intertidal zone in Argentina, in order to provide the basis for understanding the ecological role of this species on regional rocky shores.

MATERIAL AND METHODS

Study Area

The study was conducted in the intertidal zone of La Estafeta (38°10'S, 57°38'W), located 15 km south of Mar del Plata harbour, Argentina (Fig. 1). The coast is characterized by

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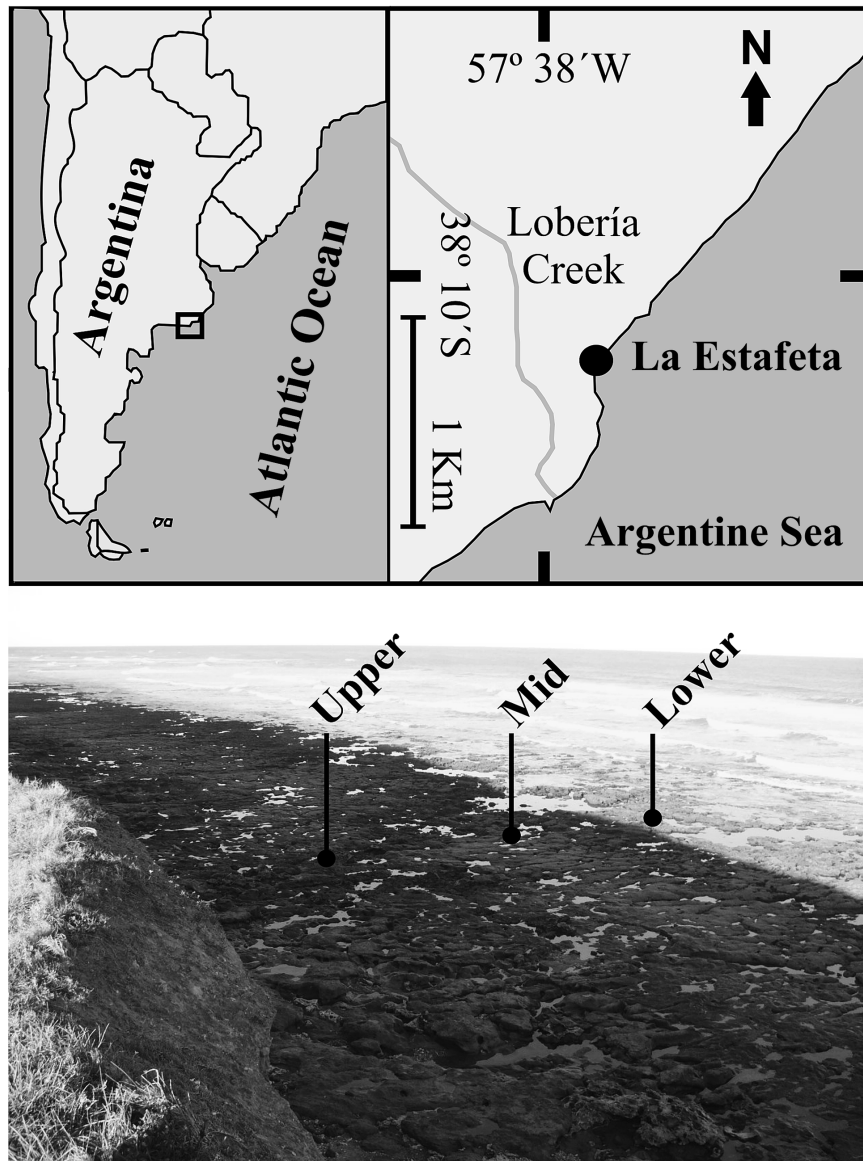


Fig. 1. Geographical localization of the study area, and a general view of the intertidal platform, including the position of sampling sites.

cliffs (height = circa 40 m) and an abrasion platform with a gentle slope ($<1\%$) and numerous tidal pools; both cliff and platform consist of consolidated sediment (loess). The distance between cliffs and the water edge during the lowest tides is circa 70 m. The tidal regime is microtidal, with mean tidal amplitude of 0.8 m (Isla, 2004). The substratum consists in covered by algae, with *Ulva rigida* (Agardh, 1823) and *Corallina officinalis* (Linnaeus, 1758) being most abundant. The mean monthly seawater temperature was obtained from the Centro Argentino de Datos Oceanográficos and air temperature from the Servicio Meteorológico Nacional (Argentina). The mean temperature of shallow seawater and air ranged between 9.3 to 20.8°C and 8 to 22.8°C, respectively and these physical variables are closely correlated ($r = 0.952$). However, during spring and summer the temperature of seawater was lower than air, a feature that was reversed in late summer and early

autumn, indicating the existence of a thermal inversion process (Fig. 2).

Field Sampling and Laboratory Procedures

Samples were collected monthly from October 2008 to September 2009. Three sampling sites were established in a gradient from the cliffs to the sea, located at 31, 47 and 58 m, respectively from the cliff and representing the high, mid and low intertidal levels (Fig. 1). Three sampling units (0.0225 m²) were taken at each site using a quadrat of 0.15 × 0.15 m and a spatula to scrape algal patches. The extracted material was fixed in 70% alcohol. In the laboratory, samples were washed and sieved through a 0.35 mm mesh-sieve; the organisms were sorted and counted using a stereomicroscope.

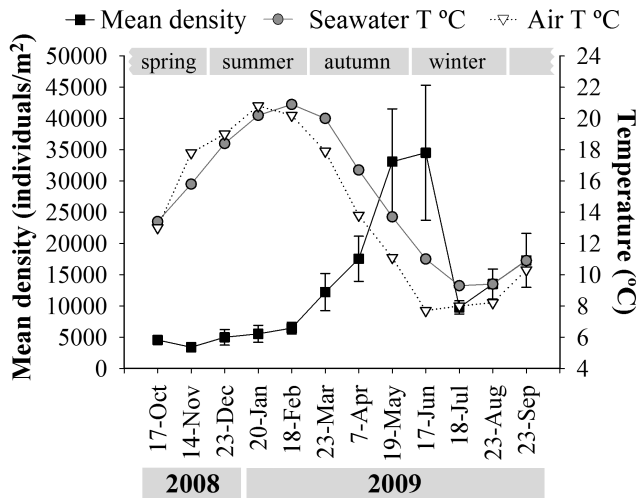


Fig. 2. Seasonal variation of seawater and air temperatures, and total population density of *T. dulongii* (mean \pm standard error).

Population Structure, Fecundity, and Size-Frequency Distributions

The individuals were classified into five groups according to Almeida (1994) and Leite et al. (2003): males (with a large cheliped), pre-ovigerous females (with small chelipeds and oostegites), ovigerous females (with small chelipeds and eggs in the marsupium), post-ovigerous females (with small chelipeds but without oostegites) and juveniles (all individuals measuring less than the smallest identifiable male, except those that had visible oostegites). They were measured from the tip of the rostrum to the tip of the pleotelson using a graduated eyepiece (total length, mm); the smallest identifiable male measured 3.06 mm.

All individuals of each group present in a sampling unit were counted and population density (individuals/m² \pm standard error) and sex ratio (males/males + total females) were calculated. The percentage of males and ovigerous females in the samples was used as an estimate of reproductive activity (Kneib, 1992). The size frequency distributions (SFD) were constructed separately for males, females, and juveniles, but since males were much less abundant than females and juveniles, two histograms were represented for each month: one for females and juveniles and the other for males. To calculate the fecundity index, 50 ovigerous females were randomly selected; they were measured (total length) and their eggs removed from the marsupium and counted.

Statistical Analyses

Parametric tests were used preferably, but when the assumptions of parametric statistics were violated, an appropriate nonparametric test was applied (Zar, 1999). Significance was assessed at $\alpha = 0.05$. The differences in monthly densities were tested using a one-way ANOVA. To determine if the density of males, females and juveniles varied among intertidal levels and months, a two-way ANOVA was used (factors: month and zones; Zar, 1999). The differences in densities of different groups of females (pre-ovigerous, ovigerous, and post-ovigerous) were tested through a two-way ANOVA (factors: month and population group; Zar, 1999). Student-Newman-Keuls (SNK) test was used for multiple compar-

isons of means (Zar, 1999). To test the deviation of sex ratio from an expected ratio of 1:1, a χ^2 -test was applied (Zar, 1999). Linear regression and the Pearson's correlation coefficient was calculated to assess the relationship between female size and the number of eggs in the marsupium (fecundity index; Zar, 1999). A Mann-Whitney rank sum test was used to evaluate differences in the size of females and males. Seasonal variation in the size of ovigerous females were tested through a Kruskal-Wallis ANOVA, followed by an all pairwise multiple comparison procedure (Dunn's test; Zar, 1999). Modal components of each SFD were estimated with the method developed by McDonald and Pitcher (1979) (MIX program; see Bas et al. (2005) for details of procedure, parameters and restrictions of the method). Differences between consecutive modes were compared with one-way ANOVA and modal values were compared between males and females with one-way ANOVA for each mode separately. Growth was described by the seasonalized von Bertalanffy (VBGF) equation and was estimated with the Elefan I program (Pauly and David, 1981). The growth model was fitted separately for each sex.

RESULTS

Population Density and Distribution

The population density of *T. dulongii* in the intertidal of La Estafeta varied markedly during the study period (One-way ANOVA, $P < 0.001$; Fig. 2). It was low during most of spring and summer, increased during autumn, while water and air temperature decreased, and reached its maximum values at the end of this season (ca. 35 000 individuals/m² in May and June; SNK test, $P < 0.05$). Later, density decreased at the beginning of winter, the period with lowest temperatures (ca. 8 000 individuals/m² in July). Finally, both density and temperature increased at the end of winter (density reached ca. 15 000 individuals/m² in September).

The density of males, females and juveniles differed among zones and months (Two-way ANOVA, $P < 0.05$; Table 1; Fig. 3). Density of males was homogeneous in the intertidal zone and did not vary between months from October to August, remaining below than 1000 individuals/m² (SNK test, $P > 0.05$) although in September it was significantly higher in the high and mid intertidal zones (more than 1800 individuals/m²) than in the low intertidal zone (SNK test, $P < 0.05$; Fig. 3a). The density of females remained below 15 000 individuals/m² from October to April and from July to August, and did not differ between areas (SNK test, $P > 0.05$; Fig. 3b). However, significant differences among areas were observed in May, June and September. In May density was higher in the low intertidal zone, where it reached its maximum value ($40\,178 \pm 9050$ individuals/m²; SNK test, $P < 0.05$); in June it was higher in the mid zone ($36\,022 \pm 8444$ individuals/m²; SNK test, $P < 0.05$); and in September it was higher in the mid and high intertidal zones (ca. 20 000 individuals/m²; SNK test, $P < 0.05$). Density of juveniles did not vary between areas during spring and summer, remaining below 8000 individuals/m², but during autumn it was higher in the mid and low intertidal zones, reaching values of ca. 12 000 individuals/m² (SNK test, $P < 0.05$). In June, density was higher in the mid inter-

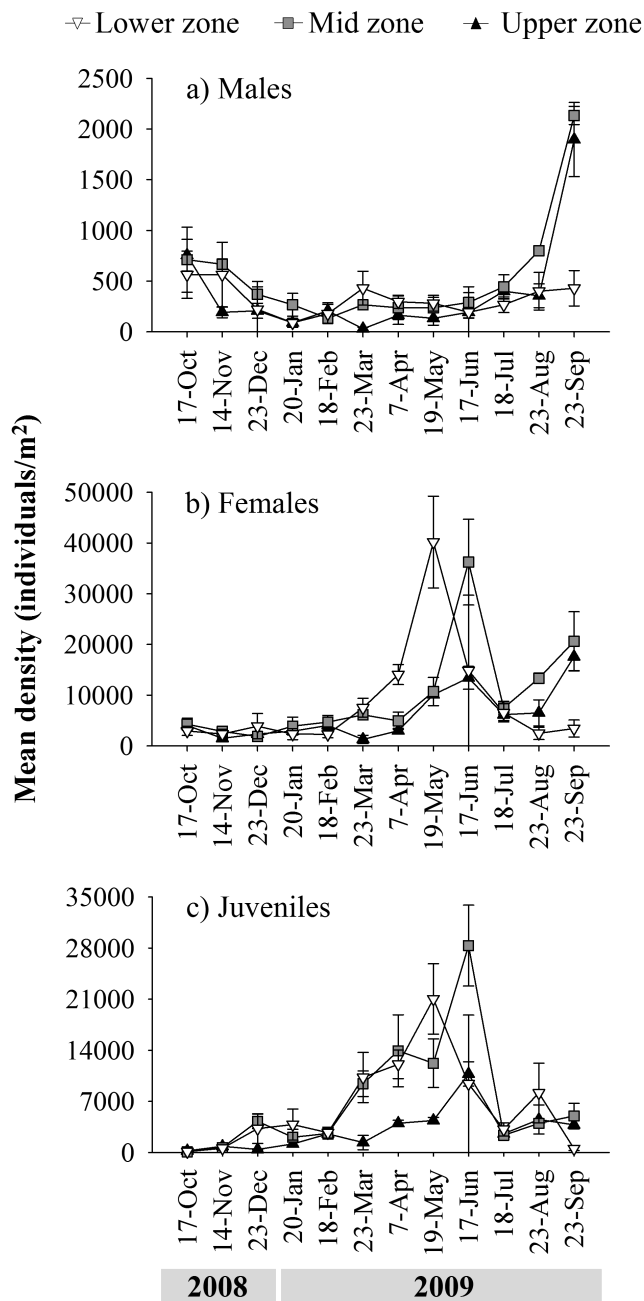


Fig. 3. Seasonal variation of density (mean \pm standard error) at three intertidal zones. a, males; b, females; c, juveniles, of *T. dulongii*.

tidal zone, where it reached its maximum value ($28\,333 \pm 5533$ individuals/m²; SNK test, $P < 0.05$; Fig. 3c).

Densities of the different groups of females (ovigerous, pre-ovigerous, and post-ovigerous) varied among groups and months (Two-way ANOVA, $P < 0.001$, Table 1). From October to March it did not differ significantly between groups (SNK, $P > 0.05$), while from April to September post-ovigerous females were more abundant (ca. 5000–17 000 individuals/m²; SNK test, $P < 0.05$). The density of ovigerous and pre-ovigerous females did not differ significantly between months (ovigerous: 659 ± 67 individuals/m², pre-ovigerous females: 1343 ± 147 individuals/m²; SNK test, $P > 0.05$).

Table 1. Results of two-way ANOVA for comparison of densities: variation of population groups (males, females and juveniles) between months and zones; and variation of female groups (ovigerous, pre-ovigerous and post-ovigerous females) among months and groups. df, degrees of freedom; MS, mean squares.

| Comparison | Source of variation | df | MS | F | P |
|---------------|----------------------|-----|------------|-------|--------|
| Males | Month | 11 | 559.39 | 17.45 | <0.001 |
| | Zone | 2 | 222.41 | 6.94 | 0.002 |
| | Month \times Zone | 22 | 118.41 | 3.69 | <0.001 |
| | Error | 69 | 32.06 | | |
| Females | Month | 11 | 193 951.47 | 10.97 | <0.001 |
| | Zone | 2 | 62 402.11 | 3.53 | 0.035 |
| | Month \times Zone | 22 | 74 929.39 | 4.24 | <0.001 |
| | Error | 69 | 17 672.95 | | |
| Juveniles | Month | 11 | 107 400.34 | 11.44 | <0.001 |
| | Zone | 2 | 80 651.81 | 8.59 | <0.001 |
| | Month \times Zone | 22 | 23 942.04 | 2.55 | 0.002 |
| | Error | 69 | 9390.17 | | |
| Female groups | Month | 11 | 59 001.94 | 7.56 | <0.001 |
| | Group | 2 | 418 210.21 | 53.61 | <0.001 |
| | Month \times Group | 22 | 38 827.34 | 4.98 | <0.001 |
| | Error | 279 | 7800.94 | | |

Ovigerous females were always present but their proportion with respect to total females reached maximum values ($>15\%$) in spring and summer (Fig. 4a). The increase and decrease of the percentage of ovigerous females occurred earlier in the low, later in the mid and even later in the high intertidal zone, reaching a maximum value in October, October/November, and December, respectively (Fig. 4a). Similarly, the percentage of juveniles with respect to the total number of individuals increased and decreased earlier in the low intertidal than in the other zones (Fig. 4b).

Sex Ratio, Reproductive Activity, and Fecundity

The mean sex ratio value was 0.08 ± 0.01 and differed significantly from the expected 1:1 (χ^2 -test, $P < 0.05$). The monthly sex ratio varied throughout the study period, but it was always female biased (Fig. 5a). The highest sex ratio was recorded in November (0.162 ; χ^2 -test, $P < 0.05$), it decreased from January to July, reaching the minimum in June (0.012 ; χ^2 -test, $P < 0.05$), and increased to values similar to those observed in October 2008 from August and September. The proportion of males was lower than that of ovigerous females except in July and August (Fig. 5a).

A linear regression was found between the number of eggs per brood and female length ($r = 0.899$, $P < 0.001$; Fig. 6). Due to the low variance associated with the data, the regression equation can be considered a good predictor of fecundity ($r^2 = 0.808$). The mean number of eggs observed (\pm standard deviation) was 47.2 ± 25.4 ($n = 50$) per female.

Length-Frequency Analysis

The mean size of juveniles was 2.32 ± 0.48 mm. The sizes of males and females differed significantly (Mann-Whitney rank sum test, $T = 3\,474\,961$, $P < 0.001$). Males had a mean length of 4.32 ± 0.25 mm and were moderately larger than females, which measured 4.18 ± 0.77 mm (Dunn's test, $P < 0.05$). However, the maximum

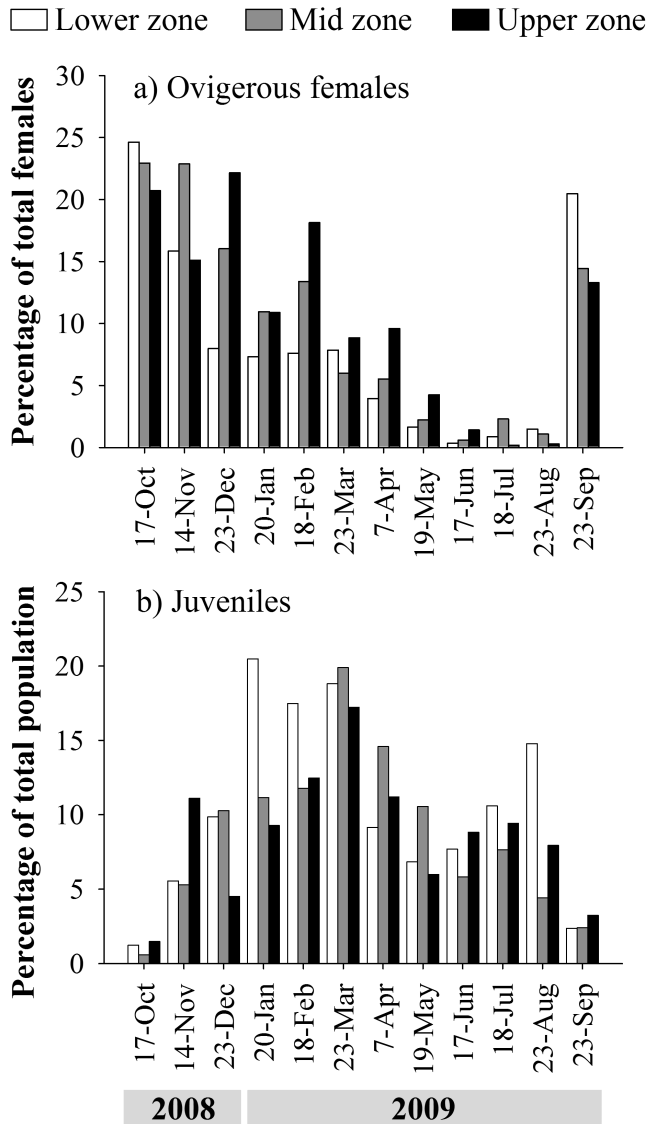


Fig. 4. Monthly percentage of *T. dulongii* in three intertidal zones, in relation to the total females and total population, respectively. a, females; b, juveniles.

size (7.28 mm) corresponded to females. Moreover, the smallest differentiated female measured 1.77 mm. The mean size of ovigerous females varied seasonally (Kruskal-Wallis ANOVA, $H = 237.36$, $df: 11$, $P < 0.001$). In spring, summer and winter the ovigerous females were larger than 4.30 mm, whereas in autumn they were smaller, measuring less than 4 mm (Dunn's test, $P < 0.05$; Fig. 5b).

The SFDs were polymodal in all months sampled, with 6-7 modes (females), 4-5 modes (males) and 2-3 modes (juveniles) but the displacement of modes between successive months did not show a clear pattern. On the other hand, the Elefan I program allowed to identify two cohorts along the sampling period in both sexes and coexisted during part of the year. The first cohort included large individuals that disappeared in January 2009 (females) or December 2008 (males). The second cohort corresponded to individuals recruited in November 2008 that increased their size until September 2009, when the sampling ended (Fig. 7). The

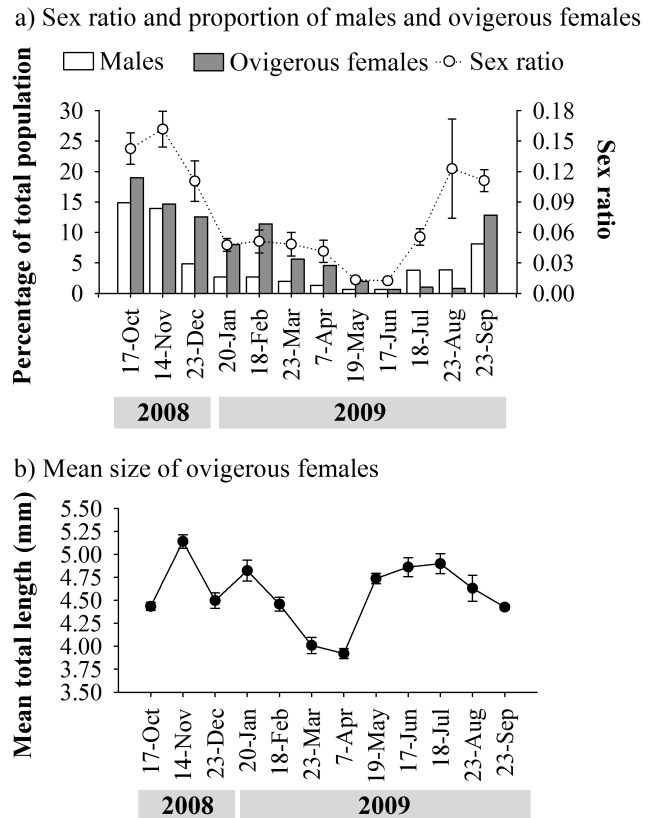


Fig. 5. a, proportion of males and ovigerous females during the sampling period, respect of the total population, and seasonal variation of sex ratio; b, mean total length of ovigerous females over months, of *T. dulongii*.

SFDs remained similar during the winter months, suggesting that growth was interrupted during the cold season.

The growth parameters obtained by Elefan I (Fig. 7) fitted very well to a seasonal model. The K coefficient was higher for males (0.92 year^{-1}) than for females (0.6 year^{-1}), the asymptotic size L_{∞} was 7.29 mm TL for females and 6.11 mm TL for males.

DISCUSSION

The population of *T. dulongii* showed two successive phases. Although the continuous presence of males, pre-ovigerous and ovigerous females, and juveniles indicated that reproduction and recruitment occurred throughout the year, as

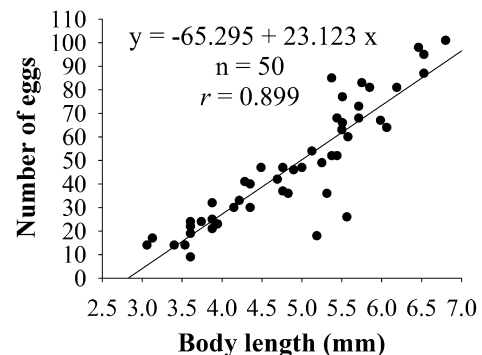


Fig. 6. Relationship between the number of eggs and the total body length of ovigerous females of *T. dulongii*.

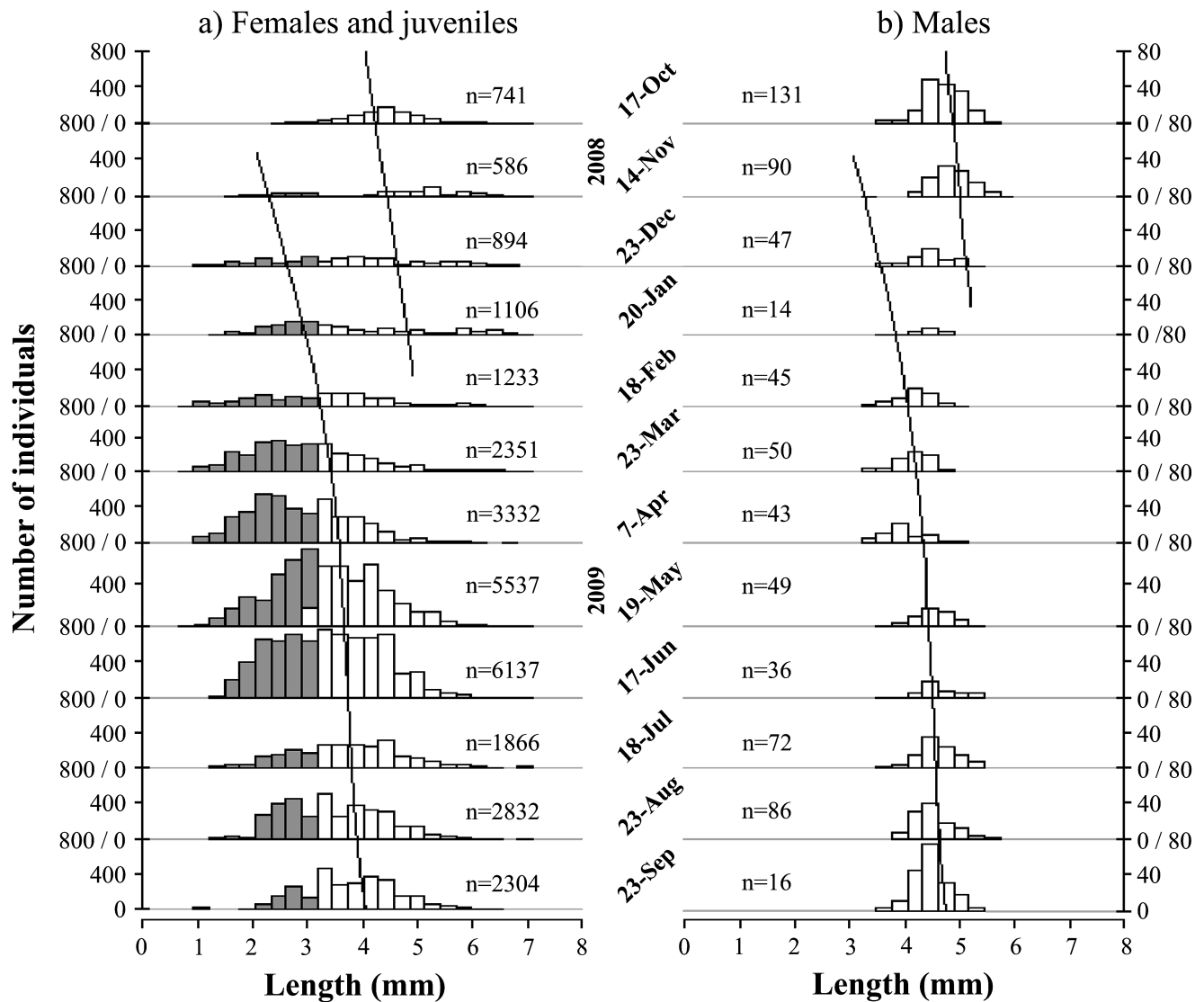


Fig. 7. Length frequency distribution and fitted growth curves of each cohort found by Elefan I. a, total females (white bars) and juveniles (gray bars); b, males, of *T. dulongii*.

has also been recorded in other littoral tanaids (Mendoza, 1982; Masunari, 1983; Modlin and Harris, 1989; Kneib, 1992; Leite et al., 2003), there is a main reproductive season in spring and summer and, to a lesser extent, early autumn. During this intense reproductive period, population density was low and the proportion of ovigerous females oscillated between 10 and 25%, depending on the month and the intertidal zone considered. This phase was followed by a strong density increase during autumn and early winter, which should be the consequence of an intense recruitment. Later, densities dropped during the coldest winter days, suggesting a negative effect of temperatures below 8–10°C. Finally, the rise in temperature observed by the end of winter seemed to be correlated with a slight density increase, corresponding to the reduced number of ovigerous females in winter. A similar seasonal relationship has been reported for different species of tanaids (Mendoza, 1982; Masunari, 1983; Kneib, 1992), although other species have their highest densities in spring and summer (Modlin and Harris,

1989; Leite et al., 2003; Rosa and Bemvenuti, 2006; Penafirme and Soares-Gomes, 2009).

The combined data of population density and annual changes in size frequency distributions and size of ovigerous females suggests that individuals recruited in summer and early autumn grew quickly, matured at a reduced size, and continued growing and reproducing until they disappeared in July and August. This coincides with the maximum size reached by both sexes, suggesting high mortality of larger organisms in winter. However, a second group of individuals that recruited in late autumn, and even in winter, could survive the colder months, grew in the following spring, matured at a larger size and disappeared during summer of the following year. The estimated longevity was about 8–9 months, and these values are similar to those obtained in *Monokalliapseudes schubartii* (Mañé-Garzon, 1949), another intertidal tanaid species of the temperate Southwestern Atlantic (Fonseca and D’Incao, 2003; Leite et al., 2003). Furthermore, this life history strategy with two

recruitment periods, has been reported for two species of tanaids (Modlin and Harris, 1989; Leite et al., 2003), and seems to be a common pattern in benthic invertebrates that inhabit the coast of Argentina such as amphipods (Obenat et al., 2006) and polychaetes (Obenat, 2002).

The proportion of males in the population remained below that of females throughout the study period. Several explanations for this female-biased sex ratio have been proposed in other tanaid populations: a higher male mortality rate due to fighting behavior within males, which would cause serious injuries; cessation of feeding activity after reaching sexual maturity; and a sex difference in reproductive behavior, since males migrate from tube to tube searching for partners resulting in high exposure to predators while females remain in their refuges (Mendoza, 1982; Highsmith, 1983). Nevertheless, male density did not vary significantly throughout the year, except in September, indicating that male mortality rate was likely constant during most months. On the other hand, it is possible that the juvenile group included males sexually mature but not differentiated externally by the morphology of the chelipeds (Hamers and Franke, 2000), which may obscure the real sex-ratio. Hermaphroditism, observed in some species of tanaids (Bückle-Ramirez, 1965; Highsmith, 1983; Stoner, 1986; Modlin and Harris, 1989; Kneib, 1992; Drumm and Heard, 2007; Pennafirme and Soares-Gomes, 2009) was not detected in *T. dulongii* (in fact only 2 of 31769 individuals had intersex characteristics): consequently, this phenomenon could not explain the observed bias in sex ratio.

The positive linear relationship in the fecundity index has also been observed in other tanaids (Masunari, 1983; Messing, 1983; Schmidt et al., 2002; Toniollo and Masunari, 2007) but the number of embryos of *T. dulongii* was higher than in other species (Messing, 1983). The great fecundity would offset the high mortality rate of 29% and 57% recorded in the developmental stages manca I and II, respectively (Hamers and Franke, 2000).

The growth curves estimated from SFDs showed that the development of females took more time than in males, as was also observed by Hamers and Franke (2000) in laboratory cultures of *T. dulongii*: the development of females comprises more instars and time than in males. This difference may be due to the fact that the development is more complex in females than in males (Hamers and Franke, 2000).

The population dynamics differed across the three intertidal levels, probably as a consequence of differences in the environmental conditions. Although no information is available on these differences in the study area, a gradient of abiotic, e.g., air exposure and water submersion, and the consequent changes in temperature and oxygen availability, and biotic, e.g., predation and competence, conditions is characteristic of all intertidal ecosystems (Bertness, 1999). Males were homogeneously distributed in the intertidal zone except in September, when their density increased in the upper and mid zones. Females and juveniles presented a uniform distribution during spring and summer, when density is low, but they predominated in the mid and lower zones when density reached the autumn peaks. These two zones, with greater availability of water, seem to be more suitable

sites for settlement and growth whereas water retention and oxygen availability, necessary for development of juveniles, should be reduced in the upper zone (Johnson and Atramadal, 1982a). The increase of juvenile and female density observed in autumn took place first in the low intertidal zone and later in the high and mid intertidal zones. The simultaneous density increase in the mid zone and the decrease in the low intertidal zone could be explained by two alternative hypothesis: 1) individuals migrated from the low to the mid zone, or 2) no exchanges occurred between zones, and the population increases and declines in the different zones were asynchronous, i.e., earlier in the lower zone. Although migrations among zones were observed in intertidal tanaids (Kneib, 1992), it is not possible to verify this process in the La Estafeta population with the available information.

In conclusion, the population of *T. dulongii* in La Estafeta has strong seasonal dynamics, with reproduction concentrated in spring and summer, and recruitment in autumn and early winter. Females are highly fecund, maximum density was unusually high and the life span of the individuals is less than a year. On the other hand, the population dynamics differed along the intertidal gradient but the causes of the observed differences and the exchange between zones should be object of further research.

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