Life history and population dynamics of the enigmatic tanaid *Chondrochelia dubia* (Tanaidacea: Leptocheliidae) in a tropical seaweed bed

Rodrigo V. A. Alves [1], Flávia Lucena Frédou [2], Nykon Craveiro [1], Leandro Nolé Eduardo [3],
José S. Rosa Filho [1,4]

[1] Laboratório de Bentos, Departamento de Oceanografia, Universidade Federal de Pernambuco, Av. Prof. Moraes Rego,
1235, 50740-550, Recife, Pernambuco, Brazil.
(RVAA) (Corresponding author) E-mail: rodrigovnicius@gmail.com. ORCID-iD: https://orcid.org/0000-0002-3288-5582
(NC) E-mail: nykoncraveiro@gmail.com. ORCID-iD: https://orcid.org/0000-0001-8296-5217
(JSRF) E-mail: souto.rosa@ufpe.br. ORCID-iD: https://orcid.org/0000-0002-5496-7706
[2] Laboratório de Estudos de Impactos Antrópicos na Biodiversidade marinha e Estuarina, Departamento de Pesca e Aquicul-
tura, Universidade Federal Rural de Pernambuco. Rua Manuel de Medeiros, s/n, 52171-900, Recife, Pernambuco, Brazil.
(FLF) E-mail: fredou@ufrpe.br. ORCID-iD: https://orcid.org/0000-0001-5492-7205
[3] Research Unit of Marine Biodiversity, Exploitation and Conservation (MARBEC), Univ. Montpellier, CNRS, Ifremer,
IRD, Sète, France.
(LNE) E-mail: leandronole@hotmail.com. ORCID-iD: https://orcid.org/0000-0003-2369-4175
[4] The Marine Biological Association of the UK, The Citadel Hill Laboratory, Plymouth, Devon, PL1 2PB, UK.

Summary: The present study describes the population dynamics and life history parameters of the enigmatic tanaid *Chon-drochelia dubia* collected in Paiva Beach, tropical coast of Brazil. The region was impacted by a large, unexpected oil spill from August to October 2019. Samples were taken monthly between July 2019 and July 2020 in beds of the red seaweed *Jania capillacea*. The abundance of individuals was negatively correlated with monthly rainfall, with higher abundances in drier months. There was an unexpected significant drop in abundance in September, possibly caused by contact with the crude oil, but the population recovered fully within two months. The parameters of the von Bertallanfy growth equation, calculated for the first time for the species, were L_{inf}=5.26 mm; k=3.36 year^{-1}; t_0=0.0. Compared with other studies, the specimens are very small (2.04 ± 0.95 mm in length), females reach sexual maturity very early (L_{50}=2.3 mm), and natural mortality is high (Z=M=5.77 year^{-1}), indicating an opportunistic life strategy. This study reinforces the bioindication potential of *C. dubia* and the use of bootstrapped length-based methods to estimate key population parameters in small marine invertebrates.

Keywords: epifauna; Peracarida; Brazilian oil spill; reef; macroalgae; leptocheliids.

Ciclo de vida y dinámica poblacional de la enigmática tanaide *Chondrochelia dubia* (Tanaidacea: Leptocheliidae) en un lecho de algas tropicales

Resumen: El presente estudio describió la dinámica poblacional y los parámetros del ciclo de vida del enigmático tanaidáceo *Chondrochelia dubia* recolectado en la playa de Paiva, costa tropical de Brasil. La región se vio afectada por un gran derrame de petróleo inesperado de agosto a octubre de 2019. Se tomaron muestras mensualmente entre julio de 2019 y julio de 2020 en lechos de algas rojas *Jania capillacea*. La abundancia de individuos se correlacionó negativamente con la precipitación men-sual, con mayor abundancia en los meses más secos. Hubo una inesperada caída significativa de la abundancia en septiembre, posiblemente causada por el contacto con el petróleo crudo, sin embargo, la población se recuperó por completo en dos meses. Los parámetros de la ecuación de crecimiento de von Bertallanfy, calculados por primera vez para la especie, fueron: L_{inf}=5.26 mm; k=3.36 año^{-1}; t_0=0,0. En comparación con otros estudios, los ejemplares son muy pequeños (2.04 ± 0.95 mm de longitud), las hembras alcanzan la madurez sexual muy temprano (L_{50}=2.3 mm), y la mortalidad natural es relativamente alta (Z=M=5.77 año^{-1}), lo que indica una estrategia de vida oportunista. Este estudio refuerza el potencial de bioindicación de *C. dubia* y el uso de métodos *bootstrap* basados en la longitud para estimar parámetros de población clave en pequeños invertebrados marinos.

Palabras clave: epifauna; Peracarida; derrame de petróleo brasileño; arrecife; macroalgae; leptoquelidos.

INTRODUCTION

Marine vegetated habitats such as seaweed and seagrass beds harbour diverse and abundant epifaunal communities as they act as shelter, feeding and reproduction grounds for many species (Carvalho et al. 2018, Martínez-Laiz et al. 2018, Tano et al. 2016). Epifauna is usually dominated by crustaceans of the superorder Peracarida, such as amphipods, isopods and tanaids (Carvalho et al. 2018, Tano et al. 2016). These organisms contribute to the elevated secondary production in macrophyte habitats and act as an important link between primary producers and consumers from higher trophic levels (Tano et al. 2016). Tanaidacea is a diverse order of small peracarid crustaceans with more than 1500 described species worldwide, which occur from intertidal to abyssal zones, inhabiting soft, interstitial and biogenic substrates in a wide variety of ecosystems (e.g. estuaries, mangroves, seagrass meadows, coral reefs and deep sea) (Blazewicz-Paszkowycz et al. 2012, Kakui et al. 2021).

Several complex reproductive and parental behaviours have been observed in Tanaidacea, such as ritualistic fights between males, courtship and the maintenance of a brood nursery for "newborn" larvae (Buckle Ramirez 1965, Highsmith 1983, Johnson and Attramadal 1982). In tube-dwelling species such as *Chondrochelia dubia* and *Tanais dulongii*, successful males enter the female tube, where copulation takes place (Highsmith 1983, Johnson and Attramadal 1982). Fertilized eggs develop within the female marsupium until the first postmarsupial stage (manca II) is achieved (Masunari 1983). In *Tanais dulongii,* released manca II larvae keep contact with the mother until manca III stage, when they leave the mother's brood nursery to build their own tubes (Johnson and Attramadal 1982). Tanaid postmarsupial development is usually divided into two or three larval (manca) stages, neutrum, and preparatory and copulatory males and females, with slight variations (Holdich and Jones 1983, Leite et al. 2003, Toniollo and Masunari 2007).

Leptocheliids such as *Chondrochelia dubia* (Krøyer, 1842) are frequently found in high abundance in many shallow-water habitats such as seaweeds, corals and soft sediment worldwide (Guţu 2016, Mendoza 1982, Stoner 1986). These organisms are typically tube-dwellers that build their tubes from sediment particles and faecal pellets held together by secreted mucus with the help of the pereopods (Krasnow and Taghon 1997, Mendoza 1982). Most tanaids are raptorial feeders that consume detritus and its associated organisms (e.g. diatoms, bacteria and nematodes) by seizing and breaking up food particles with their mouthparts (Holdich and Jones 1983). As in other species of Leptocheliidae, *C. dubia* show strong sexual dimorphism, with males having much larger antennules (first antenna), chelae, eyes and walking legs (pereopods) (Bamber 2010, Mendoza 1982, Stoner 1986). The female has short antennules with only three longer articles and also short gnathopods with small chelae, whereas the male has large gnathopods with a prominent propodus and each antennule has a long flagellum. Males also have reduced mouthparts (Gardiner 1975).

The taxonomic history of *Chondrochelia dubia* goes back to over 180 years ago when Krøyer (1842) described *Tanais dubia* (now *C. dubia*) from specimens collected in Salvador, northeastern Brazil, and *Tanais savignyi* (now *C. savignyi*) from Madeira, Portugal. These species were later transferred to the genus *Leptochelia*, and then *Chondrochelia* by Guţu (2016). In the last century, many new species of the genus were described, while the Brazilian taxon *Chondrochelia dubia* was "found" in very distinct places worldwide (Bamber 2010). Most of these species were synonymized under the wide "*Leptochelia dubia* group", which may include several cryptic species in many continents (Bamber 2010). All members of the "*Leptochelia dubia* group" were then synonymized under the cosmopolitan *L. dubia* by Sieg (1983), which started a debate over whether the senior synonym should be *L. dubia* or *L. savignyi* (Bamber 2010). Two major efforts were recently made to solve the problematic "*Leptochelia dubia* group": Bamber (2010) made a redescription of *C. savignyi* and synonymized some North Atlantic and Mediterranean species under *C. savignyi*, and a robust revision made by Guţu (2016) added a new subfamily, seven genera and 21 species to the Leptocheliidae family. Consequently, the "*Leptochelia dubia* group" was to a large extent dissolved into several different taxa, including the "Brazilian species" discovered by Krøyer (1842) that is now named *Chondrochelia dubia*. It is now evident that *C. savignyi* and *C. dubia* should no longer be considered synonymous (Bamber 2010, Jarquín-González and Carrera-Parra 2022) and that *C. dubia* is not a cosmopolitan species, since Jarquín-González and Carrera-Parra (2022) recently rejected its hypothetical occurrence in the Mexican Caribbean and Gulf Coast with molecular data.

Though it is very common in several shallow-water environments, only a few studies have focused on the population dynamics of Leptocheliidae (Buckle Ramirez 1965, Masunari 1983, Modlin and Harris 1989, Stoner 1986). Population dynamics studies combined with life histories and morphometric data are powerful tools for understanding ecosystem function at different spatial and temporal scales, managing harvested and threatened species, and quantifying biotic responses to environmental change (Pennafirme and Soares-Gomes 2009, Rumbold et al. 2015). In late 2019, the Brazilian coast was heavily impacted by the largest oil spill in tropical oceans so far (Soares et al. 2020), enabling us to study the potential impacts of this disaster in coastal marine biota. Herein, we aim to describe the population dynamics and life history parameters of *Chondrochelia dubia* on the northeast coast of Brazil (Paiva Beach). Additionally, we make inferences about the effects of the 2019 oil spill on the populations of *C. dubia*. This is also the first study to estimate the natural mortality rate, longevity, maturation and parameters of von Bertalanffy's growth equation (L_∞, k and t_0) for the tanaid *C. dubia*. Unlike previous studies on Tanaidacea, we used robust bootstrapped versions of the classical length-based methods to quantify key population parameters.

MATERIALS AND METHODS

Study area

Paiva Beach (8°16'S, 34°56'W) is an open ocean tropical sandy beach approximately 7.8 km long located in the Cabo de Santo Agostinho municipality (Pernambuco State, northeast Brazil) (Holanda 2020). The sandstone reefs of Paiva Beach are elongated and occur parallel to the shore (Laborel 1970). The reef line closest to the beach is 2.5 km long and 1 km wide and densely colonized by macroalgal assemblages that are typically found in the tropical phycogeographic region (Horta et al. 2001). The climate is tropical hot/humid, with average annual temperatures above 25°C throughout the year (Domingues et al. 2017). The tidal regime can be classified as a mesotidal semi-diurnal type, with tide height averaging 0.7 m (neap tide) to 2.5 m (spring tide) (Domingues et al. 2017). The reefs and their diverse intertidal communities were severely impacted by the 2019 Brazilian Oil Spill. In only one week (19-28 October 2019), more than 1000 t of crude oil were collected from the Cabo de Santo Agostinho municipality alone (Craveiro et al. 2021). Although less perceptible, oil strains started appearing in Pernambuco's beaches in August 2019 (Soares et al. 2020), months before the main sheet of crude oil arrived at Paiva Beach.

Sampling design and laboratory procedures

Sampling was performed monthly from July 2019 to July 2020. In March 2020, samples were not taken because of COVID-19 lockdown restrictions. On each sampling occasion, ten fronds of the red seaweed *Jania capillacea* were collected in intertidal tide pools. The fronds were wrapped with plastic bags to prevent motile animals from escaping and then removed from the substrate. Samples were fixed with 4% saline formalin. In the laboratory, the samples were sieved (0.3 mm mesh size) and the retained epifaunal organisms were sorted under the stereomicroscope. Specimens of *C. dubia* were separated, counted and preserved in 70% ethanol. For each month, approximately 120 to 170 individuals were randomly chosen (in some months fewer than 120 individuals were found) to be measured from the tip of the carapace to the end of the telson with a stereo microscope with an eyepiece reticle (body length, mm). For males, the length and width of chelae were measured. The individuals were classified into five categories, as proposed by Masunari (1983): juveniles/mancas (larval MII and MIII stages); pre-ovigerous (preparatory) females (those with oostegites); ovigerous females (those with marsupia); non-reproductive females (those with adult appearance but no sign of reproductive activity); and males (those with characteristic male features) (Fig. 1).

Statistical analysis

Monthly densities and lengths of *C. dubia* were log-transformed and compared by one-way ANOVA followed by pairwise Tukey tests. Chi-square tests (χ^2)
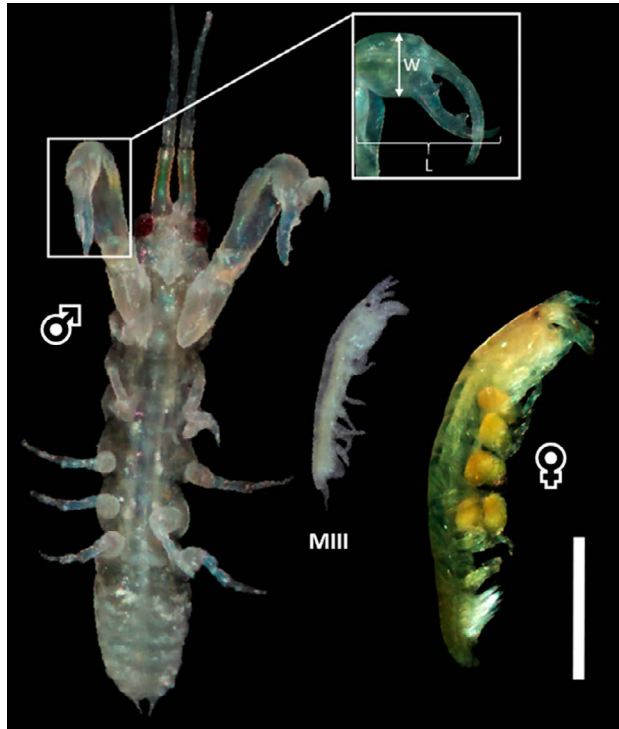

Fig. 1. – Fixed specimens of *Chondrochelia dubia* (Krøyer, 1842) collected in Paiva Beach, northeastern Brazil: adult male (♂) (left); manca III juvenile (centre) and ovigerous female (♀) (right). L, chela length; W, chela width. Scale bar, 1 mm.

were performed to compare sex ratio between months and size classes. The parameters of the von Bertalanffy growth function (VBGF) were estimated through the ELEFAN_GA_Boot method, which is based on a bootstrapped genetic algorithm that provides a range of likely best fits for the VBGF parameters (Schwamborn et al. 2019). This approach is highly applicable for rapid assessment in data-poor situations such as data collected from short time periods (e.g. one year) (Mildenberger et al. 2017). Intervals of L_∞, k and t_0 (pooled data) were chosen based on published studies about similar species from the southwestern Atlantic Ocean (Almeida 1994, Fonseca and D'Incao 2003, Leite et al. 2003, Pennafirme and Soares-Gomes 2017, Rumbold et al. 2015). Analyses were made in the *TropFishR* (Mildenberger et al. 2017) and *fishboot* (Schwamborn et al. 2019) packages.

The growth performance index (Φ') was calculated from von Bertalanffy's equation parameters as Pauly and Munro (1984):

$$\Phi' = \log k + 2 \cdot \log Linf$$

The length at which 50% of females are sexually mature (L_{50}) was estimated through a logistic function using two sets of variables: length-frequency (LFQ) data and categorical "gonadal maturation stages" (Torrejon-Magallanes 2020). Since the mean length of the individuals at MIII stage (1.75 mm) is lower than the smallest reproductive female (2.1 mm), all specimens in this category were treated as "immature". L_{50} was calculated as

$$Pi = A \cdot (1 + e^{(-r(Lt - L50))})^{-1}$$

where Pi is the proportion of reproductive females for each (0.2 mm) size class; A is the curve asymptote; r is a rate parameter related to the speed of size change from non-reproductive to reproductive status; L_t is the total length (mm); and L_{50} is the size at first maturity (mm) (Fontoura et al. 2009).

Morphometric maturity in males was estimated using a regression analysis where X (body length) is considered the explanatory variable and the classification of maturity (juveniles, 0; adults, 1) is considered the response variable (binomial) through the form (Torrejon-Magallanes 2020):

$$Pcs = 1 / (1 + e^{-(\beta_0 + \beta_1 \cdot X)})$$

where Pcs is the probability of an individual being mature at a determinate X length. β_0 (intercept) and β_1 (slope) are estimated parameters. Both gonadal (females) and morphometric (males) maturities were calculated using the "sizeMat" package (Torrejon-Magallanes 2020).

The instantaneous mortality rate (Z) was calculated through a linear capture curve based on length composition data (Sparre and Venema 1998). Estimates for maximum individual age within the population were based on Taylor (1958). The maximum longevity (t_{max}) was calculated from 95% of the asymptotic length, where

$$t_{max} = (2.996/k) + t_0$$

All data analyses were performed using R software (R Core Team 2022). For all tests a significance level of 5% was considered.

RESULTS

A total of 1513 individuals (583 females, 34 males and 896 mancas) were included in the analysis. The abundance of *C. dubia* varied significantly between months (F=10.55; p<0.01) and was negatively correlated with monthly rainfall (S=458, Rho=-0.601; p=0.04). Months with the highest abundances were August, November and December 2019 (Fig. 2A).

Body lengths varied significantly between months (F=19.9; p<0.01). In general, the smallest individuals were found in August 2019 (1.58±0.99 mm), whereas the largest ones were found in February (2.63±0.93 mm) and April 2020 (2.61±0.9 mm) (Fig. 2B). Specimens were categorized into six developmental stages (Fig. 3): MII (0.99±0.2 mm), MIII (1.75±0.3 mm), neutrum (3.05±0.48 mm), males (2.82±0.4 mm), pre-ovigerous females (2.87±0.35 mm) and ovigerous females (3.16 ± 0.39 mm).
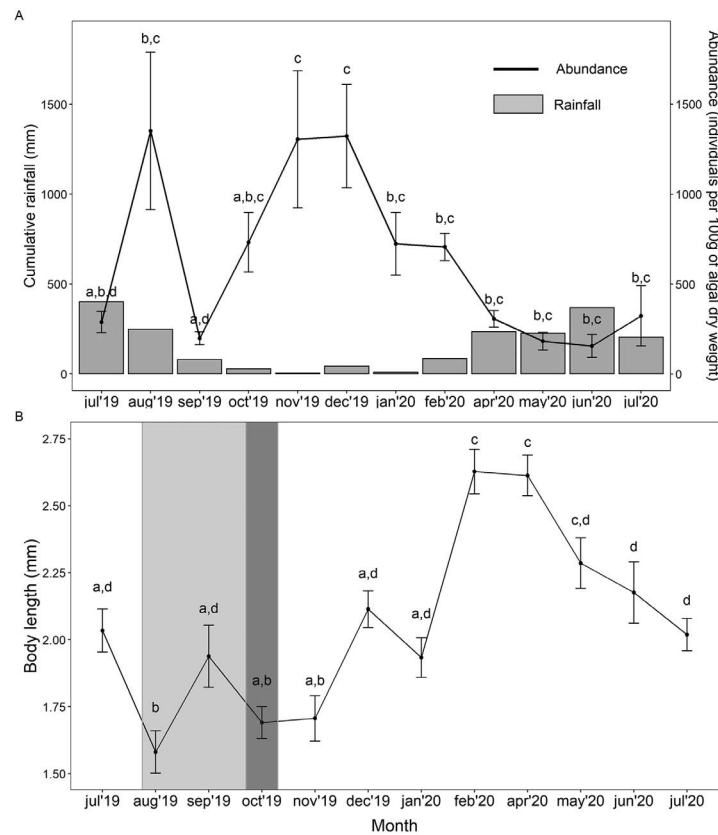

Fig. 2. – A, abundances of *Chondrochelia dubia* between July 2019 and July 2020 (black line) and cumulative rainfall (grey bars). B, body length (mm) of *C. dubia* between July 2019 and July 2020. The light grey rectangle indicates the period of weak oil arrival at the location (August and September 2019) and the dark grey rectangle indicates the period of strong oil arrival (October 2019). Vertical bars represent standard errors and letters indicate the results of Tukey tests (p<0.05).
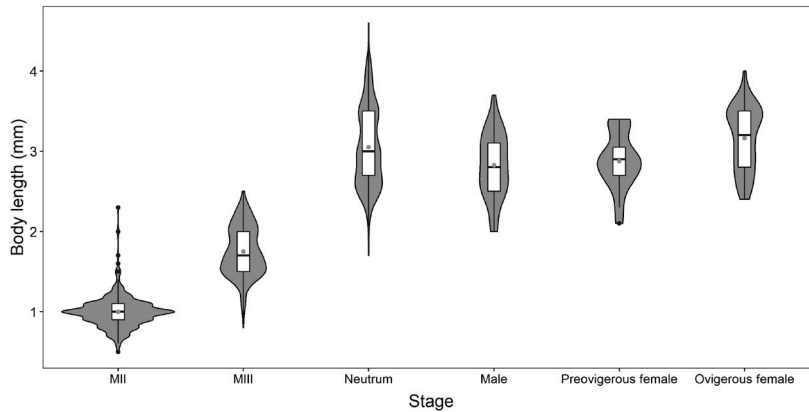
Fig. 3. – Violin plot combined with boxplot of length distributions within different developmental stages in *Chondrochelia dubia*. Grey dots are the mean values.

The population was dominated by non-reproductive individuals. Those with clear sexual characteristics (males and ovigerous and pre-ovigerous females) accounted for less than 10% of the total. *Chondrochelia dubia* had multiple cohorts throughout the year. Reproductive individuals had discrete abundance peaks throughout the year, especially in December (Fig. 4). Except for February and April, juveniles (MII and MIII stages) accounted for more than 50% of all individuals in all months. The sex ratio was significantly female-biased in all months and size classes. The general sex ratio was approximately 17:1 and maximum female dominance occurred in November 2019 (no males) and July 2020 (56 females: 1 male) (Table 1).

Female size at first maturity was 2.3 mm (Fig. 5A). For males, the inflection point, which indicates the size of morphometric maturity, was 3.0 mm (Fig. 5B). Longevity (t_{max}) was 0.89 years (10-11 months) and natural mortality (M=Z), 5.77 year^{-1}. There was a positive and significant correlation between body size and chela length (R^2=0.64; $p<0.01$) and body size and chela width (R^2=0.57; $p<0.01$) in males. The parameters of the von Bertalanffy growth formula were L_∞=5.26 mm; k=3.36 year^{-1}; t_0=0.0 (Fig. 6).

DISCUSSION

Populational fluctuations and morphometry

The maximum abundance of *C. dubia* in Paiva Beach (tropical Brazilian coast) occurred in drier months, particularly in August, November and De-
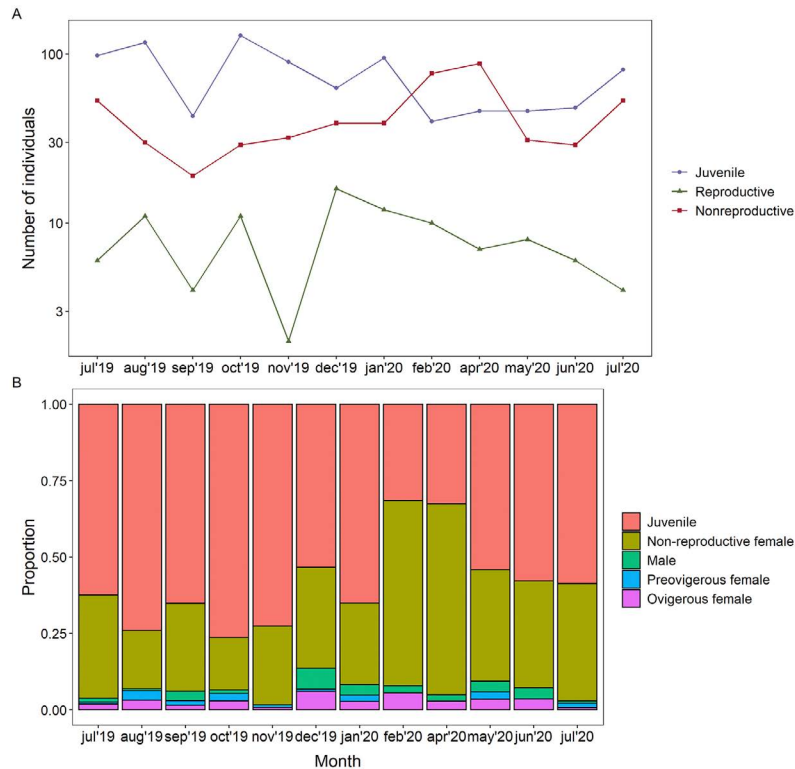

Fig. 4. – A, number of juvenile, non-reproductive and reproductive individuals (males, pre-ovigerous and ovigerous females) per month. B, proportion of different sex categories of *Chondrochelia dubia* between July 2019 and July 2020.

Table 1. – Number of males and females, sex ratio of *Condrochelia. dubia* between July 2019 and July 2020, and results of chi-squared tests per month and size class.

| Months	Females	Males	F:M ratio	Chi-squared	p-value
2019/07	57	2	33.5:1	59.362	<0.01
2019/08	40	1	40:1	36.214	<0.01
2019/09	21	2	12.5:1	17.926	<0.01
2019/10	38	2	19:1	42.481	<0.01
2019/11	34	-	-	34.028	<0.01
2019/12	47	9	5.2:1	31.641	<0.01
2020/01	46	5	9.2:1	37.123	<0.01
2020/02	84	3	28:1	77.538	<0.01
2020/04	92	3	30.6:1	87.485	<0.01
2020/05	36	3	12:1	35.021	<0.01
2020/06	32	3	10.6:1	27.225	<0.01
2020/07	56	1	56:1	51.158	<0.01
Total	583	34	17.14:1	453.17	<0.01
Size classes (mm)	Females	Males	F:M ratio	Chi-squared	p-value
1.5	2	1	2:1	-	-
2	34	4	8.5:1	20.25	<0.01
2.5	229	16	14.3:1	184.44	<0.01
3	162	12	13.5:1	127.59	<0.01
3.5	129	1	129:1	124.07	<0.01
4	26	-	-	24.038	<0.01
4.5	1	-	-	-	-
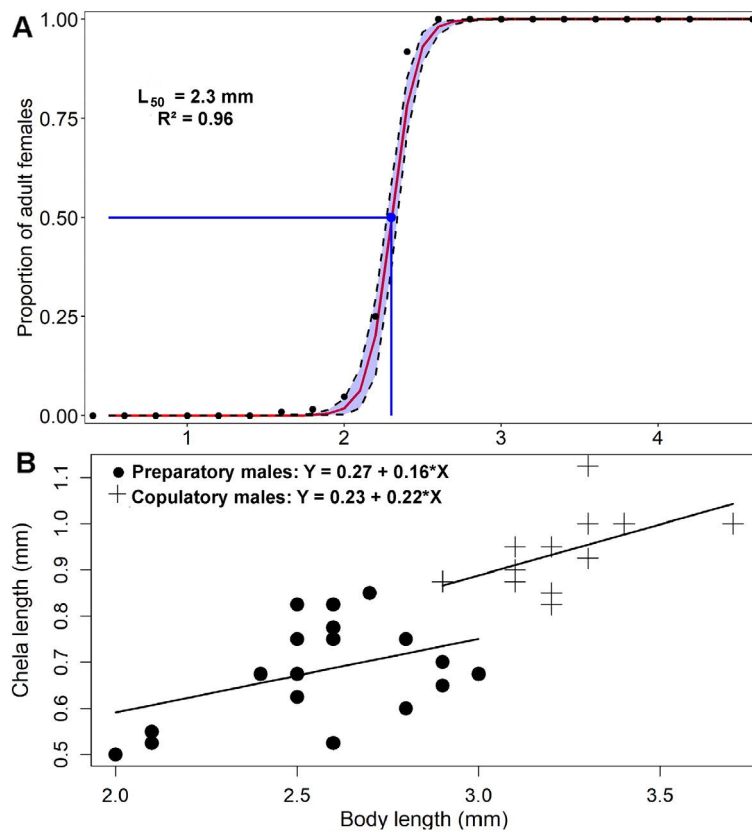
Fig. 5. – A, logistic curve and size at first maturity (L_{50}) for females of *Chondrochelia dubia*. Blue envelope represents the 95% confidence interval. B, regression lines indicating morphometric maturity in males of *C. dubia*.
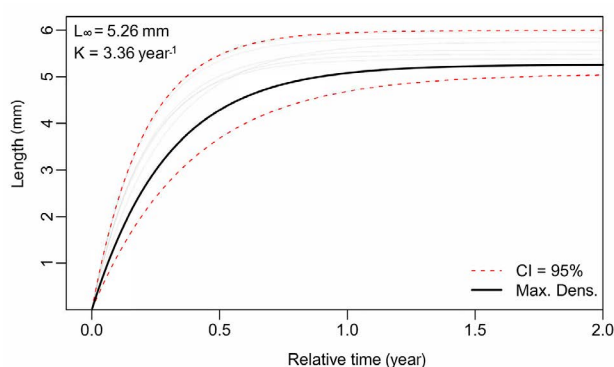
Fig. 6. – Von Bertalanffy growth curve and parameters for *Chondrochelia dubia* (pooled sexes). CI=95% confidence interval.

cember 2019. Despite the stable conditions of tropical environments, even slight variations in temperature, photoperiod, salinity and nutrient concentration might cause perceptible oscillations in population size and structure (Pandian 2016). Estuarine tanaid species have generally shown abundance peaks in rainy periods and under mesohaline conditions (Modlin and Harris 1989, Pennafirme and Soares-Gomes 2009). Marine species, in contrast, are generally more abundant during the dry season, when salinity is higher (de Souza et al. 2013, Tuya et al. 2001). Warmer temperatures in the dry season may also enhance microbial growth (Longo et al. 2019), which might contribute to the detritus chain, which is useful for both feeding and tube-building in Tanaidacea (Krasnow and Taghon 1997). In the rainy season, wave action, river discharge and sediment resuspension are considerably higher (Medeiros et al. 2001), which may cause higher mortality owing to physical and chemical stressors and reduction of available algal biomass.

There was a significant reduction in the size of individuals in August and October/November 2019. Despite the arrival of oil in these months, abundances continued to grow, so the lower body lengths might be a consequence of the recruitment of new juveniles into the population instead of a mass mortality event. The months of August (end of the rainy season), October and November (peak of the dry season) coincide with the highest salinities. However, other factors rather than just salinity might help to explain this pattern, such as the decrease in predators and/or competitors, or better conditions for the seaweed that provides refuges. However, a significant reduction in abundance was observed in September, the beginning of the dry season. This unusual decrease might have been caused by the contact with the oil that killed mainly juveniles, who are more vulnerable to harmful effects of pollutants than adults (Keesing et al. 2018). However, the population continued to grow and quickly recovered in the following months, which can be seen as the second peak in November/December. In laboratory experiments, *C. dubia* has shown to be relatively tolerant to changes in water chemistry (Araújo-Silva et al. 2022). Much of its resistance is attributed to the construction of tubes, which keep these animals protected from external agents and may help them colonize a wide variety of habitats with-

in medium and infralittoral zones (Araújo-Silva et al. 2022).

Male size of morphometric maturity was 3.0 mm, and males larger than that were very rare. When males moult into their mature phase, they lose their functional mouthparts and cannot feed anymore, so they must die soon after reproduction (Highsmith 1983, Gardiner 1975), which explains the almost complete absence of males larger than 3 mm. Also, a positive correlation was observed between body length and chela length in males. The differential growth rate of chelae has an important role in crustacean reproduction (Ewers-Saucedo 2019). In Tanaidomorpha, chelipeds are used to access the female tube, hold females during mating and fight with other males (Buckle Ramirez 1965, Highsmith 1983, Johnson and Attramadal 1982). The copulatory male is considered the only free walking instar, so developed chelipeds are essential to climb and hold onto algae in turbulent environments (Johnson and Attramadal 1982). These features might give a reproductive advantage to larger males (Highsmith 1983). Another possible function of male aggression in leptocheliids is the exclusion of other males of sympatric species that might cohabit the algal frond (Stoner 1986).

A large size overlap between the sexes, mainly among more advanced developmental stages, was recorded. This is mainly because of the progressive decrease in growth rate with age (Sparre and Venema 1998). Pre-ovigerous females have a very small growth from the preparatory to marsupial stages because they allocate more resources to reproduction than to somatic growth (Masunari 1983). The largest individuals in our samples were female. This is probably because of the low survival rate and premature deaths of males (Mendoza 1982). More specifically, the largest individuals found were in fact non-reproductive adult females. It is very likely that they were multiparous females with interspaced "pregnancies" (Masunari 1983). The wide overlap between non-reproductive individuals with adult appearance (neuters) and reproductive ones suggests the existence of at least one intermediary instar between successive marsupial stages in *C. dubia* (Fig. 3). However, we did not find external marks (as in Johnson and Attramadal 1982) or any direct sign of previous "pregnancies" in large non-reproductive females.

Reproduction and sex ratios

The scarcity of reproductive individuals was notable. A few observations might explain this annual pattern, such as high natural mortality (5.77 year^{-1}) and possible competition among individuals to mate; the aggressiveness of males and possible formation of "harems" or highly condensed mating aggregations (Stoner 1986); interspaced "pregnancies" with intermediary instars (multiparity); and pre-ovigerous females with microscopic oostegites in early development, only visible through histological analysis (Masunari 1983). The last two factors might have produced a bias in the counting of reproductive/non-reproductive individuals.

The maintenance of a skewed sex ratio towards females during the entire year has also been observed in

many previous studies on tanaids (e.g. Leite et al. 2003, Masunari 1983, Modlin and Harris 1989). Biased sex ratios have long been observed in several crustacean species (Ewers-Saucedo 2019). Some evolutionary and ecological mechanisms might explain the highly female-biased sex ratio in *C. dubia* (Ewers-Saucedo 2019):

1. Local mate competition: Because males add little to increase the mother's fitness, this favours the production of the lowest number of males sufficient to fertilize the highest number of females possible. This strategy is common in brooding and low-dispersive taxa, where brothers frequently compete for mating. Stoner (1986) proposed that aggregations with high densities of females might actually benefit males, since it would be easier for them to find partners.

2. Sexual selection: Producing males is a high-cost activity, because they have to grow up and compete to have a chance of mating—because of this, only females in good condition are likely to generate more males, making them less frequent in the population.

3. Environmental sex determination: Warm temperatures can turn the sex ratio towards females (Masunari 1983), and the stable, tropical climate of the study area might help maintain the female-skewed sex ratio year-round despite the seasonal oscillations.

4. Sex specific mortality: In Tanaidacea, the small relative number of males has been mainly attributed to their sexual behaviour: males experience higher mortality than females as a result of competition and aggressive behaviour with other males and are more vulnerable to predators because they have to walk to the female tube to mate (Highsmith 1983). Developed males also lack functional mouthparts, which might significantly decrease their lifespan (Highsmith 1983).

5. Sex reversal: Diverse reproductive strategies are observed in Tanaidomorpha and Apseudomorpha, including gonochoristic development and simultaneous, protandrous and protogynous hermaphroditism (Gardiner 1975).

The last strategy has been widely proposed to occur in many species of Tanaidacea (Gardiner 1975). It has been theorized that protogyny is an effective strategy for maximizing fitness (reproductive success) in all life stages (Highsmith 1983). Basically, males take too long to be able to reproduce (they must grow enough to fight with other males), whereas females mate as soon as they reach maturity. There is therefore a selective pressure for being a female at small (younger) stages and then becoming a male at larger (older) stages, because only the large males will be successful (Highsmith 1983). Alternatively, protogyny may also have evolved as a mechanism for counterbalancing the high mortality of males (Leite et al. 2003).

Although it is observed in many tanaids, there is no clear evidence that *C. dubia* is a sequential hermaphroditic species. If that were true, it would be expected to observe a dominance of one sex in smaller size classes and a gradual shift towards the other sex in larger size classes (Ewers-Saucedo 2019). The opposite occurred in Paiva Beach, where the sex ratio was strongly female-biased in all size classes. However, this might still be true if only a small percentage of females is able to become male. It has been observed in similar species that dominant males can inhibit sex reversal of nearby females (Highsmith 1983), which might keep the number of males in the aggregation low. The presence of two types of males based on their size differences has been treated as more evidence of protogynous hermaphroditism in Tanaidacea. The smallest males were considered gonochoristic (male-born) whereas the largest ones were protogynous (female-born) (Gardiner 1975). Interestingly, individuals identified as "*Leptochelia dubia*" collected from different parts of the West Coast of the USA have been treated either as dioecious (Mendoza 1982) or hermaphroditic (Highsmith 1983) on different occasions. Considering the lack of detailed natural observations, the taxonomic uncertainties and the geographic distances (tanaids are known to have low dispersive capacity; Bamber 2010), the best way to solve questions regarding the reproductive behaviour of *C. dubia* in the tropics would be to cultivate these organisms under controlled and realistic conditions.

Life histories and population growth

The year-long presence of reproductive adults and juveniles indicates continuous reproductive activity, a common pattern observed in many crustacean species, especially in the tropics (Pandian 2016, Pennafirme and Soares-Gomes 2009). Specimens in Paiva Beach are much smaller (2.04±0.95 mm in length) than other tanaid species from the southwestern Atlantic (Table 2), and their natural mortality is relatively high. *C. dubia* also has multiple short cohorts, a relatively high growth rate (k) and a short lifespan (<11 months). All of these features indicate that it has a short and opportunistic life strategy (Pennafirme and Soares-Gomes 2009).

Latitudinal trends in life history parameters are commonly observed in Tanaidacea (Pennafirme and Soares-Gomes 2017). Warmer temperatures generally accelerate growth and maturity in ectotherms (Sudo 2003), and tropical marine invertebrates generally have shorter lifespans and smaller individual sizes than their temperate counterparts (Cardoso and Defeo 2004). Furthermore, unlike *Monokalliapseudes schubartii* and *Tanais dulongii* (Table 2), *C. dubia* is a seaweed-dweller, meaning that its size is highly dependent upon the interstitial size and volume of the host algae (Hacker and Steneck 1990). However, in a subtropical area in southern Brazil, Fonseca and D'Incao (2003) found a growth rate (k) of 4.54 year^{-1} for *M. schubartii*. It is possible that other factors rather than temperature, such as food quality/availability (Berrigan and Charnov 1994), were responsible for the higher growth rate of this species than of our tropical species. The population studied by Fonseca and D'Incao (2003) inhabits a nutrient-rich protected estuarine bay (Patos Lagoon), which is very different from the open, nutrient-variable waters of tropical Brazilian beaches.

Table 2. – Tanaid species and their respective von Bertallanfy population growth parameters estimated in previous studies from the southwestern Atlantic. M, natural mortality; SST, sea surface temperature (mean) (Boyer et al. 2018).

Species	Location	Coordinates	SST (°C)	L_∞ (mm)	k (year^{-1})	t_0	L_{50} (mm)	φ'	Longevity (year)	M (year^{-1})	Reference
Tanais dulongii	Mar del Plata, Argentina	38°02'S; 57°32'W-38°10'S; 57°38'W	14-15	7-8	0.55-0.63	-	-	-	-	-	Rumbold et al. 2015
Monokalliapseudes schubartii	Patos Lagoon, Rio Grande do Sul, Brazil	32°01'S; 52°07'W	19	13.22	4.54	0	6.6	2.9	1	-	Fonseca and DIncao 2003
Monokalliapseudes schubartii	Mel Island, Paraná, Brazil	25°33'S; 48°19'W	21	11	3	0	-	2.6	0.66 – 1	-	Almeida 1994
Monokalliapseudes schubartii	Araçá Region, São Paulo, Brazil	23°49'S; 45°24'W	23	10.7	3	0	-	2.5	1	-	Leite et al. 2003
Monokalliapseudes schubartii	Itaipu Lagoon, Rio de Janeiro, Brazil	22°58'S; 43°02'W	25	11.74	2.91	-0.04	5.9	2.6	0.84	0.99	Pennafirme and Gomes 2017
Chondrochelia dubia	Paiva Beach, Pernambuco, Brazil	8°16′S; 34°56′W	27-28	5.26	3.36	0	2.3	1.97	0.89	5.77	Present study

The absence of other studies that address the population parameters of *C. dubia* makes it difficult to evaluate the influence of environmental variables and regional variability in the growth of this species. However, compared with other Tanaidacea species of the southwestern Atlantic, *C. dubia* also showed the lowest growth performance index (Φ'). Zamora-Sarabia et al. (2022) found a negative correlation between Φ' and sea surface temperature for a commercially important fish species in the southern Gulf of California. This correlation might explain the low Φ' value compared with other tanaid populations from colder areas at higher latitudes (Table 2). Combined with the high mortality rate and low percentage of reproductive individuals, *C. dubia* apparently faces harsh environmental conditions at Paiva Beach, such as resource limitation, high temperatures, predation and strong hydrodynamics (Domingues et al. 2017). Moreover, the size of the largest individual found (4.6 mm in length) was about 87% of the theoretical maximum length (L_{inf}=5.26 mm). It is possible that these natural stressors are a strong limitation for the growth and survival of these organisms. This may make the studied population of *C. dubia* vulnerable to extreme climatic events caused by anthropogenic warming and/or El Niño oscillations (Zamora-Sarabia et al. 2022), although Araújo-Silva et al. (2022) showed that this species is still more tolerant to warming effects than other tropical peracarids. Growth parameters such as Φ' are often used as an important reference for stock management and choosing appropriate species for aquaculture (Mathews and Samuel 1990, Pauly and Munro 1984, Zamora-Sarabia et al. 2022). Because peracarids have been recently studied as a valuable food resource for aquaculture (Abundez et al. 2021, Guevara et al. 2005), the present study should be taken into consideration for future decisions regarding the commercial use of this species.

In conclusion, *C. dubia* at Paiva Beach (tropical Brazilian coast) has a short-living, opportunistic life history that may be favoured by high-salinity conditions. The sex ratios are heavily female-skewed throughout all months and size classes. The species was apparently little impacted by the 2019 Oil Spill at the populational level, a sign of high tolerance to environmental impacts and great plasticity of lifestyle, which are interesting features of a possible bioindicator species. This study reinforces the need for cultivation techniques in order to solve key questions regarding the reproductive behaviour of the species and the high applicability of robust, bootstrapped length-based methods in population studies of small marine invertebrates.

ACKNOWLEDGEMENTS

REFERENCES

Abundez J., Moreno G., Simoes N., et al. 2021. Marine amphipods (*Parhyale hawaiensis*) as an alternative feed for the lined seahorse (*Hippocampus erectus*, Perri 1810): Nutritional value and feeding trial. PeerJ. 9: 1-28.
https://doi.org/10.7717/peerj.12288

Almeida M. 1994. *Kalliapseudes schubartii* Mañé-Garzón, 1949 (Tanaidecea-Crustacea): Dinâmica populacional e interações com a macrofauna bêntica no Saco do Limoeiro, Ilha do Mel (Paraná, Brasil). MSc thesis, Universidade Federal do Paraná, 75pp.

Araújo-Silva C., Sarmento V., Santos P. 2022. Climate change scenarios of increased CO_2 and temperature affect a coral reef peracarid (Crustacea) community. Mar. Environ. Res. 173: 1-11.
https://doi.org/10.1016/j.marenvres.2021.105518

Bamber R. 2010. In the footsteps of Henrik Nikolaj Krøyer: The rediscovery and redescription of *Leptochelia savignyi* (Krøyer, 1842) sensu stricto (Crustacea: Tanaidacea: Leptocheliidae). Proc. Biol. Soc. Wash. 123: 289-311.
https://doi.org/10.2988/10-14.1

Berrigan D., Charnov E. 1994. Reaction Norms for Age and Size at Maturity in Response to Temperature: A Puzzle for Life Historians. Oikos. 70: 474-478.
https://doi.org/10.2307/3545787

Blazewicz-Paszkowycz M., Bamber R., Anderson G. 2012. Diversity of Tanaidacea (Crustacea: Peracarida) in the world's oceans - how far have we come? PLoS ONE. 7: 1-11.
https://doi.org/10.1371/journal.pone.0033068

Boyer T., Baranova O., Coleman C., et al. 2018. NOAA Atlas NESDIS 87, Silver Spring, MD, 207 pp.

Buckle Ramirez L.F. 1965. Untersuchungen über die Biologie von *Heterotanais oerstedi* Kröyer (Crustacea, Tanaidacea). Zeitschrift Für Morphologie Und Ökologie Der Tiere. 55: 714-482.
https://doi.org/10.1007/BF00406235

Cardoso R., Defeo O. 2004. Biogeographic patterns in life history traits of the Pan-American sandy beach isopod *Excirolana braziliensis*. Estuar. Coast. Shelf Sci. 61: 559-568.
https://doi.org/10.1016/j.ecss.2004.06.021

Carvalho N., Grande H., Rosa Filho J., Jacobucci G. 2018. The structure of gammarid amphipod (Crustacea, Peracarida) assemblages associated with *Sargassum* (Phaeophyta, Fucales) and their link with the structural complexity of algae. Hydrobiologia. 820: 245-254.
https://doi.org/10.1007/s10750-018-3661-5

Craveiro N., Alves R., Menezes J., et al. 2021. Immediate effects of the 2019 oil spill on the macrobenthic fauna associated with macroalgae on the tropical coast of Brazil. Mar. Pollut. Bull. 165: 1-8.
https://doi.org/10.1016/j.marpolbul.2021.112107

de Souza F., Gilbert E., de Camargo M., Pieper W. 2013. The spatial distribution of the subtidal benthic macrofauna and its relationship with environmental factors using geostatistical tools: A case study in Trapandé Bay, southern Brazil. Zoologia 30: 55-65.
https://doi.org/10.1590/S1984-46702013000100007

Domingues E.C., Schettini C.A.F., Truccolo E.C., Oliveira Filho J.C. de. 2017. Hidrografia e correntes da Plataforma Continental de Pernambuco. Rev. Bras. de Recur. Hidr. 22: 1-17.
https://doi.org/10.1590/2318-0331.0217170027

Ewers-Saucedo C. 2019. Evaluating reasons for biased sex ratios in Crustacea. Invertebr. Reprod. Dev. 63: 222-230.
https://doi.org/10.1080/07924259.2019.1588792

Fonseca D., D'Incao F. 2003. Growth and reproductive parameters of *Kalliapseudes schubartii* in the estuarine region of the Lagoa dos Patos (southern Brazil). J. Mar. Biolog. Assoc. U.K. 83: 931-935.
https://doi.org/10.1017/S0025315403008087h

Fontoura N., Braun A., Milani P. 2009. Estimating size at first maturity (L50) from Gonadossomatic Index (GSI) data. Neotrop. Ichthyol. 7: 217-222.
https://doi.org/10.1590/S1679-62252009000200013

Gardiner L. 1975. The Systematics, Postmarsupial Development, and Ecology of the Deep-Sea Family Neotanaidae (Crustacea: Tanaidacea) (Vol. 170). Smithsonian Institution Press, City of Washington, 274 pp.
https://doi.org/10.5479/si.00810282.170

Guevara M., Lodeiros C., Donato M., et al. 2005. Nutritional quality of *Metamysidopsis insularis* Brattegard (Crustacea: Mysidacea). Aquac. Nutr. 11: 315-319.
https://doi.org/10.1111/j.1365-2095.2005.00361.x

Guţu M. 2016. Systematic Novelties of the Enigmatic Universe of the Leptocheliids: Crustacea: Tanaidacea. ePublishers, Bucharest, 205 pp.

Hacker S., Steneck R. 1990. Habitat Architecture and the Abundance and Body-Size-Dependent Habitat Selection of a Phytal Amphipod. Ecology. 71: 2269-2285.
https://doi.org/10.2307/1938638

Highsmith R. 1983. Sex Reversal and Fighting Behavior: Co-evolved Phenomena in a Tanaid Crustacean. Ecology. 64: 719-726.
https://doi.org/10.2307/1937194

Holanda T., Gonçalves R., Lino A., et al. 2020. Morphodynamic classification, variations and coastal processes of Paiva Beach, PE, Brazil. Rev. Bras. de Geomorfol. 21: 235-251.
https://doi.org/10.20502/rbg.v21i2.1796

Holdich D., Jones J. 1983. Tanaids (Synopses of the British Fauna) (Vol. 27). Cambridge University Press, Cambridge, 112 pp.

Horta P., Amancio E. Coimbra C., Oliveira E. 2001. Considerações sobre a distribuição e origem da flora de macroalgas marinhas brasileiras. Hoehnea. 28: 243-265.

Jarquín-González J., Carrera-Parra L. 2022. *Chondrochelia* Guţu, 2016 (Crustacea, Peracarida, Tanaidacea, Leptocheliidae) from North America: new species, redescription and distribution using morphological and molecular data. PeerJ. 10: 1-47.
https://doi.org/10.7717/peerj.12773

Johnson S., Attramadal Y. 1982. Reproductive Behaviour and Larval Development of *Tanais cavolinii* (Crustacea: Tanaidacea). Mar. Biol. 71: 11-16.
https://doi.org/10.1007/BF00396987

Kakui K., Fleming J., Mori M., et al. 2021. Comprehensive Transcriptome Sequencing of Tanaidacea with Proteomic Evidences for Their Silk. Genome Biol. Evol. 13: 1-11.
https://doi.org/10.1093/gbe/evab281

Keesing J., Gartner A., Westera M., et al. 2018. Impacts and Environmental Risks of Oil Spills on Marine Invertebrates, Algae and Seagrass: A Global Review from an Australian Perspective. In: Hawkins S., Evans A., et al. (eds), Oceanography and Marine Biology. CRC Press, pp. 2-61.
https://doi.org/10.1201/9780429454455-5

Krasnow L., Taghon, G. 1997. Rate of tube building and sediment particle size selection during tube construction by the tanaid crustacean, *Leptochelia dubia*. Estuaries. 20: 534-546.
https://doi.org/10.2307/1352612

Krøyer H. 1842. Nye Arter af Slaegten Tanais. Naturhistorisk Tidsskrift Ser. I. 4: 167-188.

Laborel J. 1970. Les peuplements de madréporaires des côtes tropicales du Brésil. Annales de l'Universit'e d'Abidjan (Ecologie), Abidjan, 265 pp.

Leite F., Turra A., Souza, E. 2003. Population biology and distribution of the tanaid *Kalliapseudes schubarti* Mañé-Garzon, 1949, in an intertidal flat in southeastern Brazil. Braz. J. Biol. 63: 469-479.
https://doi.org/10.1590/S1519-69842003000300013

Longo P., Mansur K., Leite F., Passos F. 2019. The highly diverse gastropod assemblages associated with *Sargassum* spp. (Phaeophyceae: Fucales) habitats. J. Mar. Biolog. Assoc. U.K. 99: 1295-1307.
https://doi.org/10.1017/S0025315419000304

Martínez-Laiz G., Ros M., Navarro-Barranco C., Guerra-García J. 2018. Habitat selection of intertidal caprellid amphipods in a changing scenario. Behav. Process. 153: 16-24.
https://doi.org/10.1016/j.beproc.2018.05.005

Masunari S. 1983. Postmarsupial development and population dynamics of *Leptochelia* Sa Vignyi (Kroyer, 1842) (Tanaidacea). Crustaceana. 44: 151-162.
https://doi.org/10.1163/156854083X00776

Mathews C., & Samuel, M. 1990. Using the growth performance index Φ' to choose species aquaculture: an example from Kuwait. Aquabyte 3: 2-4.

Mendoza J. 1982. Some Aspects of the Autecology of *Leptochelia dubia* (Krøyer, 1842) (Tanaidacea). Crustaceana. 43: 225-240.
https://doi.org/10.1163/156854082X00164

Mildenberger T., Taylor M., Wolff M. 2017. TropFishR: an R package for fisheries analysis with length-frequency data. Methods Ecol. Evol. 8: 1520-1527
https://doi.org/10.1111/2041-210X.12791

Modlin R., Harris P. 1989. Observations on the natural history and experiments on the reproductive strategy of *Hargeria rapax* (Tanaidacea). J. Crustac. Biol. 9: 678-586.
https://doi.org/10.1163/193724089X00593

Pandian T. 2016. Reproduction and Development in Crustacea. CRC Press, India, 316 pp.
https://doi.org/10.1201/b20080

Pauly D., Munro J. 1984. Once more on the comparison of growth in fish and invertebrates. Fishbyte. 2: 1-21.

Pennafirme S., Soares-Gomes A. 2009. Population biology and reproduction of *Kalliapseudes schubartii* Mañé-Garzón, 1949 (Peracarida, Tanaidacea) in a tropical coastal Lagoon, Itaipu, Southeastern Brazil. Crustaceana 82: 1509-1526.
https://doi.org/10.1163/001121609X12487811051589

Pennafirme S., Soares-Gomes A. 2017. Population dynamics and secondary production of a key benthic tanaidacean, *Monokalliapseudes schubarti* (Mañé-Garzón, 1949) (Tanaidacea, Kalliapseudidae), from a tropical coastal lagoon in southeastern Brazil. Crustaceana. 90: 1483-1499.
https://doi.org/10.1163/15685403-00003704

R Core Team. 2022. R: A language and environment for statistical computing.

Rumbold C., Obenat S., Spivak E. 2015. Comparison of life history traits of *Tanais dulongii* (Tanaidacea: Tanaididae) in natural and artificial marine environments of the south-western Atlantic. Helgol. Mar. Res. 69: 231-242.
https://doi.org/10.1007/s10152-015-0432-9

Schwamborn R., Mildenberger T., Taylor, M. 2019. Assessing sources of uncertainty in length-based estimates of body growth in populations of fishes and macroinvertebrates with bootstrapped ELEFAN. Ecol. Modell. 393: 37-51.
https://doi.org/10.1016/j.ecolmodel.2018.12.001

Soares M., Teixeira C., Bezerra L., et al. 2020. Oil spill in South Atlantic (Brazil): Environmental and governmental disaster. Marine Policy. 115: 1-8.
https://doi.org/10.1016/j.marpol.2020.103879

Sparre P., Venema S. 1998. Introduction to tropical fish stock assessment - Part I: Manual. FAO, Rome, 423 pp.

Stoner A. 1986. Cohabitation on Algal Habitat Islands by Two Hermaphroditic Tanaidacea (Crustacea: Peracarida). J. Crustac. Biol. 6: 719-728.
https://doi.org/10.1163/193724086X00523

Sudo H. 2003. Effect of temperature on growth, sexual maturity and reproduction of *Acanthomysis robusta* (Crustacea: Mysidacea) reared in the laboratory. Mar. Biol. 143: 1095-1107.
https://doi.org/10.1007/s00227-003-1160-2

Tano S., Eggertsen M., Wikström S., et al. 2016. Tropical seaweed beds are important habitats for mobile invertebrate epifauna. Estuar. Coast. Shelf Sci. 183: 1-12.
https://doi.org/10.1016/j.ecss.2016.10.010

Taylor C. 1958. Cod Growth and Temperature. ICES J. Mar. Sci. 23: 366-370.
https://doi.org/10.1093/icesjms/23.3.366

Toniollo V., Masunari S. 2007. Postmarsupial development of *Sinelobus stanfordi* (Richardson, 1901) (Tanaidacea: Tanaidae). Nauplius. 15: 15-41.

Torrejon-Magallanes J. 2020. sizeMat: Estimate Size at Sexual Maturity (R package version 1.1.2).

Tuya F., Pérez J., Medina L., Luque A. 2001. Seasonal variations of the macrofauna from three seagrass meadows of *Cymodocea nodosa* off Gran Canaria (Central-eastern Atlantic Ocean). Cienc. Mar. 27: 223-234.
https://doi.org/10.7773/cm.v27i2.462

Zamora-Sarabia F., Arreguín-Sánchez F., de Anda-Montañez, J.A., Jacob-Cervantes M. 2022. Effect of sea surface temperature on the growth performance of the thread herring *Opisthonema libertate* (Günther, 1868) in the southern Gulf of California. Lat. Am. J. Aquat. Res. 50: 31-38.
https://doi.org/10.3856/vol50-issue1-fulltext-2746