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# First results on the life cycle and population dynamics of the tanaid *Zeuxo holdichi* Bamber, 1990 colonizing concrete blocks deployed on oyster tables (Bay of Seine, eastern part of the English Channel)

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**Abstract:** The tanaid *Zeuxo holdichi* is common in intertidal and shallow waters on the French side of the English Channel, with very high abundances along the Calvados coast. The abundances and population dynamics of *Z. holdichi* were studied during a one-year experiment of benthic colonization of artificial blocks placed upon intertidal oyster culture tables 0.5 m above the seabed. Bi-monthly sampling shows that the colonization was rapid, with abundances reaching 2,000 individuals per m$^2$ in four months. Two peaks were observed at the end of September and the beginning of November, when the abundances exceeded 21,000 individuals per m$^2$. Allometry measurements show that the length of the cephalothorax is a good proxy to estimate the total length of the individuals. The population is mainly composed of male and female adults measuring up to 5.35 mm. Ovigerous females are present from the middle of June to the end of the study, with a high occurrence in August-October. The number of embryos ranges from 5 to 89 for a mean fecundity of 24 embryos per brood pouch. The mean size of the females is 3.5 mm. The mean female/male ratio is 4.28. Considering these traits of life, *Z. hodichi* possesses high ability to rapidly colonize virgin hard substrates.

***Keywords :*** *Zeuxo holdichi, Bay of Seine, fecundity, abundances*

## 1. Introduction

Since its description in 1990 based on specimens from Arcachon Bay, in the southern part of the Bay of Biscay, the tanaid *Zeuxo holdichi* Bamber, 1990 has been reported at several locations ranging from the North-eastern Atlantic to the English Channel (EC) coast of France (Foveau *et al.*, 2018) as well as in the western approaches of the EC (Scilly Islands, UK). It has also been reported along the Atlantic coast of Spain and Portugal and in the southern part of the North Sea (Cunha *et al.*, 1999; Esquete *et al.*, 2011; Bamber, 2011; Faasse, 2013). It was recently reported for the first time in the Mediterranean Sea in the Venice Lagoon (Del

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Pasqua *et al.*, 2022). However, the native origin of *Z. holdichi* and its alien status in the Mediterranean Sea remain uncertain. Based on recent records of this tanaidomorph species in North Atlantic waters, Faasse (2013) has suggested that *Z. holdichi* might not be native to Europe. This is because crustacean faunas, including tanaids, have been well investigated in Atlantic regions and it would seem exceptional to discover new native crustacean species in well-investigated North-eastern Atlantic areas. The genus (subgenus *Parazeuxo*) is present in the Macaronesian islands though. Bamber (2012) mentions *Z.* (*Parazeuxo*) *exsargasso* from the Cape Verde and Canary Islands (formerly only known from floating Sargassum near Bermuda) and *Z.* (*Parazeuxo*) *coturnix* n. sp. from Cape Verde and Madeira. Moreover, as indicated by Faasse (2013), *Zeuxo holdichi* has no congeners in the north-European waters, which further suggests that its origin may be elsewhere. Another argument supporting this hypothesis is the molecular study performed by Larsen *et al.* (2014) indicating that *Z. holdichi* has closer genetic relationships with the Pacific *Zeuxo normani* (Richardson, 1905) than with other North Atlantic species, as mentioned also by Foveau *et al.* (2018). Furthermore, *Z. holdichi* could be a Non-Indigenous Species involuntarily introduced by humans probably via the transfer of oysters or hull fouling (Leclerc and Viard, 2018). Moreover, *Z. holdichi* could also be an invasive species in the English Channel, due to its rapid progression, particularly along the French coast of the English Channel (Foveau *et al.*, 2018).

Studies on the life cycle and dynamics of tanaids, which are mainly small species with low abundance, concerned mainly intertidal populations from North and South America, such as *Hargeria rapax* (Harger, 1879) on Northwest Atlantic coasts (USA) (Kneib, 1992; Modlin and Harris, 1989); *Kalliapseudes schubartii* Mañé-Garzón, 1949 along the Brazilian coast (Fonseca and D'Incao, 2003; Leite *et al.*, 2003; Pennefirme and Soares-Gomes, 2009); *Sinelobus stanfordi* (Richardson, 1901) from other South-American environments (Slivak *et al.*, 2013; Ferreiraa *et al.*, 2015); *Tanais dulongii* (Audouin, 1826) from the Argentinian coast (Rumbold *et al.*, 2012, 2014, 2015b,b) and north-western Atlantic Ocean populations (Attramadal, 1982; Borowky, 1983; Hamers and Franke, 2000) and *Leptochelia dubia* (Krøyer, 1842) along the California coast (Mendoza, 1982). Masunari (1983) has described the post-marsupial development and population dynamics of *Leptochelia savignyi* (Krøyer, 1842) from Brazil, while Messing (1983) has studied the post-marsupial development and growth of *Pagurapseudes largoensis* (McSweeny, 1982) from a shallow population off south-eastern Florida (North-western Atlantic Ocean).

Ambrosio *et al.* (2014) suggested that tanaids are opportunistic species, and proposed the potential use of tanaids as biological indicators of water quality. Along the same lines, de la Ossa Carretero *et al.* (2010) studied the sensitivity of *Apseudopsis latreillii* (Milne Edwards, 1828) to sewage pollution along the Mediterranean coast of Spain.

Within the RECIF-project framework, an ecological engineering approach has been proposed by incorporating the crushed shells of the queen scallop *Aequipecten opercularis* (Linnaeus 1758) into concrete to develop innovative building materials for artificial reefs (Foveau *et al.*, 2015; Dauvin and Foveau, 2019). In the framework of this project, an inventory was drawn up of the sessile and vagile macrofauna recorded over a period from March 2014 to February 2015 during a survey of concrete blocks positioned on oyster culture tables in the intertidal zone near

Luc-sur-Mer area on the Calvados coast (eastern basin of the EC) (Foveau *et al*., 2015; Dauvin and Foveau, 2019; Dauvin *et al*., 2021). More than 100, 000 individuals of the tanaid *Zeuxo holdichi* were collected during the survey (Foveau *et al*., 2018), allowing us to study the pattern of colonization and the population structure of this species over a period of one year.

## 2. Materials and Methods

### 2.1. Experimental strategy

At the beginning of the experiment (19–20 March 2014), 75 blocks (20 × 20 × 40 cm) (total surface 0.6 $m^2$) were placed 0.5 m above the sea bed on oyster culture tables used in the intertidal zone of Luc-sur-Mer, Normandy (49°19'15"N; 0° 20'55"W) located in the southern part of the Bay of Seine, eastern basin of the English Channel) (Dauvin and Foveau, 2019; Dauvin *et al*., 2021). The oyster tables are submerged to a water depth of 6.5 m at high tide, located in the infralittoral fringe composed mainly of coarse sediment and natural rocky substrates corresponding to the EUNIS (European Nature Information System) code A5. 125; *Mastocarpus stellatus* and *Chondrus crispus* habitat on very exposed to moderately expose lower eulittoral rock. *Zeuxo holdichi* was counted only on blocks containing 40% of crushed queen scallop *Aequipecten opercularis* (Linnaeus, 1758) shells and 25% porosity. The blocks were collected about every 15 days between 1 April 2014 and 4 February 2015, on a total of 22 sampling dates. At the laboratory, the blocks were immerged in tanks under stagnant conditions for at least 24h. Then, the seawater was filtered on a 0.5-mm mesh sieve to collect the motile fauna including the tanaid *Z. holdichi*. Finally, we had checked whether any fauna remained on the blocks. The retained material was fixed with 96% alcohol.

### 2.2. *Zeuxo holdichi* treatment

The abundances of *Z. holdichi* are expressed per 1 $m^2$. The number of *Zeuxo holdichi* was low at the beginning of the study (04 April to 29 July 2014), thus we examined them all. During the rest of the study (12 August 2014 to 02 February 2015), only a sub-sample of 100 individuals taken randomly was recovered and stored in alcohol to study temporal changes of the population structure. Then, a photo of each individual was taken under an Olympus SZX16 binocular using an E6PL3 Olympus camera. Before photographing each individual, it was necessary to calibrate the binocular, because the measurement software (ImageJ) did not allow automatic calibration of the photos. Thus, a picture was taken of graph paper for each amplification of the binocular: i.e. x7, x8, x10, x12.5, x16, x20, x25, x32, x40, x50, x63, x80, x100 and x115. The software ImageJ took measurements in pixels and a conversion factor was applied to convert the measurements of *Z. holdichi* in pixels to measurements in mm following the ratio given in Table 1. Dorsal views were taken, and also lateral views in the case of ovigerous females (Fig. 1).

Following Bamber's (1990) description of the species, 11 segments were measured: cephalothorax, pereonites 1, 2, 3, 4, 5 and 6, pleonites 1, 2 et 3, pleonites 4 + 5 + pleotelson (Fig. 2). A supplementary measurement was made of the width of the cephalothorax.

Female and male of *Z. holdichi* can be distinguished by their morphological characters. The female has a triangular cephalothorax, which is wider than it is long. Pereonites 2 to 5 are successively longer than the previous one. Pereonite 6 is also smaller than pereonite 4. Moreover, mature females carry oostegites and sometimes embryos in their marsupial pouch. The numbers of embryos were counted in a subset of ovigerous females. For the male, the cephalothorax is

**Table 1.** Summary of the conversion factors calculated for each magnification of the binocular Olympus SZX16.

| Magnification | μm | Pixel | μm/pixel |
|---|---|---|---|
| 7 | 24000 | 3841 | 6.25 |
| 8 | 20000 | 3724 | 5.37 |
| 10 | 16000 | 3705 | 4.32 |
| 12.5 | 12000 | 3471 | 3.46 |
| 16 | 8000 | 2965 | 2.70 |
| 20 | 6000 | 2775 | 2.16 |
| 25 | 6000 | 3475 | 1.73 |
| 32 | 4000 | 2996 | 1.35 |
| 40 | 3000 | 2794 | 1.07 |
| 50 | 2000 | 2338 | 0.86 |
| 63 | 2000 | 2966 | 0.67 |
| 80 | 1000 | 1891 | 0.53 |
| 100 | 1000 | 2370 | 1.42 |
| 115 | 1000 | 2772 | 0.36 |

**Fig. 1** Photos of *Z. holdichi* showing an ovigerous female seen in profile (top), an ovigerous female seen from behind (in the middle) and a male seen from the back (bottom). Photo by Manon Jean.

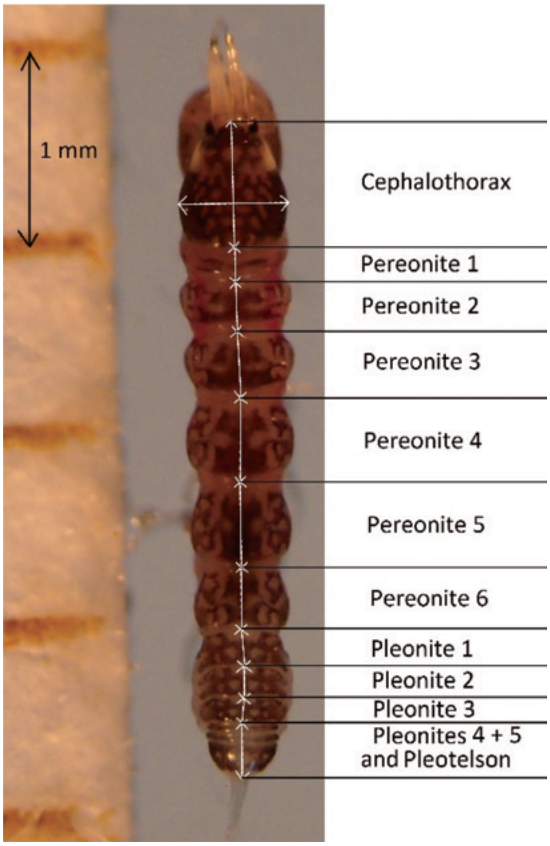

**Fig. 2** Measures performed on each individual *Z. holdichi* (female). Photo by Manon Jean.

longer than wide, with pereonites and pleonites proportionally smaller in relation to their width. Its chelipeds are also more developed than in the female in most cases.

The individuals with a total length less than 1.5 mm were considered as juveniles; the other individuals were classified as female or male and then counted to determine the sex-ratio, i.e. the ratio between females and males.

The Pearson correlation coefficient for each allometry linear relationship between the length or width of the main segments and the total length of the body was calculated using R software, and the significance of all analyses was assessed at $p < 0.01$ and $< 0.001$. Moreover, 500

**Table 2.** Numbers of females, males and juveniles in the total population from 20 March to 29 July then for 100 examined individuals per date. Sex-ratio females/males and individuals per m$^2$.

| Dates | Females | % ovigerous females | Juveniles | Males | Sex-Ratio | Individuals per m$^2$ |
|---|---|---|---|---|---|---|
| 03/20/2014 | 0 | 0 | 0 | 0 | | 0 |
| 04/01/2014 | 0 | 0 | 0 | 0 | | 0 |
| 04/17/2014 | 0 | 0 | 0 | 0 | | 0 |
| 04/30/2014 | 2 | 0 | 0 | 2 | 1 | 7 |
| 05/15/2014 | 2 | 0 | 0 | 2 | 1 | 7 |
| 05/29/2014 | 0 | 0 | 0 | 4 | 1.14 | 7 |
| 06/16/2014 | 8 | 50 | 0 | 7 | 2 | 25 |
| 06/30/2014 | 4 | 0 | 0 | 2 | 0.5 | 10 |
| 07/16/2014 | 1 | 0 | 0 | 2 | 1.37 | 5 |
| 07/29/2014 | 11 | 18 | 0 | 8 | 3.95 | 32 |
| 08/12/2014 | 79 | 14 | 1 | 20 | 2.81 | 2853 |
| 08/27/2014 | 73 | 14 | 1 | 26 | 3.71 | 3740 |
| 09/10/2014 | 78 | 18 | 1 | 21 | 5.13 | 5745 |
| 09/26/2014 | 77 | 18 | 8 | 15 | 3.62 | 13758 |
| 10/06/2014 | 76 | 14 | 3 | 21 | 6.31 | 6400 |
| 10/24/2014 | 82 | 5 | 5 | 13 | 6.46 | 20053 |
| 11/05/2014 | 84 | 13 | 3 | 13 | 5.27 | 21120 |
| 11/24/2014 | 79 | 0 | 6 | 15 | 10.87 | 9280 |
| 12/08/2014 | 87 | 1 | 5 | 8 | 12.57 | 13820 |
| 12/12/2014 | 88 | 0 | 5 | 7 | 3.17 | 5653 |
| 01/06/2015 | 73 | 0 | 4 | 23 | 2.09 | 2640 |
| 01/20/2015 | 67 | 3 | 1 | 32 | 2.09 | 4320 |
| 02/01/2015 | 92 | 2 | 1 | 7 | 13.14 | 2133 |

individuals (males and females) were taken randomly to establish an overall relation between the Total Length (Lt) and the length of the Cephalothorax (Lc).

## 3. Results

### 3.1. Abundances

The first individuals (2 males and 2 females) on the blocks were observed on 30 April, i.e. 1.5 month after the beginning of the experiment and one months after the first sampling. The abundance remained very low (7–32 individuals per m$^2$) before the 12th of August, after which the abundances reached 2,853 individuals per m$^2$, then remained high 2,000 individuals per m$^2$ throughout the rest of the experiment (Table 2; Fig. 3).

The peaks of abundance occurred at the beginning of November with 21,120 individuals per m$^2$, but remained higher than 5,000 individuals per m$^2$ from 9 September to 22 December 2014. During the winter at the end of the study, the abundance was 2,130 individuals per m$^2$ on 4 February 2015 (Fig. 3).

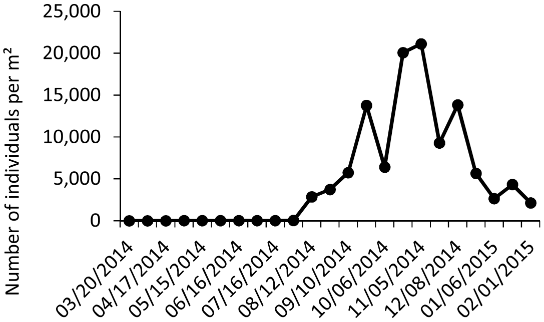

**Fig. 3** Evolution of individuals per $m^2$ of *Zeuxo holdichi* from March 2014 to February 2015.

**Table 3.** Correlation coefficient of Pearson ($R^2$) calculated for each allometry linear relationship between the length or width of the main segments of the *Zeuxo holdichi* body and the total length of 1,061 females and 200 males. * $p < 0.01$ and ** $p < 0.001$.

| | Females | Males |
|---|---|---|
| Cephalothorax length | 0.93** | 0.88** |
| Cephalothorax width | 0.93** | 0.84** |
| Perionite 1 | 0.68* | 0.32 |
| Perionite 2 | 0.91** | 0.79** |
| Perionite 3 | 0.95** | 0.88** |
| Perionite 4 | 0.96** | 0.90** |
| Perionite 5 | 0.97** | 0.90** |
| Perionite 6 | 0.94** | 0.69** |
| Pleonite 1 | 0.87** | 0.80** |
| Pleonite 2 | 0.89** | 0.81** |
| Pleonite 3 | 0.77* | 0.61* |
| Pleotelson | 0.80** | 0.61* |

### 3.2. Allometry

Table 3 gives the values of the Pearson correlation coefficient ($R^2$) between total length and the length of different segments for 1,061 females and 220 males.

Except for the Pereonite 1/total length, all the other allometric variables show a significant scaling relationship with total length. The cephalothorax length was easy to determine, thus providing a good means of describing the structure of a *Z. holdichi* population. The Total Length ($Lt$) and the Length of the Cephalothorax ($Lc$) relationship is $Lt = 0.1788 \times Lc + 0.0058$ with a Pearson correlation coefficient of 0.96 ($p < 0.01$) (Fig. 4).

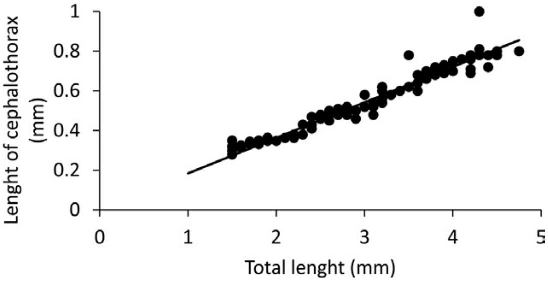

**Fig. 4** Relationship between the total length and the length of the cephalothorax established from 500 individuals of *Zeuxo holdichi* (males and females) all seasons confounded.

### 3.3. Sex-ratio

A total of 1,311 individuals were sexed, yielding a mean sex-ratio of 4.28, with 1,063 females and 248 males. The sex-ratio shows a seasonal variation, with a regular increase from < 4.0 at the beginning of the study to higher values in the autumn and winter, reaching a first peak at the end of November and the beginning of December 2014 (10.87–12.57) and a second peak at the beginning of February 2015 (13.14) (Table 2).

### 3.4. Fecundity

Ovigerous females were counted in the populations from the middle of June 2014, when 50% females were ovigerous (but only 8 females were collected on the block), to the end of the study in February. Moreover, the main period of presence of ovigerous females extended from the end of July to the beginning of November, when 5 to 18% of the females carried embryos.

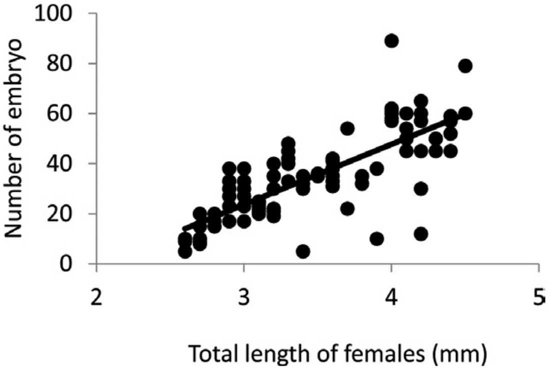

**Fig. 5** Relationship between total length of females and number of embryos counted in the marsupial pouch.

The numbers of embryos per female were counted on 89 females and varied from 5 for the smallest individuals （2.6 mm） to 89 for 4.0 mm, while ovigerous females show a minimum size of 2.6 mm and a maximum size of 4.5 mm （Fig. 5）. The mean number of embryos per female is 24 （+ /− Standard Deviation of 17）. We found a positive linear relationship between the size of females and the number of embryos, with a Pearson correlation coefficient of 0.59 （$p < 0.01$）: Number of embryos = 24,114; Total Length = 18.701.

### 3.5. Population structure

Figure 6 shows the structure of the *Z. holdichi* population at 13 dates from the 18th August 2014 to the 4th February 2015 （in terms of total length of individuals） when the abundance exceeds 2,000 individuals per $m^2$. The analysis of these size-classes allows us to underline four main points. Firstly, the size of the collected individuals ranges from 0.95 mm for the smallest to 5.35 mm for the largest. Secondly, the numbers of juveniles （size $<$ 1.5 mm） are always very low, showing that the colonization of the present blocks has been ensured by the drifting of individuals and not by the recruitment of juveniles on the blocks. Thirdly, the size-frequency histograms indicate the presence of two main cohorts throughout the experiment. The first cohort grouped together most of the measured individuals with a mean size of 2.4 mm （young individuals） and a second cohort with a low number of individuals and a mean size of 3.8 mm （adult individuals）. Fourthly it was not possible to identify any displacement of size-classes （increase in the length of individuals） of these two cohorts during the six months of the experiment.

## 4. Discussion

This study represents the first time that the biology and popûlation of *Zeuxo holdichi* has been investigated in detail. Firstly, in common with numerous other tanaids, this species is tubicolous and fixes its tubes in anfractuosities of the blocks or on macroalgae colonizing the blocks （Foveau *et al.*, 2015）. *Z. holdichi* are found on the blocks 1.5 months after immersion at the end of April 2015 but show dense populations at the beginning of August 2015 only four months after the start of the study （Fig. 6）. The species found favourable conditions for their establishment and development on blocks placed on oyster tables 0.50 m above the seabed in the intertidal zone at Luc-sur-Mer. Moreover, the barnacle *Balanus crenatus* Bruguière, 1789 grows as a pioneer species on the blocks, but dies away some months after their emplacement; in this way, the barnacle wall plates offer a new protected habitat for *Z. holdichi* （Dauvin and Foveau, 2019; Dauvin *et al.*, 2021）. *Z. holdichi* is very abundant on the blocks from the middle of October to the middle of December, i.e. from seven to nine months after immersion （Fig. 6）. From then on, the population decreases towards the end of the study.

As very low numbers of juveniles （sieved on

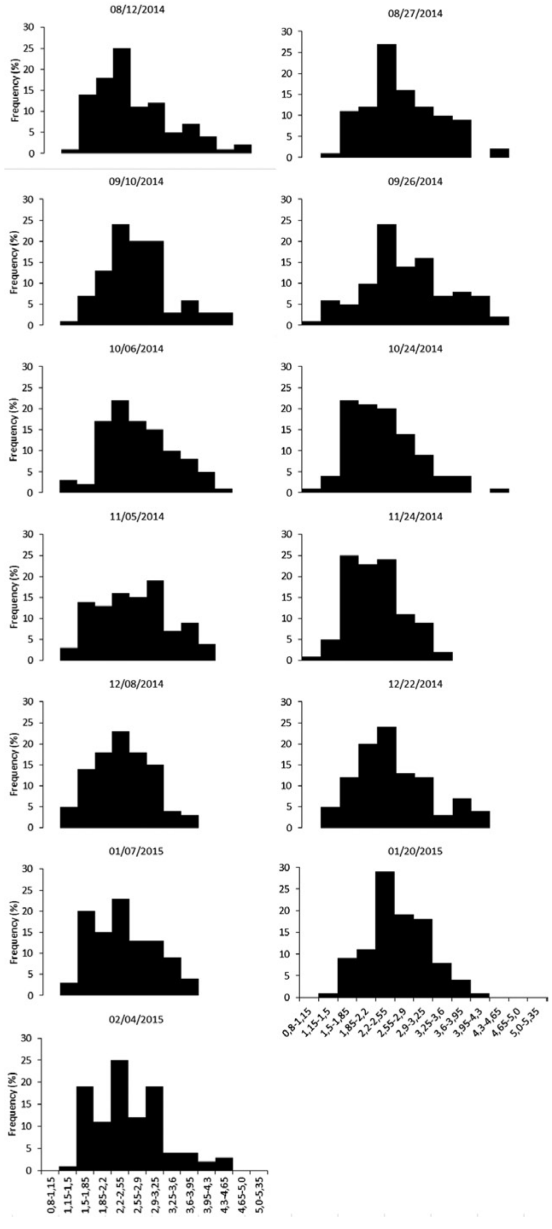

**Fig. 6** Size-frequency distribution of *Zeuxo holdichi* at Luc-sur-Mer (Bay of Seine) between August 2014 and February 2015. Total length of individuals are in mm and frequency is in % of measured individuals.

0.5 mm mesh, which probably insufficient to collect all the smallest individuals) are recorded on blocks in spite of the high abundances of adults including ovigerous females, we hypothesize that the juveniles can also settle on coarse sediment and rocky substratum around the blocks. In the Rade de Cherbourg in the North Cotentin, on the French side of the English Channel, *Zeuxo holdichi* has also been recorded on soft-bottom habitats (Foveau *et al.*, 2018; Dauvin *et al.*, 2020). At this site, the species is found under or near salmon cages on heterogeneous sediments ranging from coarse sand to mud. Nevertheless, its abundance reaches only 80 individuals per m$^2$ under the cages on sand and gravel with a low percentage of fine particles (Dauvin *et al.*, 2020). The same sediment type is observed under the oyster tables at Luc-sur-Mer (Dauvin and Foveau, 2019; Dauvin *et al.*, 2021). Due to the swimming ability of tanaids, young females and adult males of *Z. holdichi* can migrate at night in the water column in relation to their diel migration (Alldredge and King, 1980). In accompaniment of diel migration, drifting of *Zeuxo holdichi* could be also suggested as another source permitting the colonisation of elevated blocks (Thiel and Gutow, 2005; Riera, 2014). Both swimming and drifting seem favourable behaviour to colonise the blocks placed 0.5 m above the sea bed.

The life cycle of the tubicolous *Hargeria rapax* (Harger, 1879) has been studied in the salt marshes on Sapelo Island (Georgia, USA) in tropical environments (Kneib, 1992). The abundance is higher in winter (29,000 individuals per m$^2$). Although reproductive females are present throughout the year, two peaks in reproductive activity occur in autumn and spring Modlin and Harris (1989) have investigated a *H. rapax* population in tidal pools of Dauphin Island on the Alabama coast (USA) of the Gulf of Mexico where abundances reach a maximum at the beginning of the summer (up to 100,000 individuals per m$^2$). Females are present throughout the year, but ovigerous females peak in June and

January. Fonseca and D' Incao (2003) have studied the growth and reproduction of *Kalliapseudes schubartii* Mañé-Garzón, 1949 in the Patos Lagoon (Rio Grande do Sul State, southern Brazil). The reproductive activity was observed in spring and summer, and several cohorts appeared in the population during the year. The population biology of this species was similarly studied in the Araçá region (São Sebastião, Brazil) (Leite *et al.*, 2003), where several cohorts with continuous reproduction were identified over the year and the longevity was estimated as 12 months. Later, Pennefirme and Soares-Gomes (2009) studied *K. schubartii* in the Itaipu tropical coastal lagoon (Southeastern Brazil). This species showed a seasonal pattern of abundances, with the proportion of mature females larger than males over the year. Slivak *et al.* (2013) observed a population of *Sinelobus stanfordi* (Richardson, 1901) on the North coast of Rio Grande do Sul state (Southern Brazil). The ovigerous females, juveniles and males showed a continuous reproductive activity throughout the year in this tropical environment. Ferreiraa *et al.* (2015) investigated the ecology of a population of *S. stanfordi* along 155 km of shoreline within the Río de la Plata Estuary (Argentina). The juveniles were abundant in spring and summer, whereas mature individuals predominated in the winter. Females were always twice as abundant as males, and ovigerous females were collected at all seasons. The populations of *Tanais dulongii* (Audouin, 1826) were studied in detail by Rumbold *et al.* (2012, 2014, 2015a, b) around Mar del Plata in the North of Argentina. Reproductive individuals and juveniles were present throughout the year, whereas two main recruitment periods were identified, in spring and in summer, while the life span was 9–12 months.

In contrast with tropical environments, in temperate environments, the reproductive period is mainly concentrated in the summer and at the beginning of autumn (August to October for *Z. holdichi* in the English Channel), with probably one cohort per year versus numerous cohorts in tropical tanaid populations. The structure of the population at Luc-sur-Mer is characterized by two main cohorts, the main cohort present along the study with a mean size of 2.4 mm corresponding to young individuals in 2014 and a secondary cohort with a low number of adult individuals produced in 2013 with a mean size of 3.8 mm and observed until the end of 2014. The largest individuals disappeared at the end of 2015, showing that the longevity attains 16 months. The species is therefore univoltine, with only one cohort and a single year-class per year.

Females are more numerous than males. This pattern is a general feature among the tanaids: for *Zeuxo holdichi*, the mean females/males ratio is 4.28, with high values reaching 13.14. The sex-ratio is strongly female-biased for *Tanais dulongii* (Rumbold *et al.*, 2012, 2014, 2015a, b), with a sex ratio of 1.8 for *Hargeria rapax* (Modlin and Harris, 1989) and a dominance of females for *Sinelobus stanfordi* (Slivak *et al.*, 2013) and *Leptochelia dubia* (Mendoza, 1982), while the sex-ratio is near 1 (1.1) in *Pagurapseudes largoensis* (Messing, 1983). Highsmith (1983) has observed protogynous behaviour in the case of *Leptochelia dubia*, with all the smallest males being derived from females that have reversed sex. Moreover, the females tend not to reverse their sex when males are present and males show a high mortality rate; for *L. dubia*less than 5% of the adults are male. This behaviour could be generalized for other tanaids as *Z. holdichi*, explaining the dominance of females in the populations.

In the Luc-sur-Mer population, the mean

number of embryos was 24, ranging from 5 to 89 for females measuring between 2.6 to 4.5 mm with a positive relationship between the total length of females and the number of embryos in the marsupial pouch. Among the 484 individuals collected from the Rade de Cherbourg in the North Cotentin (English Channel) (Foveau *et al.*, 2018), 112 were ovigerous females. The numbers of embryos carried by these females has been counted (unpublished data), yielding a fecundity which varies from 10 embryos for the smallest females (2. 3 mm) up to a maximum of 112 embryos for the largest female (5.3 mm), corresponding to a mean fecundity of 27 (+ /- SD 17). In the case of the Luc-sur-Mer population, there is a positive relationship between the size of the females and the number of embryos, with a Pearson correlation coefficient of 0.62 ($p < 0.01$). *Z. holdichi* in the English Channel shows a high fecundity compared to other tanaid species, with an egg development estimated at 1.5 month at Luc-sur-Mer. For *Z. holdichi* Bamber (1990) reported 50 eggs for a brooding female collected in the Arcachon basin in the south of the Bay of Biscay.

For *Pagurapseudes largoensis*, the number of embryos ranges from 4–17 (Messing, 1983), while the mean fecundity is 18 ± 8 eggs per female, with a maximum of 37 and a minimum of five eggs in *Sinelobus stanfordi* (Ferreira *et al.*, 2015), and between 15 and 20 for *Tanais cavolinii* (Johnson and Attramadal, 1982). A mean number of eggs of 50 varying from 5 for a 1.5 mm female to 80 for a 5.5 mm female had been reported for *Tanais dulongii*, Rumbold *et al.*, 2015b). Similarly, *Kalliapseudes schubartii* shows a high fecundity, with a maximum of 86 eggs observed in females having a total length of 6.6 mm (Fonseca and D'Incao, 2003); for this same species, Pennafirme and Soares-Gomes (2009) reports a mean fecundity of 18 ± 11 ranging from 1 to 63 eggs, while Leite *et al.* (2003) reports a mean value of 12 eggs (1 to 31) (Leite *et al.*, 2003).

The fecundity of *Zeuxo holdichi* measured in our one-year and one-site study is among the highest reported for studied tanaid species. Taking into account the presence of two peaks of abundance of the population at Luc-sur-Mer (Table 2), it is possible to estimate the number of juveniles produced by the population. On 26th September, the estimated abundance was 13,758 individuals per $m^2$, and females carrying a brood pouch at that date represented 18% of the population, i.e. 2,476 individuals per $m^2$. With a mean fecundity of 24, the number of juveniles produced would be 59,435 individuals per $m^2$. On 5th November, the estimated abundance was 21,120 individuals per $m^2$, when females with a brood pouch represented 13% of the population, i.e. 2,745 individuals per $m^2$. With a mean fecundity of 24, the number of produced juveniles would be 65,895 individuals per $m^2$.

Commonly, tanaids populations can be very abundant with densities higher than those observed for *Z. holdichi* in the English Channel (21,000 individuals per $m^2$). Highsmith (1983) reported an average density > 50,000 individuals per $m^2$ for a North-American population of *Leptochelia dubia.* Kneib (1992) reported a winter peak of 29,000 individuals per $m^2$ for *Hargeria rapax* on the coast of Georgia (USA), while the same species reaches abundances of 100,000 individuals per $m^2$ along the Alabama coast (Modlin and Harris, 1989). High abundances of the tanaid *Apseudopsis latreillii* have also been recorded on soft-bottom communities of the North Cotentin (English Channel), where abundances reach 23,000 individuals per $m^2$ These *A. latreillii* abundances are among the highest recorded for this species in the worldwide ocean; a maximum of 43,000 individuals per m$^2$ is reported in the Dubai creek of the Persian Gulf (DAUVIN *et al.*, 2020).

Several authors have suggested an opportunistic life strategy for tanaids. LEITE *et al.* (2003) and PENNAFIRME and SOARES-GOMES (2009) reported that high fecundity, continuous reproduction in tropical environments, linked to fast growth and brief longevity, supported an opportunistic life strategy for *Kalliapseudes schubarti* (LEITE *et al.*, 2003). SLIVAK *et al.* (2013) considered that *Sinelobus stanfordi* is an opportunistic species due to its wide geographic range and high variety of habitats. The life traits of *Zeuxo holdichi*, as well as its high fecundity and its presence in numerous habitats along the English Channel, all indicate an opportunistic behaviour. Future studies in other locations should provide evidence to confirm this opportunistic strategy, i.e. the ability to colonise diverse soft-bottom and hard bottom habitats on the intertidal and shallow waters, as well its swimming and drifting behaviour.

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