

Maturation time and clinging behaviour of the invasive amphipod *Caprella scaura* Templeton, 1836 under laboratory conditions

Tiempo de maduración y comportamiento de sujeción al sustrato del anfípodo invasor *Caprella scaura* Templeton, 1836 en condiciones de laboratorio

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Palabras clave: Caprélidos, *Caprella scaura*, ciclo de vida, crecimiento, reproducción, comportamiento de sujeción al sustrato.

ABSTRACT

Since *C. scaura* was detected for the first time in the Mediterranean Sea, it has been reported in several Mediterranean countries and on the East Atlantic coast. Although the abundance patterns, seasonal fluctuations, small scale distribution, and mass culture of *C. scaura* have been studied in localities where this species is invasive, there is currently no information available describing its life history or attachment behaviour. Thirty six *C. scaura* juveniles were monitored until they reached maturation. No sexual traits appeared until instar IV and the maturation time was shown to be 24.7 ± 1.5 days (mean \pm standard deviation). At this time, the length of males was 4.5 ± 0.5 mm and of females was 4.1 ± 0.3 mm. The values measured for *C. scaura* were of the same order as the values estimated for other native and/or cryptogenic species inhabiting the same area (Strait of Gibraltar): *C. dilatata* (26.3 days), *C. equilibra* (29.0 days) and *Phtisica marina* (24.5 days). The invasion potential of *C. scaura* seems therefore not to be directly explained by a shorter maturation time, whereas other factors such as the presence of parental care and/or different response to environmental conditions could be involved. The clinging behaviour

(moving, upright, bending, parallel), scraping and grooming were also noted for *C. scaura*. Upright was the dominant posture for both sexes in both natural (bryozoan *Bugula neritina*) and artificial (meshes) substrata. The percentage of time spent in the *parallel* position was significantly higher for males than females both in natural (males: 25.7%, females: 2.8%) and artificial substrata (males: 31.3%, females: 3.6%), probably due to the presence of the brood pouch in females. The grooming frequency was higher in natural substrata than in artificial ones. Therefore, it seems that the substratum can influence caprellid behaviour but the ultimate consequences of substratum availability on the behaviour, population dynamics and/or life history in natural conditions should be further investigated.

RESUMEN

Desde que se detectó la presencia de *C. scaura* en el Mediterráneo, la especie se ha citado en varios países mediterráneos y en la costa este del Atlántico. Aunque los patrones de abundancia, las fluctuaciones estacionales, la distribución a pequeña escala y el cultivo de esta especie ya se han estudiado, no existe información sobre su ciclo de vida y comportamiento de sujeción al sustrato. Se mantuvieron en condiciones de laboratorio 36 juveniles de dos hembras de *C. scaura* hasta que alcanzaron la madurez. Las primeras diferencias entre sexos no se encontraron hasta la instar IV y el tiempo de maduración fue de $24,7 \pm 1,5$ días (media \pm desviación típica). En este momento, la longitud de los machos fue de $4,5 \pm 0,5$ mm, y la de las hembras $4,1 \pm 0,3$ mm. Los valores obtenidos para *C. scaura* fueron del mismo orden que los valores estimados para otras especies nativas y/o criptogénicas de la misma zona (Estrecho de Gibraltar): *C. dilatata* (26,3 días), *C. equilibra* (29,0 días) y *Phthisica marina* (24,5 días). Por tanto, el potencial invasor de *C. scaura* parece no relacionarse directamente con un tiempo de maduración más corto, y probablemente influyan otros factores tales como la presencia de cuidado parental y/o diferente respuesta a las condiciones ambientales. Se caracterizó también el comportamiento de sujeción al sustrato, categorizado en las pautas “moviéndose”, “erguido”, “encorvado” y “paralelo”, así como el “raspado” del sustrato, o el “filtrado”. La postura erguida fue la dominante en ambos sexos tanto en el sustrato natural (briozoo *Bugula neritina*) como en el artificial (mallas). El porcentaje de tiempo en posición paralela fue significativamente más alto en machos que en hembras tanto en sustrato natural (machos: 25.7%, hembras: 2.8%) como en sustrato artificial (machos: 31.3%, hembras: 3.6%), probablemente debido a la presencia del marsupio en las hembras. La frecuencia del “filtrado” fue superior en sustrato natural que en el artificial. Por tanto, parece que el sustrato puede influir en el comportamiento de los caprellidos, pero las últimas consecuencias que la disponibilidad de un sustrato u otro puede tener sobre el comportamiento, dinámica población y/o ciclo de vida en condiciones naturales, son aún desconocidas y deben investigarse en detalle.

INTRODUCTION

Caprellids are small crustaceans belonging to the order Amphipoda which live on algae, hydrozoans, bryozoans, sponges, seagrasses, sediment and other marine invertebrates (Guerra-García, 2001). They feed mainly on detritus and secondarily on microalgae, dinoflagellates, hydroids, sponges, polychaetes and crustaceans (Guerra-García & Tierno de Figueroa, 2009; Guerra-García *et al.*, 2014). Caprellids constitute an important link between primary producers and higher trophic levels in marine ecosystems (Woods, 2009), being considered as useful marine bioindicators (Guerra-García & García-Gómez, 2001; Takeuchi *et al.*, 2001; Ohji *et al.*, 2002; Guerra-García *et al.*, 2009) and as a potential resource in aquaculture (Woods, 2009; Baeza-Rojano *et al.*, 2010).

Caprellids represent an interesting group with regards to studying human-mediated dispersal since they have a limited dispersal capability resultant of an absence of a larval stage (see Ros *et al.*, 2015 and references therein). Caprellids are very successful colonisers of artificial hard substrata and can reach high densities in harbours and marinas, including biofouling on ship hulls (Frey *et al.*, 2009; Ashton *et al.*, 2010; Guerra-García *et al.*, 2015). Indeed, the role of marinas and recreational boating in the occurrence and distribution of exotic caprellids has recently been highlighted (Ashton *et al.*, 2010; Ros *et al.*, 2013, 2015).

Alongside *Caprella mutica* Schurin, 1935, *Caprella scaura* Templeton, 1836 is among the invasive caprellid species with the highest dispersal potential (Ashton *et al.*, 2008; Ros *et al.*, 2014a). Since *C. scaura* was detected for the first time in the Mediterranean Sea (Sconfiatti & Danesi, 1996) it has been reported in several Mediterranean countries (Ros *et al.*, 2014a and references therein; Fernández-González & Sánchez-Jerez, 2014) and also on the east Atlantic coast (Guerra-García *et al.*, 2011; Minchin *et al.*, 2012; Ramalhosa & Canning-Clode, 2015; Gillon *et al.*, 2016). The recent expansion of this widespread species suggests that it is in a phase of active colonisation and should be followed with the utmost attention (Galil *et al.*, 2014). As pointed out by Minchin *et al.* (2012), *C. scaura* has proved to (1) be able to reach high densities (i.e. 12925 ind/m²) (Martínez & Adarraga, 2008), (2) outcompete native congeners (Ros *et al.*, 2015), (3) extend its geographical distribution (Ros *et al.*, 2014a) and (4) exhibit aggressive behaviour among individuals, especially males in the presence of receptive females (Lim & Alexander, 1986; Schulz & Alexander, 2001). It is mainly a detritivorous species (Guerra-García & Tierno de Figueroa, 2009) which also displays parental care (Lim & Alexander, 1986; Aoki, 1999).

Caprella scaura has been characterised by a complicated taxonomic history. Since the species was originally described by Templeton (1836) from

Mauritius, it has been reported as several forms or varieties from numerous areas of the world. Recent morphological and molecular studies (Ros *et al.*, 2014a; Cabezas *et al.*, 2014) have suggested that (1) *Caprella scaura typica* from Brazil and *C. scaura scaura* from Mauritius correspond to the same “variety”, (2) this “variety” is the only one expanding its distribution range and (3) the other “varieties” of the *C. scaura* complex could represent distinct species each with a restricted distribution. The “variety” studied in the present work correspond with *C. scaura scaura/typical*.

In future ecological studies conducted in different geographical areas it is therefore important to properly describe the variety/form/subspecies to which the *C. scaura* specimens belong. This is essential in order to understand the invasion profile and to assess adequate control strategies of the variety which is spreading. Recent studies (see for example Ojaveer *et al.*, 2014, 2015) have reviewed the European directives concerning invasions in Europe and have provided recommendations for the handling and management of invasive species in the marine environment. All strategies have reached the agreement that the involvement of expert taxonomists and utilisation of a combination of morphological and molecular tools are critical in the detection and proper identification of invasive species, especially small invertebrates. An adequate identification of these species is the starting point for improved management by governments and authorities in response to the demands of European strategies.

Although the abundance patterns, seasonal fluctuations, small scale distribution and mass culture of *C. scaura* have been studied in localities along the Mediterranean and East Atlantic coasts where this species is invasive (Martínez & Adarraga, 2008; Guerra-García *et al.*, 2011, 2016; Minchin *et al.*, 2012; Baeza-Rojano *et al.*, 2013; Prato *et al.*, 2013; Ros *et al.*, 2013, 2015), there is limited information available regarding its life history and attachment behaviour. The main objective of this paper is therefore to provide preliminary data of maturation time and clinging behaviour for the invasive *C. scaura scaura/typica* in the invaded area.

MATERIAL AND METHODS

Sampling and laboratory procedure

Caprella scaura specimens were collected from colonies of *Bugula neritina* in June 2015 from La Línea Marina-Club Marítimo Linense, Cádiz (36°09'36"N, 5°21'34"W). In previous studies conducted in 2011, La Línea Marina was dominated by *C. equilibra* and *C. scaura* was absent (Guerra-García *et al.*, 2015). In the last 4 years, *C. scaura* has invaded this marina, reached high densities and has competitively displaced *C. equilibra*. Colonies

of bryozoans attached to floating pontoons, buoys and ropes of the marinas were handpicked. Preliminary sorting was conducted *in situ* to ensure an adequate quantity of specimens for laboratory use. Individuals were transported to the laboratory in plastic containers. Aeration was provided using battery powered air pumps and small bryozoan colonies were provided for attachment (see Baeza-Rojano *et al.*, 2013). The containers were stored in an insulating box to minimise temperature fluctuations.

To study the maturation time, two ovigerous females (females I and II) were selected and isolated in individual glass containers of 120 ml with a diameter of 6.5 cm and a height of 6 cm (see Baeza-Rojano *et al.*, 2011). A 1 mm plastic mesh was used as a substratum for attachment and was replaced weekly. Twenty five juveniles from female I and eleven juveniles from female II were monitored until they reached maturation. The juveniles were kept with their mother during the first two instars. After this hatchlings were introduced into new glass containers in groups of a maximum of three individuals. At the time of maturation, males and females could be clearly differentiated and both sexes were reproductively active. The caprellids were maintained at 20°C with a photoperiod of 12 h light: 12 h dark. The seawater used for culture had a salinity of 35.5 psu and was treated by filtration (through a 0.45 µm Millipore filter) and UV irradiation. The seawater in each container was changed daily (Baeza-Rojano *et al.*, 2011). Specimens were fed daily *ad libitum* with a diet consisting of *Artemia* nauplii, phytoplankton and detritus. *Artemia* nauplii were hatched from cysts maintained (1-2 days) in a Brine Shrimp Hatchery Hobby® with seawater at 25°C. The nauplii used for the experiments were not enriched. The phytoplankton consisted of a mixture of freeze-dried microalgae (Easy Reefs®) containing *Phaeodactylum*, *Tetraselmis* and *Nannochloropsis* (1:1:1, percentage in dry weight). The detritus consisted primarily of fish faeces and also of uneaten feed pellets and was obtained by scraping the bottoms of aquaculture tanks used for the culture of *Argyrosomus regius* at the IFAPA center “El Toruño” experimental aquaculture station (Cádiz, Spain). All the caprellid specimens were observed daily under a binocular microscope. Juveniles that were released from the brood pouch were classified as instar I and subsequent instars were identified by each successive molt, in accordance to the system adopted by Takeuchi & Hirano (1991). At each instar stage the body length was measured (using the mesh of 1 mm as a reference) whilst the caprellid pereonites remained straightened over the mesh.

To study the clinging behaviour of *C. scaura* the methodology of Takeuchi & Hirano (1995) and Guerra-García *et al.* (2002) was adopted, with some variations. To avoid alterations in behaviour resultant of the transfer of caprellids between containers or examinations under a stereomicroscope (see e.g. Takeuchi & Hirano, 1995; Guerra-García *et al.*, 2002), aquaria of

dimensions 20 cm x 13 cm x 13 cm each containing 3 L seawater were used and the clinging behaviour was examined using a handheld magnifying glass. The caprellids were maintained at 20°C with a photoperiod of 12 h light: 12 h dark and a salinity of 35.5 psu. Feeding was conducted daily with a mixed diet consisting of *Artemia* nauplii, phytoplankton and detritus (described above). To explore whether variations in clinging behaviour occurred between substrata, the natural substratum (*Bugula neritina*) and an artificial substratum (30 cm x 50 cm folded and compacted plastic mesh with 6 mm diameter pores; see mesh number 2 in Baeza Rojano *et al.*, 2013) were used. Substrata were held down with 2 small pebbles. Four aquaria were used to maintain the 40 adult specimens (20 males and 20 females) during the observations: Aquarium 1 (10 males, natural substratum), Aquarium 2 (10 females, natural substratum), Aquarium 3 (10 males, artificial substratum), Aquarium 4 (10 females, artificial substratum). Observations of each specimen were taken for 10 minutes and the clinging behaviour was noted. The clinging behaviour was categorised in 4 postures: moving (crawling over the substratum with an inchworm-like movement), upright (grasping the substratum with pereopods 5-7, or 6-7 with the anterior pereonites held away from the substratum and gnathopod 2 usually extended laterally), bending (grasping the substratum with gnathopod 1 and pereopods 5-7, with the body pereonites bent in the shape of an inverted U or V) and parallel (grasping the substratum with gnathopod 1 and pereopods 5-7 with the body pereonites straight and parallel to the substratum) (Takeuchi & Hirano, 1995; Guerra-García *et al.*, 2002). In addition to the attachment behaviour, the duration of scraping as described by Caine (1974, 1977) and the frequency of grooming (measured as the number of times that the antennae were folded and brought towards the mouthparts) were also recorded. The latter behaviour is thought to be associated with filtering suspended materials (Takeuchi & Hirano, 1995).

Statistical analyses

To explore whether the percentage of time spent in each posture was different in males and females and if it varied according to the substratum, a two-way ANOVA was conducted with the following factors: 'Substratum' a fixed factor with two levels: Natural substratum (*Bugula neritina*) vs Artificial substratum (mesh), and 'Sex' a fixed factor orthogonal with 'Substratum' consisting of two levels: males vs females.

Prior to ANOVAs, the homogeneity of variances was tested with Cochran's C-test. Data were transformed with square root in cases where variances were not homogeneous. Where variances remained heterogeneous, even with data

transformation, untransformed data were analysed, as ANOVA is a robust statistical test and is relatively unaffected by the heterogeneity of variances, particularly in balanced experiments (Underwood, 1997). In such cases, to reduce type I error, the level of significance was reduced to <0.01 (this was indicated in the Tables as $p<0.01$ in the Cochran's test section). Analyses were conducted with GMAV5 (Underwood *et al.*, 2002) and multivariate analyses were carried out using the PRIMER v.6 plus PERMANOVA package (Clarke & Gorley, 2001).

RESULTS AND DISCUSSION

Maturation time

Of the 36 juveniles monitored (25 from female I and 11 from female II), only 13 (6 males and 7 females) reached maturation. No sexual traits appeared until instar IV. The maturation time was 24.7 ± 1.5 days (mean \pm standard deviation) (Fig. 1, Table 1). At this time, the length of male specimens was 4.5 ± 0.5 mm and the length of female specimens was 4.1 ± 0.3 mm. After 30 days, the length of males was 5.3 ± 1.1 mm and the length of females was 4.4 ± 0.3 mm (Fig. 1).

Previous literature has shown the maturation time at 20°C of other caprellids to range from 19.5 days (*C. generosa*) to 35.0 days (*C. cristibrachium*) (Table 1). The value measured for *C. scaura scaura/typica* is of the same order as the values estimated for other native and/or cryptogenic species inhabiting the same area (Strait of Gibraltar): *C. dilatata* (26.3 days), *C. equilibra* (29.0 days) and *Phtisica marina* (24.5 days). These are three typical fouling species. Other caprellids more adapted to live in natural habitats (such as *C. grandimana*, see Table 1) has also been studied, showing a maturation time of 38.4 days cultivated at 17°C (relatively close to 20°C). Therefore, the invasion potential of *C. scaura* seems not to be directly explained by a shorter maturation time and therefore other factors such as parental care and/or different responses to environmental conditions (e.g. Lim & Alexander, 1986; Aoki, 1999; Ros *et al.*, 2015) could possibly be involved. On the other hand, the values obtained during the present study for *C. scaura scaura/typica* (24.7 days) are lower than those obtained for *C. scaura diceros* (32.0 days, Sakaguchi, 1989), which has a restricted distribution around Japanese waters (Ros *et al.*, 2014a). It must however be taken into account that the values for maturation time were obtained from experimental evidence under laboratory conditions, thus could vary to those of specimens in the field. It is interesting to note that the smaller body size found for *C. scaura scaura/typica* ovigerous females in the field (at Mallorca

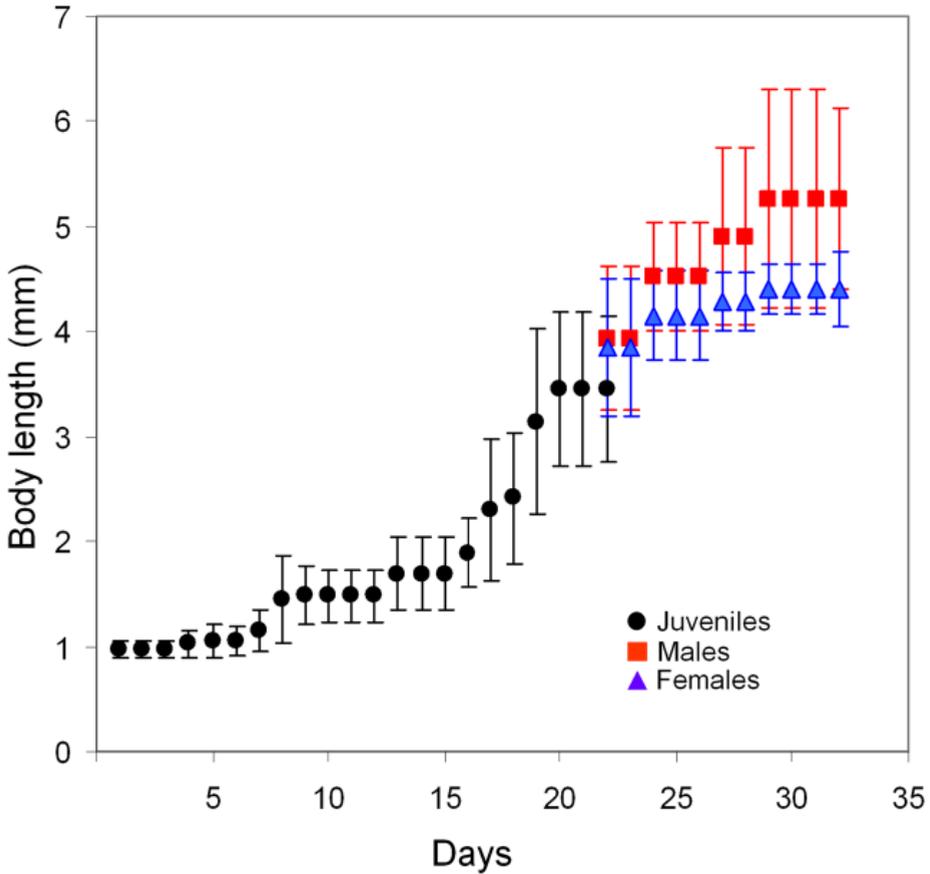


Fig. 1.—Body growth pattern of *Caprella scaura*. Data represent the mean and standard deviation.
 Fig. 1.—Patrón de crecimiento de *Caprella scaura*. Los datos representan los valores medios y la desviación típica.

island) is about 4.2-4.3 mm (see Fig. 4 in Ros *et al.*, 2013), very similar to that found during the present study. The temperature at the moment of collection was also very similar in both studies. Regardless of the species, Table 1 clearly shows an inverse relationship between temperature and maturation rates. This inverse relationship in caprellids indicates that the maturation rate decreases considerably with decreasing temperatures (Hosono, 2014).

The short maturation time required for *C. scaura* probably justifies its potential for large scale culture for aquaculture purposes. In fact, Baeza-Rojano *et al.* (2013) have maintained a mass culture of *C. scaura* using nauplii of *Artemia* and microalgae as a feed source, obtaining abundances 50 times higher after 3 months. These authors demonstrated that the caprellid

Table 1.—Average maturation time of female caprellids reported in literature. Modified from Hosono (2014).

Tabla 1.—Tiempo medio requerido para alcanzar la madurez de hembras de caprélidos. Datos tomados de la literatura. Modificado de Hosono (2014).

<i>Species</i>	<i>Temperature</i> (°C)	<i>Maturation</i> (Days)	<i>References</i>
<i>Caprella acanthogaster</i> Mayer, 1890	5	120.5	Hosono (2014)
<i>C. brevirostris</i> Mayer, 1903	20	27.5	Takeuchi & Hirano (1991)
<i>C. cristibrachium</i> Mayer, 1903	20	35.0	Hosono (2006)
<i>C. danilevskii</i> Czerniavski, 1868	20	20.0	Takeuchi & Hirano (1991)
<i>C. dilatata</i> Kroyer, 1843	20	26.3	Baeza-Rojano & Guerra-García (2013)
<i>C. equilibra</i> Say, 1818	20	29.0	Baeza-Rojano & Guerra-García (2013)
<i>C. generosa</i> Arimoto, 1977	20	19.5	Takeuchi & Hirano (1991)
<i>C. grandimana</i> Mayer, 1882	17	38.4	Baeza-Rojano <i>et al.</i> (2011)
<i>C. laeviuscula</i> Mayer, 1903	12	44.2	Gardella (1962)
<i>C. mutica</i> Schurin, 1935	5	140.7	Instar X estimated based on the growth curve in Hosono (2011)
<i>C. mutica</i>	10	54.0	Instar VII in Boos (2009)
<i>C. mutica</i>	10	56.9	Instar X in Hosono (2011)
<i>C. mutica</i>	14	24-26	Cook <i>et al.</i> (2007)
<i>C. mutica</i>	15	41.3	Instar X in Hosono (2011)
<i>C. mutica</i>	16	38.1	Instar VII in Boos (2009)
<i>C. mutica</i>	20	31.6	Instar X in Hosono (2011)
<i>C. okadai</i> Arimoto, 1930	20	20.6	Takeuchi & Hirano (1992)
<i>C. scaura</i> Templeton, 1836 [diceros]	20	32.0	Sakaguchi (1989)
<i>C. scaura</i> [scaura/typica]	20	24.7	Present study
<i>Phtisica marina</i> Slabber, 1769	20	24.5	Baeza-Rojano & Guerra-García (2013)

C. scaura may be readily cultured at high densities with a variety of mesh morphologies allowing for a more efficient use of tank volume and improved handling. Nevertheless further studies are required to quantify the incubation time, number of eggs and juveniles in order to properly characterise the whole life history of this species.

Clinging behaviour, scraping and grooming

The data obtained for clinging behaviour, scraping and grooming for males and females in both natural and artificial substrata are included in Table 2. In

Table 2.—Average time and range spent in each clinging type of behaviour and scraping, and frequency of grooming for *Caprella scaura*. Data are mean values of 10 specimens.

Tabla 2.—Tiempo medio y rango dedicado a cada comportamiento de sujeción al sustrato y raspado, así como la frecuencia del “filtrado” de *Caprella scaura*. Los datos representan el valor medio de 10 ejemplares.

	<i>Clinging behaviour</i>				<i>Scraping</i>		<i>Grooming</i>
	<i>Moving</i>	<i>Upright</i>	<i>Bending</i>	<i>Parallel</i>	<i>Bending</i>	<i>Parallel</i>	
	(%)	(%)	(%)	(%)	(%)	(%)	(times)
<i>Bugula neritina</i>							
Males	3.0	68.2	3.1	25.7	1.7	9.2	9.7
	(0-6.9)	(26.4-97.3)	(0-9.1)	(0-63.7)	(0-5.7)	(0-46.5)	(6.0-14.0)
Females	3.9	92.9	0.4	2.8	0.3	0	11.0
	(0.1-9.6)	(81.7-99.2)	(0-1.8)	(0-13.6)	(0-1.0)		(6.0-16.0)
<i>Artificial substrate</i>							
Males	7.3	60.0	1.4	31.3	1.2	3.4	6.7
	(0-22.9)	(10.2-100)	(0-7.6)	(0-87.3)	(0-7.7)	(0-13.8)	(3.0-10.0)
Females	3.0	74.4	18.9	3.6	1.4	0	9.1
	(0-10.8)	(2.6-98.7)	(0-96.5)	(0-33.1)	(0-5.8)		(3.0-12.0)

general, specimens mainly attached to the substratum in an *upright* posture. No significant differences were observed between sexes or substrata for time spent *bending* or *moving*, or for scraping behaviour (Table 3). It is worth noting however, that females in an artificial substratum spent a higher percentage of time bending (18.9%) in comparison to females in a natural substratum (0.4%) or males (3.1% in natural substratum and 1.4% in artificial substratum). The percentage of time spent in the *parallel* position was significantly higher for males than for females both in natural (males: 25.7%, females: 2.8%) and artificial substrata (males: 31.3%, females: 3.6%). Oppositely, females spent more time in the *upright* position than males. Despite both sexes being observed in the upright position for a longer duration in *B. neritina* than in the artificial mesh, these differences were not significant (Table 3).

Although females showed a higher frequency of grooming than males, differences were not significant between sexes ($p=0.0587$, see Table 3) however natural substrata resulted in significantly more times grooming (Males: 9.7 times, Females: 11.0 times) than artificial ones (Males: 6.7 times, Females: 9.1 times) ($p=0.0139$, see Table 3).

Previous studies on the clinging behaviour of caprellids (Takeuchi & Hirano, 1995; Guerra-García *et al.* 2002) have concluded that a combination of the upright posture accompanied by frequent grooming indicated filtering to be the primary mechanism of feeding. Likewise, these authors suggested a parallel posture to represent scraping. The use of gnathopod 1 in a parallel stance is also a physiological adaptation to tolerate increased wave energy (Takeuchi & Hirano, 1995). Caine (1978) suggested that caprellids usually occur only in habitats where their morphology maximises feeding effectiveness, finding differences in the feeding mechanisms of caprellids inhabiting different substratum. It has been shown that ontogenetic shifts in diet enable polychaetes to overcome their physiological limitations, particularly in juveniles which have been observed seeking better quality prey items in order to overcome feeding rate limitations (Hentschel, 1998). Ontogenetic dietary shifts in *C. scaura* were also observed by Ros *et al.* (2014b) between juveniles on substrata of *B. neritina* and *Zoobotryon verticillatum*. This gives rise to the possibility that *C. scaura* are better adapted to optimising their feeding techniques than *C. equilibra*, a congener which is being competitively displaced by *C. scaura* (see Ros *et al.*, 2015). The clinging behaviour of *C. equilibra* has previously been well documented. Guerra-García *et al.* (2002) demonstrated that this species spent the majority of the time (90%) in the upright position and exhibited a high number of times grooming (Page *et al.*, 2006), suggesting that *C. equilibra* is primarily a filter feeder, aided by dense setae to improve particle capture on the ventral surface of antenna 2 (Guerra-García *et al.*, 2002). Alan (1970) also concluded that filtering was the primary feeding mechanism of *C. equilibra*, although also observed a shift towards active predation from the species using gnathopods and antennae where crustacean prey was present, indicating a preference of this diet when it is available. Scraping in a bending or parallel posture has also been previously observed in *Caprella equilibra*, albeit for very short durations (Alan, 1970; Keith, 1969). In the present study, it can be observed that *C. scaura* also spends the majority of time in the upright posture (60.0%-92.9%), however exhibits a grooming frequency of between 6.7 and 11 times, far lower than the 21 times observed for *C. equilibra* by Guerra-García *et al.* (2002). Furthermore, *C. scaura* was observed scraping in the parallel and bending positions for longer periods than has been described for *C. equilibra* in previous literature (Guerra-García *et al.*, 2002), suggesting that it is more adapted to the scraping feeding mechanism. The longer time observed in the parallel position for *C. scaura* could also suggest that it is more resistant to the mechanical impacts of wave energy than *C. equilibra*.

Females of *C. scaura* spent more time than males in the upright posture. This could probably be related to the presence of the brood pouch making the parallel position difficult for females, since eggs need aeration continuously.

Variations in clinging behaviour for *C. scaura* between substrata were also observed, where artificial substrata resulted in less time upright and less times grooming. The frequency of grooming is thought to be associated with filtering suspended materials (Caine, 1974; Takeuchi & Hirano, 1995) so it is expected that the higher proportion of upright measured in the natural substratum involves a higher frequency of grooming. Probably, in *B. neritina*, caprellids can find better refuge than in the mesh, remaining more cryptic among the bryozoan branches thus reducing the risk of predation whilst grooming in the upright position. In fact, Ros *et al.* (2013) found abundance differences between *C. scaura* populations inhabiting *B. neritina* and another bryozoan, *Tricellaria inopinata*. *T. inopinata* presents more defensive structures than *B. neritina* such as frontal spines or lateral avicularia, which may hinder the movement of caprellids within the colony. Moreover, *T. inopinata* is more compact than *B. neritina*, therefore caprellids may have more difficulty penetrating the inner parts of the colony. This could explain why for the samples of *T. inopinata*, caprellids were commonly found on the surface of the colony more exposed to predators, whereas for *B. neritina* caprellids were found throughout. In the present study *C. scaura* were observed clinging along the whole branches of *B. neritina*, while in the mesh the specimens were located on the surface thus may have reduced the time spent upright in order to reduce exposure to predators. It seems therefore that the substratum can influence caprellid behaviour, although the ultimate consequences of substratum availability on the behaviour, population dynamics and/or life history should be further investigated.

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