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**Peracáridos y Picnogónidos de las praderas de
fanerógamas de la ensenada de O Grove: ecología
y faunística**

**Peracarids and Pycnogonids of the seagrass meadows
in O Grove inlet: Ecology and faunistics.**

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Certifican:

Que la presente Memoria de Doctorado Internacional titulada **PERACÁRIDOS Y PICNOGÓNIDOS DE LAS PRADERAS DE FANERÓGAMAS DE LA ENSENADA DE O GROVE: ECOLOGÍA Y FAUNÍSTICA**, que **Dña. Patricia Esquete Garrote** presenta para optar al grado de Doctor con Mención Internacional por la Universidad de Vigo, ha sido realizada bajo nuestra dirección en el departamento de Ecología y Biología Animal de la Universidad de Vigo.

Y considerando que cumple con los requisitos necesarios para ser considerada como un trabajo de Tesis Doctoral con Mención Internacional, autorizamos su presentación ante la Comisión Académica del Programa de Doctorado en Oceanografía y la Comisión de Estudios de Posgrado de la UVIGO.

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A mis padres

“Todas las generalizaciones son peligrosas, incluso ésta”

Alejandro Dumas

“La unidad es la variedad, y la variedad en la unidad es la ley suprema del universo”

Sir Isaac Newton

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Abstract

The Galician rias are singular and complex estuarine systems of great economic importance. Nevertheless, the ecological role of seagrass meadows in Galician rias has been only partially assessed. Because of the importance of Peracarid faunas in benthic assemblages and the lack of studies on Pycnogonids synecology, in this work, species diversity, patterns of distribution and temporal fluctuations of peracarids and pycnogonids are studied in sediments colonized by two species of seagrass (*Zostera marina* and *Z. noltii*) in O Grove (Ria de Arousa, NW Spain), an inlet with high level of anthropogenic influence.

Both taxocoenoses showed higher values of abundance and species diversity than other similar environments in the Northeast Atlantic. The spatial distribution of the peracarid assemblages was characterized by high numerical dominances due to a few species, particularly Tanaidaceans. The temporal study at a subtidal *Z. marina* meadow showed a strongly seasonal pattern defined by great fluctuations of the populations. Analyses pointed out a high correlation among the granulometric features of the sediment and the faunistic attributes. Abundance of peracarid taxa showed a strongly seasonal pattern. Temporal variations in the population dynamics of the pycnogonid *Achelia echinata* suggest a strong coupling with the life history of the seagrass.

A detailed observation of the specimens obtained during the study revealed the presence of a new species of Tanaidacean, *Apseudopsis adami* sp. nov. In addition, the amphipod *Perioculodes aequimanus* is reported for the first time in the Atlantic Ocean. The latter species is well established in the inlet and is one of the numerically dominant peracarid species.

The species of the genus *Apseudopsis* can be diagnosed, regardless the developmental stage of the specimen, by a combination of the following characters: the shape of the rostrum, the presence/absence of apophyses on pereonites and the spination of the first pereopod. Some differences have been found in the postmarsupial development and population structure of the two species present in the inlet; such differences can be attributed to habitat partitioning that would permit the coexistence of two congeneric species.

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I. Introducción y Métodos

1. INTRODUCCIÓN

1.1. LAS RÍAS DE GALICIA Y LAS FANERÓGAMAS MARINAS

Las rías son zonas costeras formadas a partir de valles fluviales inundados por el mar, en un proceso que culminó durante los periodos interglaciares del Cuaternario (Von Richthofen, 1886; Pannekoek, 1970; Méndez & Vilas, 2005). En las rías de Galicia, la parte más externa recibe fuerte influencia oceánica, mientras que las zonas más abrigadas pueden ser consideradas un verdadero estuario tanto desde el punto de vista hidrográfico como sedimentológico ya que reciben aportes fluviales y de escorrentía (Evans & Prego, 2003; Méndez Martínez *et al.*, 2011).

Las rías gallegas son singulares sistemas acuáticos costeros, complejos y productivos, en los que se desarrollan actividades de gran importancia económica tales como pesca, marisqueo, cultivo de moluscos, y también actividades turísticas y navegación recreativa (Figueiras *et al.*, 2002; Méndez & Vilas, 2005). Los fenómenos estacionales de afloramiento en la región son responsables de una elevada productividad primaria (Fraga, 1981; Figueiras *et al.* 2002; Méndez Martínez *et al.*, 2011) que favorece el asentamiento y crecimiento de especies, muchas de ellas de interés comercial. Estas rías albergan además gran variedad de hábitats, tanto de sustratos rocosos como sedimentarios, que han demostrado ser particularmente ricos en biodiversidad y abundancia de especies bentónicas (e. g. López-Jamar & Mejuto, 1985; Garmendia *et al.*, 1988; Moreira & Troncoso, 2007; Lourido *et al.*, 2008).

Las fanerógamas marinas, a diferencia de la mayoría de las algas, presentan tejidos especializados en el transporte y almacenamiento de sustancias, la fijación, la captación de agua y nutrientes, y la reproducción. La presencia de raíces y rizomas les permiten colonizar sustratos blandos como arenas y fangos, y captar nutrientes del sedimento y el agua intersticial (Hemminga & Duarte, 2000; Quintas, 2005). Tienen un aspecto herbáceo, pudiendo alcanzar los 120 cm de longitud, y viven sumergidas (aunque algunas son intermareales) en aguas poco profundas, dado que precisan un mínimo de intensidad lumínica relativamente alto (Abal *et al.*, 1994). El número de

especies de angiospermas marinas es relativamente reducido, existiendo unas 50 especies repartidas en 12 géneros (Hemminga & Duarte, 2000; Quintas, 2005). En las costas europeas, son comunes las siguientes (Short & Coles, 2001): *Ruppia marítima* L., *Ruppia cirrhosa* (Petagna) Grande, *Halophila stipulacea* (Forsskål) Ascherson, *Posidonia oceanica* (L.) Delile, *Cymodocea nodosa* (Ucria) Ascherson, *Zostera marina* L. y *Zostera noltii* Hornem., siendo estas tres últimas las especies presentes en el litoral atlántico de la Península Ibérica.

Las fanerógamas marinas son elementos clave en los ecosistemas costeros de todo el mundo (Hemminga & Duarte, 2000). La presencia de praderas en estuarios favorece el establecimiento y mantenimiento de altos valores de diversidad en las comunidades bentónicas (Fredette *et al.*, 1990; Montadouin & Sauriau, 2000; Whitlow & Grabowski, 2012). Esto es debido a que influyen en el medio y en los organismos bentónicos de diferentes modos: Por un lado, debido a su estructura tridimensional, aumentan la complejidad y heterogeneidad del hábitat creando mayor número de nichos que en zonas no vegetadas (Currás *et al.*, 1993; Attrill *et al.*, 2000). Por otro lado, desde un punto de vista geomorfológico, estabilizan el sustrato y reducen la velocidad de la corriente cerca del fondo, por lo que aumentan las tasas de sedimentación y reducen la erosión, facilitando el depósito de sedimento y materia orgánica, lo que a su vez afecta positivamente al establecimiento y supervivencia de muchas especies bentónicas (Orth *et al.*, 1984; Short & Neckless, 1999; Koch, 2001; Cochón y Sánchez, 2005; Böstrom *et al.*, 2006; Hasegawa *et al.*, 2008). Además, su alta productividad las convierten en una parte importante de la cadena trófica (Orth, 1976), ya que además son responsables de una parte importante de la producción primaria y el carbono fijado mediante fotosíntesis en el medio marino (Duarte, 1999). Las praderas de fanerógamas sirven como refugio y dan recursos alimenticios a juveniles de numerosas especies de moluscos, crustáceos y peces potencialmente comerciales (Orth, 1976; Short & Neckless 1999), y por lo tanto su presencia resulta vital para la conservación y restauración de los ambientes en los que viven (Jackson *et al.*, 2001; Heck *et al.*, 2003).

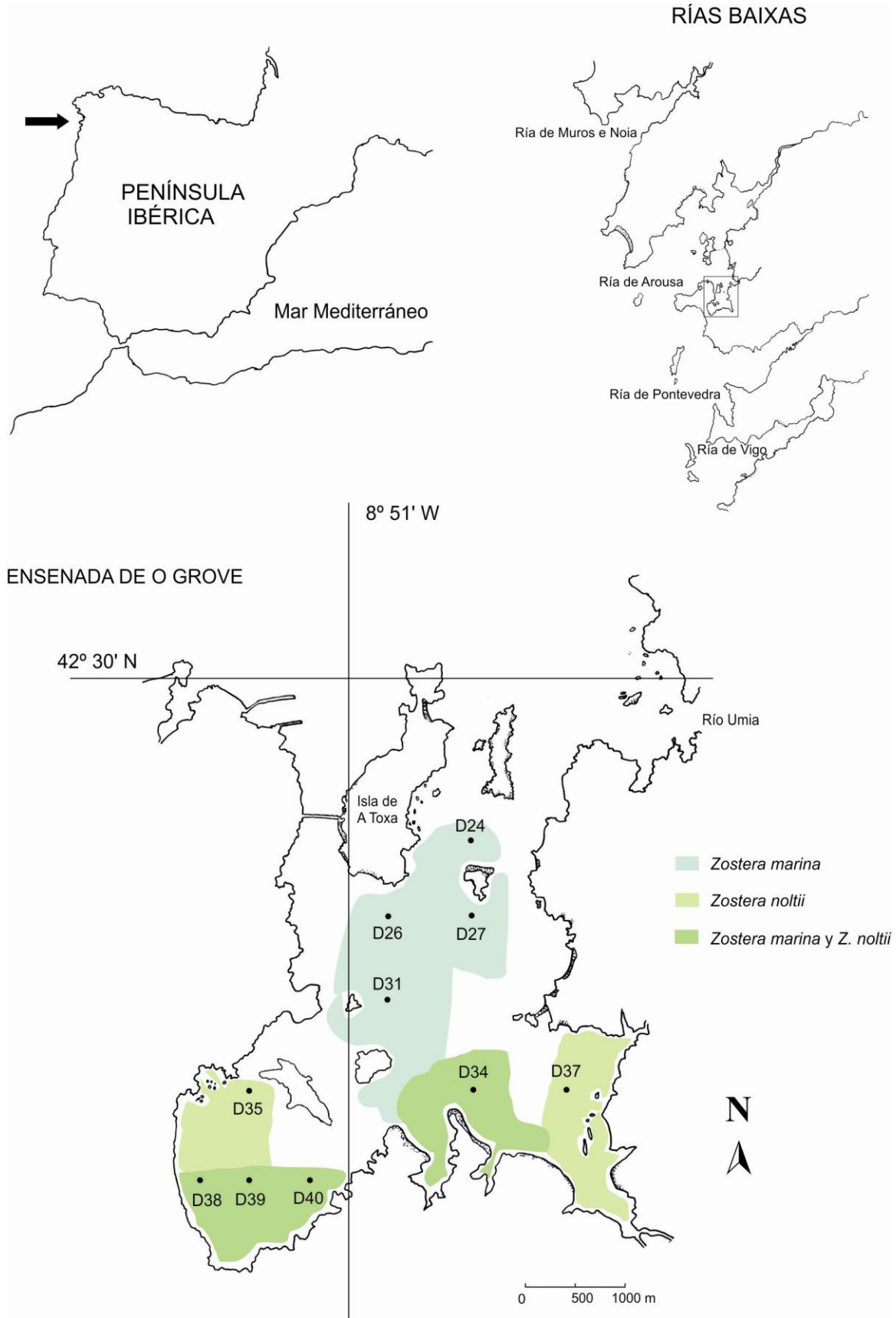


Figura 1. Localización de la Ensenada de O Grove y las estaciones de muestreo

La ensenada de O Grove

En las rías de Galicia, las zonas más internas, abrigadas y poco profundas a menudo están colonizadas por fanerógamas. Las praderas más extensas se encuentran en la ensenada de O Grove, en el extremo suroeste de la ría de Arousa entre 42°41'–42°28'N y 9°01'–8°44'W (Figura 1). Esta ensenada, a pesar de estar situada cerca de la boca de la ría, se halla protegida de la influencia oceánica por la península de O Grove. Se trata de un sistema estuárico, influenciado por aportes de agua dulce procedentes de la desembocadura de varios ríos estacionales que vierten en el margen este de la parte interna. La parte central de la ensenada la ocupa una pradera monoespecífica de *Zostera marina*, mientras que sus zonas más abrigadas albergan praderas de *Zostera noltii* y praderas mixtas de ambas especies. La distribución de los sedimentos en los fondos de zosteráceas fue estudiada en profundidad por Quintas (2005): sus estudios mostraron un predominio de fracciones sedimentarias finas, pudiéndose distinguir un fondo de arena fangosa en la pradera de *Z. marina* central, y fango y fangos arenosos en las praderas de *Zostera noltii* y mixtas (Figura 1).

La ensenada de O Grove cuenta con un gran interés tanto socioeconómico como ambiental. Por un lado, se trata de una zona muy poblada, con un alto grado de presión urbanística, y una importante actividad pesquera. En ella se desarrollan diversas actividades como son el marisqueo y el cultivo de mejillón en batea. Por otro lado, la gran cantidad de hábitats que presenta la ensenada, y muy especialmente la presencia extensiva de fanerógamas en la parte más interna favorecen la presencia de gran diversidad faunística, tanto de invertebrados bentónicos como de aves acuáticas.

Antecedentes

Por su importancia social y económica, las rías de Galicia han sido objeto de diversos estudios faunísticos en las últimas décadas; diversos autores han estudiado diversidad y distribución de la fauna bentónica dentro de las rías (e. g. Anadón, 1980; López-Jamar, 1978a, b, 1981, 1982; Mora, 1980, 1982; Abella *et al.* 1996; Currás,

1990; López-Jamar & Mejuto, 1985; Junoy, 1988, 1996; Sánchez-Mata & Mora 1999a, b; Lourido 2005, 2009, 2010; Rodil *et al.*, 2009;). También han sido estudiados los diversos hábitats que éstas albergan (e. g. Anadón, 1981; Besteiro 1986; Besteiro & Urgorri, 1987; Besteiro *et al.* 1990; Garmendia *et al.*, 1998; Moreira, 2003; Cacabelos, 2005; Cacabelos 2009, 2010) Asimismo, existe un número considerable de trabajos dedicados a la sinecología o distribución de grupos concretos (e. g., Margalef, 1958; Cadée, 1968; Urgorri, 1974; Anadón, 1975; Cristobo *et al.*, 1988; Troncoso, 1990; Troncoso & Urgorri 1991; Francesch & López-Jamar, 1991; Parapar, 1991; Reboreda, 1995; Olabarria *et al.*, 1997, 1998, 1999; Moreira *et al.*, 2005, 2006, 2008a, b, 2010; Lourido *et al.*, 2006, 2008a, b; Cacabelos, 2010; Aneiros, 2011). También son destacables los trabajos dedicados a la evaluación del impacto producido por los desastres ocasionados por el derrame de combustibles acaecidos en la zona en los últimos años (e. g. Sánchez-Mata, 1996; Garmendia, 1997; Parra & López-Jamar 1997; Gómez-Gesteira & Dauvin, 2005; Carro *et al.*, 2006).

Es gracias a todos estos estudios que conocemos la biodiversidad que albergan las rías gallegas, sus variaciones en el espacio y en el tiempo. Este conocimiento es de un valor incalculable para hacer valoraciones sobre los efectos de las variaciones ambientales y la actividad humana en el ecosistema y, en última instancia, las actividades socioeconómicas que se desarrollan en las rías.

No obstante, y pesar de que en las zonas más protegidas de las rías sus fondos están generalmente colonizados por fanerógamas, pocos estudios se han centrado en estos ecosistemas y el papel que juegan éstas en la ecología de las rías como centros de biodiversidad, refugio y fuente de alimento para especies potencialmente comerciales. A este respecto destacan los trabajos de Currás (1990), Currás & Mora (1990, 1992), Currás *et al.* (1993), y Penedo (1999). Otros autores, en estudios sobre comunidades bentónicas, han hecho mención a la fauna que albergan los fondos de fanerógamas de las zonas más internas de las rías (e. g. Junoy, 1988; Parapar, 1991; Olabarria, 1995; Moreira, 2003; Cacabelos, 2005, y Cacabelos *et al.*, 2008). Estas praderas también han sido tratadas desde un punto de vista fitológico en trabajos como los de Izco & Sánchez (1996, 2002). Cochón & Sánchez (2005), estudian el

descenso de las poblaciones de *Zostera* en la ría de Pontevedra. En un trabajo más amplio, Laborda *et al.* (1997) describen la distribución de *Zostera noltii* en el litoral norte de España.

La ensenada de O Grove se incluye en varios trabajos desarrollados en la ría de Arousa: Rodríguez *et al.* (1987) y Vilas (1999) abordaron la sedimentología y geología de toda la ría, y Rosón *et al.* (1995) la oceanografía. Cadée (1968), en un estudio malacológico, incluyó doce estaciones de muestreo en O Grove; Mora (1980, 1982) estudió la fauna bentónica de toda la ría, con cuatro estaciones en O Grove. Los estudios de Rolán (1992), Rolán *et al.* (1985), Quintas *et al.* (2005) y Bañón *et al.* (2008) pusieron de manifiesto la presencia de varias especies de moluscos típicamente mediterráneos en la ensenada de O Grove, probablemente como consecuencia de la importación de especies comerciales para el cultivo. El estudio faunístico más exhaustivo llevado a cabo en O Grove fue el de Quintas (2005), quien analizó las biocenosis de moluscos y poliquetos de O Grove. Sus estudios revelaron que las praderas de fanerógamas de la esta ensenada albergan una gran diversidad faunística, y que las comunidades de ambos grupos son estables en la ensenada.

1.2. LOS PERACÁRIDOS

Los peracáridos (Superorden Peracarida) son un grupo de crustáceos ampliamente diversificado, con más de 12000 especies conocidas, distribuidas en 9 órdenes, abarcando aproximadamente un tercio de todos los crustáceos (Spears *et al.*, 2005). Se caracterizan fundamentalmente por poseer un marsupio o cámara incubatriz formada en la mayoría de los casos por ramificaciones de las extremidades (Poore, 2005). Calman (1909) propuso una serie de sinapomorfías para definir al grupo, además de la presencia de marsupio: un caparazón que deja libres al menos cuatro segmentos torácicos, el primer segmento torácico fusionado con la cabeza y una mandíbula con una lámina articulada llamada *lacinia mobilis* (excepto en formas parásitas y algunas formas muy modificadas). Sin embargo, tales caracteres no son

aplicables en el caso de algunos órdenes, y la diagnosis para el Superorden Peracarida es en nuestros días objeto de intenso debate (Spears *et al.*, 2005).

Los peracáridos forman uno de los taxones más diversificados y numéricamente dominantes en las comunidades bentónicas (e. g. Cartes *et al.*, 2001; Dauby *et al.*, 2001; Moreira *et al.*, 2008), mostrando una gran variedad de modos de alimentación y ocupado todos los nichos posibles en el medio marino. Además, contribuyen significativamente a la producción del bentos (Mancinelli & Rossi, 2002) y suponen una fuente de alimento considerable para otras especies bentónicas y peces demersales, constituyendo un elemento importante para el sistema trófico (Dauvin, 1988; Takeuchi & Hino, 1997; Takahashi *et al.*, 1999; Cartes *et al.*, 2001; Lourido *et al.*, 2008). Además, las especies herbívoras de peracáridos son muy importantes en el control de los epífitos de las fanerógamas en las praderas submarinas (Jernakoff & Nielsen, 1997; Duffy & Harvilicz, 2001). Como ejemplo ilustrativo, se han comprobado incrementos de más del 400% en la biomasa del perifiton en praderas de *Zostera marina* tras retirar ciertas especies de caprélidos (Caine, 1980).

La macrofauna bentónica en general, y los peracáridos en particular se ven afectados por las condiciones ambientales, de manera que su distribución, abundancia y la variación espaciotemporal de las comunidades dependen en gran medida de dichas condiciones (Chintiroglou *et al.*, 2004; De-la-Ossa-Carretero, 2011; De-la-Ossa-Carretero *et al.*, 2011a). En el caso de los crustáceos peracáridos esto se debe a que muestran una amplia variedad de respuestas a los factores ambientales (Cunha *et al.*, 1999; Paganelli *et al.*, 2005), la cual se debe a su vez a la gran radiación adaptativa del grupo (Moreira *et al.*, 2008). Por ejemplo, muchas especies se alimentan de especies epífitas, o directamente del alga o fanerógama sobre la que viven, y tienden a situarse sobre hojas y frondes (e. g. anfípodos de las familias Ampithoidae y Caprellidae, así como la mayoría de los isópodos), dependiendo por tanto de la cobertura de las especies vegetales (Guerra-García *et al.*, 2001a; Duffy & Harvilicz, 2001; González *et al.*, 2008). Otros, como la mayoría de los cumáceos, tanaidáceos y algunas familias de anfípodos, son detritívoros y viven enterrados en el sedimento o construyen tubos o

madrigueras, y su presencia en un determinado hábitat depende sobre todo de la granulometría del sedimento (Jones, 1976; Oakden, 1984; Lourido *et al.*, 2008).

Por todo ello, diversos autores (Bellan-Santini, 1981; Conradi & López González, 2001; Chintiroglou *et al.*, 2004; Guerra-García & García-Gómez, 2004, 2005; Gómez Gesteira & Dauvin, 2000; De-la-Ossa-Carretero, 2011; De-la-Ossa-Carretero *et al.*, 2010a, b, 2011a, b, entre otros) señalan a las poblaciones de peracáridos como buenos bioindicadores del estado y la calidad de los ecosistemas marinos. Esto es gracias a una serie de particularidades que los hacen especialmente sensibles a cambios en el medio: la carencia de una etapa larvaria dispersiva, su escasa movilidad que les impide hacer grandes desplazamientos para escapar a dichos cambios, y unos ciclos de vida relativamente largos. Sin embargo, la sensibilidad de las poblaciones es mayor o menor dependiendo de la especie y/o el grupo trófico (King *et al.*, 2006; De-la-Ossa-Carretero *et al.*, 2011b); por ejemplo, las especies que construyen tubos o madrigueras se ven menos afectadas por contaminantes que las que se entierran (De-la-Ossa-Carretero, 2011). Así mismo, ciertas especies, como *Apocorophium acutum* (Chevreux, 1908), *Ampithoe helleri* Karaman, 1975 y *Ampithoe ramondi* Audouin, 1826, han sido propuestas como indicadores de un mal estado de conservación en praderas de fanerógamas (Zakhama-Sraieb *et al.*, 2006).

Como resultado de todo lo expuesto, la importancia del conocimiento de las comunidades de peracáridos se debe tanto a su papel fundamental en el sistema trófico del bentos como a la relación de las poblaciones de las distintas especies con las condiciones ambientales y con el resto de especies del sistema bentónico.

Antecedentes

En relación al conocimiento de los Peracáridos costeros de la Península Ibérica, son destacables los recientes inventarios de Cumáceos ibéricos (Corbera, 1995) e Isópodos de la Península y Baleares (Junoy & Castelló, 2001), así como el de los anfípodos presentes en fondos de arena fina (De-la-Ossa-Carretero *et al.*, 2010a). Es de destacar, asimismo, el también necesario incremento en trabajos de índole ecológica,

particularmente de aquellos peracáridos asociados a algas intermareales, como los realizados por el profesor José Guerra y colaboradores (e. g., Guerra-García *et al.*, 2009; Izquierdo & Guerra-García, 2010). Otros trabajos destacables, centrados en áreas más concretas son los de Castelló (1984, 1985), Castelló & Carballo (2001), y Sánchez *et al.*, (2001), sobre isópodos, y Marques & Bellan-Santini (1990) Dauvin & Bellan-Santini (1996) Bachelet *et al.* (2003) y Carvalho *et al.* (en prensa) sobre anfípodos de diversas zonas del litoral ibérico, y los de Barberá Cebrián (2002) sobre misidáceos de las praderas de fanerógamas del sureste peninsular. En definitiva, todos estos inventarios y catálogos se caracterizan por su aportación de nuevas citas, poniendo de manifiesto que aún falta mucho por conocer acerca de la fauna ibérica. Así lo atestigua también el número considerable de nuevas especies que se han descrito en los últimos años, muchas de ellas fruto de los estudios anteriormente mencionados (e. g. especies de anfípodos descritos por Guerra-García *et al.*, 2001b, 2002; Sturaro & Guerra-García, 2012; Myers *et al.*, 2010 y Tato *et al.*, en prensa; e isópodos descritos por Castelló, 1997, 2002, y Castelló & Poore, 1998).

En las rías de Galicia, destacan sobre todo los estudios realizados en otras rías y ensenadas similares a O Grove (i. e. Moreira *et al.*, 2008a y b; Lourido *et al.*, 2008, Cacabelos *et al.*, 2009), en los que se hace mención a los lechos de fanerógamas en las zonas abrigadas. Estos trabajos ponen de manifiesto que los fondos sedimentarios de las rías albergan una fauna de peracáridos particularmente diversa en comparación a otros fondos similares de las costas europeas. También son destacables los trabajos de la Dra. Reboreda (e. g. Reboreda, 1995; Reboreda & Urgorri, 1995; Reboreda & Otero 1990), centrados en isópodos, que aportan nuevas citas para la península y para el Atlántico oriental.

No son pocos los estudios de carácter ecológico o faunístico que abordan la relación de las comunidades faunísticas en los lechos de fanerógamas. Entre los que se centran en el estudio de los peracáridos podemos mencionar, además de los ya citados, los de Stoner *et al.* (1983), Brearley & Walke (1995), Cunha *et al.* (1999), Barberá-Cebrián *et al.* (2002), Gambi *et al.* (2005), Winfield *et al.* (2007), González *et al.* (2008) y Scipione & Zupo (2010).

1.3. LOS PICNOGÓNIDOS

La clase Pycnogonida es un grupo de artrópodos también conocido como “arañas de mar”, sin afinidades claras con ningún otro grupo zoológico y consideradas como grupo hermano del resto de los Euarthropoda (Bamber, 2007; 2010b). El grupo está formado por más de 1300 especies, repartidas de forma desigual entre 77 géneros; asimismo, los picnogónidos están presentes en todos los hábitats marinos desde los trópicos hasta aguas polares y desde aguas someras hasta las profundidades abisales (Arnaud & Bamber, 1987; Munilla, 1999; Bamber, 2010b; Soler i Membrives, 2010). En los últimos años, los picnogónidos han sido objeto de un creciente interés debido a sus particularidades, y a la controversia creada con respecto a su posición filogenética dentro de los Euarthropoda (ver Wheeler & Hayashi, 1998; Giribet *et al.*, 2001, 2005; Scholzt & Edgecombe, 2006; Bamber, 2007; Ungerer & Scholzt, 2009).

La clase Pycnogonida se define por una serie de autoapomorfías (Dunlop & Arango, 2005; Soler i Membrives, 2010): un tronco reducido, que obliga a los sistemas digestivo y reproductor a extenderse hacia las prolongaciones laterales o encontrarse reducidos, una probóscide externa prominente, abdomen extremadamente reducido y la presencia de un par de apéndices ventrales en el segmento cefálico llamados ovígeros.

Los picnogónidos son animales predominantemente bentónicos, con algunos representantes batipelágicos (Child & Harbison, 1986; Pagès *et al.*, 2007), de movimientos lentos, que se alimentan principalmente de presas sésiles tales como algas, hidrozoos, actiniarios y briozoos (Wyer & King, 1974; Bamber & Davis, 1982; Bamber, 2010b). La mayoría son de vida libre, aunque se han descrito algunas especies comensales y parásitas (Arnaud, 1978; Benson & Chivers, 1960; Russel & Hedgpeth, 1990; Soler i Membrives, 2010) asociadas a diversos hospedadores tales como poríferos, cnidarios, moluscos y equinodermos. En general, y debido a su escasa movilidad, la abundancia y distribución de los picnogónidos depende de la

disponibilidad de alimento (Roberts, 1981; Arnaud & Bamber, 1987). Otros factores, como gradientes de salinidad (Wolff, 1976) e hidrodinamismo (Munilla León & San Vicente, 2000) también influyen en su abundancia y distribución a escala local.

Antecedentes

Los estudios que tratan la sinecología de este grupo son escasos; de hecho, la mayoría de los datos disponibles de picnogónidos en aguas templadas proceden de estudios más amplios sobre ecología de comunidades bentónicas, en los que rara vez se encuentran abundancias relevantes. No obstante, podemos destacar a este respecto a Arnaud y Bamber (1987), quienes publicaron una revisión completa que incluye datos sobre alimentación, hábitat y biogeografía. En otros trabajos señalables, Wolf (1976) estudia la distribución de picnogónidos a lo largo de varios estuarios y su tolerancia a la salinidad, y Wyer & King (1974) tratan la alimentación de las especies británicas. De Haro (1966, 1965) y Munilla (1991) estudian las especies presentes en lechos de algas pardas, y Genzano (2002) la relación con hidroideos. Por su parte, De Haro (1967), Pérez-Ruzafa & Munilla (1991), estudiaron los picnogónidos presentes en praderas de fanerógamas, y Chimenz *et al.* (1993) comparan la diversidad en una pradera de *Posidonia oceanica* con las encontradas fondos de algas coralinas y fondos no vegetados.

Entre los trabajos de carácter taxonómico que tratan los picnogónidos litorales en el Atlántico nordeste destacan los de Bouvier (1923) para las costas francesas, King & Crapp (1971), King (1974) y Bamber *et al.* (1997), en las islas británicas, Chimnez *et al.* (1979, 1993) y Krapp (1973), en el sur de Italia, Bamber & Costa (2009), en Azores y Stock (1990, 1991) en la región macaronésica, y una completa sinopsis con claves de identificación de las especies del nordeste atlántico ha sido recientemente publicada por Bamber (2010b). Los picnogónidos de las costas de la Península Ibérica fueron estudiados por Munilla León (1987, 1993, 1997), quien recogió datos de todo el litoral ibérico. Otros trabajos de menor envergadura son los de De Haro (1965, 1966, 1967) y Munilla (1988, 1991,) y Pérez-Ruzafa & Munilla (1991), quienes aportan listas de las especies encontradas en diferentes puntos del litoral ibérico mediterráneo. Munilla

(1987) recogió las especies citadas hasta el momento en las costas del Norte de la península, incluyendo las rías de Vigo, y Pontevedra, y la costa de Lugo. Lamentablemente, no existen más trabajos centrados en picnogónidos de las rías, ni en la costa gallega.

1.4. BIODIVERSIDAD, CONSERVACIÓN Y TAXONOMÍA

La biodiversidad, entendida como riqueza específica (=número de especies), es uno de los valores del ecosistema que se utilizan como parámetro para determinar la importancia de conservar un área determinada. A menudo, las figuras de protección se aplican para asegurar la conservación de la biodiversidad, y un inventario previo de ésta es exigido para declarar áreas protegidas (e. g., BOE, Real Decreto 1599/2011, de 4 de noviembre, en el que se establecen los criterios de integración de espacios marinos en la RAMPE). Al mismo tiempo, la composición específica y la abundancia de ciertas especies bentónicas sirven como indicadores del estado de conservación o degradación de un determinado ecosistema, de la presencia de contaminantes, y de la presión ejercida por la presencia humana (Bellan-Santini, 1981; Conradi & López González, 2001; Chintiroglou *et al.*, 2004; Guerra-García & García-Gómez, 2004, 2005; Seitz *et al.*, 2009; De-la-Ossa-Carretero, 2011; De-la-Ossa-Carretero *et al.*, 2010a, b, 2011a, b)

Por lo tanto, tan importante resulta la realización de estudios de carácter ecológico como que éstos se sustenten sobre una correcta y exhaustiva identificación de todas las especies que conformen el estudio, para que los análisis provean de una información precisa y fiable las condiciones y procesos que se suceden en el medio (Hogg *et al.*, 1998; Fernández *et al.*, 2000). Sin embargo, frecuentemente el número de especies es subestimado en estudios bentónicos debido a dificultades taxonómicas; esto ocurre especialmente con los grupos menos estudiados a este respecto, como son los cumáceos y tanaidáceos (Cunha *et al.*, 1999; Blazewicz-Paszkowycz *et al.*, 2012), o aquellos con una gran variación intraespecífica, generalmente relacionada con

diferencias entre sexos o los diferentes estadios del desarrollo (Blazewicz-Paszkowycz *et al.*, 2012).

En este sentido, en los últimos años, algunos autores (Bamber, 2010a; Larsen & Froufe, 2010; Blazewicz-Paszkowycz *et al.*, 2012 entre otros) han comenzado a señalar e insistir en la importancia de extender las descripciones de nuevas especies y los trabajos taxonómicos a todos los estadios de desarrollo del individuo, y de incluir la variación intraespecífica para así facilitar la identificación del gran número de juveniles que suele aparecer en las muestras procedentes de estudios bentónicos, especialmente cuando se sospecha la existencia de especies simpátricas del mismo género. Este tipo de estudios se hacen especialmente necesarios en especies que, perteneciendo a grupos morfológicamente conservativos, presentan gran variabilidad intraespecífica. Los peracáridos en general, y los tanaidáceos en particular son un buen ejemplo de ello, ya que los machos y juveniles a menudo no comparten caracteres específicos con las hembras, existen machos polimórficos, y variaciones ontogénicas en los caracteres taxonómicos. Esto se complica debido al carácter conservativo de la morfología del grupo, que resulta problemática a la hora de identificar juveniles; los juveniles comparten caracteres en especies próximas y al mismo tiempo se diferencian significativamente de los adultos de su misma especie (Larsen, 2001; Larsen & Froufe, 2010). Como consecuencia, se han descrito en numerosas ocasiones especies nuevas basándose erróneamente en caracteres dimórficos o diferencias merísticas entre juveniles y adultos (Larsen, 2001; Gardiner, 1975; Bamber, 2010a).

La caracterización de una especie y su discriminación con respecto a especies próximas en grupos de este tipo puede hoy realizarse mediante técnicas de taxonomía morfológica (como en Bamber, 2010a) o bien moleculares (como en Larsen, 2001), o idealmente, por medio de una combinación de ambas (Larsen & Froufe, 2010; Blazewicz-Paszkowycz *et al.*, 2012). No obstante, una vez determinada la validez de una especie es importante definir los caracteres que llevan a la identificación positiva e inequívoca de cualquier individuo, sea cual sea el género o estadio de desarrollo. Del mismo modo, para poder estudiar la estructura poblacional de una especie es importante definir los caracteres que permitan identificar dichos estadios.

Consecuentemente, tanto la descripción de nuevas especies como los trabajos sobre el ciclo de vida y desarrollo morfológico de las especies resultan indispensables para el desarrollo de los estudios bentónicos que se realizan en la actualidad, y para asegurar unos resultados precisos.

2. OBJETIVOS

Como se ha comentado anteriormente, a pesar de la importancia de los Crustáceos Peracáridos en la estructura de las comunidades bentónicas y los procesos que en ellas se suceden, no existe ningún estudio exhaustivo sobre este grupo en la ensenada de O Grove. Por otro lado, los estudios faunísticos centrados en Picnogónidos son escasos en Galicia, y los estudios referentes a su ecología prácticamente inexistentes. Dado el interés socioeconómico del ecosistema bentónico de la ensenada, y para suplir estas carencias, se ha realizado un estudio ecológico de ambos grupos en la ensenada de O Grove. También, dada la importancia de los estudios taxonómicos que permitan la correcta identificación de las especies, especialmente aquellas más comunes, se ha querido contribuir a dicho conocimiento con el estudio detallado de una especie de anfípodo previamente no registrada en el área geográfica y dos especies de tanaidáceos abundantes en la ensenada, pertenecientes a un género actualmente en revisión.

- El estudio de las comunidades de peracáridos y picnogónidos se ha realizado con los siguientes objetivos específicos:
 1. Caracterizar la variabilidad espacial de ambas biocenosis dentro de la ensenada.
 2. Conocer la variación estacional de dichas biocenosis.
 3. Estudiar las posibles relaciones de la distribución espacial y temporal de ambos grupos con los parámetros abióticos ambientales y sedimentarios.

Dada la importancia de una correcta identificación de los ejemplares tanto en estudios faunísticos como ecológicos, se han estudiado con detenimiento aquellos de los géneros *Apseudopsis* Norman, 1899 (Apseudidae: Tanaidacea) y *Periocolodes* Sars, 1895 (Amphipoda: Oedicerotidae) para ayudar a esclarecer sus particularidades morfológicas.

- Los ejemplares del género *Periocolodes* fueron examinados, dibujados, descritos, cuantificados y medidos con los siguientes objetivos específicos:

4. Documentar la presencia de *Periocolodes aequimanus* (Kossmann, 1980) fuera del mar Mediterráneo.
 5. Determinar las diferencias morfológicas que presentan las dos especies del género *Periocolodes* presentes en la ensenada: *P. aequimanus* y *Periocolodes longimanus* (Bate & Westwood, 1868).
 6. Especificar e ilustrar los caracteres diagnósticos de *P. aequimanus*.
- Los ejemplares del género *Apseudopsis* fueron examinados, dibujados, descritos, cuantificados y medidos con los siguientes objetivos específicos:
7. Redescribir la especie *Apseudopsis latreillii* (Milne-Edwards, 1828).
 8. Describir una nueva especie de dicho género, *Apseudopsis adami* Esquete & Bamber, 2012.
 9. Caracterizar los estadios de desarrollo de ambas especies.
 10. Identificar aquellos caracteres taxonómicos que no presentan variación intraespecífica y sí interespecífica, y sirven por tanto para identificar cada una de las especies.
 11. Identificar aquellos caracteres taxonómicos que presentan variación intraespecífica, pero son estables en cada estadio de desarrollo, y sirven por tanto para distinguir los mismos.
 12. Determinar la estructura poblacional de ambas especies en el área de estudio.

3. MATERIAL Y MÉTODOS

3.1. METODOLOGÍA DE MUESTREO. UN PROYECTO A ESCALA REGIONAL

En 1996 se llevó a cabo un muestreo a escala espacial mediante draga Van Veen en diez puntos que abarcaron aquellas áreas de la ensenada de O Grove correspondientes a fondos sedimentarios colonizados por las fanerógamas marinas *Zostera marina* y *Zostera noltii* (ver Figura 1). Posteriormente, entre 1998 y 1999 se completaron dichos muestreo con un seguimiento bimensual en un punto situado sobre una pradera sublitoral de *Z. marina* situada en la parte central de la ensenada. Ambos muestreos fueron realizados como parte de un de un proyecto de carácter regional que tenía como objetivo la caracterización faunística y ecológica de los fondos sedimentarios de cuatro ensenadas (Baiona, San Simón, Aldán y O Grove) repartidas por la costa suroccidental de Galicia. La metodología y protocolos seguidos durante dichos muestreos se describe con detalle en Moreira (2003; ensenada de Baiona), Cacabelos (2005; ensenada de San Simón), Quintas (2005; ensenada de O Grove) y Lourido (2009; ría de Aldán).

A partir de las muestras recogidas en los lechos de fanerógamas de la ensenada de O Grove se ha elaborado la tesis doctoral que es objeto de esta memoria. Los métodos referidos a la obtención del material faunístico y datos abióticos utilizados para la realización del presente trabajo se encuentran especificados en el capítulo 1, y una descripción detallada de las técnicas puede consultarse en Quintas (2005).

El material estudiado en esta Memoria procede, por tanto, de muestras recolectadas en diez puntos de muestreo (Noviembre 1996), y de aquellas correspondientes a seis períodos diferentes (Mayo 1998 a Marzo 1999), con periodicidad bimensual, en uno de dichos puntos.

3.2. MATERIAL EXAMINADO

Para la realización de esta tesis doctoral han sido examinados un total de 21820 ejemplares de peracáridos y picnogónidos procedentes de diez puntos de muestreo situados en las praderas de zosteráceas de la ensenada de O Grove (Figura 1). Una relación de las especies identificadas y su abundancia en cada punto de muestreo puede consultarse en los Anexos 2 y 3.

Adicionalmente, se solicitó material relativo a la especie *Apseudopsis latreilli* procedente de su localidad tipo al Museo Nacional de Historia Natural de París (MNHN), para compararlo con los ejemplares encontrados en O Grove y confirmar los caracteres morfológicos de la especie. El material que fue enviado consistió en dos ejemplares, un macho adulto y una hembra ovígera, recogidos en Le Petit Nord (noroeste de Francia) por E. L. Bouvier y por C. Bate y J. O. Westwood, respectivamente, en el año 1895. Ambos ejemplares fueron designados como neotipos dado que el material tipo no fue encontrado en ningún museo de Europa y se consideró perdido en consecuencia.

Además, fueron examinados 31 ejemplares adicionales de *Apseudopsis latreilli* procedentes de las islas de Scilly (Inglaterra), recolectados por R. N. Bamber en 2010.

3.3. METODOLOGÍA DE LABORATORIO

Estudio e identificación de los ejemplares

Los ejemplares fueron examinados mediante una lupa binocular y un microscopio para ser identificados a nivel específico. Algunos de ellos, bien por estar dañados o bien por tratarse de juveniles cuyos caracteres taxonómicos no están bien definidos en la literatura, sólo pudieron ser identificados a nivel genérico o de familia. Una vez identificados y cuantificados, se conservaron en etanol al 70% en tubos de plástico etiquetados con información relativa a la estación de muestreo, réplica

espacial o temporal (R1 a R5), fecha de obtención de la muestra de la que procedían, y luz de malla del tamiz del que fueron separados (0.5 ó 2.0 mm).

Ilustración y mediciones

Para ilustrar aquellos caracteres taxonómicos de interés, se seleccionaron ejemplares de las especies y estadios a estudiar, los cuales fueron diseccionados y dibujados mediante una cámara clara conectada a un microscopio. Las mediciones de los ejemplares individuales se llevaron a cabo mediante un ocular milimetrado. En los casos en que existía un gran número de ejemplares (capítulos 4 y 5) se utilizó un analizador de imagen conectado a una lupa binocular.

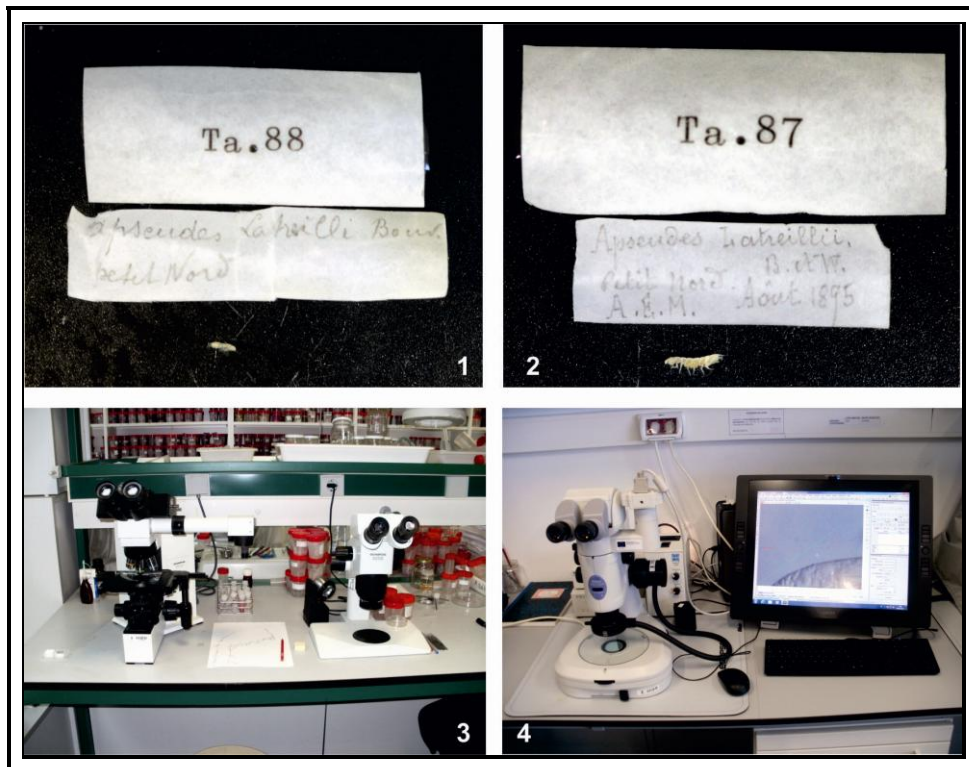


Figura 2. 1 y 2, material faunístico procedente del Muséum National d'Histoire Naturelle (París). 3, Lupa binocular y microscopio equipado con cámara clara. 4, Lupa binocular conectada al analizador de imagen de la Estación de Ciencias Marinas de Toralla.

La longitud total de los anfípodos fue medida desde el rostro hasta el margen posterior de la última placa epimeral. En el caso de los tanaidáceos, se midió desde el extremo distal del rostro hasta el margen distal del pleotelson. La longitud de los picnogónidos fue medida desde el margen anterior del cefalón hasta el margen

posterior de los últimos procesos laterales. Todas las medidas se tomaron axialmente, dorsalmente en el cuerpo y las antenas, y lateralmente en otros apéndices.

Nomenclatura

Los diferentes trabajos taxonómicos, tratados y claves de identificación de los grupos estudiados difieren, a menudo, en la nomenclatura taxonómica empleada. En los crustáceos, y dentro de un mismo grupo, son frecuentes las controversias en cuanto a la terminología referida a las mismas partes del cuerpo. En este trabajo se ha seguido, para los tanaidáceos apseudomorfos, la terminología propuesta por Bamber & Shearer (2005); así, el primer par de antenas son denominadas anténulas, y el segundo par, antenas. Del mismo modo, las primeras maxilas son denominadas maxílulas y las segundas maxilas. El primer par de pereópodos (de un total de seis pares) es el par inmediatamente posterior a los quelípedos. Se denominan segmentos aquellas subdivisiones de partes del cuerpo que aparecen repetidas en serie, tales como las de los flagelos de las antenas o las de los urópodos, mientras que aquellas subdivisiones con musculatura independiente (tales como las partes en que se dividen los pereiópodos) se denominan artículos. El término “espinas” es usado para designar aquellas piezas cuticulares ornamentales articuladas y rígidas, sin función sensitiva. Las piezas ornamentales articuladas, más o menos flexibles y/o con función sensitiva se consideran setas. Por último, aquellas no articuladas son denominadas apófisis.

En el caso de los anfípodos, se ha seguido la nomenclatura utilizada por Ledoyer (1993). Consecuentemente, cada antena del primer y segundo par son consideradas como antena 1 y antena 2, respectivamente; el mismo razonamiento se ha utilizado en el caso de la nomenclatura de los dos pares de maxilas. Cada uno de los miembros del primer par de apéndices tras las piezas bucales es el gnatópodo 1, al que sigue el gnatópodo 2, y a éste a su vez les siguen los pereópodos del 3 al 7.

La identificación de los estadios de desarrollo postmarsupial en apseudomorfos se ha basado en Gardiner (1975), con las modificaciones sugeridas por Messing (1981), también usado en los trabajos de Messing (1983) y Pereira Leite & Pereira Leite (1997).

Depósito de ejemplares

Algunos ejemplares de las especies que consideramos de especial interés, además de la serie tipo de una nueva especie de tanaidáceo, fueron depositados en el Museo Nacional de Ciencias Naturales (Madrid, MNCN).

3.4. TRATAMIENTO DE LOS DATOS

Los datos de abundancia de los taxones identificados fueron sometidos a una serie de análisis numéricos, y a continuación relacionados con los valores de los parámetros abióticos ambientales y sedimentarios determinados por Quintas (2005), correspondientes a las mismas muestras que las estudiadas en esta Memoria. Ello fue realizado con el objetivo de describir e interpretar la composición y estructuración de la fauna de peracáridos y picnogónidos asociada a los fondos de zosteráceas de la ensenada.

En las siguientes secciones se detallan los parámetros bióticos determinados a partir de la matriz de datos correspondientes así como los análisis realizados.

A. PARÁMETROS DE RIQUEZA Y ESTRUCTURA DE LA COMUNIDAD

Abundancia (N) – Número de individuos de una especie o conjunto de especies en una estación o conjunto de estaciones.

Densidad – Número de individuos de una especie o conjunto de especies por unidad de superficie.

Dominancia (D%) – Porcentaje de individuos de una especie en una estación o conjunto de estaciones respecto al número de total de individuos de todas las especies presentes.

$$D_{ij} \% = 100 \cdot (X_{ij} / N_{ij})$$

D_{ij} : dominancia de la especie i en la muestra j

X_{ij} : número de individuos de la especie i en la muestra j

N_j : número total de individuos de todas las especies en la muestra j

Se han considerado especies dominantes en una estación o en el conjunto de la ensenada a aquellas especies con un valor de dominancia superior al 1%

Riqueza específica (S) – Número de especies presentes en una estación o conjunto de estaciones.

El número de especies es el concepto más antiguo y simple de diversidad, pero resulta una medida incompleta al no discriminar entre las especies más comunes y abundantes y aquellas raras o escasas.

Diversidad – Es un parámetro determinado tanto por el número de especies como de la distribución del número de individuos entre las mismas. El índice que hemos utilizado como medida de la diversidad es el de Shannon-Wiener (H') (Shannon & Weaver, 1963) derivado de la teoría de la información:

$$H' = - \sum_{i=1}^n p_i \cdot \log p_i$$

$$p_i = n_i / N$$

n_i : nº de individuos de la especie i en la muestra

Este índice se mide en bits o unidades de información, y toma valores positivos desde 0, cuando todos los individuos pertenecen a la misma especie, hasta un número más o menos elevado y teóricamente infinito, cuando los individuos están repartidos equilibradamente en especies distintas. En este trabajo se han calculado los valores de H' con el logaritmo en base 2 como se ha hecho en otros estudios que tratan la diversidad de peracáridos en rías y ensenadas similares (Lourido *et al.*, 2008, Moreira *et al.* 2008a, b; Cacabelos, 2010, entre otros), con objeto de que los resultados sean fácilmente comparables y posibilitar la unificación de conocimientos.

Diversidad relativa o equidad de Pielou (J') – Viene determinado por la relación entre la diversidad real y la diversidad máxima. La diversidad máxima sería la alcanzada cuando todas las especies de la muestra tuviesen la misma abundancia.

$$J' = H' / H'_{máx.} \qquad H'_{máx.} = \log_2 S$$

S: número de especies presentes en la muestra

Los valores de J' oscilan entre 0 y 1; valores débiles indican la dominancia de una o más especies y por lo tanto una población poco estable y heterogénea y valores próximos a 1 indican una buena repartición de los ejemplares entre las diferentes especies y por tanto una población más homogénea y estable. Este parámetro puede considerarse como un complemento del índice de diversidad pues indica la homogeneidad o estabilidad de la abundancia de las especies presentes en la muestra en cuestión.

B. ANÁLISIS MULTIVARIANTE

Los análisis univariante realizados son especie-independientes, por lo que no han podido ser utilizados a la hora de hacer comparaciones entre la composición faunística de las estaciones. Por ello, se han realizado análisis multivariante especie-dependientes con el objeto de determinar la estructura de las comunidades bentónicas y su variabilidad espacial y estacional en función de su composición. En el presente estudio se han seguido los esquemas metodológicos propuestos por Clarke

(1993), basadas en las propuestas de Field *et al.*, (1982) y descritas en Clarke y Warwick (1994), consistentes en:

1. Representación de la estructura de la comunidad a través de análisis de clasificación y ordenación de las muestras correspondientes a las estaciones o períodos.
2. Determinación de las especies responsables de los agrupamientos de las muestras.
3. Test para analizar las diferencias espaciales en la estructura de la comunidad.
4. Análisis de las relaciones entre las variables bióticas y abióticas.

Se ha realizado un análisis normal o en modo “q”, con el que se trata de buscar la relación (similitud o disimilitud) entre estaciones en base a su composición específica. Para ello se han utilizado técnicas específicas de clasificación (UPGMA) y ordenación (MDS).

Los análisis fueron realizados por medio del paquete estadístico PRIMER 6 (Plymouth Routines In Multivariate Ecological Research).

Índice de similitud de Bray-Curtis

Con el objeto de determinar las afinidades entre estaciones de muestreo o especies se utilizó el índice de similitud de Bray-Curtis (Bray & Curtis, 1957), cuya notación es:

$$S_{jk} = 1 - \sigma_{jk}$$

S_{jk} : similitud entre las muestras j y K

σ_{jk} : disimilitud entre las muestras j y k, sumando todas las especies

$$\sigma_{jk} = \frac{\sum_{i=1}^p |y_{ij} - y_{ik}|}{\sum_{i=1}^p |y_{ij} + y_{ik}|}$$

y_{ij} : valor de la especie i en la muestra j

y_{ik} : valor de la especie i en la muestra k

Es un índice cuantitativo y presenta la ventaja, respecto a otros índices de similitud, de no verse afectado por las dobles ausencias de especies y de incluir las presencias simples. Sin embargo, es muy sensible a los valores extremos, dando más importancia a las especies más abundantes que a las raras (Digby & Kempton, 1987), por lo que los datos originales de la matriz de abundancia fueron transformados por medio de la raíz cuarta (Clarke & Warwick, 1994). Esta transformación consigue reducir el efecto de las especies más abundantes a la similitud entre dos estaciones, de forma que las menos abundantes contribuyan en mayor medida a esta similitud.

Se ha expresado en términos de porcentaje:

$$S_{jk} = 100 \cdot (1 - \sigma_{jk})$$

Los valores de este índice variarán entre 0, cuando las muestras comparadas no tengan ninguna especie en común, y 100, cuando los valores para todas las especies sean idénticos en ambas muestras

Técnicas de clasificación y agrupamiento jerárquico

Las técnicas de clasificación se aplican con el objetivo de obtener una clasificación en la que se observe si existe cierta estructura o agrupamientos de muestras debido a su similitud en base a la composición faunística. Para ello, hemos utilizado el análisis CLUSTER (dentro de PRIMER), que utiliza el algoritmo de agrupación UPGMA (“Unweighted Pairgroup Method Using Arithmetic Averages”), y se aplica sobre la matriz triangular de datos de similitud. El resultado gráfico es un dendrograma en el que las muestras aparecen dispuestas en grupos en función de su

similitud media, de forma que los componentes de un grupo sean muy similares entre sí y muy disimilares del resto.

Sin embargo, este análisis de clasificación presenta una serie de limitaciones (Field *et al.*, 1982) como la de presentar un carácter unidimensional, lo cual permite que a partir de una misma matriz de similitud puedan crearse dos o más configuraciones posibles. Por ello se aconseja utilizarlo en conjunción con métodos de ordenación con el objeto de contrastar los resultados obtenidos.

Técnicas de ordenación

Los análisis de ordenación representan las muestras a lo largo de ejes en función de su composición específica. El resultado es un diagrama en que las estaciones se representan por puntos en un espacio multidimensional, de forma que la distancia entre dos puntos (muestras) es proporcional a la similitud en la composición específica de sus comunidades (Estacio, 1996). En general, los métodos de ordenación permiten conocer las relaciones entre muestras, como en este caso, reduciendo las dimensiones del espacio original y acumulando la mayor parte de la varianza en el sentido de unos pocos ejes principales (dos o tres).

En este trabajo se ha aplicado el nMDS (“Non-Metric Multidimensional Scaling”), a partir de la matriz de similitud basada en el índice de Bray-Curtis. Para cuantificar la fiabilidad de la ordenación de las muestras resultante se ha empleado el coeficiente de estrés de Kruskal (Kruskal & Wish, 1978). Valores de este índice inferiores a 0,1 nos indican que se puede realizar una representación gráfica muy fiable de la disposición de las muestras. Valores mayores a 0,3 sugieren una disposición arbitraria (Clarke & Warwick, 1994).

Análisis de similitud de porcentajes entre especies (SIMPER)

El análisis SIMPER, perteneciente al paquete PRIMER, ha sido empleado para determinar las especies responsables de los agrupamientos de las estaciones. Este análisis parte de los agrupamientos proporcionados por los análisis de clasificación

para determinar, por un lado, la contribución de las especies a la similitud dentro de un grupo de (especies tipificadoras) y, por otro, la contribución de las especies a la disimilitud entre grupos (especies discriminadoras) (Estacio, 1996). El propio programa facilita el valor "Ratio": cociente entre la abundancia media de cada especie y su desviación típica. Este valor permite determinar cuáles son las especies que caracterizan un grupo y cuáles presentan mayor afinidad por determinado o determinados grupos.

Análisis de las diferencias espaciales en la estructura de la comunidad

Para contrastar las diferencias en la composición específica entre las muestras se ha utilizado el test no paramétrico ANOSIM (incluido en el paquete PRIMER) (Clarke & Green, 1988). Para ello, se parte de la matriz basada en la abundancia de cada especie en cada muestra replicada tomada en cada estación/período, y no su promedio. A partir de este procedimiento se obtiene el estadístico "R", que indica el grado de separación entre estaciones, es decir, si existen diferencias significativas en la composición faunística. R presentará un valor 0 cuando no existan diferencias entre réplicas de distintas estaciones y 1 si las réplicas de una misma estación muestran una composición idéntica entre sí y distinta a la de otras estaciones.

Análisis de la biota en relación a las variables ambientales (BIOENV)

EL análisis BIOENV (paquete PRIMER) ha sido empleado a la hora de analizar la relación entre la composición faunística de las muestras y los parámetros abióticos. Este análisis utiliza la matriz triangular de similitud entre muestras basada en el índice Bray Curtis y la abundancia de las especies, la cual relaciona con una matriz de disimilitud de datos abióticos basada en las distancias euclídeas. Esta relación se establece por medio del coeficiente de correlación armónica de Spearman (ρ_w), y el resultado es todos los valores de correlaciones máximas donde se puede observar cuáles son las variables ambientales que explicarían mejor la estructura faunística (Clarke & Ainsworth, 1993).

4. ESTRUCTURA DE LA MEMORIA

La presente memoria comienza con el estudio ecológico de los dos grupos objeto de estudio en las praderas de fanerógamas de la ensenada de O Grove, analizando tanto la distribución espacial como la dinámica temporal y su relación con los parámetros fisicoquímicos de la ensenada:

El capítulo 1 está dedicado a los peracáridos. En él se estudia la diversidad de los mismos en el área de estudio, tanto a escala espacial (en diez puntos de muestreo) como a escala temporal (partiendo de muestras recogidas bimensualmente en seis períodos consecutivos). Mediante análisis multivariante se determina la estructura de las comunidades bentónicas y su variabilidad espacial y estacional.

Esquete P., Moreira J., Troncoso J.S. 2010. Peracarid assemblages of *Zostera* meadows in an estuarine ecosystem (O Grove inlet, NW Iberian Peninsula): spatial distribution and seasonal variation. *Helgoland Marine Research* 65: 445-455.

En el capítulo 2 se estudian los picnogónidos desde un punto de vista faunístico. También se hace un estudio de la variación temporal de la estructura poblacional de *Achelia echinata*.

Esquete P., Bamber R.N., Moreira J., Troncoso J.S. En prensa. Pycnogonids (Arthropoda: Pycnogonida) in seagrass meadows: The case of O Grove Inlet (NW Iberian Peninsula). *Thalassas*.

En el capítulo 3 se documenta la presencia de una especie de anfípodo cuya distribución se consideraba restringida a costas mediterráneas, *Perioculodes aequimanus*, y se incluyen comentarios ilustrados sobre sus caracteres taxonómicos más relevantes.

Esquete P., Moreira J., Troncoso J.S. 2010. First record of *Perioculodes aequimanus* (Crustacea: Amphipoda) in the north-east Atlantic, with remarks on taxonomic characters. *Marine Biodiversity Records* 3: e112.

Los dos últimos capítulos se centran en el estudio morfológico y taxonómico de dos especies de tanaidáceos, una de ellas nueva para la ciencia, así como su desarrollo postmarsupial:

En el capítulo 4 se re-describe una de las especies de la macrofauna bentónica más frecuentes en los fondos sedimentarios de las costas europeas: el tanaidáceo *Apsudopsis latreillii* incluyendo toda la variabilidad morfológica intraespecífica que presentan los individuos de la especie; se realiza, además, un análisis de su estructura poblacional dentro de la ensenada de O Grove.

Esquete P., Bamber R.N., Moreira J., Troncoso J.S. 2012. Redescription and postmarsupial development of *Apsudopsis latreillii* (Crustacea: Tanaidacea). *Journal of the Marine Biological Association of the United Kingdom*. DOI 10.1017/S0025315411002086

Finalmente, en el capítulo 5 se describe una especie de tanaidáceo nueva para la ciencia, *Apsudopsis adami*, incluyendo también la descripción de todas las etapas del desarrollo, dimorfismo sexual y su estructura poblacional.

Esquete P., Bamber R.N., Moreira J., Troncoso J.S. 2012. *Apsudopsis adami*, a new species of Tanaidacean (Crustacea: Peracarida) from the NW Iberian Peninsula. Postmarsupial development and remarks on morphological characters. *Helgoland Marine Research*. DOI 10.1007/s10152-012-0295-2

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II. Resultados

Capítulo 1

Esquete P, Moreira J, Troncoso JS. 2011. Peracarid assemblages of *Zostera* meadows in an estuarine ecosystem (O Grove inlet, NW Iberian Peninsula): spatial distribution and seasonal variation *Helgoland Marine Research* 65(4): 445-455.

AGRUPAMIENTOS DE PERACÁRIDOS DE LAS PRADERAS DE *ZOSTERA* EN UN ECOSISTEMA ESTUÁRICO (ENSENADA DE O GROVE, N.O. DE LA PENÍNSULA IBÉRICA): DISTRIBUCIÓN ESPACIAL Y VARIACIÓN ESTACIONAL.

Resumen. Las rías de Galicia son sistemas complejos de gran importancia económica. Por su parte, las fanerógamas marinas son elementos clave de la biocenosis bentónica, ya que favorecen el mantenimiento de una gran diversidad faunística. Sin embargo, el papel ecológico de estas praderas dentro de las rías gallegas no ha sido evaluado adecuadamente hasta el momento. Los crustáceos peracáridos constituyen un importante componente numérico de la fauna de sustratos blandos, interviniendo de forma significativa en la estructura de las comunidades bentónicas. En este capítulo, se estudian los patrones de distribución, la diversidad específica y la fluctuación estacional de los peracáridos de los sedimentos estuáricos colonizados por dos especies de *Zostera* (i.e. *Zostera marina* y *Z. noltii*) en la ensenada de O Grove. La comunidad de peracáridos estudiada se caracteriza por un lado por una elevada diversidad, y por otro, por una gran dominancia numérica de un pequeño número de especies, particularmente tanaidáceos apseudomorfos. El estudio temporal en la pradera sublitoral de *Z. marina* de la parte central de la ensenada muestra un fuerte patrón estacional, el cual está definido por grandes fluctuaciones de las poblaciones de Anfípodos. Los valores más altos en el número de especies e individuos se observan en Septiembre, y los mínimos en Marzo. Los análisis muestran una alta correlación entre las características granulométricas del sedimento y la composición faunística. No obstante, la presencia de fanerógamas influye de manera destacable en las características hidrodinámicas y sedimentarias del hábitat y, consecuentemente, en los patrones espaciales y temporales observados en los agrupamientos de peracáridos en la ensenada de O Grove.

Peracarid assemblages of *Zostera* meadows in an estuarine ecosystem (O Grove inlet, NW Iberian Peninsula): spatial distribution and seasonal variation

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Abstract The Galician rias are singular and complex estuarine systems of great economic importance. Seagrasses are key elements of the ecosystem and favor the maintenance of high species diversity in benthic communities. Nevertheless, the ecological role of seagrass meadows in the Galician rias has been only partially assessed. Peracarid crustaceans are an important component of soft-bottom faunas and have great importance for the structure of benthic assemblages. In this work, species diversity, patterns of distribution and seasonal fluctuations of peracarids (Crustacea, Peracarida) are studied in estuarine sediments colonized by two species of *Zostera* (*Z. marina* and *Z. noltii*) at the O Grove inlet (Ría de Arousa, Galicia, NW Iberian Peninsula). The spatial distribution of peracarid assemblages was characterized by high numerical dominances due to a few species, particularly tanaidaceans. The temporal study at a *Z. marina* meadow showed a strongly seasonal pattern defined by great fluctuations of the amphipod population, the latter being the dominant group in abundance and number of species. The highest numbers of species and individuals were observed in September, with minimum values in March. Analyses pointed out a high correlation among the granulometric features of the studied

bottoms and the faunistic attributes. Nevertheless, the presence of the seagrasses should influence in a major way the hydrodynamic and sedimentary features of the habitat and utterly the spatial and temporal patterns observed in the peracarid assemblage in the O Grove inlet.

Keywords Peracarida · *Zostera* · Seagrass · Assemblages · Distribution · Dynamics

Introduction

The presence of seagrass meadows in estuaries favors the establishment and maintenance of high species diversity in benthic assemblages (Fredette et al. 1990; Montadoun and Sauriau 2000). This is mostly due to their role as ecosystem engineers (Jones et al. 1994; Hasegawa et al. 2008): seagrasses reduce current velocities, and thus influence sedimentation rates. They also constitute a source of organic matter, which positively affects the establishment and survival of many benthic, particularly epifaunal species (Orth et al. 1984; Böstrom et al. 2006; Hasegawa et al. 2008). Furthermore, seagrass meadows represent a nursery habitat for fishes and invertebrates and are therefore crucial for the conservation and restoration of marine environments (Heck et al. 2003).

Peracarids (Crustacea: Peracarida) are one of the dominant taxa in benthic assemblages (Cartes et al. 2001) and are considered good indicators of the environmental conditions (Chintiroglou et al. 2004; Guerra-García and García-Gómez 2004). Besides, peracarids represent an important element of the trophic system (Cartes et al. 2001). Thus, the study of this group is a useful tool to evaluate the health and state of conservation of ecosystems.

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The Galician rias (NW of Spain) are singular, complex and productive estuarine systems, which support activities of great economic importance such as littoral fishing, mussel culture and other kinds of exploitation of sea food resources (Figueiras et al. 2002). In addition, the rias house a variety of hard- and soft-bottom habitats with high numbers of species (Garmendia et al. 1998; Moreira and Troncoso 2007). Because of their social and economic importance, the rias have been the subject of several faunistic studies in the last years (e.g. Junoy and Viéitez 1988; Currás and Mora 1991; Olabarria et al. 1998; Cacabelos et al. 2008; Lourido et al. 2008; Moreira et al. 2008b). However, there is a lack of studies on the fauna inhabiting seagrass meadows along the Galician coast. The ecological role of seagrass meadows in the Galician rias has not yet been properly assessed, despite the importance of seagrasses for the functioning of the ecosystem (Heck and Thoman 1981; Orth et al. 1984; Ersoy Karaçuha et al. 2009).

The O Grove inlet is of high economic and ecological importance due to mussel culture and tourism, on the one hand, and the presence of the extensive seagrass meadows, on the other hand. In fact, *Zostera marina* L. and *Z. noltii* Hornem. meadows cover the major part of the intertidal and shallow subtidal sediments of the inlet; this contributes to habitat complexity and thus to high values of benthic biodiversity (Quintas 2005).

As a starting point for a better understanding of the role of *Zostera* meadows in the ecosystem of the Galician rias, we (1) characterized the peracarid assemblage present in the *Zostera* spp. beds of the O Grove inlet and (2) studied possible seasonal changes of this assemblage in a representative *Zostera marina* bed.

Materials and methods

Study area and sampling procedures

The Ensenada de O Grove is located in the southern part of the Ria de Arousa (Galicia, NW Iberian Peninsula), between 42°41'–42°28'N and 9°01'–8°44'W (Fig. 1). It is a sheltered inlet, influenced by high precipitations in autumn/winter and affected seasonally by freshwater input from several streams. The peracarid fauna inhabiting the *Zostera* meadows at O Grove was studied at both spatial and temporal scales. The spatial study was done in December 1996 and comprised 10 sampling sites to assure a representative coverage of the seagrass meadows, which are composed of *Z. marina*, *Z. noltii* or both of them (Fig. 1). For the temporal study, samples were taken bimonthly between May 1998 and March 1999 in site D27, a subtidal area colonized by *Z. marina*, which was assumed to be less affected by salinity fluctuations than meadows located in

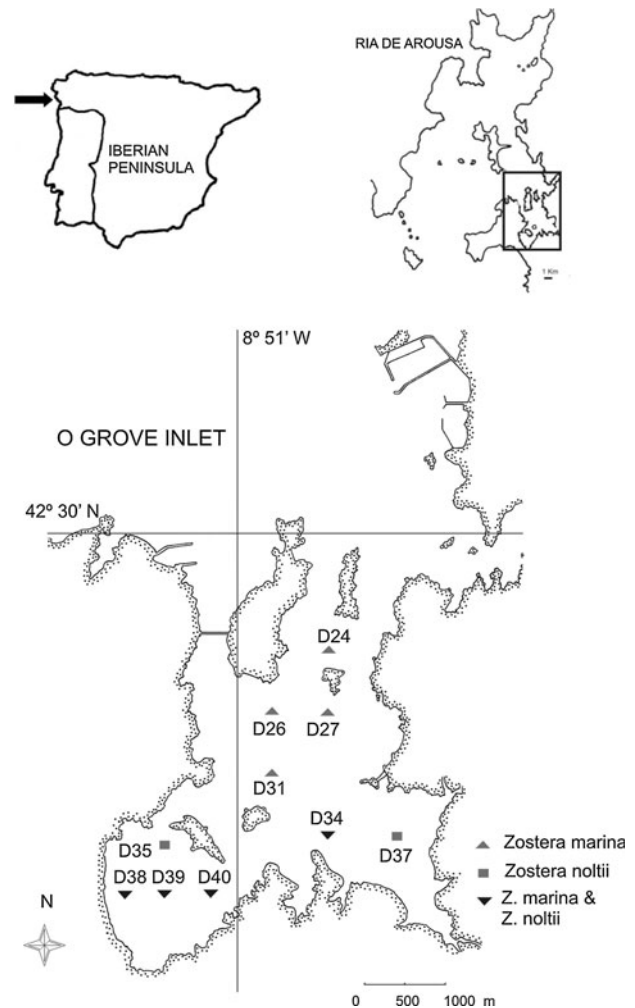


Fig. 1 Location of the O Grove inlet and sampling sites

the innermost parts of the inlet. This site was furthermore selected because of its high peracarid diversity and the good state of conservation of the meadow.

The spatial study was part of a larger project on the benthic environment of the Ria de Arousa. In order to unify the sampling procedure across different kinds of soft substrata, samples were taken by means of a Van Veen grab. Usually, studies on benthic faunas of seagrass meadows are performed by collecting samples with corers or quadrats (e.g. Blanchet et al. 2004; Fredriksen et al. 2005; González et al. 2008). Nevertheless, the grab used here was considered to take representative samples of the bottom; anyway, samples were discarded when the grab closed on *Zostera* roots and a substantial part of the sample could have been lost. Five replicate samples were taken at each site, thus covering a total area of 0.28 m² per site. Samples were sieved through a 0.5-mm mesh and fixed in 10% buffered formalin for later sorting and identification of the fauna. An additional sample was taken at each site for granulometric analyses and to determine calcium carbonate and organic

matter content. Also, a sample of the bottom water was taken by means of a Niskin bottle. The following granulometric fractions were distinguished: gravel (>2 mm), very coarse sand (1–2 mm), coarse sand (0.5–1.0 mm), medium sand (0.25–0.50 mm), fine sand (0.125–0.250 mm), very fine sand (0.063–0.125 mm) and silt/clay (<0.063 mm). Median grain size (Q_{50}) and the sorting coefficient (S_0) were also determined for each site. Calcium carbonate content (%) was estimated by treating the sample with hydrochloric acid in a Bernard Calcimeter, and the total organic matter content (TOM, %) was estimated from the weight loss of samples dried in a furnace for 4 h at 450°C. Temperature and pH of bottom seawater were measured in situ, by means of a portable microprocessor model HI9025C (Hanna instruments). Salinity was measured by means of a refractometer model S/Mill-E (Atago).

For the study of possible seasonal changes in the fauna, samples were taken at site D27 in May, July, September and November 1998, as well as in January and March 1999 by Scuba divers. At each sampling date, the seagrass cover of five replicate quadrats of 0.0625 m² each was harvested; the shoot and rhizome fractions (the latter including the sediment) were kept separately in plastic bags. An additional sample of sediment was taken for granulometric analyses and to determine calcium carbonate and organic matter content. Salinity, pH and temperature were measured in situ. Samples destined for faunal analysis were sieved through a 0.5-mm mesh and fixed in 10% buffered formalin.

Data analyses

Univariate measures were calculated for each sampling site and date: total abundance (N), number of species (S), Shannon–Wiener's diversity index (H' , as \log_2) and Pielou's evenness (J'). Peracarid assemblages (spatial study) and patterns of seasonal changes (site D27) were determined through non-parametric multivariate techniques as described by Clarke and Warwick (1994), using PRIMER 6 (Plymouth Routines in Multivariate Ecological Research) software package. The Bray–Curtis similarity index was applied on the fourth-root transformed data (to downweight the contribution of the most abundant species). Data were previously averaged through the five replicates for each site/date thus obtaining a centroid. Classification of sampling sites/dates was done by cluster analysis based on the group-average sorting algorithm and tested by Simprof test. Non-metric multidimensional scaling (nMDS) was used to produce a visual representation of the ordination of centroids. The SIMPER analysis served to identify the species that contributed most to the differentiation of the groups of samples (sampling sites/dates). The possible relationship between the peracarid assemblages

and the measured environmental variables was analyzed by the BIO-ENV procedure. All variables expressed in percentages were previously transformed by $\log(x+1)$.

Results

Spatial distribution

Environmental variables

Sediments were composed mainly of muddy sand, with relatively high percentages of fine and very fine sand (up to 64.6 and 47.9%, respectively) and silt/clay (up to 61.6% in site D37). Salinity was relatively low (maximum 33‰) especially for sites 34 and 37 (around 20‰). Content in TOM was high (up to 15.55%), whereas content in calcium carbonate was low (<10.5%). Values of the studied variables are detailed for each site in Table 1.

Fauna

A total of 15,523 individuals belonging to 113 species were identified (those with >1% of dominance are detailed in Table 2). Tanaids accounted for 52% of the specimens, with *Apseudes latreillii* (Milne-Edwards, 1828) being the numerically dominant species (40.2%). Amphipods were the group best represented in number of species (83) and constituted 35.8% of the specimens. The least represented group was cumaceans, which accounted for only 3.12% of the total abundance.

The highest number of species was found in site D27 (60); diversity (H') and evenness (J') indexes were low for this site (H' : 2.05; J' : 0.51). Both H' and J' were highest for sites D38, D39 and D40 (H' : 3.74–4.07; J' : 0.73–0.78).

The ANOSIM test showed significant differences in faunistic composition among sites (global R : 0.823, $P < 0.001$). The cluster dendrogram and the graphic representation of the nMDS analysis revealed the existence of three major groups of sites (Fig. 2). Group A (similarity level of 60%) comprised four sites located in the central part of the inlet and colonized by *Z. marina* (D24, D26, D27 and D31). The species that mostly contributed to the similarity were the tanaids, *Apseudes latreillii* and *Zeuxo holdichi* Bamber, 1990, followed by the caprellids, *Caprella acanthifera* Leach, 1814 and *Pariambus typicus* (Krøyer, 1884). Group B was composed of two sites colonized by both species of seagrasses, situated in the sheltered south-western part of the inlet (D38 and D39; similarity of 70%). *Uromunna* spp., *Microdeutopus* spp., *Gammarella fucicola* (Leach, 1814) and *Apseudes talpa* (Montagu, 1808) were the taxa determining this group. Site D35 was also included in this group (similarity of 60%),

Table 1 Spatial study: environmental variables measured in different sites

	D24	D26	D27	D31	D34	D35	D37	D38	D39	D40
T sed. (°C)	12.50	11.10	11.60	13.40	12.70	13.50	12.90	12.60	12.70	12.80
T bottom water (°C)	14.60	10.00	9.90	16.70	13.00	15.30	13.20	13.20	13.00	13.30
pH sed.	7.36	7.53	7.41	7.39	7.27	7.46	7.20	7.30	7.29	7.26
pH bottom water	7.76	7.90	7.85	7.81	7.74	7.89	7.74	7.71	7.70	7.73
Salinity (‰)	29.00	30.00	32.00	32.50	30.00	30.50	20.00	33.00	33.00	32.00
Gravel	1.87	4.44	0.38	1.95	0.23	0.68	1.03	5.77	1.05	22.38
Very coarse sand	0.50	2.38	0.21	0.57	0.14	0.53	0.36	1.09	0.37	3.95
Coarse sand	0.97	4.56	0.45	0.91	1.83	1.54	1.86	2.81	1.00	5.00
Medium sand	3.82	10.19	2.37	4.76	10.97	14.48	3.88	5.13	4.72	9.71
Fine sand	40.14	46.14	37.80	58.03	20.85	64.63	11.77	18.51	43.58	18.36
Very fine sand	40.68	25.89	47.89	23.20	33.93	11.40	19.49	29.66	31.07	13.17
Silt/clay	12.01	6.41	10.90	10.59	32.05	6.75	61.61	37.02	18.22	27.44
Q ₅₀	0.12	0.17	0.11	0.16	0.18	0.19	0.10	0.11	0.13	0.18
S ₀	1.52	1.50	1.48	1.45	1.82	1.30	2.31	1.70	1.61	1.99
TOM (%)	3.93	1.37	2.98	2.80	5.08	1.32	15.55	10.75	3.32	7.10
Carbonate content (%)	7.58	10.05	8.46	8.69	7.22	10.46	5.41	7.40	9.59	7.17

Granulometric fractions in %, *T sed* temperature of the sediment, *T bottom water* temperature of the bottom water, *pH sed* pH of the sediment, *pH bottom* pH of the bottom water, *Q₅₀* median grain size, *S₀* sorting coefficient, *TOM* total organic matter

although this was not supported by the Simprof test. Group C (similarity 50%) was formed by two sites located near the mouth of rivers in the south-east (D34, with both *Z. marina* and *noltii*; D37, only with *Z. noltii*) and another site hosting both seagrasses (D40); the latter was situated on the other side of the inlet, near site D39. The species that most contributed to the similarity of this group were the isopods, *Idotea chelipes* (Pallas, 1766) and *Idotea balthica* (Pallas, 1772), followed by the amphipods, *Corophium sextonae* Crawford, 1937 and *C. insidiosum* Crawford, 1937.

The BIO-ENV procedure revealed that the combination of salinity, gravel, fine sand and silt/clay had the highest correlation with the faunal composition, according to the values of the Spearman's rank correlation coefficient (ρ_w : 0.734). The variable that showed the best correlation was silt/clay (ρ_w : 0.603).

Seasonal changes

Environmental variables

The temperature of the bottom water reached a minimum in March (12.4°C) and a maximum in July (25.2°C). Fine and very fine sand were the dominant granulometric fractions throughout the year at site D27 (20.9–58.0% and 11.4–40.7%, respectively). Coarser granulometric fractions were present in small percentages, showing some variation over the study period. Silt/clay fraction showed more or

less constant values, reaching the maximal content in January (32.1%). Calcium carbonate and organic matter contents showed slight variations over the year, with maximal values in March (TOM, 4.6%; calcium carbonate, 9.9%). Details are shown in Table 3.

Fauna

A total of 5,768 individuals belonging to 83 species were found in the study period. Amphipods were dominant in number of the specimens (69.4% of total abundance), followed by tanaids (21.8%), isopods (8%) and cumaceans (0.8%). Amphipods were also numerically dominant at each sampling date except for July, when tanaidaceans were the dominant group (Fig. 3). The dominant species was the amphipod, *Gammarella fucicola* (23.6% of total abundance), followed by the tanaid, *Zeuxo holdichi* (18.6%), and the caprellid, *Phtisica marina* Slabber, 1769 (16.6%; Fig. 4).

The highest numbers of species and individuals were observed in September, minimal numbers in March. Diversity (H') and evenness (J') were minimal in summer–autumn, reaching the highest values in January (Table 4).

The ANOSIM test showed significant differences in faunistic composition among all sampling dates (global R : 0.634, $P < 0.001$). Cluster analysis and nMDS ordination showed two defined groups of samples (Fig. 5): spring–summer (May and July; group A) and autumn–winter (November, January and March; group B). The September

Table 2 Spatial study: list of the peracarid orders and most abundant species (>1% dominance) with abundances (individuals/0.28 m²) in the different sampling sites, total abundances and dominance (%)

	D24	D26	D27	D31	D34	D35	D37	D38	D39	D40	Total	D (%)
AMPHIPODA (total)	437	510	1,064	267	858	126	68	1,116	671	444	5,561	35.82
<i>Stenothoe monoculoides</i> (Montagu, 1815)	21	9	6	3	23	3	0	10	4	87	166	1.07
<i>Gammarus tigrinus</i> Sexton, 1939	0	1	1	0	213	0	1	10	0	1	227	1.46
<i>Gammarella fucicola</i> (Leach, 1814)	17	22	516	18	0	1	2	170	69	5	820	5.28
<i>Melita palmata</i> (Montagu, 1804)	0	0	1	0	0	6	6	0	0	157	170	1.09
<i>Perioculodes aequimanus</i> (Kossmann, 1880)	28	5	7	8	1	11	0	55	105	68	288	1.85
<i>Harpinia pectinata</i> Sars, 1891	12	55	78	16	0	11	0	33	39	0	244	1.57
<i>Dexamine spinosa</i> (Montagu, 1813)	25	5	28	12	0	0	0	74	34	0	178	1.15
Aoridae indet.	0	1	0	1	12	0	0	246	16	4	280	1.80
<i>Microdeutopus</i> spp.	13	9	17	30	60	6	3	166	81	27	412	2.65
<i>Microdeutopus versiculatus</i> (Bate, 1856)	2	64	1	0	96	0	1	0	1	0	165	1.06
<i>Siphonocetes sabatieri</i> de Rouville, 1894	0	0	0	0	0	7	0	0	149	0	156	1.00
<i>Pariambus typicus</i> (Krøyer, 1804)	22	17	178	25	0	0	0	0	1	0	243	1.56
ISOPODA (total)	14	76	100	60	55	26	449	199	94	194	1,267	8.16
<i>Cyathura carinata</i> (Krøyer, 1847)	0	74	2	0	1	6	3	15	6	68	175	1.13
<i>Uromunna</i> spp.	12	0	10	57	2	16	0	180	87	4	368	2.37
CUMACEA (total)	196	10	96	26	0	26	0	58	70	3	485	3.12
<i>Iphinoe trispinosa</i> (Goodsir, 1843)	173	2	30	8	0	5	0	9	10	3	240	1.55
TANAIDACEA (total)	1,456	1,411	2,711	1,424	0	258	0	662	248	30	8,200	52.82
<i>Apeudes latreillii</i> (Milne- Edwards, 1828)	1,394	806	2,699	1,250	0	37	0	30	24	0	6,240	40.20
<i>Apeudes talpa</i> (Montagu, 1808)	0	530	0	0	0	15	0	61	117	3	726	4.68
<i>Leptocheilia savignyi</i> (Kroyer, 1842)	0	0	0	1	0	12	0	400	51	1	465	2.99
<i>Zeuxo holdichi</i> Bamber, 1990	59	70	6	173	0	194	0	171	23	4	700	4.51
Pielou's evenness (J')	0.42	0.54	0.35	0.38	0.72	0.67	0.68	0.74	0.79	0.74		
Shannon-Wiener's diversity index (H')	2.39	3.07	2.05	2.04	3.72	3.62	2.94	4.07	4.48	3.74		

sampling appeared separated from both groups. Group A (70% similarity) was defined by *Zeuxo holdichi*, *Stenothoe monoculoides* (Montagu 1815), *Uromunna* spp. and *Microdeutopus* spp. Group B (60% similarity) was characterized by *Z. holdichi*, *S. monoculoides* and *Gammarella fucicola*. In the x-axis, the September sampling appeared to be closest to group A (70% similarity), but this was not supported by the Simprof test.

The BIO-ENV procedure revealed that the combination of pH, temperature of bottom water and content in medium sand, very fine sand and silt/clay had the highest correlation with peracarid fauna, according to the Spearman's rank correlation coefficient (ρ_w : 0.532).

Discussion

The *Zostera* meadows at the O Grove inlet have a very diverse peracarid fauna, with a total of 113 taxa identified in this study. The assemblages were numerically dominated

by tanaidaceans (53% of the total abundance) and amphipods (36%); on the other hand, amphipods were the peracarid order with the highest number of species (85). The high numerical dominance of tanaidaceans was mostly due to *Apeudes latreillii*, particularly in sites colonized by *Zostera marina*.

The species composition of the studied seagrass meadows was typical for north-east Atlantic estuarine sediments (Cunha et al. 1999; Dauvin et al. 2009). However, in other similar estuarine environments of the North Atlantic and the Mediterranean, whether colonized by seagrasses, the number of peracarid species was often smaller and tanaidaceans were very scarce or even absent (Cunha et al. 1999; Cartes et al. 2007; Dauvin et al. 2009). In seagrass meadows, the total number of species was usually high, although tanaidacean densities were much lower than in the present study (Gambi et al. 1992; Sfriso et al. 2001; Paganelli et al. 2005; Ersoy Karacuha et al. 2009). In general, amphipods were dominant in most of the studies listed above. This dominance may be explained by the fact

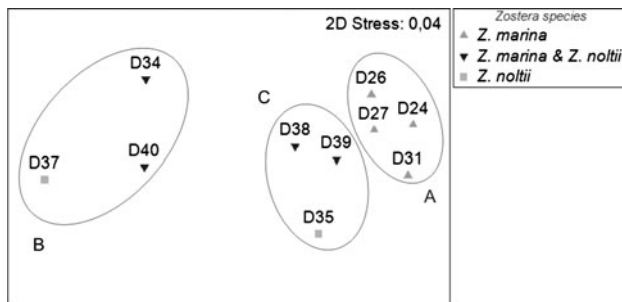


Fig. 2 nMDS ordination of sampling sites showing the groups determined by cluster analysis. The *Zostera* species present in each site are also indicated

that amphipods are highly diversified both taxonomically and in terms of niche occupation (habitat preferences, feeding habits) and life strategies (e.g. Lancellotti and Trucco 1993; Nelson et al. 1982). Seagrass meadows in turn provide a variety of microhabitats and food sources (vegetal biomass, detritic deposits, epiphytes on seagrasses) to be colonized and exploited by amphipods.

High densities of the tanaid, *Apseudes latreilli*, have recently been reported in several studies and have often been linked to organic and/or inorganic pollution (Cruz et al. 2003; Guerra-García and García-Gómez 2004; Tomasetti et al. 2009). According to Riggio (1996), *A. latreilli* is found frequently in sediments with detritic deposits. In the O Grove inlet, organic matter contents are high in general, and extensive mussel culture also

contributes to a significant detritus input. These features, together with the pollution related to intense vessel activities, may have favored the establishment of large populations of *A. latreilli* in the inlet.

Recent benthic studies of several Galician rias have pointed out a particular richness in peracarid species when compared to similar environments of the North Atlantic (Lourido et al. 2008; Moreira et al. 2008a, b). The granulometric characteristics of the sediment have been suggested the main factor in structuring those assemblages. Nevertheless, in the study area, the presence of the seagrasses undoubtedly contributes to the establishment and structure of the peracarid assemblage by providing, for example, an increased habitat complexity. Furthermore, seagrasses enhance sedimentation rates and organic matter supply and are crucial for the sedimentary features of the habitat (Böstrom et al. 2006; Hasegawa et al. 2008). As expected, the organic matter contents measured in the *Zostera* meadows at the O Grove inlet was high, and multivariate analysis indicated that peracarid assemblages were positively correlated with the granulometric composition, especially with the silt/clay fraction. This granulometric fraction is easily suspended and drifted away by hydrodynamism in spite of the presence of the seagrasses (Hasegawa et al. 2008), and then distributed irregularly across the meadows. This provides the basis for restricted distributions of infaunal species in the meadows depending on species-specific differences in granulometric preferences. Indeed, we observed that infaunal species such as

Table 3 Seasonal study: environmental variables measured in site D27 at different dates

	May	July	September	November	January	March
T sed. (°C)	19.30	18.80	19.60	16.90	21.20	12.30
T bottom water (°C)	21.50	25.20	20.10	17.20	21.20	12.40
pH sed.	7.25	7.28	7.19	7.45	7.56	6.38
pH bottom water	8.05	7.79	7.66	7.73	7.55	7.58
Salinity (‰)	32.00	34.70	40.40	40.80	32.70	41.00
Gravel	1.9	4.4	0.4	1.9	0.2	0.7
Very coarse sand	0.5	2.4	0.2	0.6	0.1	0.5
Coarse sand	1.0	4.6	0.4	0.9	1.8	1.5
Medium sand	3.8	10.2	2.4	4.8	11.0	14.5
Fine sand	40.1	46.1	37.8	58.0	20.9	64.6
Very fine sand	40.7	25.9	47.9	23.2	33.9	11.4
Silt/clay	12.0	6.4	10.9	10.6	32.1	6.7
Q ₅₀	3.050	2.950	2.183	2.283	1.283	4.600
S ₀	8.089	8.506	8.406	8.183	8.511	9.930
TOM (%)	0.1932	0.1745	0.1963	0.1725	0.2505	0.1747
Carbonate content (%)	1.339	1.470	1.345	1.689	1.567	1.597

Granulometric fractions in %, *T sed* temperature of the sediment, *T bottom water* temperature of the bottom water, *pH sed* pH of the sediment, *pH bottom* pH of the bottom water, *Q₅₀* median grain size, *S₀* sorting coefficient, *TOM* total organic matter

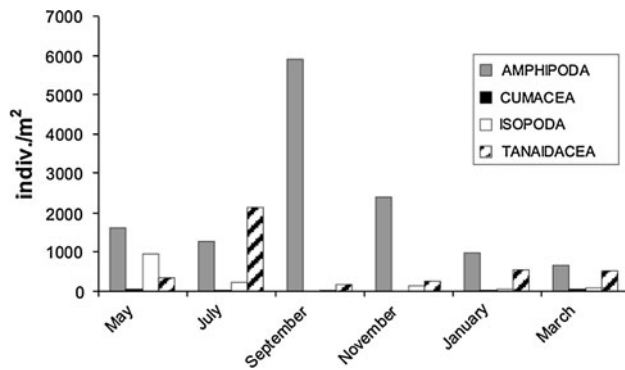


Fig. 3 Total abundance (individuals per m²) of the four peracarid orders per sampling date at site D27

Pariambus typicus and *A. latreillii*, which have been related with the silt/clay fractions (Guerra-García et al. 2003), contributed significantly to the characterization of the assemblages.

Peracarid assemblages of the *Zostera marina* meadows in the center of the inlet constituted a definite group (A) in the cluster analysis. The assemblages corresponding to the other two groups (B and C) were found in meadows composed of *Z. noltii* or a mixture of both species. Group C (sites D35 and D37) is clearly defined in the nMDS ordination and is located close to the mouth of several rivers. The differences in those peracarid assemblages might be related to the different conditions in salinity observed across the inlet. In wet climates, macrofaunal distributions in estuaries are influenced by salinity gradients (Talley et al. 2000). Indeed, salinity affects peracarids in estuarine areas more than any other environmental factor (Paganelli et al. 2005). In fact, in the sites of group C, euryhaline species such as *Idotea balthica*, *I. chelipes*, *Corophium acherusicum* Costa, 1851, *C. insidiosum*, *Gammarus tigrinus* Sexton, 1939, and *G. insensibilis* Stock, 1966, were more abundant than in the sites of the other two groups, while

species less tolerant to changes in salinity (i.e. tanaidaceans) were completely absent. In conclusion, our results suggest that the spatial variations in peracarid assemblages found at the O Grove inlet are related to three main factors: sediment characteristics, seagrass species composition and salinity conditions.

In the second part of the study (seasonal changes in the peracarid assemblage of a subtidal *Z. marina* meadow; D27), the numbers of species and total numbers of individuals were generally lower than in the samples (including those from D27) taken for the first (spatial) part of the study. This might be due to the different sampling techniques, as scuba diving (used in the seasonal study) might expose peracarids to a higher rate of disturbance than a Van Veen grab (applied in the spatial study). Indeed, some peracarid taxa tend to escape or bury into the sediment when disturbed; for example, Guerra-García and García-Gómez (2008) observed that tanaidaceans are able to bury actively to deeper levels when disturbed by a sampling device. That would explain in particular the low abundances of *Apseudes latreillii* compared to those found for the same site in the spatial scale study.

The studied peracarid assemblage showed clear seasonal changes. There was a decline in the total abundances and numbers of species from autumn through winter for all orders of peracarids, while diversity and evenness indexes increased. This seasonality in peracarid assemblages is typical of temperate latitudes (Cunha et al. 1999; Moreira et al. 2008a; Ersoy Karaçuha et al. 2009). The reasons may be diverse: Frequent rains characterize winter and autumn periods at the area of study, altering the salinity conditions in estuarine habitats, and thus leading to changes in the benthic assemblages (Szedlmayer and Able 1996; Cunha et al. 1999). Furthermore, life histories with seasonal changes in reproductive activity and dispersal may explain variations of the benthic crustacean assemblages over the annual cycle (Cunha et al. 1999; Moreira et al. 2008a).

Fig. 4 Total abundance (individuals per m²) of *Phtisica marina*, *Gammarella fucicola*, *Uromunna* spp. and *Zeuxo holdichi* per sampling date at site D27

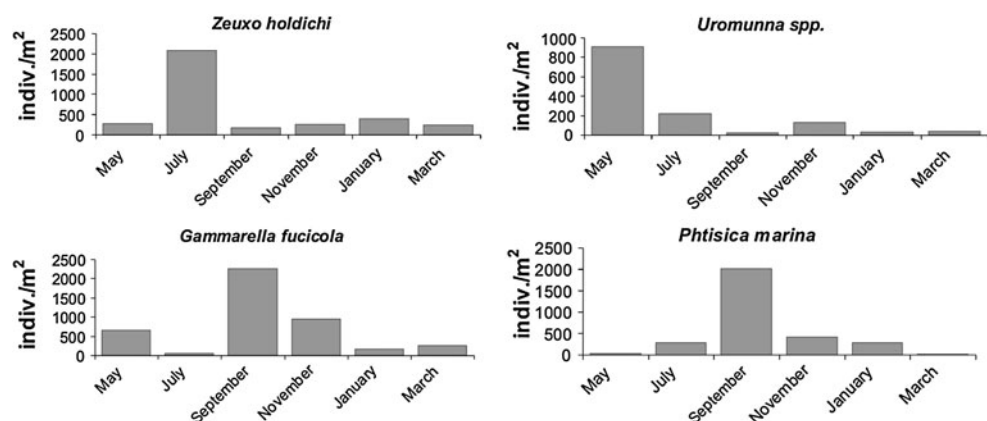
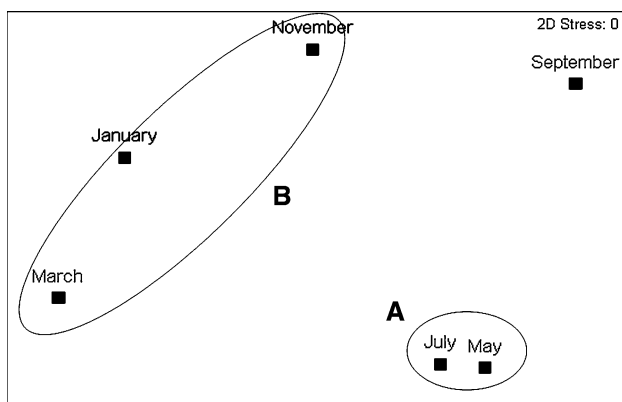


Table 4 Faunistic parameters for each sampling date at site D27

	<i>S</i>	<i>N</i>	<i>J'</i>	<i>H'</i>
May	40	925	0.64	3.39
July	33	1,146	0.52	2.63
September	42	1,911	0.52	2.82
November	38	876	0.64	3.36
January	35	499	0.70	3.59
March	33	411	0.68	3.41

S number of species; *N* total number of individuals (individuals/0.31 m²); *H'* Shannon–Wiener's diversity index; *J'* Pielou's evenness

**Fig. 5** nMDS ordination of bimonthly samples (centroids) collected at site D27 showing the groups determined by cluster analysis

In the present study, amphipods showed the highest number of species and made the greatest contribution to the total abundance. Amphipod populations also showed great fluctuations through the study period (Fig. 3). These results agree with those of other studies done in similar environments in the northern hemisphere (e.g. Gambi et al. 1992; Dias and Hassal 2005; Quiroz-Vázquez et al. 2005; Ersoy Karaçuha et al. 2009). Dias and Hassal (2005) suggested that amphipods living in seagrasses and feeding on (live or decaying) *Zostera* eat faster show higher growth rates and also may have larger broods than other groups such as isopods, which might contribute to the numerical dominance and seasonality of their populations.

The life history of the seagrasses can also affect associated organisms via seasonal fluctuations in organic matter supply and alterations of sedimentation rates (Jones et al. 1994; Quiroz-Vázquez et al. 2005; Böstrom et al. 2006; Hasegawa et al. 2008). In particular, *Zostera marina* shows

a clear seasonal dynamics, with elongation of the leaves and rhizomes in spring–summer and spreading of seeds in winter (Hasegawa et al. 2007). This may be reflected in changes of the peracarid faunas, as indicated by the present study. Indeed, some dominant species of the *Zostera* beds in the O Grove inlet (e.g. *Gammarella fucicola*, *Phtisica marina*, *Uromunna* spp. and *Aapseudes latreillii*, among others) showed great variations in density through seasons (Fig. 4). Guerra-García et al. (2001) reported similar fluctuations of densities for the caprellid, *P. marina*, influenced by the life cycle of the seaweed, which it is associated with. González et al. (2008) found a correlation between the abundance of *P. marina* and seagrass biomass in *Zostera* meadows. Likewise, high abundances of *G. fucicola* have been related to detritus accumulation in seagrass meadows right after the decay of the leaves (Lepoint et al. 2006). Furthermore, the increase in seagrass biomass favors the establishment of epiphytic algae, which bloom in August and provide additional food for secondary producers (Hasegawa et al. 2007). This leads to high rates of the secondary production, with grazers such as amphipods of the families Dexaminidae and Amphitoidae as well as most of the isopods reaching their greatest abundances after late summer (Fredette et al. 1990).

The life cycle of *Z. marina* has been reported to be coupled the breeding and development of certain peracarids. An illustrative example is given by Nakaoka (2002), who reported the tanaidacean *Zeuxo* not only feeding on *Z. marina* seeds, but also using the spathes for reproduction and nursery. Indeed, we found large numbers of *Zeuxo holdichi* in summer, just after the anthesis of the seagrass (Fig. 4).

In conclusion, peracarid assemblages in *Zostera* meadows in the O Grove inlet are rich and diversified. These findings from the subtidal benthic system of the Galician rias again demonstrate the important ecological role of the seagrasses. As the rias are strongly affected by urbanization and pollution, conservation of these peculiar habitats will be crucial for the preservation of the local biodiversity.

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Appendix

See Table 5.

Table 5 List of peracarid species found during the period of study

Order Amphipoda

Lysianassa ceratina (Walker, 1889)
Tryphosites longipes (Bate & Westwood, 1861)
Amphipoda indet.
Ampelisca spp.
Ampelisca brevicornis (A. Costa, 1853)
Ampelisca gibba Sars, 1882
Ampelisca serraticaudata Chevreux, 1888
Ampelisca spinifer Reid, 1951
Ampelisca spinipes Boek, 1861
Ampelisca tenuicornis Liljeborg, 1855
Ampelisca typica (Bate, 1856)
Amphilochus spencebatei (Stebbing, 1876)
Peltocoxa marioni Catta, 1875
Leucothoe incise Robertson, 1892
Leucothoe lilleborgi Boek, 1861
Leucothoe spinicarpa (Abildgaard, 1879)
Stenothoe monoculoides (Montagu, 1815)
Gammaridae indet.
Gammarus spp.
Gammarus crinicornis Stock, 1966
Gammarus insensibilis Stock, 1966
Gammarus tigrinus Sexton, 1939
Gammarella fucicola (Leach, 1814)
Abludomelita gladiosa (Bate, 1862)
Melita dentata (Kroyer, 1842)
Melita herguensis Reid, 1939
Melita palmata (Montagu, 1804)
Urothoe elegans (Bate, 1857)
Urothoe grimaldii Chevreux, 1895
Urothoe pulchela (Costa, 1853)
Periculodes aequimanus (Kossmann, 1880)
Periculodes longimanus (Bate & Westwood, 1868)
Harpinia spp.
Harpinia antennaria Meinert, 1890
Harpinia crenulata (Boeck, 1871)
Harpinia delavallei Chevreux, 1910
Harpinia laevis Sars, 1891
Harpinia pectinata Sars, 1891
Apherusa bispinosa (Bate, 1856)
Apherusa henneguyi Chevreux & Fage, 1925
Apherusa jurinei (Milne-Edwards, 1830)
Dexamine spinosa (Montagu, 1813)
Ampithoe spp.
Ampithoe gammaroides (Bate, 1856)
Ampithoe helleri Karaman, 1975
Ampithoe neglecta Lincoln, 1976
Ampithoe ramondi Audouin, 1826
Ampithoe rubricata (Montagu, 1808)
Sunamphitoe pelgica (Milne-Edwards, 1830)

Table 5 continued

Aoridae indet.
Lembos spp.
Lembos websteri Bate, 1857
Leptocheirus pilosus Zaddach, 1844
Microdeutopus spp.
Microdeutopus anomalus (Rathke, 1843)
Microdeutopus chelififer (Bate, 1862)
Microdeutopus damnoniensis (Bate, 1856)
Microdeutopus gryllotalpa Costa, 1853
Microdeutopus stationis Della Vale, 1893
Microdeutopus versiculatus (Bate, 1856)
Gammaropsis maculata (Johnston, 1827)
Gammaropsis sophiae (Boeck, 1861)
Gammaropsis palmata (Stebbing & Robertson, 1891)
Microprotopus maculatus Norman, 1867
Photis longipes (Della Valle, 1893)
Monocorophium spp.
Monocorophium ascherusicum (Costa, 1851)
Monocorophium insidiosum Crawford, 1937
Monocorophium sextoane Crawford, 1937
Siphonocetes kroyeranus Bate, 1856
Siphonocetes striatus Myers & McGrath, 1979
Siphonocetes sabatieri de Rouville, 1894
Colomastix pusilla Grube, 1861
Erichthonius punctatus (Bate, 1857)
Jassa falcata Montagu, 1808
Caprellidae indet.
Caprella sp.1
Caprella sp.2
Caprella equilibra Say, 1818
Caprella penatis Leach, 1814
Caprella acanthifera Leach, 1814
Pariambus typicus (Krøyer, 1884)
Phthisica marina Slabber, 1769
Pseudoprotella phasma Montagu, 1804
Order Isopoda
Arcturidae indet.
Astacilla longicornis (Sowerby, 1806)
Cyathura carinata (Krøyer, 1847)
Idotea spp.
Idotea baltica (Pallas, 1772)
Idotea chelipes (Pallas, 1776)
Idotea granulosa Rathke, 1843
Idotea neglecta Sars, 1897
Jaera albifrons Leach, 1814
Janira maculosa Leach, 1814
Janiropsis sp.
Munna spp.
Uromunna spp.
Lekanesphaera levii (Argano & Ponticelli, 1981)

Table 5 continued

Order Cumacea

- Bodotria pulchella* (Sars, 1879)
Iphinoe tenella Sars, 1878
Iphinoe trispinosa (Goodsir, 1843)
Nannastacidae indet.
Nannastacus spp.
Cumella spp.
Cumella pygmaea Sars, 1865
Pseudocuma longicorne (Bate, 1858)
Pseudocuma simile G.O. Sars, 1900

Order Tanaidacea

- Apseudopsis latreilli* (Milne-Edwards, 1828)
Apseudes talpa (Montagu, 1808)
Akanthophoreus gracilis (Krøyer, 1842)
Leptocheilia savignyi (Krøyer, 1842)
Tanaïs dulongii (Audouin, 1826)
Zeuxo holdichi Bamber, 1990

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Capítulo 2

Esquete P, Bamber RN, Moreira J, Troncoso JS. In press. Pycnogonids (Arthropoda: Pycnogonida) in seagrass meadows: The case of O Grove Inlet (NW Iberian Peninsula). *Thalassas*.

PICNOGÓNIDOS (ARTHROPODA: PYCNOGONIDA) EN PRADERAS DE FANERÓGAMAS: EL CASO DE LA ENSENADA DE O GROVE (N.O. DE LA PENÍNSULA IBÉRICA).

Resumen. La clase Pycnogonida es un grupo de artrópodos exclusivamente marinos, actualmente considerados como grupo hermano del resto de los Euarthropoda. Son organismos predominantemente bentónicos, que se alimentan de presas sésiles tales como hidrozoos, briozoos y algas. Hasta la fecha, son escasos los estudios cuantitativos que han tratado la ecología de los Picnogónidos. En este capítulo se estudia la fauna de picnogónidos presente en las praderas de *Zostera spp.* en un ambiente estuárico del noroeste de la península Ibérica, incluyendo su distribución espacial y las variaciones estacionales de densidad y diversidad. Los datos cuantitativos obtenidos muestran que la taxocenosis de Picnogónidos asociada a las fanerógamas es rica y diversa. Las especies mejor representadas en términos de abundancia y distribución son *Callipallene tiberi*, *Achelia echinata* y *Anoplodactylus pygmaeus*. Los valores de abundancia total muestran un patrón fuertemente estacional, con los mayores registros en el mes de Septiembre y los más bajos en Marzo. Las variaciones temporales en la abundancia de *A. echinata* sugieren un patente acoplamiento con el ciclo vital de *Zostera marina*, que se explica por la proliferación de epífitos que sirven de recurso alimentario para los Picnogónidos.

PYCNOGONIDS (ARTHROPODA: PYCNOGONIDA) IN SEAGRASS MEADOWS: THE CASE OF O GROVE INLET (NW IBERIAN PENINSULA)

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ABSTRACT

Quantitative studies dealing with the ecology of the Pycnogonida (Arthropoda) are scarce. In this work, the pycnogonid fauna present in the seagrass meadows (*Zostera* spp.) of an estuarine environment in NW Spain are studied, including spatial distribution and intra-annual seasonal variations of density and diversity. Quantitative sampling showed that the pycnogonid taxocoenosis associated with seagrass meadows was rich and diverse. The best represented species in terms of distribution and abundance were *Callipallene tiberi*, *Achelia echinata* and *Anoplodactylus pygmaeus*. Abundances showed a strongly seasonal pattern, with the highest values in September and lowest in March. Temporal variations in the population dynamics of *A. echinata* suggest a strong coupling with the life story of the seagrass *Zostera marina*, which in turn determines the availability of food resources for the pycnogonid assemblage.

KEYWORDS: Pycnogonida, diversity, distribution, seagrass, Atlantic Ocean

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INTRODUCTION

The class Pycnogonida is an exclusively marine group of arthropods also known as “sea spiders”, with no clear affinities to any other group and considered as a sister group to the rest of the Euarthropoda (Bamber, 2007; 2010). Pycnogonids are predominantly benthic, slow-moving organisms, and feed mainly on sessile prey such as algae, hydroids, actinians and bryozoans (Wyer and King, 1974; Bamber and Davis, 1982); generally, their abundances depend on the availability of food resources (Roberts, 1981; Arnaud and Bamber, 1987). Other factors such as salinity gradients (Wolff, 1976) and hydrodynamics (Munilla León and San Vicente, 2000) have also been reported to influence their local abundance and distribution.

Quantitative studies dealing with the ecology of pycnogonids are scarce (but see Wolff, 1976; Arnaud and Bamber, 1987 and references therein; Munilla, 1991; Pérez-Ruzafa and Munilla, 1991; Genzano, 2002; Soler i Menbrives et al., in press). In fact, most of the data available for tropical and temperate areas come from wider studies on benthic community ecology where pycnogonids are rarely found in high numbers; these data usually do not allow the determination of relevant patterns in their environmental needs, ecological role or population dynamics.

Seagrass meadows constitute complex habitats and are considered as “ecosystem engineers” because they favour the settlement and maintenance of high benthic species diversity in temperate and tropical waters (Montadouin and Sauriau, 2000; Hasegawa et al., 2008) including of pycnogonids (Arnaud and Bamber, 1987; Chimenz et al., 1993). However, pycnogonids may play an important role in seagrass meadows because of their feeding on sessile epibiont organisms which settle there; therefore, understanding their distribution patterns, habitat preferences and temporal dynamics will be necessary to assess the structure and functioning of assemblages inhabiting those habitats.

In this work, the composition and diversity of the pycnogonid assemblage present in the seagrass meadows (*Zostera marina* L. and *Z. noltii* Hornem.) of an estuarine environment (O Grove inlet, NW Spain) is studied quantitatively at a spatial and temporal scale. In particular, the dynamics and structure of a population of *Achelia echinata* is investigated and related to the presence and the life history of the seagrasses.

MATERIAL AND METHODS

The O Grove inlet is an estuarine environment situated in the northwest coast of the Iberian Peninsula between 42°41' –42°28'N and 09°01' –08°44'W. Most of its intertidal and shallow subtidal sediments are covered by meadows of *Zostera marina*

and *Z. noltii*. The area is subjected to seasonal freshwater inputs from several streams and a high level of precipitation in autumn/winter.

In December 1996, benthic samples were taken with the aim of characterizing the spatial distribution of the macrofaunal assemblages present in the meadows. Five replicate samples were taken from each of ten sites by means of a van Veen grab covering a total area of 0.28 m² for each site (Table 1); additional details on location and abiotic features of the sampling sites may be found in Esquete et al. (2010). A sample of the bottom water was taken by means of a Niskin bottle and salinity, temperature and pH were measured in situ.

In addition, samples were taken bimonthly between May 1998 and March 1999 at a subtidal *Z. marina* meadow (corresponding to site 3; see Table 1) to study the seasonal dynamics of the fauna. This site was selected for the good state of conservation of the *Zostera* meadow; furthermore, it was assumed that it would be less affected by salinity fluctuations than meadows situated in more sheltered areas. For this study, samples were taken by SCUBA divers, collecting five replicate quadrats of 0.065 m² in each occasion. The shoot and the rhizome fractions of the seagrass (the latter including the sediment) were kept separately in plastic bags and their fauna sorted separately. Abiotic parameters were measured following the same methodology as in the previous phase.

For both studies, samples were sieved through a 0.5 mm mesh and fixed in 10% buffered formalin. Specimens were later sorted, identified, and preserved in 70% ethanol. Specimens were measured using a stereomicroscope fitted with a micrometer eyepiece.

Pycnogonid classification follows that used by Bamber (2007; 2010). The body length of specimens was measured from the anterior margin of the cephalon to the posterior margin of the last lateral processes.

RESULTS

Spatial study

A total of 232 individuals belonging to 9 species was found in 9 out of 10 sampling sites in December 1996 (Table 1). The most abundant species was *Callipallene tiberi* (Dohrn, 1881) (85 individuals, 36.6% of total abundance) followed by *Achelia echinata* Hodge, 1864 (72 indiv., 31.0% of total abundance) and *Anoplodactylus pygmaeus* (Hodge, 1864) (56 indiv., 24.6% of total abundance) (Figure 1). These three species accounted for the 91% of the total pycnogonid abundance. The most widespread species in the inlet was *A. pygmaeus* (present in 8 out of 10 sites), followed by *C. tiberi* (7 sites).

	1	3	4	5	6	7	8	9	10	Total	D
<i>Achelia echinata</i>	6	37	11	-	3	7	2	6	-	72	31.0
<i>Nymphon gracile</i>	-	-	1	-	-	-	-	-	-	1	0.4
<i>Callipallene brevirostris</i>	-	-	-	1	-	-	-	-	-	1	0.4
<i>Callipallene emaciata</i>	-	-	-	3	-	-	-	3	3	9	3.9
<i>Callipallene spectrum</i>	-	-	-	2	-	-	2	-	-	4	1.7
<i>Callipallene tiberi</i>	-	10	2	40	1	-	14	10	8	85	36.6
<i>Anoplodactylus petiolatus</i>	2	-	-	-	-	-	-	-	-	2	0.9
<i>Anoplodactylus pygmaeus</i>	5	7	6	5	22	2	2	7	-	57	24.6
<i>Endeis spinosa</i>	1	-	-	-	-	-	-	-	-	1	0.4
Number of species	4	3	4	5	3	2	4	4	2	9	
Total abundance	14	54	20	51	26	9	20	26	12	232	
Seagrass	M	M	M	M/N	N	N	M/N	M/N	M/N		
Depth (m)	0.6	5.9	0.3	0.3	0.3	0.3	0.3	0.3	0.3		
pH	7.7	7.8	7.8	7.7	7.9	7.7	7.7	7.7	7.7		
Temperature (°C)	14.6	9.9	16.7	13.0	15.3	13.2	13.2	13.0	13.3		
Salinity (‰)	29.0	32.0	32.5	30.0	30.5	20.0	33.0	33.0	32.0		

Table 1. Pycnogonid species found at ten sites (1 to 10) in the O Grove inlet in December 1996 showing abundance per site (individuals/0.28 m²), total abundance, numerical dominance (D, %), seagrass species (*Z. marina*: M; *Z. noltii*: N) and values of selected environmental variables of seawater.

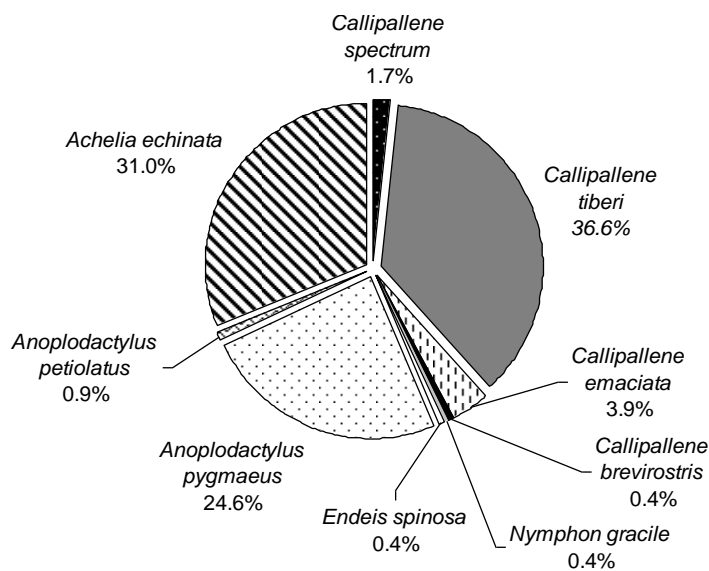


Figure 1. Total relative abundance (%) of pycnogonid species found in the O Grove inlet in December 1996.

Temporal study

During the studied period, 297 individuals belonging to 7 species were found (Table 2). *Achelia echinata* was by far the numerically dominant species, accounting for 72.1% of total abundance (214 individuals), followed by *Anoplodactylus pygmaeus* (13.1% of total abundance, 39 indiv.).

The maximal values of number of species and of individuals were obtained in September (88 individuals, 7 species); the lowest abundance was recorded in May (26 indiv.). *Achelia echinata* was present on all sampling occasions (6) followed by *A. pygmaeus*, *C. tiberi* and *N. gracile* (5 each).

	1998				1999		Total
	May	July	September	November	January	March	
<i>Achelia echinata</i>	14	36	63	42	34	25	214
<i>Nymphon gracile</i>	2	1	2	-	3	4	12
<i>Callipallene emaciata</i>	-	-	3	1	5	-	9
<i>Callipallene spectrum</i>	-	-	3	4	-	-	7
<i>Callipallene tiberi</i>	4	1	2	1	-	3	11
<i>Anoplodactylus pygmaeus</i>	6	-	13	7	11	2	39
<i>Endeis spinosa</i>	-	1	2	1	1	-	5
Number of species	4	4	7	6	5	4	7
Total abundance	26	39	88	56	54	34	297
Temperature (°C)	21.5	25.2	20.1	17.2	21.2	12.4	
pH	8.0	7.8	7.7	7.7	7.5	7.6	
Salinity (‰)	32.0	34.7	40.4	40.8	32.7	41.0	

Table 2. Pycnogonid species found in site 3 from May 1998 to March 1999, showing abundance per month (individuals/0.28 m²) for each species, total abundance and values of selected environmental variables of seawater.

SYSTEMATICS

Class PYCNOGONIDA Latreille, 1810

Family AMMOTHEIDAE Dohrn, 1881

Genus *Achelia* Hodge, 1864

Achelia echinata Hodge, 1864

Material examined.- Spatial study (December 1996): 6 ♀♀, site 1; 12 ♀♀, 23 ♂♂, 2 juveniles, site 3; 4 ♀♀, 3 ♂♂, 3 juveniles, site 4; 3 ♂♂, site 6; 7 ♂, site 7; 1 ♀, 1 ♂, site 8; 4 ♀♀, 1 ♂, 1 juvenile, site 9. Temporal study (site 3): 7 ♀♀, 2 ♂♂, 8 juveniles, May 1998; 5 ♀♀, 4 ♂♂, 13 juveniles, July 1998; 18 ♀♀, 13 ♂♂, 32 juveniles, September 1998; 11 ♀♀, 9 ♂♂, 21 juveniles, November 1998; 16 ♀♀, 8 ♂♂, 10 juveniles, January 1999; 15 ♀♀, 9 ♂♂, 1 juvenile, March 1999.

Body size.- ♀♀: 0.5-2 mm; ♂♂: 0.6-1.1 mm; juveniles: 0.3-0.9 mm.

Distribution.- Widely distributed in the north Atlantic and Mediterranean Sea, including around the Iberian coasts (De Haro, 1965; Munilla, 1987).

Remarks.- *Achelia echinata* is a common, abundant and widespread species in the north Atlantic. In the *Zostera* meadows of O Grove, this species was very abundant, particularly in the subtidal meadow corresponding to site 3 (Tables 1, 2). The temporal study at this site provided enough individuals to allow the examination of the population dynamics of this species. There was an increase in the number of individuals from spring through summer, reaching a maximum in September and declining through autumn and winter until the following spring. The highest proportion and numbers of juveniles were found in July, decreasing to a minimum in March (Figure 2). Gravid females were found throughout the year, although in small numbers (1-5 per sample); five ovigerous males were found in March.

Family NYMPHONIDAE Wilson, 1878

Genus *Nymphon* Fabricius, 1794

Nymphon gracile Leach, 1814

Material examined.- Temporal study (site 3): 2 unsexed specimens, May 1998; 1 unsexed spec., July 1998; 2 unsexed spec., September 1998; 3 unsexed spec., January 1999; 1 ♂, 3 unsexed spec., March 1999.

Body size.- 1.8-4.5 mm. ♂ with eggs 4.6 mm.

Distribution.- Atlantic and Mediterranean European waters. Iberian Peninsula: Cantabric coast (Munilla, 1987), Ría de Vigo (Anadón, 1975).

Remarks.- In March 1999, one male was found carrying four egg masses.

Family CALLIPALLENIDAE Hilton, 1942

Genus *Callipallene* Flynn, 1929

Callipallene brevirostris (Johnston, 1837)

Material examined.- Spatial study (December 1996): 1 ♂, 1.0 mm, site 5.

Distribution.- North Atlantic, Mediterranean and Black Sea. Iberian Peninsula: Alborán Sea and Gibraltar (Munilla, 1993).

Callipallene emaciata (Dohrn, 1881)

Material examined.- Spatial study (December 1996): 3 ♀♀, site 5; 3 ♀♀, site 9; 1 ♀, 2 juveniles, site 10. Temporal study (site 3): 1 ♂, 1 ♀, 1 juvenile, September 1998; 1 juvenile, November 1998; 5 ♀♀, January 1999.

Body size.- ♀♀ 0.8-1.1 mm; ♂♂ 1.2 mm; juveniles 0.6 mm.

Distribution.- North-east Atlantic and Mediterranean Sea. Iberian Peninsula: Cantabric coast (Munilla, 1987), Ría de Vigo (Anadón, 1975), Gibraltar (Munilla, 1988), Mediterranean coast (Munilla, 1991).

Callipallene spectrum (Dohrn, 1881)

Material examined.- Spatial study (December 1996): 1 ♀, 1 ♂, site 5; 1 ♀, 1 ♂, site 8. Temporal study (site 3): 1 ♀, 2 ♂♂, September 1998; 1 ♂, 3 ♀♀, November 1998.

Body size.- ♀♀ 0.9-1.2 mm; ♂♂ 1.0-1.2 mm.

Distribution.- South of Great Britain, Atlantic coast of Spain, Mediterranean Sea (De Haro, 1965; Munilla, 1993).

***Callipallene tiberi* (Dohrn, 1881)**

Material examined.- Spatial study (December 1996): 9 ♀♀, 1 ♂, site 3; 2 ♀, site 4; 35 ♀♀, 4 ♂♂, 1 juvenile, site 5; 1 ♀, site 6; 13 ♀♀, 1 ♂, site 8; 6 ♀♀, 1 ♂, 3 juveniles, site 9; 7 ♀♀, 1 ♂, site 10. Temporal study (site 3): 1 ♀, 1 ♂, 2 juveniles, May 1998; 1 ♀, July 1998; 2 ♀♀, September 1998; 1 ♀, November 1998; 2 ♀♀, 1 ♂, March 1999.

Body size.- ♀♀ 0.8-1.3 mm; ♂♂ 1-1.2 mm; juveniles 0.6-0.7 mm.

Distribution.- British Isles, Mediterranean Sea, Canary Islands. Iberian Peninsula: SE Iberian Peninsula and Gibraltar strait (Munilla, 1991), Mediterranean coast (Munilla León and San Vicente, 2000).

Family PHOXICHILIDIIDAE Sars, 1891

Genus *Anoplodactylus* Wilson, 1878

***Anoplodactylus petiolatus* (Hodge, 1864)**

Material examined.- Spatial study (December 1996): 2 ♀♀, 1 mm, site 1.

Distribution.- Widely distributed from western to eastern Atlantic, Mediterranean and Black seas. Iberian Peninsula: Cantabric coast (Munilla, 1987), Galician Rías (Moreira and Troncoso, 2007), SE Iberian Peninsula, Gibraltar strait (Munilla 1993), Mediterranean coast (De Haro, 1967).

Anoplodactylus pygmaeus (Hodge, 1864)

Material examined.- Spatial study (December 1996): 3 ♀♀, 1 ♂, 1 juvenile, site ; 3 ♀♀, 4 ♂♂, site 3; 6 ♀♀, site 4; 1 ♀, 4 ♂♂, site 5; 13 ♀♀, 9 ♂♂, site 6; 1 ♀, 1 ♂, site 7; 2 ♀♀, site 8; 5 ♀♀, 1 ♂, 1 juvenile, site 9; 1 ♀, site 10. Temporal study (site 3): 4 ♀♀, 1 ♂, 1 juvenile, May 1998; 8 ♀♀, 3 ♂♂, 2 juveniles, September 1998; 4 ♀♀, 2 ♂♂, 1 juvenile, November 1998; 5 ♀♀, 5 ♂♂, 1 juvenile, January 1999; 2 ♀♀, March 1999.

Body size.- ♀♀ 0.6-0.8 mm; ♂♂ 0.7 mm.

Distribution.- Amphiatlantic, Mediterranean and Red seas. Iberian Peninsula: Cantabric coast (Munilla, 1987), Mediterranean coast (Pérez-Ruzafa and Munilla, 1992).

Remarks.- One ovigerous male and one gravid female were found in September 1998.

Family ENDEIDAE Norman, 1908

Genus *Endeis* Philippi, 1843

Endeis spinosa (Montagu, 1808)

Material examined.- Spatial study (December 1996): 1 ♀, site 3. Temporal study (site 3): 1 ♀, July 1998; 2 ♀♀, September 1998; 1 ♀, November 1998; 1 ♂, January 1999.

Body size.- ♀♀ 1.8-2.2 mm; ♂♂: 2.3 mm.

Distribution.- Widespread Amphiatlantic species. Iberian Peninsula: Cantabric Coast (Munilla, 1987), Ría de Vigo (Anadón, 1975), Gibraltar (Munilla, 1993), Mediterranean coast (De Haro, 1965).

Remarks.- One specimen collected in July 1998 presented one leg of the third pair abnormally small, about $\frac{1}{4}$ of the normal length.

DISCUSSION

The pycnogonid taxocoenosis found in the *Zostera* meadows of the O Grove inlet comprises species typical of European shallow environments (Arnaud and Bamber, 1987). The studied *Zostera* meadows have a richer pycnogonid fauna than those present in other shallow habitats and sedimentary substrata in the Galician rías. For example, Moreira and Troncoso (2007) and Cacabelos et al. (2009), using an identical methodology, only found two and four pycnogonid species in nearby inlets, respectively, and in much lower numbers. Likewise, extensive studies carried out in other European estuarine areas have reported similar assemblages to those found in O Grove, but characterized by lower densities for most of the species (Wolff, 1976; Pérez- Ruzafa and Munilla, 1992). In general, hard substrata with seaweed biocoenoses host more diverse assemblages (e. g. Munilla, 1991; Chimenz et al., 1993) than unvegetated sedimentary bottoms which tend to be poor in pycnogonid faunas (Chimenz and Cotarelli, 1986; Pérez Ruzafa and Munilla, 1992; Chimenz et al., 1993). However, most studies point out that pycnogonids are well represented in soft bottoms when covered by seagrass meadows (e. g. De Haro, 1967; Wolff, 1976; Arnaud and Bamber, 1987; Chimenz et al., 1993; Munilla León and San Vicente, 2000). Moreover, those have also been proposed as a “source” habitat for pycnogonids to colonise adjacent habitats (Munilla and San Vicente, 2000).

The abundance of pycnogonids in O Grove showed great seasonal fluctuations, with the highest numbers of species and individuals in September and the lowest values in spring. Particularly, in the case of *A. echinata*, the highest numbers and proportion of juveniles occurred in July, followed by a substantial increase of the total abundance of the population in September. This indicates a high rate of survival of juveniles during the summer. Likewise, the subsequent population decreased in the following sampling periods coupled with a high number of juveniles; this suggests, on the one hand, low rates of survival of adults in autumn and, in the other hand, an ongoing recruitment of juveniles through autumn. In winter-spring, the population reaches the minimum in total numbers and percentage of juveniles, suggesting that the conditions are not favourable for reproduction and survival. These results are similar to those found by Jarvis and King (1978), who pointed out that juvenile stages of *A. echinata* appear in

April and reach a maximum in August. In contrast, Munilla León (1980) found a maximum of juveniles in April, and minimum values in August-September, and suggested that such differences between different populations of the same species are due to variations in environmental conditions.

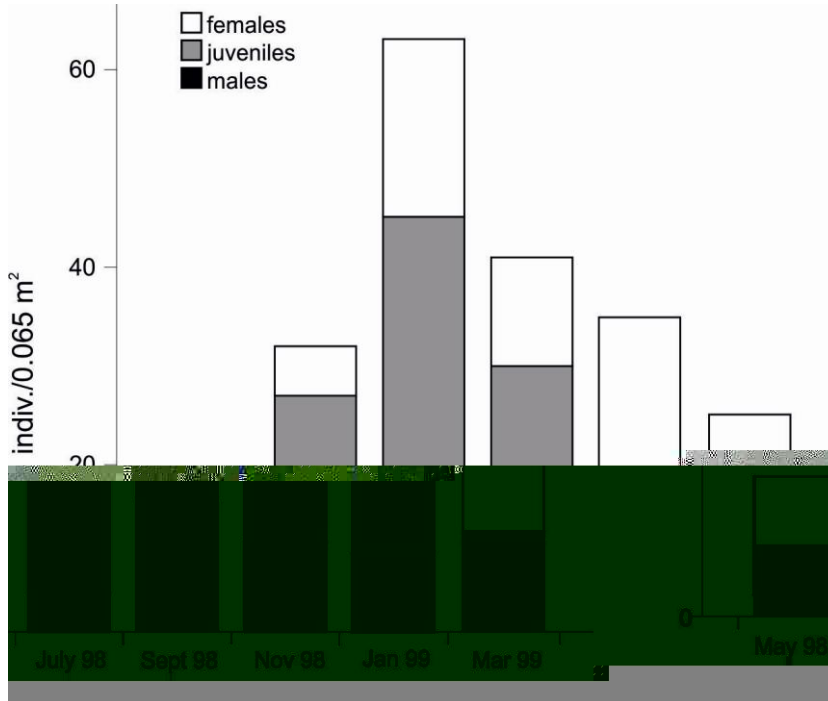


Figure 2.- Abundance (individuals/0.28 m²) of juveniles, adult females and adult males of *Achelia echinata* in site 3 from May 1998 to March 1999.

The temporal dynamics of *A. echinata* in particular (Figure 2) and that of the whole pycnogonid taxocoenosis in general (Table 2) seems to be coupled with the life cycle of *Z. marina*; thus, the seagrass shows elongation of leaves and rhizomes in spring-summer and dispersion of seeds in winter (Hasegawa et al., 2007). This coincidence of the maximal values of pycnogonid density and those of the above-ground biomass of the seagrass can be explained by the subsequent increase of surface available for epiphytic algae, hydroids and bryozoans that occurs when leaves are enlarged; these epiphytes, which bloom in August, provide a significant increase in food resources (Böstrom et al, 2006; Hasegawa et al., *opus cit.*) from which the populations of pycnogonids may benefit, therefore reaching their greatest abundances after late summer. Similarly, the highest proportions and numbers of juvenile stages coincide with this bloom of epiphytes, suggesting that the reproductive period occurs in the months previous to the maximum of food availability. Seasonal variations in abundances of secondary producers in seagrass meadows, linked to the life history of the plant and abundance of epiphytic food-species has been verified for a number of benthic zoological groups (e. g. Edgar, 1990; Böstrom et al, 2006). Indeed, previous

studies in the O Grove meadows have also shown similar fluctuations for gastropods, bivalves and several polychaete families (Quintas, 2005), isopods and amphipods (Esquete et al., in press).

In conclusion, the present study suggests that the presence of the seagrass favours the availability of food resources for pycnogonids, thereby allowing a higher diversity than in other non-vegetated habitats. Similarly, the seasonal evolution of the *Zostera* meadow would entirely determine the seasonal variations in diversity and abundance of the pycnogonids.

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Capítulo 3

Esquete P, Moreira J, Troncoso JS. 2010. First record of *Perioculodes aequimanus* (Crustacea: Amphipoda) in the north-east Atlantic, with remarks on taxonomic characters. *Marine Biodiversity Records* 3: e112.

PRIMERA CITA DE *PERIOCULODES AEQUIMANUS* (CRUSTACEA: AMPHIPODA) EN EL ATLÁNTICO NORDESTE, CON OBSERVACIONES SOBRE SUS CARACTERES TAXONÓMICOS.

Resumen. En este capítulo se documenta por primera vez la presencia del anfípodo *Periiculodes aequimanus* en el nordeste atlántico. Los ejemplares fueron recolectados en las praderas de fanerógamas de la ensenada de O Grove (noroeste de la península Ibérica), donde la especie está bien establecida y es uno de los peracáridos dominantes en términos de abundancia. Se han observado ciertas diferencias morfológicas con los individuos mediterráneos, si bien han sido consideradas dentro del rango de variación intraespecífica. Esta especie se distingue de otras especies atlánticas del género de acuerdo a las características del propodio del primer gnatópodo, la primera coxa, la base del pereópodo 7 y el pedúnculo de las antenas.

First record of *Periocolodes aequimanus* (Crustacea: Amphipoda) in the north-east Atlantic, with remarks on taxonomic characters

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In this work, we report for the first time the presence of the amphipod Periocolodes aequimanus from the north-east Atlantic. Specimens were collected in Zostera meadows located in the O grove inlet (north-western Iberian Peninsula), where the species is well established and is one of the numerically dominant peracarid species. Some morphological differences were found in comparison to Mediterranean individuals but those are regarded as due to intraspecific variation. This species can be distinguished from other Atlantic species according to the features of the propodus of the first gnathopod, the first coxa, the pereopod 7 basis and the antennal peduncle.

Keywords: Amphipoda, *Periocolodes aequimanus*, distribution, *Zostera*, north-east Atlantic

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INTRODUCTION

Periocolodes aequimanus (Kossmann, 1880) is an oedicerotid amphipod that inhabits sedimentary bottoms (Ledoyer, 1993). This species was described from the Red Sea (Kossmann, 1880, as *Oedicerus aequimanus*), and later reported from the Suez Canal (Schellenberg, 1928). There are records of this species along the Mediterranean Sea, from the Israel coasts (Sorbe *et al.*, 2002), Cyprus (Kocatas *et al.*, 2001), Aegean Sea (Ledoyer, 1993; Baxevanis & Chintiroglou, 2000; Antoniadou *et al.*, 2004; Dağlı *et al.*, 2008), Adriatic Sea (Ledoyer, 1993; Dondi *et al.*, 2003), Tyrrhenian Sea (Ledoyer, 1993; Sparla *et al.*, 1993), the Tunisian coast (Ledoyer, 1993; Zakhama-Sraieb *et al.*, 2009), France (Ledoyer, 1972, 1993) and eastern Iberian Peninsula (Cartes & Sorbe, 1999; Munilla & San Vicente, 2005).

To date, the only species of the genus *Periocolodes* Sars, 1895 reported from Atlantic European waters is *Periocolodes longimanus* (Bate & Westwood, 1868). Although there have been records of *P. aequimanus* for the Indian Ocean (Ledoyer, 1986), this species was later considered as having a distribution circumscribed to the Mediterranean and Red Seas (Ledoyer, 1993). A record pending confirmation from Brazil (Serejo, 1998, as *Periocolodes cf. aequimanus*) would expand the distribution of this species to the western Atlantic.

An examination of samples from sediments collected in the O Grove inlet (Galicia, north-western Spain) during 1996

yielded a number of specimens identified as *P. aequimanus*. This confirms, therefore, the presence of *P. aequimanus* in the Atlantic Ocean, and represents its first record for the eastern Atlantic.

MATERIALS AND METHODS

Benthic samples were taken at the O Grove, an estuarine inlet located on the north-west Atlantic coast of the Iberian Peninsula, between 42°41'–42°28'N and 9°01'–8°44'W. Most of its intertidal and shallow subtidal sediments are covered by meadows of *Zostera marina* L. and *Z. noltii* Hornem. In December 1996, ten sites were sampled by means of a van Veen grab in order to characterize the macrofaunal assemblages of these meadows. Five replicate samples were taken at each site, thus covering a total area of 0.28 m² for each site. Samples were sieved through a 0.5-mm mesh and fixed in 10% formalin for later sorting and identification of the fauna. An additional sample was taken at each site for granulometric analyses and to determine calcium carbonate content (% estimated by treatment with hydrochloric acid) and organic matter content (TOM, %, estimated from the weight loss after placing samples in a furnace for 4 hours, at 450°C). Salinity, pH and temperature measurements were taken *in situ*.

Line drawings of *Periocolodes aequimanus* were done with a camera lucida connected to a light microscope. Length of the individuals was measured from the rostrum to the posterior margin of the third epimeral plate. Nomenclature follows that used by Ledoyer (1993). Six specimens were deposited in the Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN).

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SYSTEMATICS

Order AMPHIPODA Latreille, 1816
 Suborder GAMMARIDEA Latreille, 1802
 Family OEDICEROTIDAE Lilljeborg, 1865
 Genus *Periocolodes* Sars, 1895
Periocolodes aequimanus (Kossmann, 1880)
 (Figures 1–3)

Oedicerus aequimanus Kossmann, 1880, 130, pl. 13, figures 6–8.

Periocolodes aequimanus Schellenberg, 1928, 641, figure 200. Ledoyer, 1972, 775, figure 1. Ledoyer, 1993, 600, figure 412.

MATERIAL EXAMINED

Specimens totalling 288 (1.85% of total amphipod abundance): 12 ♀♀, 2 ♂♂, 14 juveniles, 42°29.12'N 08°50.25'W, mud with *Zostera marina*, 0.8 m, coll. J.S. Troncoso, 11 December 1996; 5 ♀♀, 42°28.75'N 08°50.75'W, fine sand with rests of shells and *Z. marina*, 0.3 m, coll. J.S. Troncoso, 4 December 1996; 5 ♀♀, 2 juveniles, 42°29.75'N 08°50.25'W, mud with *Z. marina*, 5.9 m, coll. J.S. Troncoso, 4 December 1996; 6 ♀♀, 1 ♂, 1 juvenile, 42°28.25'N 08°50.75'W, fine sand with *Z. marina*, 0.3 m, coll. J.S. Troncoso, 11 December 1996; 1 ♀, 42°27.75'N 08°51.25'W, mud with *Z. marina* and *Z. noltii*, 0.3 m, coll. J.S. Troncoso, 18 December 1996; 8 ♀♀, 1 ♂, 2 juveniles, 42°27.75'N 08°51.25'W, fine sand with *Z. noltii*, 0.3 m, coll. J.S. Troncoso, 11 December 1996; 39 ♀♀, 5 ♂♂, 11 juveniles, 42°27.25'N 08°52.25'W, mud, 0.3 m, coll. J.S. Troncoso, 18 December 1996; 3 ♀♀ (MNCN 20.04/8371), 63 ♀♀, 7 ♂♂, 32 juveniles, 42°27.25'N 08°51.25'W, mud with *Z. marina* and *Z. noltii*, 0.3 m, coll. J.S. Troncoso, 18 December 1996; 1 ♀ and 2 ♂♂ (MNCN 20.04/8419), 40 ♀♀, 4 ♂♂, 21 juveniles, 42°27.25'N 08°51.75'W, mud with *Z. marina* and *Z. noltii*, 0.3 m, coll. J.S. Troncoso, 18 December 1996.

ADDITIONAL COMPARATIVE MATERIAL

Periocolodes longimanus (Bate & Westwood, 1868). Fifty-nine specimens: 33 ♀♀, 1 ovigerous ♀, 4 ♂♂, 7 juveniles, 42°29.12'N 08°50.25'W, mud with *Z. marina*, 0.8 m, coll. J.S. Troncoso, 11 December 1996; 2 ♀♀, 1 unsexed, 42°28.75'N 08°50.75'W, fine sand with rests of shells and *Z. marina*, 0.3 m, coll. J.S. Troncoso, 4 December 1996; 3 ♀♀, 1 ♂, 42°29.75'N 08°50.25'W, mud with *Z. marina*, 5.9 m, coll. J.S. Troncoso, 4 December 1996; 3 ♀♀, 1 ♂, 42°28.25'N 08°50.75'W, fine sand with *Z. marina*, 0.3 m, coll. J.S. Troncoso, 11 December 1996; 2 ♀♀, 1 ♂, 42°27.75'N 08°51.25'W, mud with *Z. marina* and *Z. noltii*, 0.3 m, coll. J.S. Troncoso, 18 December 1996.

DESCRIPTION

Female: body length of 1.5–4.0 mm. Head with rostrum, downturned (Figure 2A). Eyes coalesced, large; often not defined in preserved specimens. Antenna 1 peduncular articles 1–3 subequal in length, flagellum—six-articulated (Figure 2B). Antenna 2 flagellum short—five-articulated (Figure 2C). Mandible with six spines (Figure 2F, G). Maxilla 1 inner lobe with one setule (Figure 2H). Maxilla 2 bilobed, reduced, with terminal setae (Figure 2I). Maxilliped

basic (Figure 2J). Gnathopods subchelated, carpal lobe long and narrow, reaching beyond end of propodus. Palm delimited by one stout spine (Figure 3A, B). Gnathopod 1 propodus ovate, 2.1–2.5 times as long as broad (Figure 3A). Gnathopod 2 propodus longer, three times as long as wide (Figure 3B). Coxa 1 oblique, with pronounced anterior distal margin (Figure 3A). Coxa 3 slightly concave on distal margin (Figure 3C). Coxa 4 with 3–4 long setae on posterodistal corner (Figure 3D). Pereiopod 3 (Figure 3E) and four dactylus at least half of length of propodus. Pereiopods 5 and 6 (Figure 3F) basis ovate, bearing long plumose setae and not plumose setae. Pereiopod 7 distinctly longer, basis not broadened (Figure 3G). Telson entire, ovate, bearing a pair of small setae (Figure 3H). Uropod 1 peduncle long, subequal in length with rami (Figure 3I). Uropod 2 reaching end of uropod 3. Uropods rami subequal. No ovigerous female in samples examined.

Male: antenna 1 peduncular articles 2 and 3 of same length. Antennal flagellum with six articles; first article approximately twice in length than the others (Figure 2D). Antenna 2 flagellum long, up to 20–30 articulated articles; articles longer than wide (Figure 2E). Antenna 2 of fully developed males reaching half or more of body length. Otherwise males similar to females. Male:female ratio: 1:6–1:10 (for any given sample with at least one male and > 10 individuals).

Subadults/juvenile stages: antennal flagellum sometimes reduced in specimens <2.5 mm long; females with antenna 1 and two flagellum with 4–5 articles. In subadult males, antenna 2 flagellum short, reaching less than 1/3 of body length; articles wider than long. Gnathopod 1 propodus stout, 1.5–2 times as long as wide.

HABITAT

This species was found in *Zostera* meadows on sediments which are mainly composed of muddy sand, with high percentages of fine and very fine sand (up to 64.6% and 47.9%, respectively), and silt/clay (up to 61.6%). Content in organic matter was high (up to 15.55%), whereas content in calcium carbonate was low (<10.5%). Salinity was relatively low (20–33‰). Values of the studied variables and number of individuals at each sampling site are detailed in Table 1.

REMARKS

There are some morphological differences of Atlantic specimens when compared with the diagnosis reported by Ledoyer (1972, 1993) for Mediterranean specimens. Thus, in our specimens, coxa 4 (Figure 3D) presents 3–4 long setae in the posterodistal margin, while Mediterranean individuals have only small setae along the distal margin. The basis of pereiopod 3 is notably broadened in Mediterranean specimens, but only slightly broadened in specimens from the O Grove (Figure 3E). Nevertheless, the features of gnathopod 1 and coxa 1 (Figure 3A), the basis of the pereiopod 7 (Figure 3G) and the antennal peduncle (Figure 2B–E) are those typical of *Periocolodes aequimanus*.

The other European species, *P. longimanus*, is very similar to *P. aequimanus* but differs in the following features: the length of the peduncle articles of antenna 1, the propodus of gnathopod 1 is more than four times longer than wide, the coxa 1 is rounded and not produced, the basis of pereiopod 3 is distinctively narrower, and the basis of pereiopod 7 is broadened (Ledoyer, 1993).

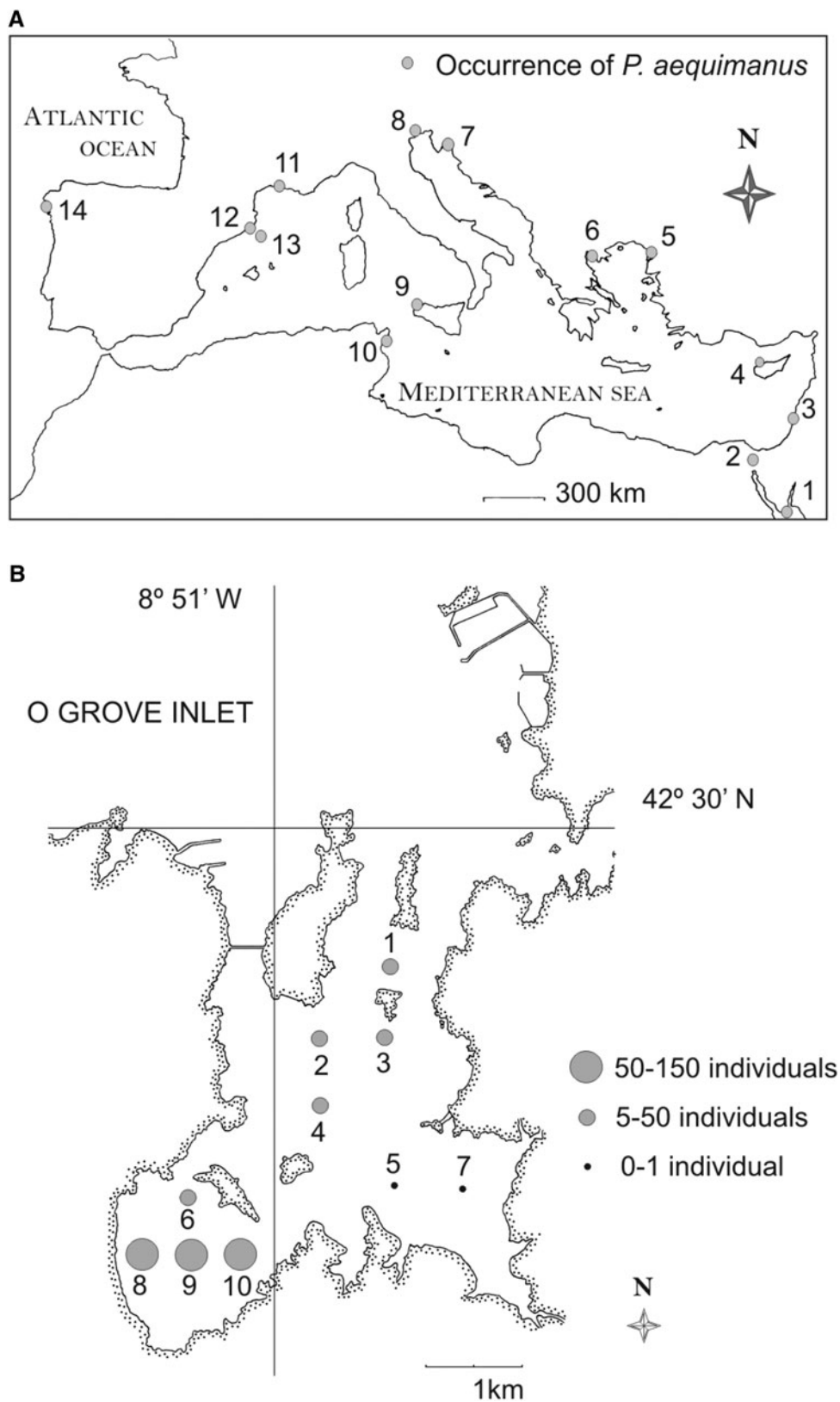


Fig. 1. (A) Records of *Perioculodes aequimanus* in European waters, including this study: 1, Red Sea (Kossmann, 1880); 2, Suez Canal (Schellenberg, 1982); 3, Israel coasts (Sorbe *et al.*, 2002); 4, Cyprus (Kocatas *et al.*, 2001); 5, Tunisian coasts (Dağlı *et al.*, 2008); 6, Aegean Sea (Ledoyer, 1993; Baxevanis & Chintiroglou, 2000; Antoniadou *et al.*, 2004); 7&8, Adriatic Sea (Ledoyer, 1993; Dondi *et al.*, 2003); 9, Sicily (Sparla *et al.*, 1993); 10, Tunisian coasts (Ledoyer, 1993; Zakhama-Sraieb *et al.*, 2009); 11, French coasts (Ledoyer, 1972, 1993); 12&13, eastern Iberian Peninsula (Cartes & Sorbe, 1999; Munilla & San Vicente, 2005, respectively); 14, Galician coast (this study); (B) location of the O Grove inlet showing the position of the sampling sites and numbers of individuals of *P. aequimanus* found at each site.

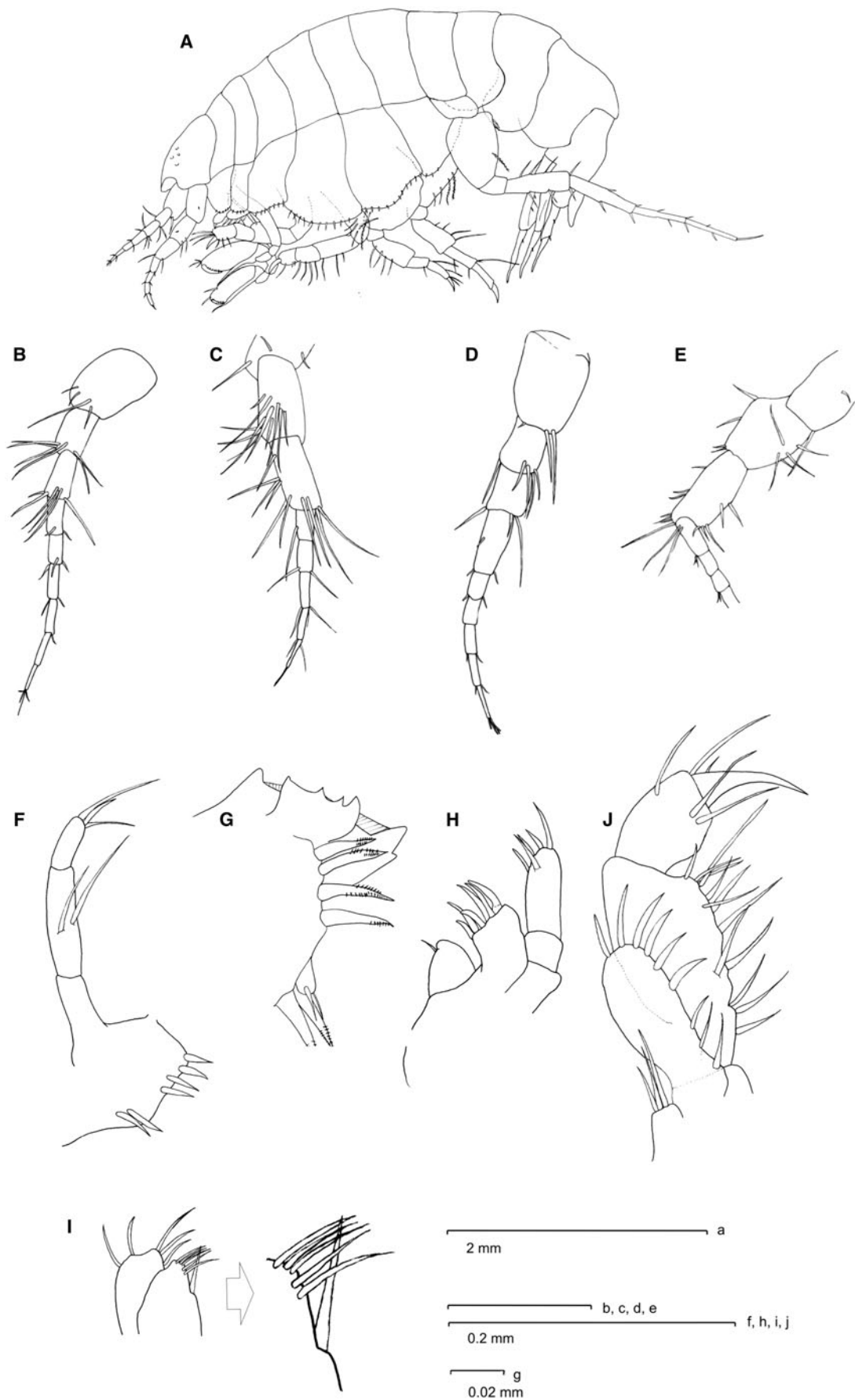


Fig. 2. *Pericolodes aequimanus*. Female: (A) entire animal, lateral view; (B) antenna 1; (C) antenna 2. Male: (D) antenna 1; (E) antenna 2. Female: (F) mandibular palp; (G) detail of the mandible; (H) maxilla 1; (I) maxilla 2; (J) maxilliped.

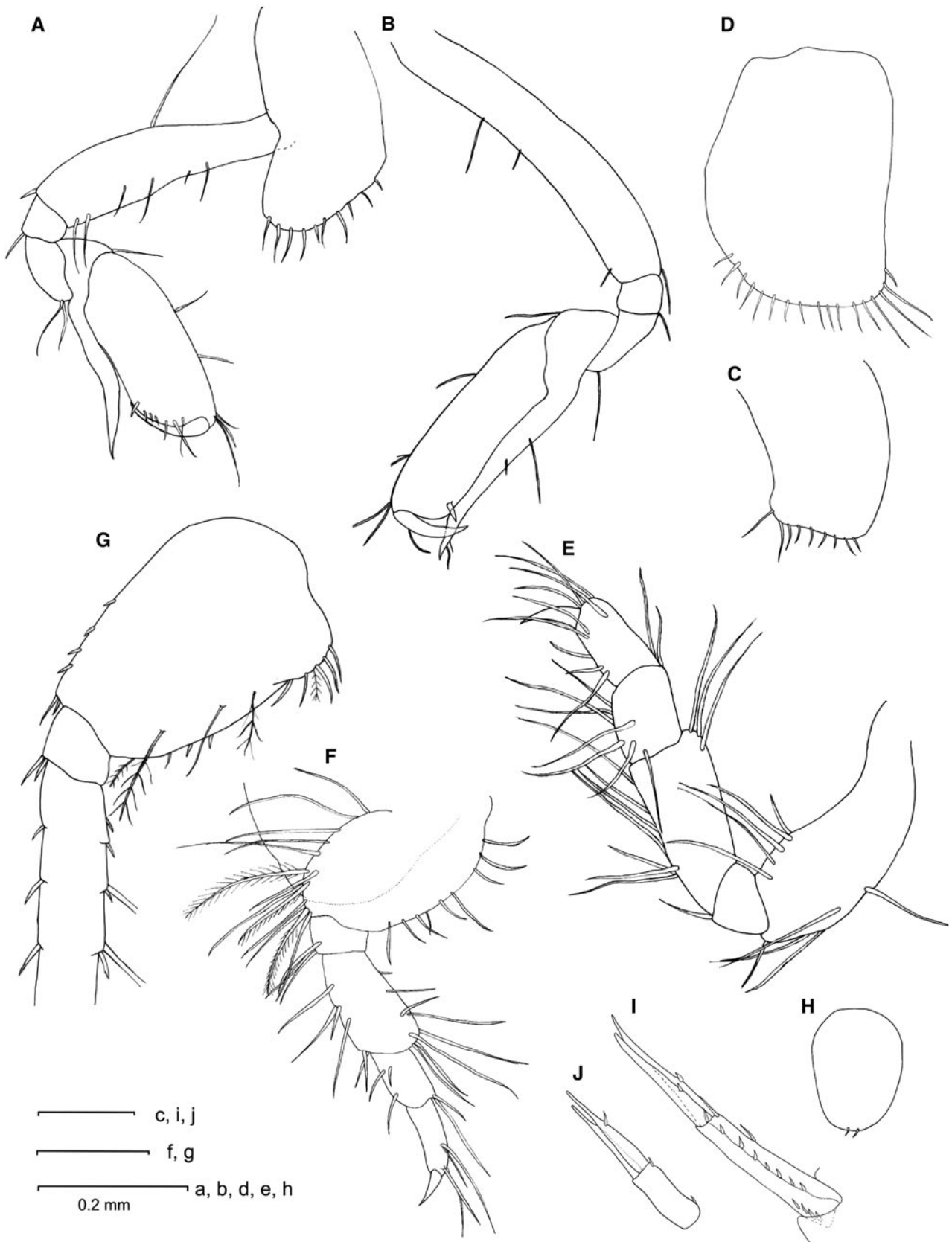


Fig. 3. *Perioculodes aequimanus*. Female: (A) gnathopod 1; (B) gnathopod 2; (C) coxa 3; (D) coxa 4; (E) pereopod 3; (F) pereopod 5; (G) pereopod 7; (H) telson; (I) uropod 1; (J) uropod 3.

Table 1. Environmental variables and number of individuals (ind 0.28 m²) of *Periculodes aequimanus* and *P. longimanus* at each sampling site. Granulometric fractions expressed in percentages (%).

Variable	Sampling site									
	1	2	3	4	5	6	7	8	9	10
Depth	0.8	0.3	5.9	0.3	0.3	0.3	0.3	0.3	0.3	0.3
T sed. (°C)	12.50	11.10	11.60	13.40	12.70	13.50	12.90	12.60	12.70	12.80
T bottom water (°C)	14.60	10.00	9.90	16.70	13.00	15.30	13.20	13.20	13.00	13.30
pH sed.	7.36	7.53	7.41	7.39	7.27	7.46	7.20	7.30	7.29	7.26
pH bottom water	7.76	7.90	7.85	7.81	7.74	7.89	7.74	7.71	7.70	7.73
Salinity (‰)	29.00	30.00	32.00	32.50	30.00	30.50	20.00	33.00	33.00	32.00
Gravel (<2 mm)	1.87	4.44	0.38	1.95	0.23	0.68	1.03	5.77	1.05	22.38
Very coarse sand (2–1 mm)	0.50	2.38	0.21	0.57	0.14	0.53	0.36	1.09	0.37	3.95
Coarse sand (1–0.5 mm)	0.97	4.56	0.45	0.91	1.83	1.54	1.86	2.81	1.00	5.00
Medium sand (0.5–0.25 mm)	3.82	10.19	2.37	4.76	10.97	14.48	3.88	5.13	4.72	9.71
Fine sand (0.25–0.125 mm)	40.14	46.14	37.80	58.03	20.85	64.63	11.77	18.51	43.58	18.36
Very fine sand (0.125–0.063 mm)	40.68	25.89	47.89	23.20	33.93	11.40	19.49	29.66	31.07	13.17
Silt/clay (<0.063 mm)	12.01	6.41	10.90	10.59	32.05	6.75	61.61	37.02	18.22	27.44
Q ₅₀	0.12	0.17	0.11	0.16	0.18	0.19	0.10	0.11	0.13	0.18
S ₀	1.52	1.50	1.48	1.45	1.82	1.30	2.31	1.70	1.61	1.99
TOM %	3.93	1.37	2.98	2.80	5.08	1.32	15.55	10.75	3.32	7.10
Carbonate content (%)	7.58	10.05	8.46	8.69	7.22	10.46	5.41	7.40	9.59	7.17
<i>Periculodes aequimanus</i> (Kossmann, 1880)	28	5	7	8	1	11	–	55	105	68
<i>Periculodes longimanus</i> (Bate & Westwood, 1868)	45	3	4	4	3	–	–	–	–	–

T sed., temperature of the sediment; T bottom water, temperature of the bottom water; pH sed., pH of the sediment; pH bottom, pH of the bottom water; Q₅₀, median grain size, S₀, sorting coefficient; TOM, total organic matter.

DISCUSSION

In general, the morphological characteristics of the Atlantic specimens examined here fit well with those described by Ledoyer (1972, 1993) for the Mediterranean *Periculodes aequimanus*, although with minor differences. Serejo (1998) found similar differences in a single specimen from Brazilian coasts, which she identified as *Periculodes cf. aequimanus*. The distal border of coxa 4 and pereopod 3 basis (Figure 3D, E) are similar in Brazilian and Iberian specimens; gnathopod 2 propodus (Figure 3B) is, however, shorter and wider in the Brazilian specimens than in those from north-west Spain. Morphological variability (e.g. number of setae, body size) is frequent between individuals from one species undergoing different conditions or inhabiting different regions (Berezina, 2007). Therefore, we consider that the minor differences found between our material and the specimens described from the Mediterranean and the Red Sea should be considered as intraspecific variations.

Taking the aforementioned intraspecific variations into account, we conclude that the shape of gnathopod 1 propodus, coxa 1, the pereopod 7 basis and the antennal peduncle can be considered the main diagnostic characters for the identification of this species, as well as for differentiation from other species within the genus. On the other hand, early juvenile or small specimens (<2 mm), in which most of the taxonomic characters are slightly or not defined at all and the antennae are not properly developed, could only be distinguished because of the oval and stout shape of the gnathopod 1 propodus.

The examination of individuals of various sizes and the range of definition of the morphological characters show that the specimens from north-west Spain have several levels of development. Besides, a high number of individuals were found in the samples (Figure 1; Table 1), even when compared with most of the aforementioned studies. These two circumstances lead to the conclusion that *P. aequimanus*

is a well-established species in the O Grove inlet, and consequently we infer that the environmental conditions in this inlet are adequate for the development of the species. Nevertheless, little is described about the ecology of this species in the available literature.

In general, *P. aequimanus* is found in warm-temperate waters (i.e. the Mediterranean Sea, the Red Sea and the coast of Brazil). However, the seawater off the north-west coast of the Iberian Peninsula is often colder than in those areas, suggesting that the temperature tolerance of this species is wider than previously thought. A recent record from the Catalonia continental slope (western Mediterranean; Cartes & Sorbe, 1999) supports this idea. On the other hand, our study seems to confirm that the preferred habitat for *P. aequimanus* corresponds to sedimentary bottoms of sheltered, shallow areas, according to most of the records for this species (Bellan-Santini, 1998; Dondi *et al.*, 2003; Antoniadou *et al.*, 2004; Basset *et al.*, 2006; Dağlı *et al.*, 2008). Indeed, in our samples, this species is much more abundant in Sites 8, 9 and 10 which are sheltered from oceanic influence and the seasonal freshwater streams that affect, for instance, Sites 5 and 7 (Figure 1). Besides, no specimens were collected at Site 7, the closest to these streams, which could indicate either that *P. aequimanus* does not tolerate frequent changes in salinity or rather the hydrodynamics derived from the freshwater flux. The nature of the substratum does not, however, seem to be a limiting condition for *P. aequimanus*; according to Ledoyer (1993) and Bellan-Santini (1998) this species can be found in a range of sedimentary types, from muddy sands to coarse sand and gravels. Other substrata on which this species has been cited include 'Amphioxus sands' (Antoniadou *et al.*, 2004), the sponge *Dysidea fragilis* (Serejo, 1998), aegagropylae of red algae (Sparla *et al.*, 1993) and artificial hard substratum (Baxevis & Chintiroglou, 2000). Other conditions, such as the high organic matter content or the presence of the seagrasses could contribute to the

maintenance of high densities of *P. aequimanus* in the O Grove inlet, but further data are necessary to test these observations.

In addition, *Periculodes longimanus* is also present in the O Grove inlet but in smaller numbers, and is absent in those sites in which *P. aequimanus* is more abundant (Table 1). The lack of data on large-scale temporal variations of the benthic assemblage at the studied area does not allow further conclusions, but benthic studies done in nearby areas (Sánchez-Mata *et al.*, 1993; Lourido *et al.*, 2008; Moreira *et al.*, 2008a, b; Cacabelos *et al.*, 2010) do frequently report *P. longimanus*, sometimes in large numbers, indicating that this species is common in sedimentary bottoms in north-west Spain. This fact could be related to competitive exclusion among these species, as was previously reported for other benthic taxa introduced in the O Grove as a consequence of ship transport, shellfish culture and trade (Rolán, 1992; Bañón *et al.*, 2008). Nevertheless, experimental work would be needed to explore that possibility.

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Capítulo 4

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REDESCRIPCIÓN Y DESARROLLO POSTMARSUPIAL DE *APSEUDOPSIS LATREILLII* (CRUSTACEA: TANAIDACEA).

Resumen. *Apseudopsis latreillii* es un Tanaidáceo común y ampliamente distribuido en el Atlántico nordeste. A pesar de ello, los trabajos previos sobre la especie no han discriminado adecuadamente los caracteres que definen su diagnóstico. Del mismo modo, la variación intraespecífica relacionada con los estadios de desarrollo no ha sido descrita hasta el momento. El conocimiento de esta variación es necesario debido a la dificultad que presenta la identificación de los juveniles, que aparecen frecuentemente en gran número en muestras recogidas en determinados sustratos; este hecho se ve agravado particularmente cuando es posible la presencia de varias especies simpátricas del mismo género. En este capítulo se describen ejemplares procedentes de tres localidades diferentes del Atlántico nordeste y se estudia la talla de 766 individuos. El estudio del desarrollo postmarsupial muestra que el primer estadio es una manca II a la que siguen dos estadios juveniles antes de alcanzar la madurez. Los machos presentan dos morfologías diferenciadas. Tras un estadio preparatorio, las hembras pasan por una secuencia de estadios copulatorios seguidos de estadios intermedios en los cuales el individuo pierde el ovisaco tras la liberación de las mancas. Los caracteres que permiten la distinción de los ejemplares de *A. latreillii*, independientemente del estadio de desarrollo del individuo, son las siguientes: rostro apuntado y doblado hacia abajo, pereonitos sin apófisis, tres espinas ventrales en el propodio y una dorsal en el mero del pereópodo 1.

Redescription and postmarsupial development of *Apseudopsis latreillii* (Crustacea: Tanaidacea)

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Apseudopsis latreillii is a common tanaidacean species widely-distributed in the north-east Atlantic, but its diagnostic characters remain unspecified. Furthermore, intraspecific variation in relation to its developmental stages has not been described. Knowledge about this variation is needed owing to the difficulty of identification of the significant number of juvenile specimens within samples, particularly when sympatric with other apseuid species. Specimens from three different localities of the north-east Atlantic have been examined, and the size of 766 individuals has been measured. Study of postmarsupial development shows that the manca II is followed by two juvenile stages before reaching maturity. Males present two possible morphologies. After a preparatory stage, females pass through a sequence of copulatory instars followed by intermediate stages in which the female loses the ovisac after manca release. Characters allowing the distinction of *A. latreillii* specimens regardless of developmental stage are the combination of a pointed and downturned rostrum, pereonites without apophyses, three ventral spines on the pereopod 1 propodus, and one dorsodistal spine on the merus.

Keywords: Tanaidacea, Apseudomorpha, *Apseudopsis latreillii*, development, manca, juvenile, preparatory, copulatory, fecundity

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INTRODUCTION

Apseudopsis latreillii (Milne-Edwards, 1828) is a common, widely-distributed tanaidacean species of the north-east Atlantic and Mediterranean coastal waters (Riggio, 1996). It inhabits sandy and muddy bottoms from the intertidal to 138 m, and has been reported in a variety of habitats, including seagrass meadows, seaweeds, estuaries and sandy beaches (Holdich & Jones, 1983a; De-la-Ossa-Carretero, 2010; Bamber, 2011). This species is often locally found in large numbers, representing an important component of benthic assemblages (Riggio *et al.*, 1996; Lourido *et al.*, 2008; Moreira *et al.*, 2008; Esquete *et al.*, 2011).

The species was first described by Milne-Edwards (1828) as *Rhæa latreillii*, from a specimen dredged near Port Louis, Brittany, on the Atlantic coast of France (Milne-Edwards, 1840; Bate & Westwood, 1868). Bate & Westwood (1868) gave a brief description and a figure of an ovigerous female attributed to this species (as *Apseudes latreillii*) on the basis of features of its rostrum, cheliped and first pereopod (which they termed the second pereopod), based on a single specimen sent to them by A.M. Norman, which they recorded as having been collected in Northumberland (north-east England) although this was a *lapsus calami* on their part (see Norman & Brady, 1909). The same specimen was in the collection

used by Sars (1886) to redescribe *Apseudes latreillii*, distinguishing it from *Apseudes talpa* (Montagu, 1808). This was the first detailed description of the species, and was accompanied with accurate figures. Sars' description (1886) differed from the original in the number of segments of the inner flagellum of the antennule, and in the spination of the first pereopod. In spite of these discrepancies, Sars' description is considered valid, and has been used to distinguish *A. latreillii* from other new, morphologically similar species (Băcescu, 1961; Sieg, 1983; Gutu, 2001, 2002). Recently, Gutu (2006) transferred *A. latreillii* to the genus *Apseudopsis* Norman, 1899.

Nevertheless, the diagnostic characters for *A. latreillii* remain unspecified, and full details of its morphology (i.e. mouthparts, pleopods, hyposphenia and pereopods 2 to 4) have never been given. Furthermore, intraspecific variations have not yet been described.

Although juveniles often represent the majority of the individuals within a population, descriptions of early developmental stages of crustaceans are rare in the literature. Knowledge about intraspecific variation between developmental stages is needed owing to the difficulty of identification of the significant number of juvenile specimens within a sample, particularly when sympatric with other apseuid species. There are cases where an excessive number of species has been described within a genus, based erroneously on intraspecific variations resulting from dimorphic characters or meristic differences between juveniles and adults (Gardiner, 1975; Bamber, 2010).

In this study, *A. latreilli* is fully redescribed and the postmarsupial development is investigated. The ultimate objectives were to determine those characters that can be used as

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diagnostic of the species, as well as those that can be used to recognize the developmental stage of a specimen. Finally, a theoretical scheme of the life history of *A. latreillii* is proposed based on the data obtained.

MATERIALS AND METHODS

Specimens were collected from O Grove inlet (north-west Iberian Peninsula; 42°41'–42°28'N 9°01'–8°44'W). Most of the intertidal and shallow subtidal sediments of the inlet are covered by meadows of *Zostera marina* L. and *Z. noltii* Hornem. In December 1996, benthic samples were taken in those *Zostera* meadows using a van Veen grab, in order to characterize the macrofaunal assemblages. Five replicate samples were taken at each site, representing a total area of 0.28 m² for each site. Samples were sieved through a 0.5 mm mesh and fixed in 10% formalin for later sorting and identification of the fauna.

Additional material examined included 31 individuals collected in 2010 in the Isles of Scilly, south-west England (see Bamber, 2011), and two specimens (one male and one female) deposited in the invertebrate collection of the Muséum National d'Histoire Naturelle (Paris, MNHN). The type material could not be found in the collection of any European museum, and consequently we can consider it lost.

Line drawings were created using a camera lucida connected to a microscope. The total lengths (from the tip of the rostrum to the end of the telson) of all individuals yielded by a single grab (766 individuals) were measured in order to obtain a significant sample of the population. Measurements were made using a stereomicroscope (Nikon SMZ-1500) connected directly to a computer with an image analyser (Nikon, NIS-Elements). Incomplete or heavily damaged individuals were excluded.

Fecundity was calculated according to Messing (1983), as the median number of offspring per ovigerous female determined as the number of eggs or larvae in the marsupium in one sample. Those with a damaged marsupium were excluded because part of the brood may have been lost.

Statistical analyses were performed using the IBM SPSS 19 software package.

Morphological terminology follows that of Bamber & Shearer (2005). Serially repetitive body-parts, such as the subdivisions of the antennal flagella and of the uropod rami are segments, while those with independent musculature (such as the parts of the pereopods) are articles. Measurements are made axially, dorsally on the body and antennae, and laterally on other appendages.

Identification of the postmarsupial developmental stages followed Gardiner (1975), Messing (1983) and Pereira Leite & Pereira Leite (1997).

RESULTS

The type material could not be found in any European collection; therefore, we accept Bate and Westwood's assumption that their material was indeed the *Rhæa latreillii* of Milne-Edwards (Bate & Westwood, 1868). Consequently, Sars' description (1886) should be accepted as corresponding to the same species.

The material deposited in the MNHN by Bate and Westwood and those from Isles of Scilly and O Grove did not show any significant morphological differences, and could be attributed to the *A. latreillii sensu* Sars (1886) and that described by Holdich & Jones (1983b). Moreover, the specimens examined from southern England and western France can be considered to originate from sites close to the type locality cited by Milne-Edwards (1828, 1840; also Bate & Westwood, 1868). As a result, in spite of discrepancies with the original description and in absence of type material, we can conclude that all these specimens are, effectively, *Apseudopsis latreillii* (Milne-Edwards, 1828).

Consequently, a female specimen from the MNHN has been designated as a neotype (MNHN-Ta 87), and a male (MNHN-Ta 88) as an alloneotype.

SYSTEMATICS

- Order TANAIIDACEA Dana, 1849
- Suborder APSEUDOMORPHA Sieg, 1980
- Family APSEUDIDAE Leach, 1814
- Subfamily APSEUDINAE Leach, 1814
- Genus *Apseudopsis* Norman, 1899
(Figures 1–11)
- Apseudopsis latreillii* (Milne-Edwards, 1828)

Rhæa Latreillii Milne-Edwards, 1828, pp. 287–301, pl. xiii. A, figures 1–8.

Rhæa Latreillii Milne-Edwards, 1840, p. 141.

Apseudes latreillii Bate & Westwood, 1868, p. 153.

Apseudes latreillii Sars, 1882, p. 14.

Apseudes latreillii Sars, 1886, pp. 82–84, pl. XVI.

Non *Apseudes latreillii*, Claus, 1888, pp. 319–333, figures 1–19 (= *Apseudes acutifrons* Sars, 1882).

Apseudes latreillei Lister, 1909, p. 477.

Apseudes latreillii Băcescu, 1961, p. 160, figure 4, pl. 1.

Apseudes latreillii Holdich & Jones, 1983b, pp. 30–31, figure 7.

Apseudes latreillii Sieg, 1983, pp. 61–66.

Apseudes latreillii Riggio, 1996, p. 614–615.

Apseudes latreillei Gutu, 2001, p. 62.

Apseudopsis latreillii Gutu, 2006, p. 61.

MATERIAL EXAMINED

North-west Iberian Peninsula

81 ♀♀, 14 ♂♂, 226 juveniles and manca, 42°29.12'N 08°50.25'W, mud with *Zostera marina*, 0.8 m, coll. J.S. Troncoso, 11 December 1996; 40 ♀♀, 10 ♂♂, 141 juveniles and manca, 42°28.75'N 08°50.75'W, fine sand with shells and *Z. marina*, 0.3 m, coll. J.S. Troncoso, 4 December 1996; 1152 ♀♀, 165 ♂♂, 2681 juveniles and manca, 42°29.75'N 08°50.25'W, mud with *Z. marina*, 5.9 m, coll. J.S. Troncoso, 4 December 1996; 134 ♀♀, 17 ♂♂, 486 juveniles and manca, 42°28.25'N 08°50.75'W, fine sand with *Z. marina*, 0.3 m, coll. J.S. Troncoso, 11 December 1996.

St Martin's, Isles of Scilly, England

16 ♀♀, 5 ♂♂, 10 juveniles, 49°57.55'N 06°17.76'W, LWST clean sand, coll. R.N. Bamber, 11 September 2010.

Petit Nord, France

Neotype: 1 ovigerous ♀ (MNHN-Ta 87), colls. C. Bate and J.O. Westwood, August 1895. Alloneotype: 1 ♂ (MNHN-Ta 88), coll. E.L. Bouvier.

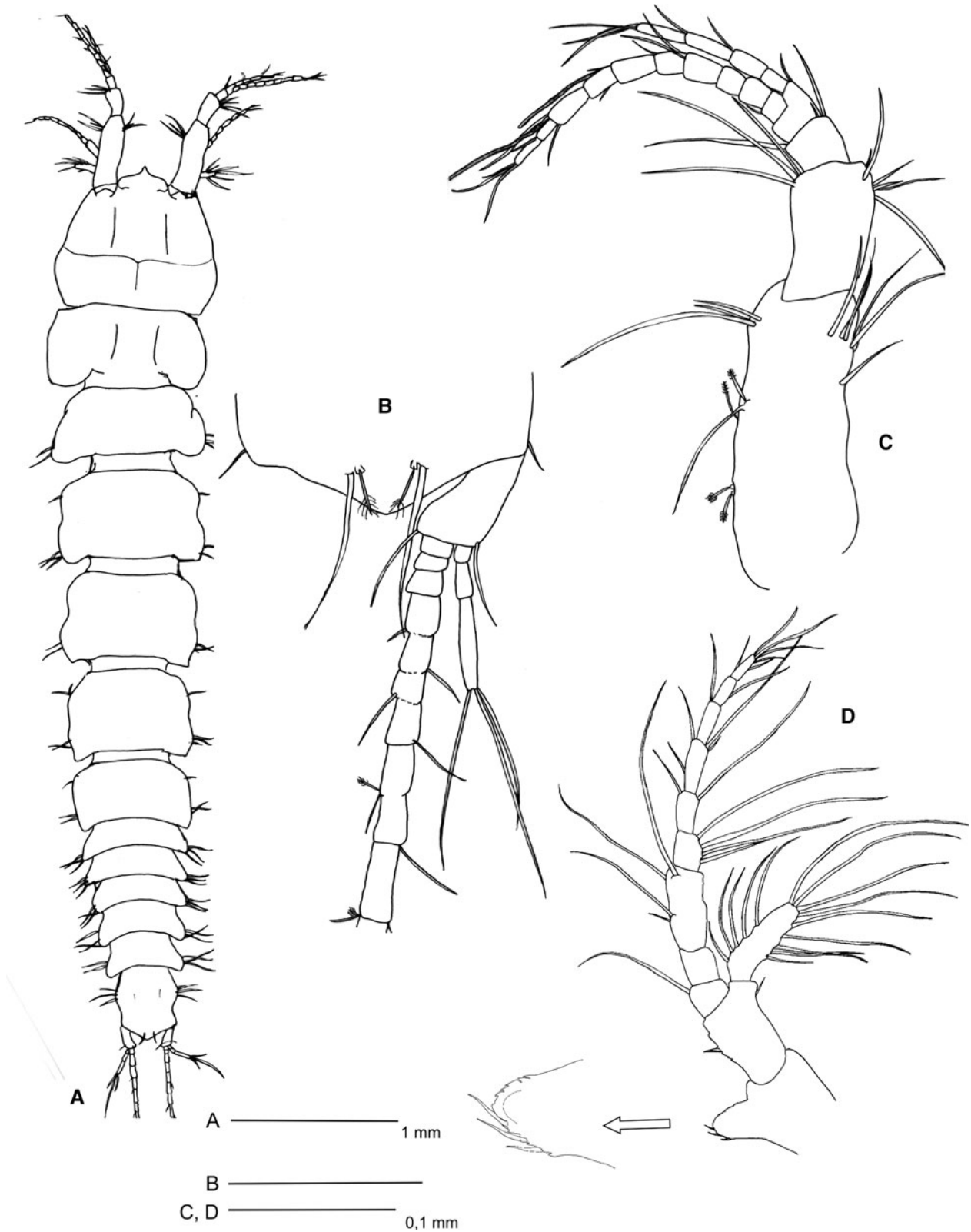


Fig. 1. *Apseudopsis latreillii*: preparatory female. (A) Dorsal view; (B) pleotelson and right uropod; (C) left antennule; (D) right antenna.

REDESCRIPTION

Female with oostegites

Total length: 3.2–5.5 mm. Body dorsoventrally flattened, elongated, slightly narrowed posteriorly, 5.7 times as long as wide. Carapace as broad as long; rostrum pointed and slightly

downturned, with rounded ‘shoulders’. Ocular lobes present, pointed. Eyes present. All pereonites with rounded corners, and setae on anterolateral and posterolateral margins. First pereonite shorter than the rest, with two posterolateral lobes. Second pereonite trapezoidal. Third to sixth pereonites



Fig. 2. *Apseudopsis latreillii*: preparatory female. (A) Labrum; (B) left mandible; (C) detail of the left mandible; (D) detail of the right mandible; (E) mandibular palp; (F) maxillule; (G) maxillular palp; (H) maxilla.

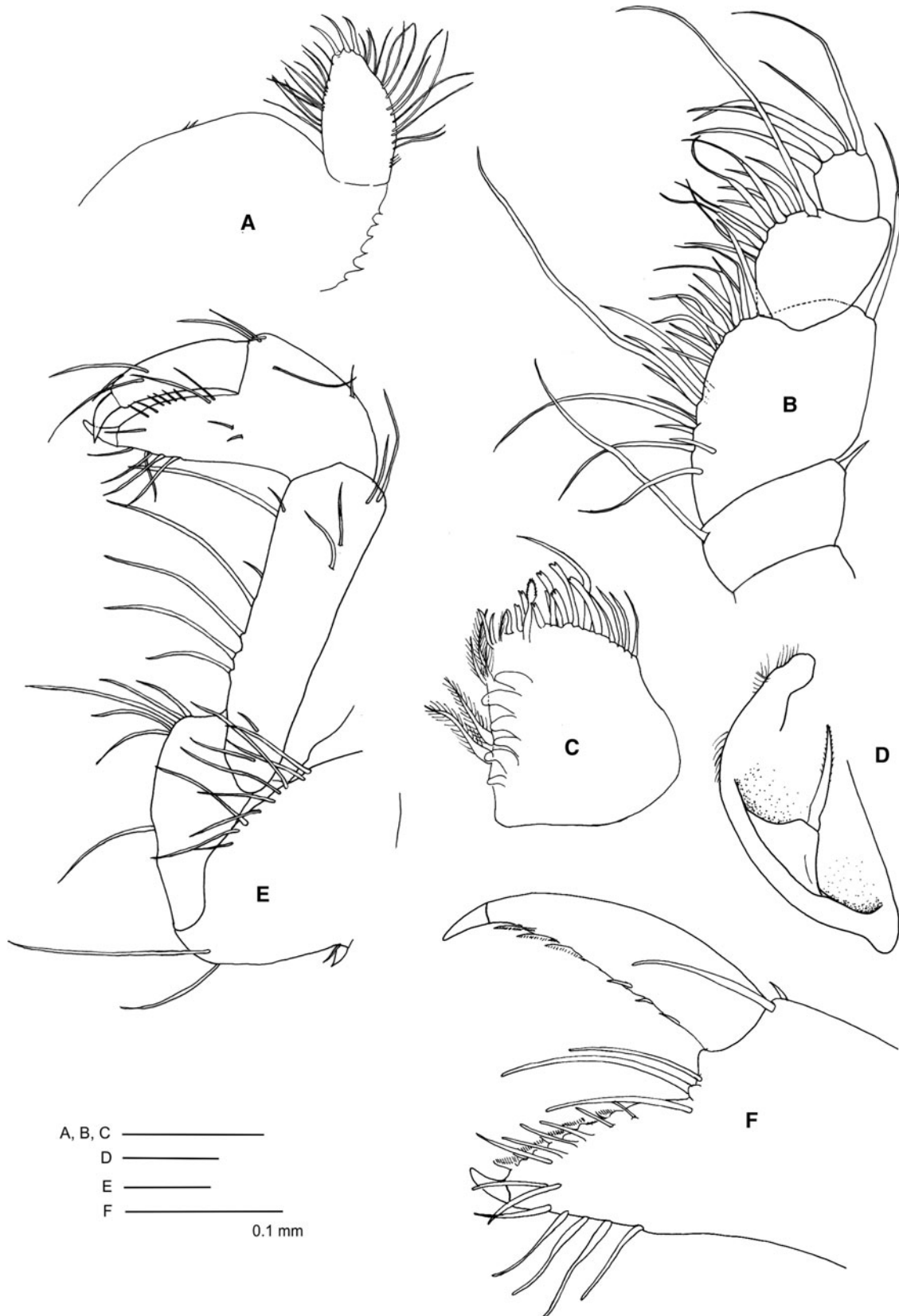


Fig. 3. *Apseudopsis latreillii*: preparatory female. (A) Labium; (B) maxilliped; (C) maxilliped endite; (D) epignath; (E) cheliped; (F) chela.

subquadrangular; fourth and fifth subequal (Figure 1A). Ventral hyposphenia present on pereonites 2 to 6. Pleon one-quarter of total length, longer than wide. Pleonites subequal,

narrower posteriorly and with ventral hypophyses. Lateral margins of all pleonites produced posteriorly, bearing lateral setae. Pleotelson as long as broad, bearing a group of 4 setae

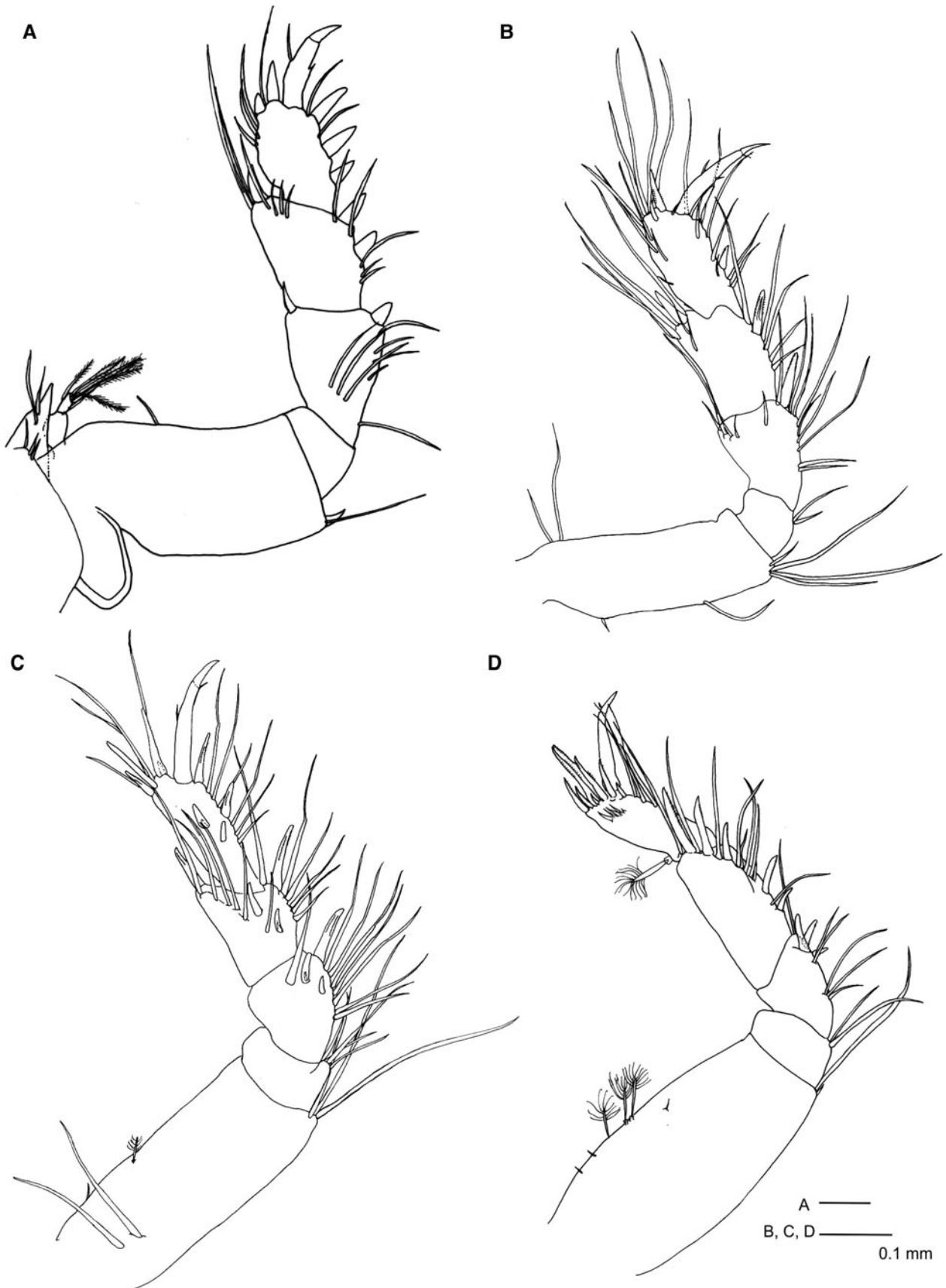


Fig. 4. *Apseudopsis latreillii*: preparatory female. (A) Pereopod 1; (B) pereopod 2; (C) pereopod 3; (D) pereopod 4.

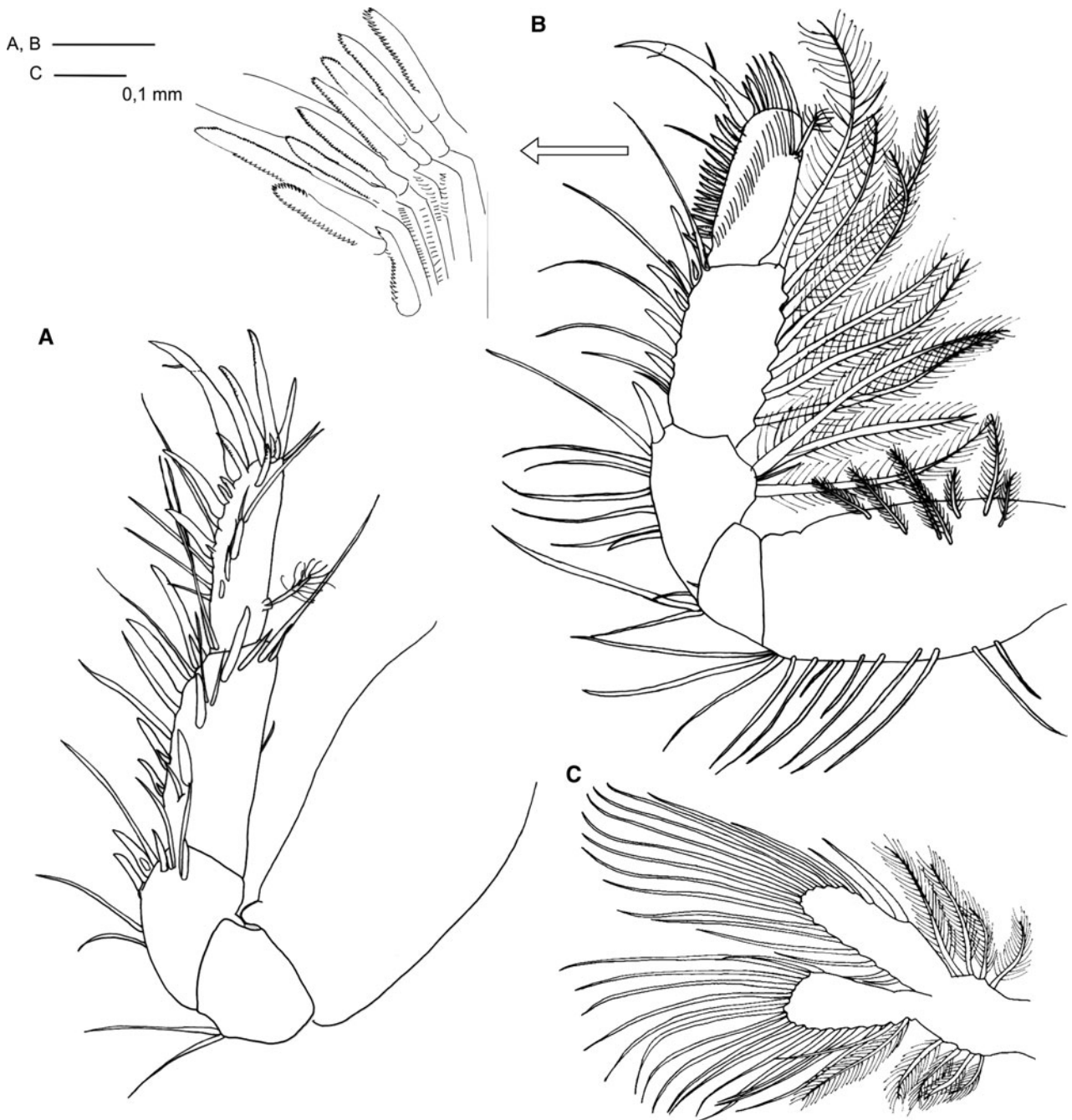


Fig. 5. *Apseudopsis latreillii*: preparatory female. (A) Pereopod 5; (B) pereopod 6; (C) pleopod 1.

on two dorsolateral protuberances (Figure 1A), two small setae on posterolateral margins, and one pair of subterminal long setae and one pair of penicillate setae (Figure 1B).

Antennule peduncle 4-articled; first article 3.7 times as long as wide, with two pairs of penicillate setae on outer margin, two medial marginal setae, and two distal groups of setae. Second article half length of first, twice as long as wide, with inner and outer distal tufts of setae. Third article one-third length of second, as long as wide, with single inner and outer distal setae. Fourth article L-shaped, as long as preceding article. Main flagellum of 10 segments, segments 6 and 8 bearing one aesthetasc each. Accessory flagellum 4-segmented (Figure 1C).

Antennal peduncle 5-articled; first article as long as wide, with an inner, serrated lobe bearing 1–3 small setae. Second

article 1.3 times as long as preceding, and 1.5 times as long as wide, bearing outer squama with marginal, long setae; inner margin denticulated, bearing one small seta. Third and fourth articles subequal, quadrangular, and $1/3$ length of second. Fifth article 1.3 times as long as the two preceding articles together, with one medial, long seta and two long, distal setae. Flagellum of 6 segments, first with four, second and third with one long, outer setae. Terminal segment bearing terminal setae (Figure 1D).

Mouthparts: labrum (Figure 2A) bilobed, setulose. Left mandible (Figure 2B) with strongly dentated pars incisiva and lacinia mobilis, setiferous lobe with 4–5 bifurcate and trifurcate setae; pars molaris crenulated, setulose (Figure 2C). Right mandible (Figure 2D) as left but without lacinia

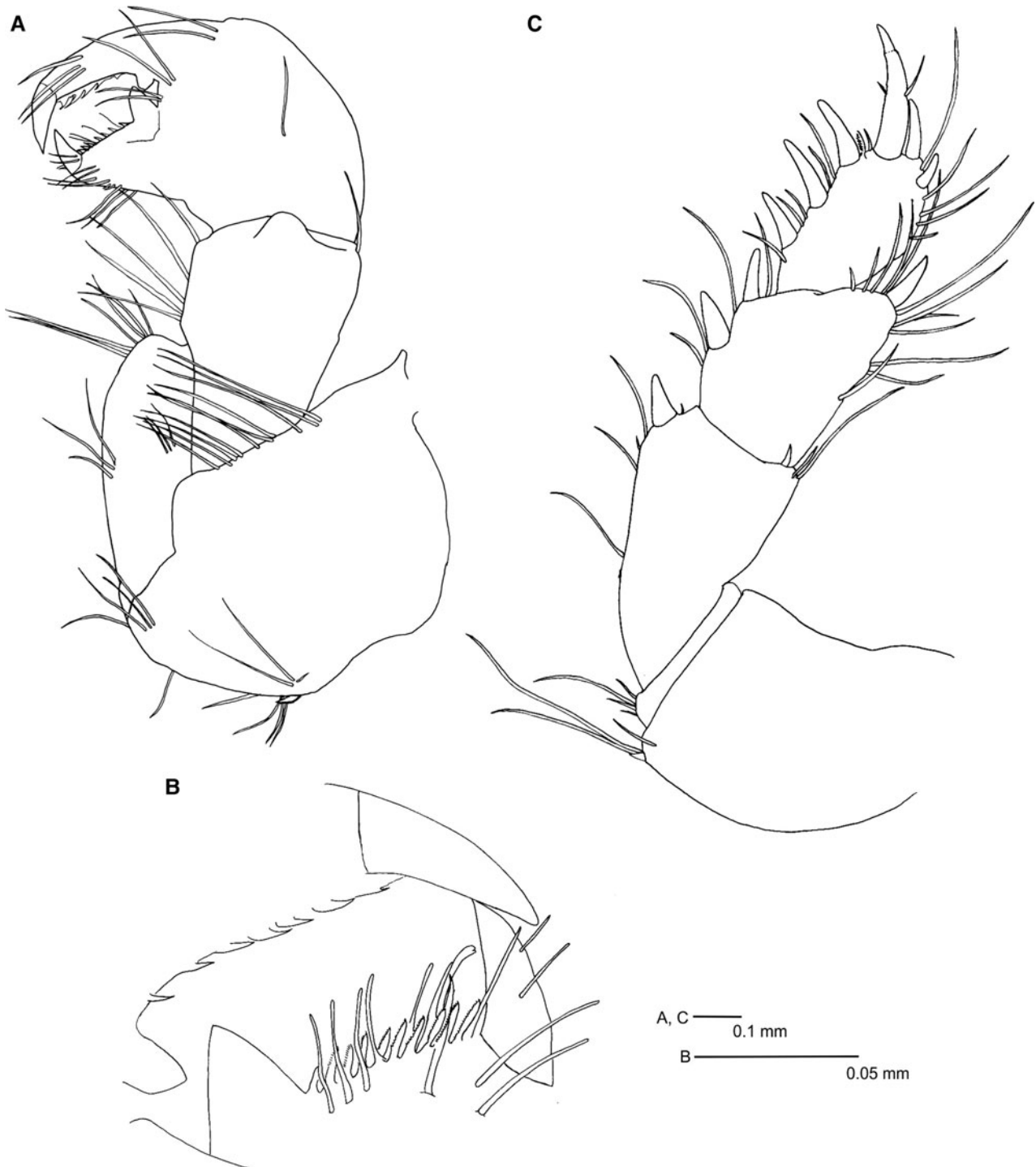


Fig. 6. *Apseudopsis latreilli*: male. (A) Cheliped; (B) chela; (C) pereopod 1.

mobilis. Mandibular palp 3-articled; first article 2.2 times as long as broad, bearing numerous setae on inner margin; second article as long as first, bearing 5 setulose setae, decreasing in length distally; third article bearing distal setae and pectinate spines (Figure 2E). Maxillule (Figure 2F) inner endite with short fine setae on inner margin, outer margin with longer fine setae and marginal apophysis, and 5 distal setulose setae; outer endite bearing 11 distal spines and two subdistal setae, inner margin with a group of fine setae, outer margin with longer fine setae; palp (Figure 2G) bearing three long simple

setae. Maxilla (Figure 2H) with margins serrated; outer lobe of inner endite with simple setae, and bifurcate, trifurcate and pectinate spines. Inner lobe of fixed endite with a row of simple setae in front of serrated setae. Outer lobe of outer endite with serrate setae and two strong outer setae. Labium (Figure 3A) with outer margin serrated, palp with 3 distal setae and marginal setae and setules. Maxilliped (Figure 3B) basis simple; palp first article with a long inner seta and an outer distal spine; second article inner margin with numerous setae, one as long as whole palp, outer margin with one distal seta; third article

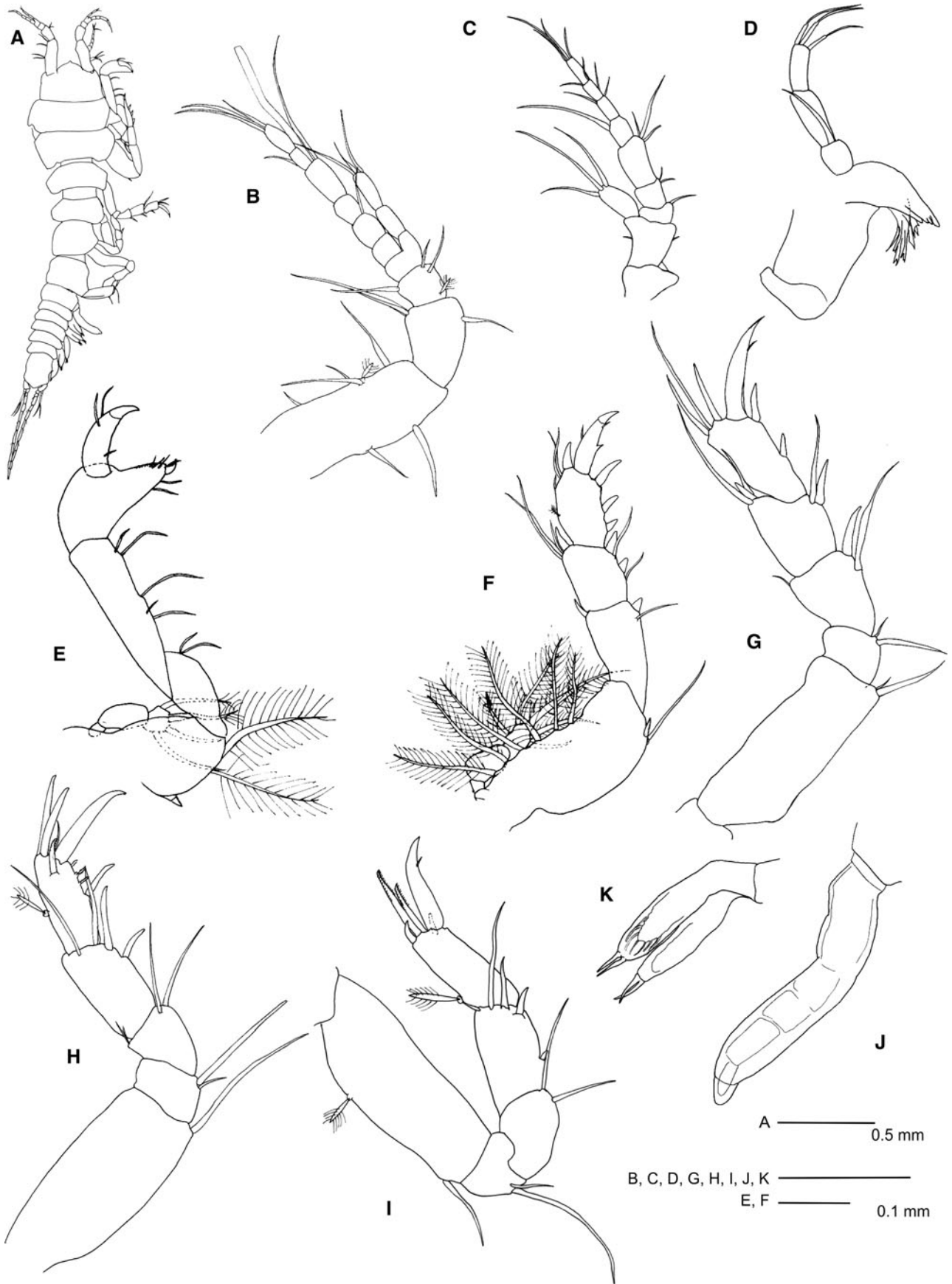


Fig. 7. *Apseudopsis latreilli*: manca II. (A) Dorsolateral view; (B) left antennule; (C) left antenna; (D) left mandible; (E) cheliped; (F) pereopod 1; (G) pereopod 2; (H) pereopod 3; (I) pereopod 5; (J) pereopod 6; (K) pleopod.

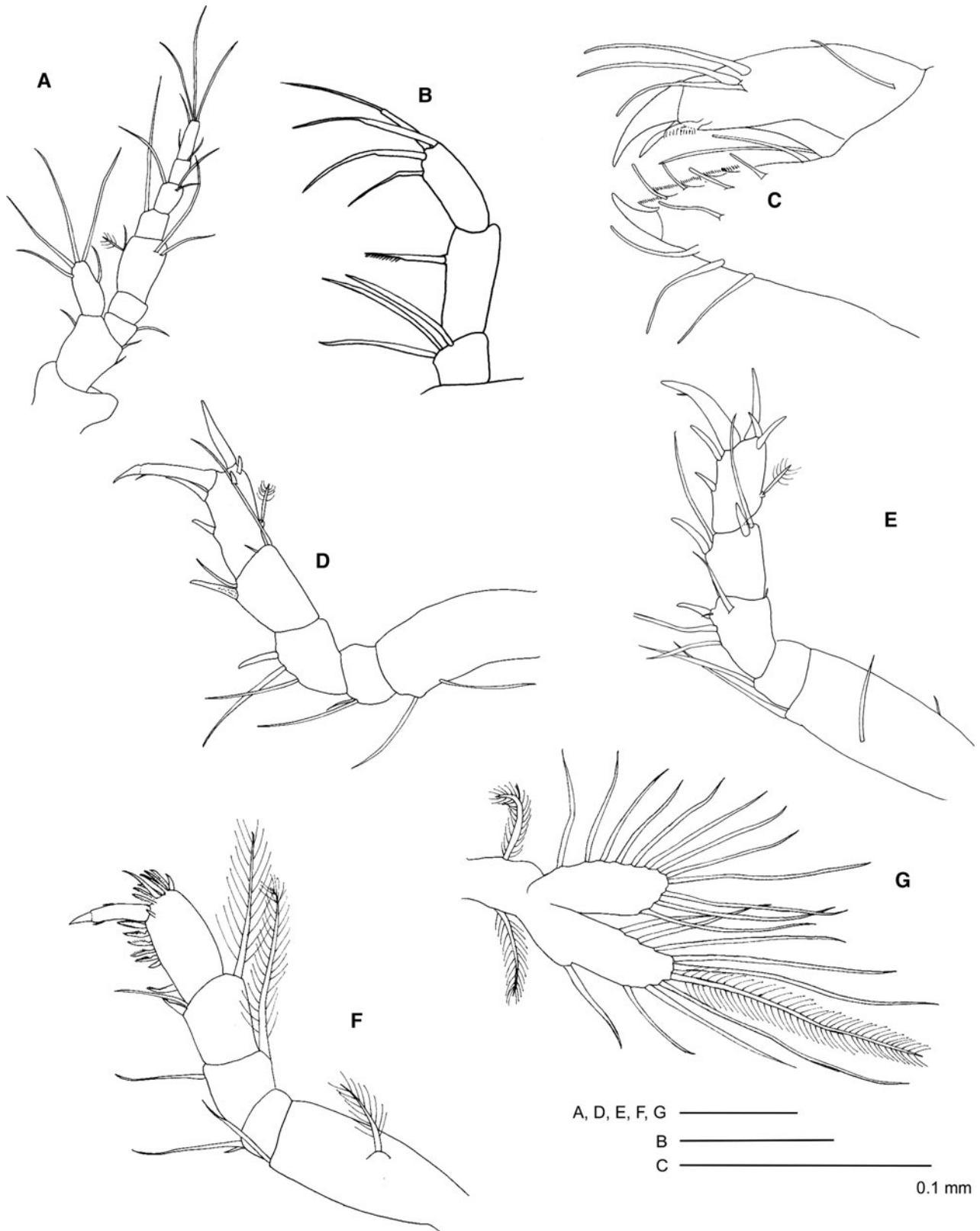


Fig. 8. *Apseudopsis latreilli*: juvenile I. (A) Left antenna; (B) mandibular palp; (C) chela; (D) pereopod 3; (E) pereopod 5; (F) pereopod 6; (G) pleopod.

with setae along inner margin, one as long as second and third articles together; distal article with long distal setae. Maxilliped endite (Figure 3C) with setulose setae on inner margin and up to six spatulate spines, and simple, bifurcate, trifurcate and

pectinate setae on distal margin. Epignath (Figure 3D) bearing a long, distally setulose spine; border sparsely setulose.

Cheliped slender (Figure 3E). Basis 1.6 times as long as broad, with a medial stout spine and a pair of long distal

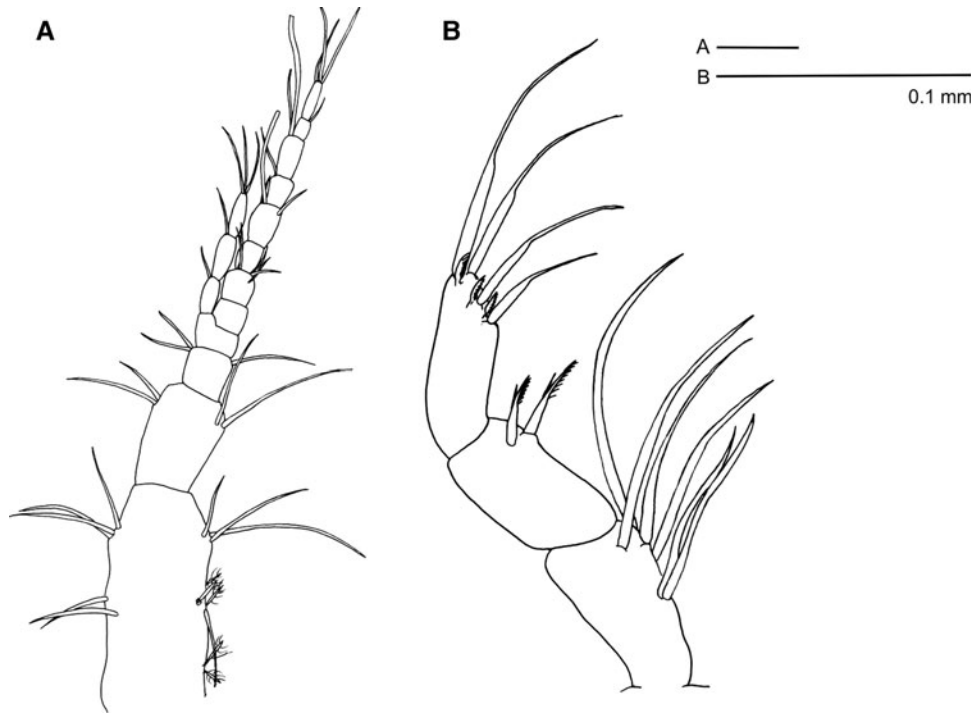


Fig. 9. *Apseudopsis latreillii*: juvenile II. (A) Right antennule; (B) mandibular palp.



Fig. 10. *Apseudopsis latreillii*: male I. (A) Cheliped; (B) chela.

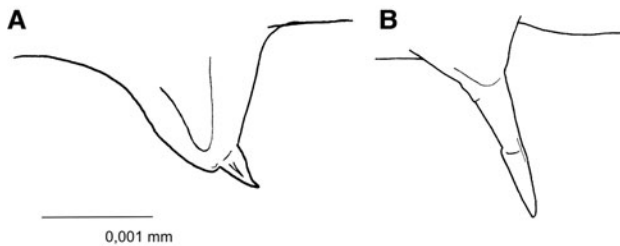


Fig. 11. *Apsudopsis latreillii*: copulatory structures. (A) Penial tubercle of male II; (B) hyposphenium of preparatory female.

setae on ventral margin, and a row of setae along dorsal margin. Exopodite (not figured) present, 3-articled; first article small, second article cylindrical, naked, distal article with 6 long, plumose setae. Merus elongate, narrower proximally, with one medial ventral seta and a ventral, distal group of setae. Carpus slender, 4.1 times as long as wide, with long setae along ventral margin and shorter ones on laterodistal surface. Chela (Figure 3E, F) fingers about as long as wide. Palm region about as long as wide, with dorsal and lateral short setae; fixed finger with a row of setae distally on ventral margin, shortening approaching claw. Cutting edge convex, with a row of fine setae and pinnate, small spines. Dactylus as long as fixed finger, with a couple of lateral setae near claw; cutting edge with small spines and pinnate spines.

Pereopod 1 (Figure 4A) with oostegite. Pronounced apophysis on coxa. Basis with exopodite, 1.5 times as long as wide, with a ventrodorsal spine accompanied by 1–3 long setae. Ischium naked. Merus narrower proximally, half length of basis, with lateral and ventral groups of setae, a ventrodorsal stout spine and a dorsodorsal spine. Carpus as long as merus, with two ventral and one dorsodorsal spine, ventral setae, short laterodorsal setae and long dorsodorsal setae. Propodus about as long as merus, with three ventral and two dorsal spines, becoming longer distally. Dactylus with one mid-dorsal fine seta, and one mid-ventral denticle. Unguis about 1/3 length of dactylus.

Pereopod 2 (Figure 4B) with oostegite. Basis 3.7 times as long as wide, with long, marginal setae, short setae, and a tuft of ventrodorsal setae. Ischium with two ventral setae. Merus, carpus and propodus with long marginal setae. Merus about 1/3 as long as basis, narrower at base, with one long ventrodorsal spine. Carpus 1.2 times as long as merus, with one ventrodorsal spine and one dorsodorsal spine. Propodus about as long as merus, with two ventral spines and one dorsodorsal spine, serrated, those on both sides of dactylus longer and slender. Dactylus slender, with one mid-ventral spinule, and one ventrodorsal setule. Unguis about 1/4 of total length of dactylus.

Pereopod 3 (Figure 4C) with oostegite. Basis 2.2 times as long as broad, with long proximal setae, smaller dorsal simple and penicillate seta, and a group of long setae on ventrodorsal corner. Ischium with a tuft of ventrodorsal setae. Merus, carpus and propodus with marginal and lateral long setae. Merus narrower at base, with one long ventrodorsal spine, and two ventrolateral shorter spines. Carpus with one long, ventrodorsal spine, one long, dorsodorsal spine, and two shorter lateral spines. Propodus slender, narrower at base, three times as long as broad and 1.3 times as long as carpus, with two long, ventral spines, two long, slender and one shorter dorsodorsal spines, and two stout lateral spines. Dactylus as in pereopod 2.

Pereopod 4 (Figure 4D) with oostegite. Basis fusiform, 2.2 times as long as broad, with dorsal small setae and 3 penicillate setae, and one long and one very short ventrodorsal setae. Ischium with 2–3 ventrodorsal setae. Merus, carpus and propodus with long ventral and distal setae. Merus with one pair of ventral spines. Carpus 2 times as long as merus, 2.5 times as long as broad, with two rows of 5 ventral spines that become longer approaching propodus. Propodus 2.7 times as long as broad and 1.3 times as long as carpus, with a long penicillate dorsal seta, a group of long terminal spines, and a marginal terminal crown of lanceolate, denticulate spines. Dactylus slender, as long as propodus, unguis about 1/5 of length of dactylus.

Pereopod 5 (Figure 5A) very similar to pereopod 4, but with basis naked, merus with two rows of 4 spines, propodus with two pairs of ventral spines, three terminal, long spines and some lanceolate, serrate spines, not forming a crown.

Pereopod 6 (Figure 5B) basis with dorsal plumose setae and ventral long, simple setae. Merus and carpus with ventral long setae and dorsal very long, plumose setae. Ischium with a tuft of ventrodorsal setae. Merus narrower proximally, with one long ventral spine. Carpus with two rows of 3–4 spines, longer when approaching propodus. Propodus ovate, as long as carpus, with a dorsal penicillate seta, and a row of lanceolate, pinnate spines along ventral and frontal border. Dactylus about as long as propodus, with a medial dorsal setule and a distal ventral setule, unguis about one-third of length of dactylus.

Pleopods (Figure 5C) biramous. Articulation not distinct. Pleopod 1 basis with 6 + 5 (six inner, five outer) plumose setae; pleopods 2–3 with 5 + 4 and pleopods 4–5 with 4 + 3 plumose setae. Both rami with numerous marginal plumose setae. Endopod longer than exopod. Inner proximal seta on endopod shorter and robust.

Uropods (Figure 1B) biramous. Basis with two distal setae. Inner ramus with around 30 segments, increasing in length towards end, some with simple or penicillate setae. Outer ramus 3-, occasionally 4-segmented. Distal segment significantly longer than the other two/three together, with long distal setae.

Male

Slightly longer than female: total length 3.6–6.1 mm. Penial tubercle (Figure 11A) on pereonite 6. Hyposphenia absent. Cheliped (Figure 6A) more robust: basis as long as broad, with row of setae on dorsal margin, group of setae and a small spine on ventrodorsal margin. Merus about 3 times as long as broad, with ventral, distal and proximal tufts of setae. Carpus narrower at base, 1.2 times as long as basis, with a row of setae on ventral margin and a blunt subterminal apophysis. Chela (Figure 6B) robust, cutting edge of fixed finger straight, with a triangular proximal apophysis. Cutting edge of dactylus with a proximal rounded apophysis; setation and ornamentation as in the female. Pereopod 1 (Figure 6C) merus dorsodorsal spine smaller than that of female; ventral spines of carpus and propodus larger. Dorsodorsal corner of carpus pronounced.

REMARKS

Apsudopsis latreillii resembles other species of the genus such as *A. acutifrons* (G.O. Sars, 1882), *A. anabensis* (Gutu, 2002), *A. bacescui* (Gutu, 2002), *A. caribbeanus* Gutu, 2006, *A. elisae* (Băcescu, 1961), *A. hastifrons* (Norman & Stebbing, 1886),

A. mediterraneus (Băcescu, 1961) and *A. ostroumovi* (Băcescu & Cărășu, 1947). These species share with *A. latreillii* the presence of a pointed rostrum with rounded shoulders, but they have apophyses or pointed corners on the pereonite margins, and more than four spines on the ventral margin of the propodus of pereopod 1. *Apseudopsis apocryphus* (Gutu, 2002) and *A. minimus* (Gutu, 2002) show a similar rostrum and 3 spines on the ventral margin of the propodus of pereopod 1, but do not have a dorsodistal spine on the merus. *Apseudopsis bruneinigma* (Bamber, 1998), *A. isochelatus* Gutu, 2006 and *A. robustus* (G.O. Sars, 1882) mostly differ from *A. latreillii* in the shape of the rostrum.

POSTMARSUPIAL DEVELOPMENT

Up to eight different stages have been identified in the life history of *A. latreillii* (apart from manca I, which occurs inside the marsupium and is not included in this work). They can be diagnosed as follows:

Manca II: Sixth pereopod with no articulation; pleopods without plumose setae around the border.

Juvenile I: All pereopods developed. Hyposphenia often absent; oostegites absent.

Juvenile II: Hyposphenia present, but no oostegites. Cheliped slender.

Preparatory female: Oostegites present. Cheliped slender.

Copulatory female: Complete marsupium.

Intermediate female: Adult females without oostegites, nor marsupium nor hyposphenians.

Male I: Rudimentary hyposphenia. Penial tubercle present. 'Intermediate' cheliped (see description).

Male II: Penial tubercle present. Cheliped robust.

Morphological characteristics of preparatory females and males II correspond with those of the adults already described. The rest of the developmental stages differ from the preparatory female, and can be described as follows (only those characters that differ from the adult female with oostegites are specified):

Manca II

Total length: 1.2–1.9 mm. Less setose in general than adult. Rostrum broad, slightly pointed. Cephalothorax about 0.22 of total length. Pereonites 1 and 2 significantly broader than rest, about 3 times as broad as long (Figure 7A). Pleotelson as in adult.

Antennular accessory flagellum 2-segmented, inner flagellum 6-segmented, with one aesthetasc on fourth segment (Figure 7B).

Antennal squama bearing three setae; flagellum 4-segmented (Figure 7C).

Mouthparts very similar to adult, except mandibular palp (Figure 7D): proximal article short, as long as broad, bearing one seta; second and third subequal in length, 2.2 times as long as first; second article naked; distal article with three simple setae.

Cheliped (Figure 7E) slender, similar to female; exopod proportionally larger; basis bearing long plumose setae.

Pereopods 1–5 (Figure 7F–I) sparsely setose by comparison to the adult.

Pereopod 1 (Figure 7F) spination as in adult; exopodite proportionally larger; basis bearing long dorsal setae.

Pereopod 2 (Figure 7G) spination similar to adult, but without terminal dorsal spine on the propodus.

Pereopod 3 (Figure 7H) merus lacking spines; two long, slender ventral spines on carpus; propodus with one dorsal penicillate seta, one slender and three lanceolate, serrated ventral spines, two long terminal spines, and one serrated, subterminal spine.

Pereopod 4 (Figure 7I) basis with one ventral penicillate seta; carpus with one ventral spine; propodus with one large penicillate seta, two long, serrated and two simple terminal spines.

Pereopod 5 similar to pereopod 4.

Pereopod 6 (Figure 7J) reduced, with no segmentation or ornamentation.

Pleopods (Figure 7K) all alike, biramous, with two terminal, short, simple setae on each ramus.

Uropod inner ramus of about 10 segments. Outer ramus as in the adult.

Juvenile I

Total length: 1.4–3.0 mm. Rostrum defined. Antennule, cheliped and pereopod 1 as in manca II.

Antenna (Figure 8A) squama bearing 5 marginal setae; flagellum of 4 segments.

Mandibular palp (Figure 8B) first article short, as long as broad, bearing three setae; second article bearing one distally setulose seta; third article as long as second, bearing 4 terminal simple setae.

Cheliped and chela as in manca II (Figure 8C).

Pereopods 1 and 2 as in adult.

Pereopod 3 (Figure 8D) merus with one ventral spine; one spine on carpus; propodus with two ventral spines, two subdistal small spines, and one long distal spine.

Pereopod 4 merus with one ventral spine; carpus with one ventral and one dorsodistal spine; propodus with two ventral and three dorsodistal spines.

Pereopod 5 (Figure 8E) similar to pereopod 4.

Pereopod 6 (Figure 8F) articulated; basis with one plumose seta, and one ventrodiscal simple seta; merus with a dorsodistal, long plumose seta and a ventral simple seta; carpus with one dorsodistal plumose seta, one ventrodiscal spine and seta; propodus border bearing several lanceolate, serrated spines.

Pleopods (Figure 8G) similar to those of adult, but with one plumose seta on inner and one on outer margin of the basis, and fewer plumose setae on margins of rami.

Uropod inner ramus of 12–16 segments.

Only some of the largest individuals had hyposphenia.

Juvenile II

Total length: 2.1–4.4 mm. Hyposphenia present. Antennular (Figure 9A) inner flagellum 3-segmented; outer flagellum 7–8-segmented, presence of aesthetascs variable, often on fourth and sixth segments.

Mandibular palp (Figure 9B) first article twice as long as broad, bearing a tuft of setae on inner margin; second article as long as first, bearing two distally setulated setae; distal article bearing four simple setae and three pectinate spines.

Cheliped as in adult female.

Pleopod setation variable.

Uropod inner ramus of about 20 segments.

Rest of appendages and mouthparts as in adult.

Male I

Total length: 3.1–5.7 mm. Mostly similar to adult female, bearing vestigial hyposphenia on pereonites 2–5, and penial tubercle on pereonite 6. Antennular accessory flagellum

4-segmented. Cheliped (Figure 10A, B) as in female, but with a triangular apophysis on cutting edge of fixed finger, in proximal position.

REMARKS

A few individuals (i.e. intermediate males and the largest juvenile II) had a different number of segments on the accessory flagellum of each antenna (3 on one, 4 on the other). Similarly, a few of the largest specimens (males and females) had a different number of segments on the outer rami of the uropods (3 and 4). These have been considered abnormalities, owing to the small proportion of cases (<2% of the total).

Apart from a general increase in the number of setae and spines in the pereopods, meristic changes that occur through the development of *A. latreilli* include: the abrupt appearance of a segmented pereopod 6 and well-developed pleopods; an increase in the number of segments in antennal and antennular flagella and uropod inner rami; and the appearance of a third article on the mandibular palp after the juvenile II. Morphometric changes include the proportional size of the cephalothorax, cheliped, pereopod 1, and the exopodite of the cheliped and pereopod 1. The penial tubercle appears on the pereonite 6 on males I, while in preparatory females a hyposphenium appears as a pointed, conical structure (Figure 11B). Earlier stages present a structure which is not yet differentiated. On the other hand, some characters do not show significant changes, remaining relatively stable from the mancae to the adults; these are the cheliped (which only changes in the males, but is very similar in the manca and the ovigerous female), the pereopod 1, and the uropod outer rami. There are no observable differences on the size of the oostegites among the preparatory females. The hyposphenia appear on the juveniles, and are only absent in the ovigerous females and adult males.

LENGTH-FREQUENCY DISTRIBUTION

The length-frequency distribution obtained (Figure 12) may, *a priori*, be divided into two normal distributions, with the juvenile stages on the left and the adult-preparatory stages on the right. There is an overlap in the size of the juvenile stages, including mancae (Figure 13). The adult-stage size-classes overlap completely on the right of the graph (Figures 12 & 14). The total length measured ranged from 1.22 mm to 6.09 mm (Table 1). In general, the largest adults were males (3.66–6.09 mm) and the smallest were preparatory males (minimum size: 3.12 mm) and preparatory females (minimum: 3.19 mm). In general, juvenile stages did not

exceed 3.8 mm, although the largest juvenile II reached 4.36 mm.

FECUNDITY AND MALE:FEMALE RATIO

Fecundity ranged from 7 to 23 potential offspring per brood (mean: 13.15; standard deviation: 5.5; mode: 13). Male:female ratio in O Grove ranged from 1:1.7 to 1:8 per sample, and between 1:4 and 1:7 per site.

DISCUSSION

Taxonomic observations and development

Some discrepancies with previous descriptions were detected. For instance, the outer rami of the uropods were described by Sars (1886), and later on by Riggio (1996) as 4-segmented; we, however, observed three segments on the vast majority of the individuals, finding four only on a few of the largest specimens. Such discrepancies can be attributed to the difficulty in distinguishing the limit between two consecutive segments. In any case, this character is not specific, and can be disregarded for identifications.

A number of characters remain constant during the post-marsupial development of *A. latreilli*. Some of these are characteristic of the genus, or at least shared by several species (i.e. morphology of the rostrum, mouthparts, cheliped and pereopods 2–6, the number of segments of the uropod outer ramus (Gutu, 2001, 2006)), and thus not reliable for species identification. On the other hand, there is not a single character that can serve as a definite diagnosis of the species. Therefore, we conclude that *A. latreilli* can be identified, regardless the developmental stage, from the following combination of morphological characters: a pointed and downturned rostrum, pereonites without apophyses, three ventral spines on the pereopod 1 propodus, and one dorsodistal spine on the merus.

Life history

The number of manca and juvenile postmarsupial stages varies among tanaidaceans (Table 2); generally, there are one or two manca stages followed by one or two distinct juveniles, each one originated through a single moult (Messing, 1983; Schmidt *et al.*, 2002). In contrast, in adults several moults lead to an increase of the body size, without the occurrence of significant meristic changes (Lang, 1953). Large size-ranges, like those on Figures 12–14, support this idea (Schmidt *et al.*, 2002). In peracarids, growth normally

Table 1. Statistical values of the size distribution for every developmental stage studied. Values in mm.

Size distribution												
	Cop Fem	Prp Fem	Int Fem	Tot Fem	Male II	Male I	Tot Male	Juv II	Juv I	Tot Juv	Manca II	Total
N	49	95	23	167	33	34	67	233	246	481	48	766
Mean	4.52	4.25	4.37	3.99	4.58	4.28	4.37	2.98	2.17	2.56	1.57	3.06
Standard deviation	0.43	0.47	0.59	0.49	0.69	0.61	0.73	0.38	0.26	0.53	0.14	0.10
Minimum	3.81	3.19	3.57	3.19	3.66	3.12	2.25	2.07	1.38	0.71	1.22	1.22
Maximum	5.57	5.52	5.57	5.57	6.09	5.68	6.09	4.36	3.04	4.36	1.94	6.09

Cop Fem, copulatory females; Prp Fem, preparatory females; Int Fem, intermediate female; Tot Fem, total females; Tot Male: total males; Juv I and Juv II, juveniles I and II; Tot Juv, total juveniles.

Table 2. Developmental stages, proposed sexual development strategy and fecundity of several species of tanaidaceans.

Family/species	Post-marsupial stages											Strategy	Fecundity	Source		
	M I	M II	M III	Juv I	Juv II	Prp Fem	Cop Fem	Int Fem	Male I	Male II						
Apseudidae																
<i>Apseudopsis latreillii</i> (Milne-Edwards, 1828)		x		x	x	x		x	x	x			Protogyny?	7-23	This paper	
<i>Apseudes heroae</i> Sieg, 1986	x	x		x	x	x		x				x	Gonochoristic	9-5	Schmidt <i>et al.</i> (2002)	
Metapseudidae																
<i>Synapseudes idios</i> Gardiner, 1973	x	?			x	x		x		?		x	x	Gonochoristic?	5-11	Gardiner (1973)
<i>Monokalliapseudes schubarti</i> (Mañé-Garzón, 1949)				x	x	x		x				x	x	Protogyny?	1-63	Pennafirme & Soares-Gomes (2009)
Pagurapseudidae																
<i>Pagurotanais largoensis</i> (McSweeney, 1982)	x	x		x	x	x		x					x	Gonochoristic	4-17	Messing (1983)
Leptocheiliidae																
<i>Heterotanais oerstedii</i> (Krøyer, 1842)			x		x		x		x			x	various	Protogyny	6-16	Bückle-Ramírez (1965)
<i>Hargeria rapax</i> (Harger, 1879)		x			x		x		x			x	x	Protogyny	-	Modlin & Harris (1989)
Tanaidae																
<i>Tanais dulongii</i> (Andouin, 1826)		x	x		?		x		x				x	Gonochoristic	up to 46	Johnson & Attramadal (1982)
<i>Allotanais hirsutus</i> (Beddard, 1886)		x			x		x		x				x	Gonochoristic	19-31	Schmidt <i>et al.</i> (2002)
Neotanaidae																
<i>Neotanais micromopher</i> Gardiner, 1975	x	x			x		x		x			x	x	Gonochoristic	-	Gardiner (1975)

M I, M II and M III, manca I-III; Juv I and Juv II, Juvenile I and II; Prp Fem, preparatory female; Cop Fem, copulatory female; Int Fem, intermediate female.

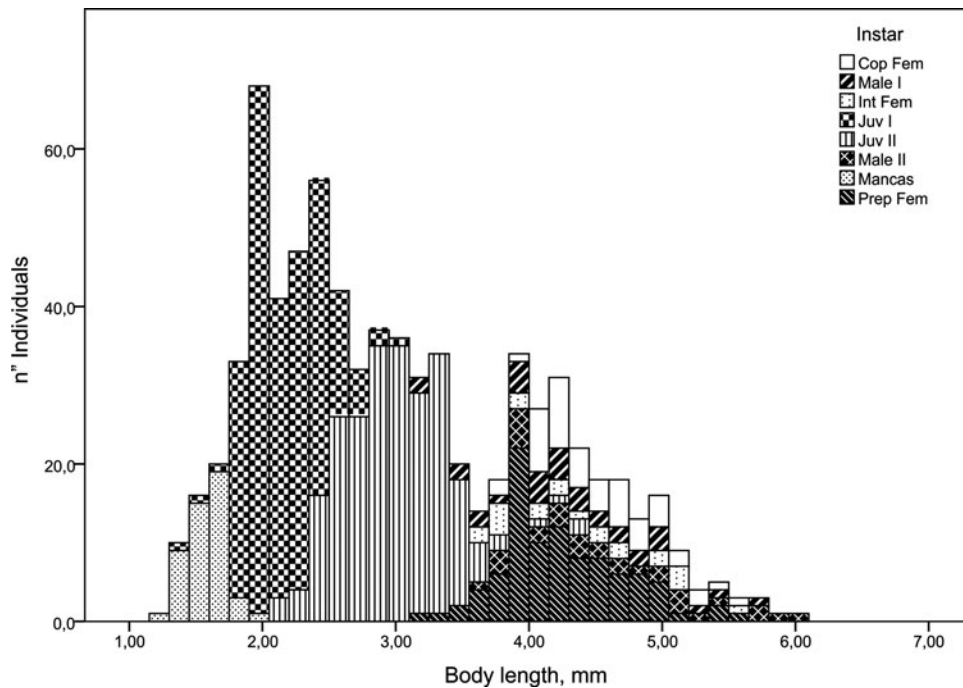


Fig. 12. Size-frequency distribution of the specimens of *Apseudopsis latreillii* yielded by a single grab from O Grove *Zostera* meadows. Cop Fem, copulatory female; Int Fem, intermediate female; Prep fem, preparatory female; Juv I-II, juveniles I and II. Sizes in μ m. Interval: 150 μ m.

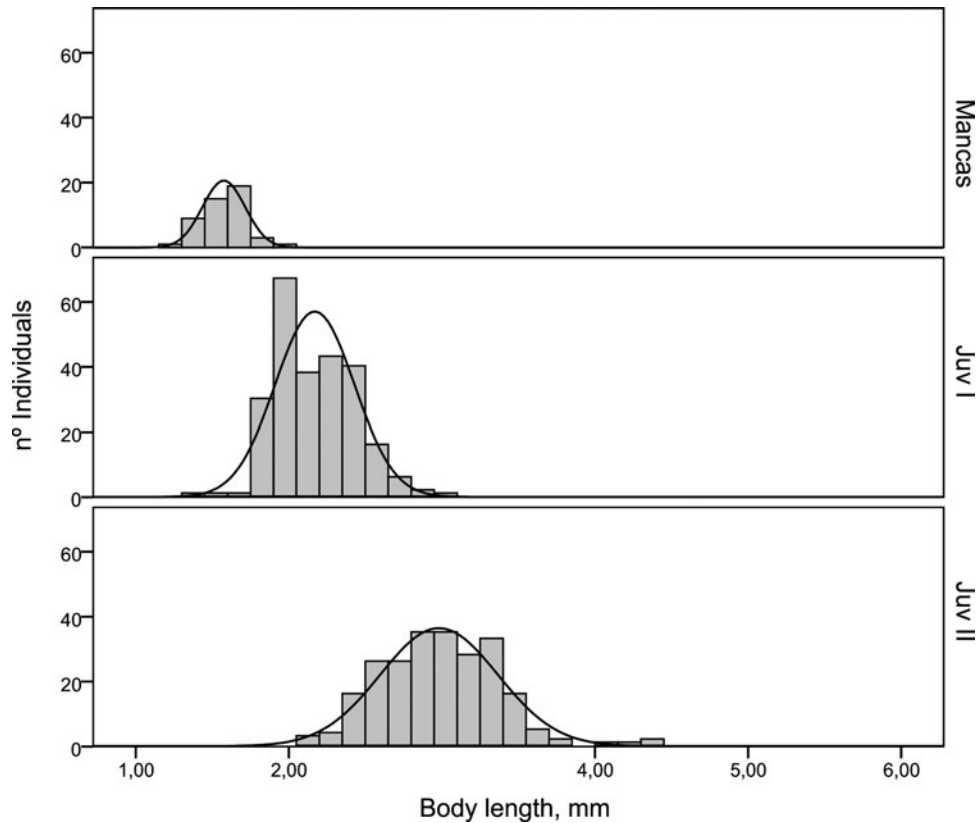


Fig. 13. Size–frequency distribution of the immature developmental stages of *Apseudopsis latreillii*. Juv I-II, juveniles I and II. Sizes in μm . Interval: 150 μm

slows down as the individuals become older (Johnson *et al.*, 2001).

Considering that the differentiation of the copulatory structure marks the passage from the juvenile to an adult stage, males I can be considered sexually mature. Consequently, developed hyposphenia (rudimentary on males I) appear to be a characteristic restricted to juveniles and females. Similarly, the 4-articled inner flagellum on the antennule arises as an indication of maturity.

The large range of the body length for copulatory females suggests the presence of more than one copulatory stage separated by moults; similarly, the females with adult characters but no oostegites nor hyposphenia, classified as intermediate, share the same range. This indicates a sequence of copulatory instars followed by intermediate stages on which the female lose the ovisac after the manca release. Lang (1953) proposed this sequence for the Apsuedidae, Johnson & Attramadal (1982) for *Tanais dulongii* (Audouin, 1826) and Gardiner (1975) for the family Neotanaidae Lang, 1956.

The occurrence of two types of male is frequent among apseudomorphans (see Table 2), and have different interpretations. For instance, Pennafirme & Soares-Gomes (2009) proposed protogynic hermaphroditism for *Monokalliapseudes schubartii* (Mañé-Garzón, 1949), considering that a female-skewed sex-ratio may indicate this strategy. Other authors (Bamber, 2010) consider that in certain tanaidomorph species males I are simply pre-adults. In *A. latreillii* males I present rudimentary hyposphenia (absent in the male II but evident on juveniles and females) and a 4-articled inner flagellum of the antennule (an adult characteristic in this species). Therefore, it seems possible that they follow either a juvenile II instar, or a preparatory female. Both origins can be

supported by their position on the length–frequency distribution, being larger than most of the juvenile II and a number of the preparatory females. The males I coincide in the size-range with the females. Because there are males I smaller than the smallest males II, it does seem equally possible that males I represent an intermediate state between juveniles and males II. Nevertheless, protogyny cannot be discarded, considering the female-skewed sex-ratio, the occurrence of large males I and the fact that sex reversal may be a facultative strategy (Bückle-Ramírez, 1965; Highsmith, 1983; Błażewicz-Paszkowycz, 2001). Experimental work would be needed to solve this question definitely (Highsmith, 1983).

Figure 15 shows a proposed life developmental sequence based on our results. Post-marsupial mancas are common among peracarids (Gardiner, 1975). While in isopods the sex can be determined from the manca stages, in cumaceans and tanaidaceans the sex is not noticeable in juveniles. Several moults occur in adult females of all peracarids, leading to at least two (usually several) breeding periods in a lifetime. In contrast, peracarid copulatory males are usually considered terminal (Gardiner, 1975; Johnson *et al.*, 2001). There are cases of terminal males among tanaidaceans (Gardiner, 1975; Johnson *et al.*, 2001), but several authors indicate more than one moult (Schmidt *et al.*, 2002; Pennafirme & Soares-Gomes, 2009). Mature males of *A. latreillii* probably moult several times before dying, during which time they are able to reproduce.

Fecundity is comparable to that of other tanaidacean species (Table 2). Although tanaidaceans have the least fecundity per female of the peracarids (Messing, 1983), they are abundant and often numerically dominant among crustaceans on sandy and muddy bottoms, reaching high densities

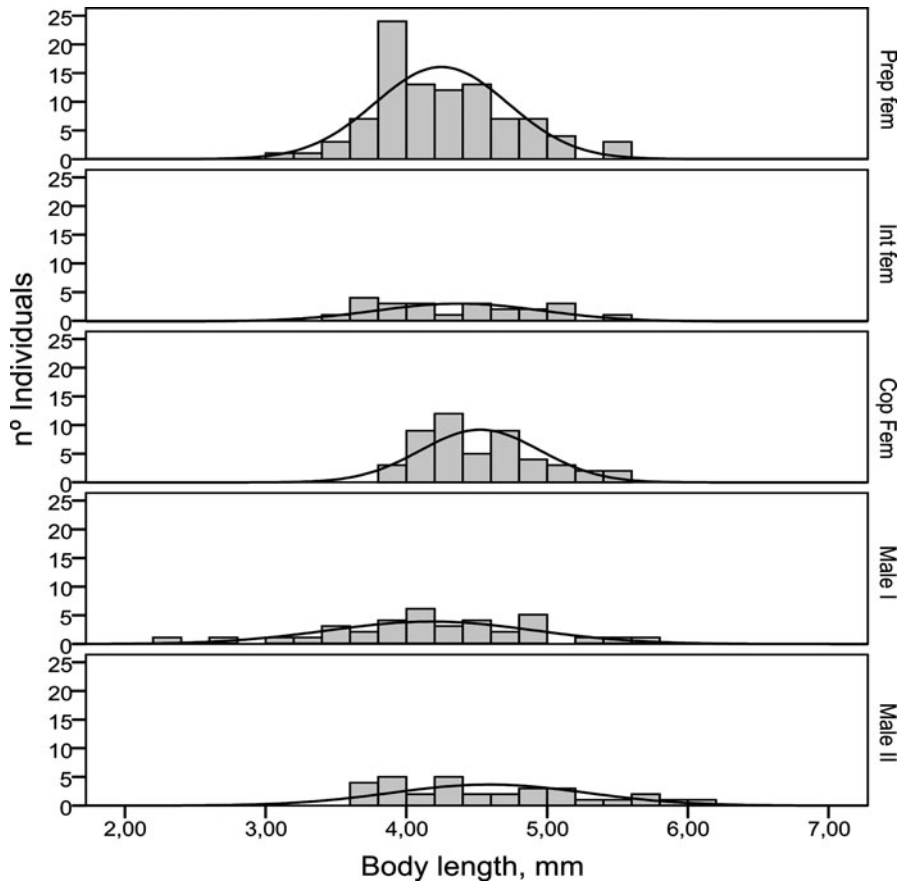


Fig. 14. Size-frequency distribution of the mature developmental stages of *Apseudopsis latreillii*. Cop Fem, copulatory female; Int Fem, intermediate female; Prep fem, preparatory female. Sizes in μm . Interval: 200 μm .

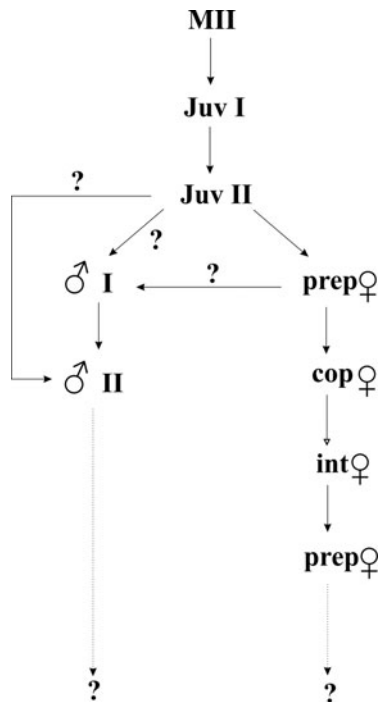


Fig. 15. Proposed life cycle scheme for *Apseudopsis latreillii*. MII, manca II; Juv I, juvenile I; Juv II, juvenile II; prep ♀, preparatory female; cop ♀, copulatory female; int ♀, intermediate female; ♂ I, male I; ♂ II, male II. Black arrows indicate one or more moults. White arrow indicates no moults implicated. Dotted arrows indicate an undetermined number of moults.

(Swennen *et al.*, 1982; Moreira *et al.*, 2008; Esquete *et al.*, 2011, among others).

CONCLUSIONS

- *Apseudopsis latreilli* can be identified, regardless of the developmental stage, from the following combination of morphological characters: a pointed and downturned rostrum, pereonites without apophyses, three ventral spines on the pereopod 1 propodus, and one dorsodistal spine on the merus.
- Through the life of *A. latreilli*, the following postmarsupial stages can be recognized: manca II, juvenile I, juvenile II, preparatory females, copulatory females, intermediate females, males I and males II.
- The number of segments of the inner flagellum of the antennule increases through the life history, and can be used as an indication of the developmental stage of the individual. Similarly, the differentiation of the copulatory structure on pereonite 6 is characteristic of the adults. A general increase of the number of setae and spines on the pereopods, as well as number of articles on the inner flagellum of the uropodal endopod occurs through the developmental history of *A. latreilli*.
- The length-frequency distribution suggests that the adults pass through a variable number of instars-moults before and after the first reproductive period.

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Capítulo 5

Esquete P, Bamber RN, Moreira J, Troncoso JS. 2012. *Apseudopsis adami*, a new species of tanaidacean (Crustacea: Peracarida) from the NW Iberian Peninsula: postmarsupial development and remarks on morphological characters. *Helgoland Marine Research* DOI: 10.1007/s10152-012-0295-2.

APSEUDOPSIS ADAMI, UNA NUEVA ESPECIE DE TANAIDÁCEO (CRUSTACEA: PERACARIDA) DEL N.O. DE LA PENÍNSULA IBÉRICA. DESARROLLO POSTMARSUPIAL Y OBSERVACIONES SOBRE CARACTERES MORFOLÓGICOS.

Resumen. En este capítulo se describe una nueva especie de tanaidáceo Apseudomorfo, *Apseudopsis adami* sp. nov., incluyendo su variación intraespecífica, a partir de ejemplares recolectados en las praderas de fanerógamas de la ensenada de O Grove. La nueva especie se caracteriza, independientemente del estadio de desarrollo del individuo, por la combinación de los siguientes caracteres morfológicos: rostro apuntado con esquinas redondeadas, cuatro espinas ventrales en el propodio del pereópodo 1 y apófisis posterolaterales en los pereonitos 2 a 5. Con respecto al desarrollo, se distinguen dos estadios antes de alcanzar la madurez, y las extremidades de los estadios más tempranos están escasamente ornamentadas con respecto a los adultos; los juveniles avanzados representan una vasta mayoría de la población estudiada, y la ornamentación de sus extremidades es similar a la de los adultos. Los machos presentan dos morfologías diferenciadas en el quelípedo. Las hembras, tras un estadio preparatorio, pasan a través de una secuencia de estadios copulatorios seguidos de estadios intermedios en los que el ovisaco se desprende tras la liberación de las manchas. El número de segmentos de los flagelos antenulares y antenales y el flagelo del urópodo, así como el desarrollo y ornamentación del palpo mandibular, son caracteres merísticos que ocurren durante el desarrollo y permiten una rápida identificación del estadio en que se encuentra el individuo.

Apseudopsis adami, a new species of tanaidacean (Crustacea: Peracarida) from the NW Iberian Peninsula: postmarsupial development and remarks on morphological characters

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Abstract A new species of apseudomorph tanaidacean, *Apseudopsis adami* sp. nov., is described, including intra-specific variation, from specimens collected in the seagrass meadows of O Grove inlet (NW Iberian Peninsula, NE Atlantic). The new species is characterized by the unique combination of the following characters: pointed rostrum with rounded shoulders, four ventral propodal spines on pereopod 1, and posterolateral pointed apophyses on pereonites 2–5, regardless of the developmental stage of the individual. Two juvenile stages were identified before reaching maturity; early juvenile limbs are scarcely ornamented in comparison to the adults. Advanced juveniles represent the vast majority of the studied population, and the limb ornamentation is similar to that of the adults. Males show two different cheliped morphologies. After a preparatory stage, females pass through a sequence of copulatory instars followed by intermediate stages in which the female loses the ovisac after manca release. The number of segments of the antennular and antennal flagella and uropod endopods, as well as the development and

ornamentation of the mandibular palp, are meristic changes that occur during development and allow rapid identification of the developmental instar.

Keywords Apseudomorpha · *Apseudopsis* · Sexual dimorphism · New species · Identification · Taxonomic characters · Development · Life history

Introduction

Tanaidacea is a group of peracarid crustaceans of ecological importance owing to their wide distribution and abundance in sedimentary and crevicial habitats (Bamber 2011). Despite being a morphologically conservative taxon at the generic level, tanaidacean species present high intraspecific variability depending on the gender and developmental stage of the individual. Such variability can make identification to species level difficult, especially when juveniles represent the majority of the individuals within a population and when sympatric species of the same genus are found (Bamber 2010; Larsen and Froufe 2010; Esquete et al. 2012). Therefore, complete descriptions that include intra-specific variation are especially important in such species, and the definition of characters that allow positive, unequivocal identification of the specimens to species level are crucial for accurate faunistic and ecological studies.

The genus *Apseudopsis* was proposed by Norman (1899) to accommodate those apseudomorph species with eye lobes fused to the carapace; this feature differentiates this genus from the closely related *Apseudes* Leach 1814. *Apseudopsis* was invalidated by Lang (1955) and reinstated by Guñu in a recent paper (2006), who listed 19 extant species worldwide (see Anderson and Bird 2011). The genus is common and widely distributed on the shallow

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sedimentary bottoms of the North Atlantic and the Mediterranean Sea (see Guñu 2002 (as *Apseudes*); Bamber et al. 2009; Bamber 2011). The only species known to date from the Atlantic coasts of Europe is *Apseudopsis latreillii* (Milne-Edwards 1828), which is considered common to abundant and therefore represents an important component of soft bottom assemblages (Riggio 1996; De-la-Ossa-Carretero et al. 2010 [as *Apseudes*]; Bamber 2011; Esquete et al. 2011, 2012).

In this study, a new species of *Apseudopsis* Norman 1899 is described, including its intraspecific variation and the taxonomic characters that allow the unequivocal identification of the species. Useful characters to determine the developmental stage of any individual of the species are defined. Additionally, a putative scheme of the life history of the new species, and ecological remarks are included.

Materials and methods

In December 1996, benthic samples were taken in O Grove inlet (NW Iberian Peninsula; 42°41′–42°28′N 9°01′–8°44′W) using a van Veen grab, in order to characterize the macrofaunal assemblages inhabiting the seagrass (*Zostera*) meadows of its sedimentary bottoms. Five replicate samples were taken at each site, representing a total sampled area of 0.28 m² for each site. Samples were sieved through a 0.5 mm mesh and fixed in 10% formalin for later sorting and identification of the fauna. An additional sample was taken at each site to determine calcium carbonate (%) and total organic matter content (%) and for granulometric analyses. Mean grain size (Q₅₀) and sorting coefficient (S₀) were determined for each sample.

Line drawings were done using a camera lucida connected to a microscope. The total lengths (from the tip of the rostrum to the end of the pleotelson) of all the specimens found in one site (642 individuals, excluding incomplete and heavily damaged specimens) were measured. Measurements were made using a stereomicroscope connected to a computer with an image analyzer at the ECIMAT marine station (University of Vigo).

Fecundity was calculated according to Messing (1983), as the mean number of offspring per ovigerous female in one sample. Females having a damaged marsupium were excluded because part of the brood may have been lost.

Statistical calculations and size-frequency distribution graphs were performed using the IBM SPSS 19 software package.

Morphological terminology follows that of Bamber and Shearer (2005); serially repetitive body parts, such as the subdivisions of the antennal flagella and those of the uropodal rami are segments, while those with independent musculature (such as the parts of the pereopods) are

articles. Measurements were made axially, dorsally on the body and antennae, and laterally on other appendages.

Identification of the postmarsupial developmental stages follows Esquete et al. (2012), as:

Juvenile I: All pereopods developed. Hyposphenia often absent; oostegites absent.

Juvenile II: Hyposphenia present, but no oostegites. Cheliped slender.

Preparatory female: Oostegites present. Cheliped slender.

Copulatory female: Complete marsupium.

Male I: Rudimentary hyposphenia. Penial tubercle present. “Intermediate” cheliped.

Male II: Penial tubercle present. Cheliped robust.

Females with adult characteristics but presenting neither oostegites nor marsupium have been considered intermediate females (according to Shiino 1937).

Type material was deposited in the Museo Nacional de Ciencias Naturales, Madrid (MNCN).

Results

Systematics

Order TANAIIDACEA Dana 1849

Suborder APSEUDOMORPHA Sieg 1980

Family APSEUDIDAE Leach 1814

Subfamily APSEUDINAE Leach 1814

Genus *APSEUDOPSIS* Norman 1899

Apseudopsis adami Esquete & Bamber, sp. nov.
(Figs. 1, 2, 3, 4, 5, 6, 7, 8 and 9)

Material examined

Type material *O Grove (NW Iberian Peninsula)*.- Holotype: ♀, 4.7 mm (MNCN 20.04/8789); allotype: ♂, 5.1 mm (MNCN 20.04/8790); paratypes: 4 ♂♂, 4 ♀♀, 6 juveniles (MNCN 20.04/8791), 42°29.12′N 08°50.25′W, mud with *Zostera marina*, 0.8 m, coll. J.S. Troncoso, 11 December 1996.

Additional examined material *O Grove (NW Iberian Peninsula)* 0.130♀♀, 68♂♂, 405 juveniles, 42°29.12′N 08°50.25′W, mud with *Zostera marina*, 0.8 m, coll. J.S. Troncoso, 11 December 1996; 254♀♀, 39♂♂, 277 juveniles, 42°28.75′N 08°50.75′W, fine sand with shells and *Z. marina*, 0.3 m, coll. J.S. Troncoso, 4 December 1996; 161♀♀, 44♂♂, 371 juveniles, 42°28.25′N 08°50.75′W, fine sand with *Z. marina*, 0.3 m, coll. J.S. Troncoso, 11 December 1996; 17♀♀, 3♂♂, 5 juveniles, 42°27.75′N 08°51.25′W, fine sand with *Z. noltii*, 0.3 m, coll. J.S. Troncoso, 11 December 1996; 10♀♀, 4♂♂, 90 juveniles,

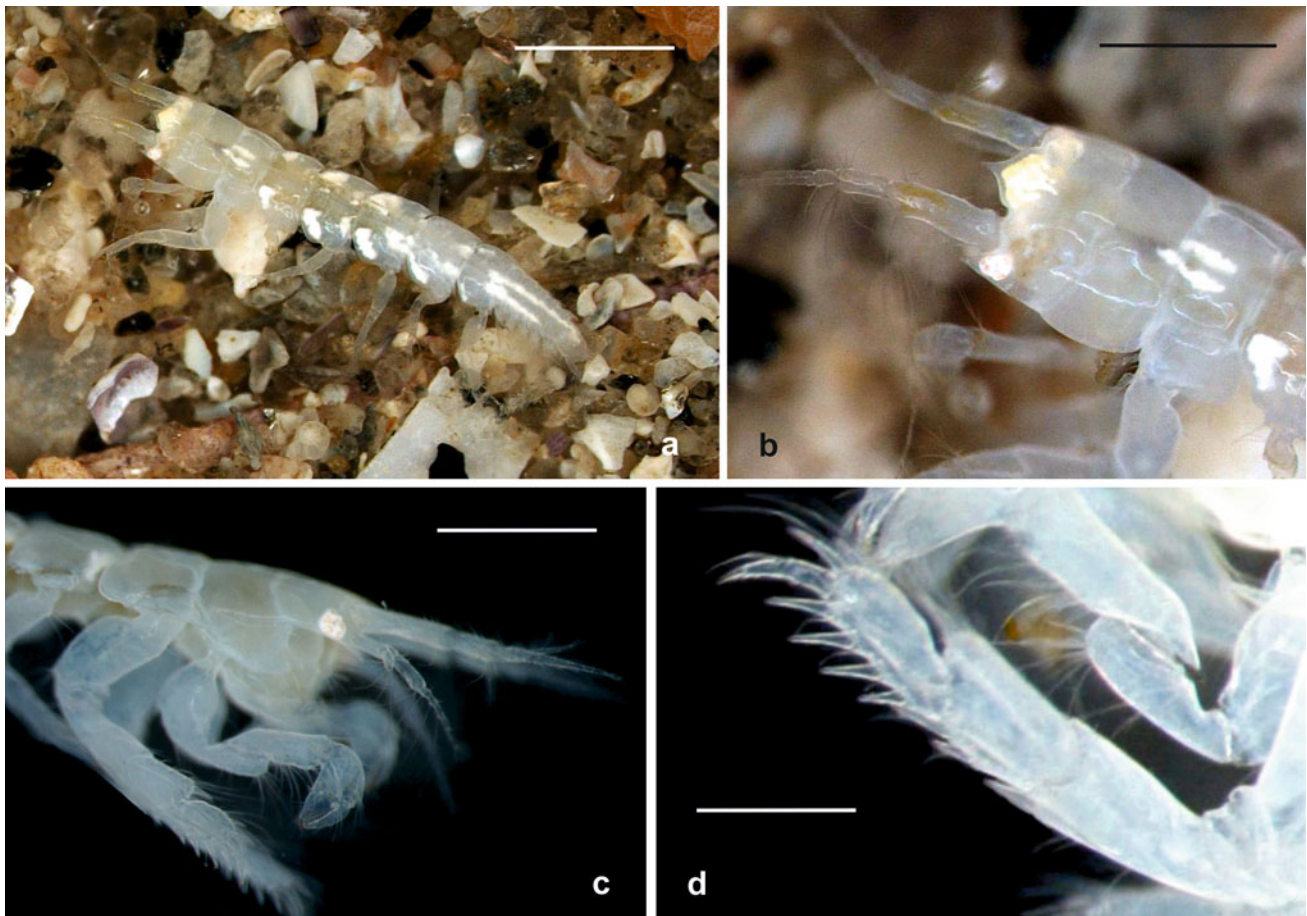


Fig. 1 *Apseudopsis adami* sp. nov. **a** Habitus. **b** Detail of the head. **c** Anterior part, lateral view. **d** Detail of pereopod 1. Scale bar: **a**, 1 mm. **b**, **c**, 0.5 mm. **d**, 0.2 mm

42°27.25'N 08°51.75'W, mud with *Z. marina* and *Z. noltii*, 0.3 m, coll. J.S. Troncoso, 18 December 1996. *Baiona* (NW Iberian Peninsula). 11♀♀, 5♂♂, 18 juveniles, 42°08.83'N 08°50.25'W, fine sand with *Z. marina*, 7 m, coll. J.S. Troncoso, 6 September 2011; 3♀♀, 1♂, 2 juveniles, 42°07.50'N 08°50.25'W, sand with shell fragments, 7 m, coll. J.S. Troncoso, 6 September 2011.

Diagnosis *Apseudopsis* with posterolateral apophyses on pereonites 2–6; rostrum pointed, slightly downturned; antennular accessory flagellum 3-segmented, main flagellum 10- or 11-segmented in adults; pereopod 1 bearing 4 ventral spines on the propodus; uropod endopod about 25- to 30-segmented, exopod 3-segmented.

Description

Female with oostegites (preparatory female)

Total length 3.1–4.8 mm. Body (Fig. 2a, b) dorsoventrally flattened, elongated, slightly narrowed posteriorly, 5.7 times as long as wide. Living specimens whitish, with

yellowish and white patches on rostrum, pereonites and pleonites (Fig. 1a). Cephalothorax about as long as broad, about 1/6 of total body length; rostrum with rounded “shoulders”, pointed and downturned. Ocular lobes present, pointed. Eyes present, with orange pigment (Figs. 1b–c and 2a, b). Pereonites bearing simple lateral setae. First pereonite about 2.6 times as broad as long, extended into two posterolateral lobes with rounded posterolateral corners. Pereonites 2–5 with posterolateral apophyses, distally angulate on pereonites 3–5. Second pereonite narrower proximally, twice as broad as long. Third pereonite 1.5 times as broad as long. Pereonites 4 and 5 subrectangular. Sixth pereonite 1.8 times as broad as long, with angulate posterolateral corners. Hyposphenium present on pereonite 6. Pleon about one-quarter of total length. Pleonites subequal, posterior pleonites narrower. Lateral margins of all pleonites produced posteriorly, bearing ventrally oriented pointed apophyses. Pleotelson 1.2 times as long as broad, bearing two groups of four lateral setae and two setae on two lateral protuberances, one pair of subterminal long setae each with adjacent penicillate seta, and one pair of terminal setae (Fig. 2c).

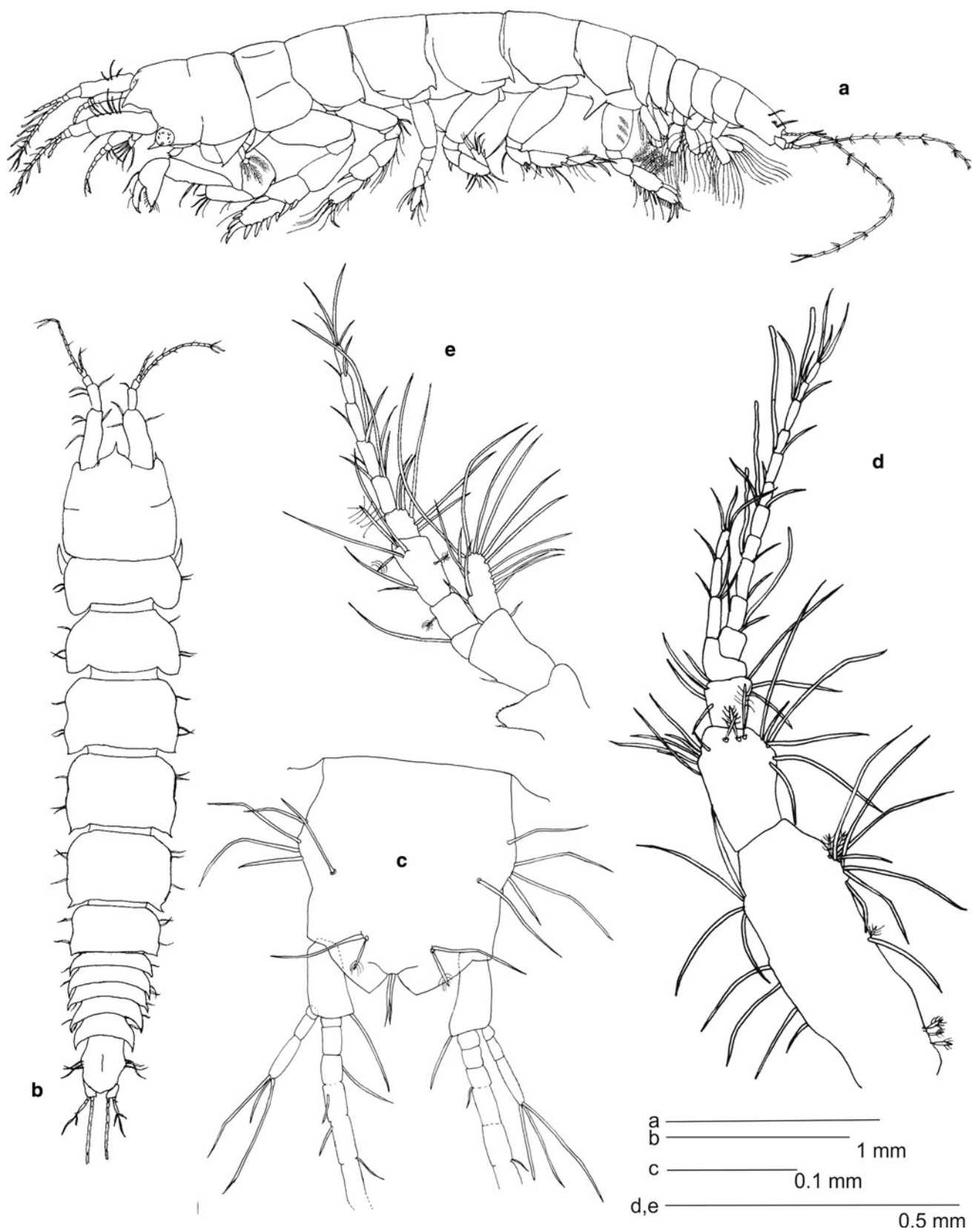


Fig. 2 *Apseudopsis adami* sp. nov. Preparatory female: **a** Habitus, lateral view. **b** Habitus, dorsal view. **c** Pleotelson. **d** Antennule. **e** Antenna

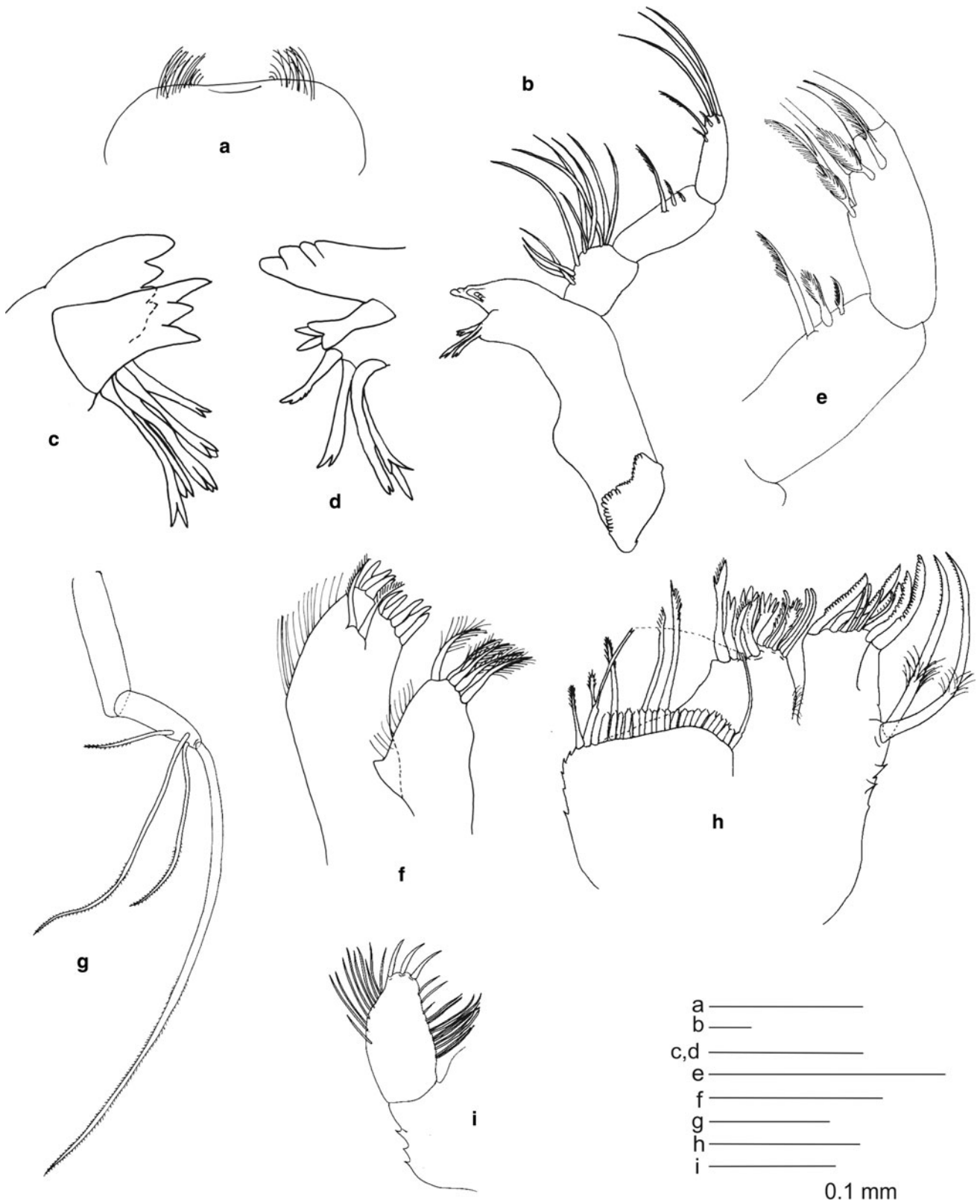


Fig. 3 *Apseudopsis adami* sp. nov. Preparatory female: **a** Labrum. **b** Left mandible. **c** Detail of the *left* mandible. **d** Detail of the *right* mandible. **e** Detail of the medial and distal segments of the mandibular palp. **f** Maxillule. **g** Maxillular palp. **h** Maxilla. **i** Labium

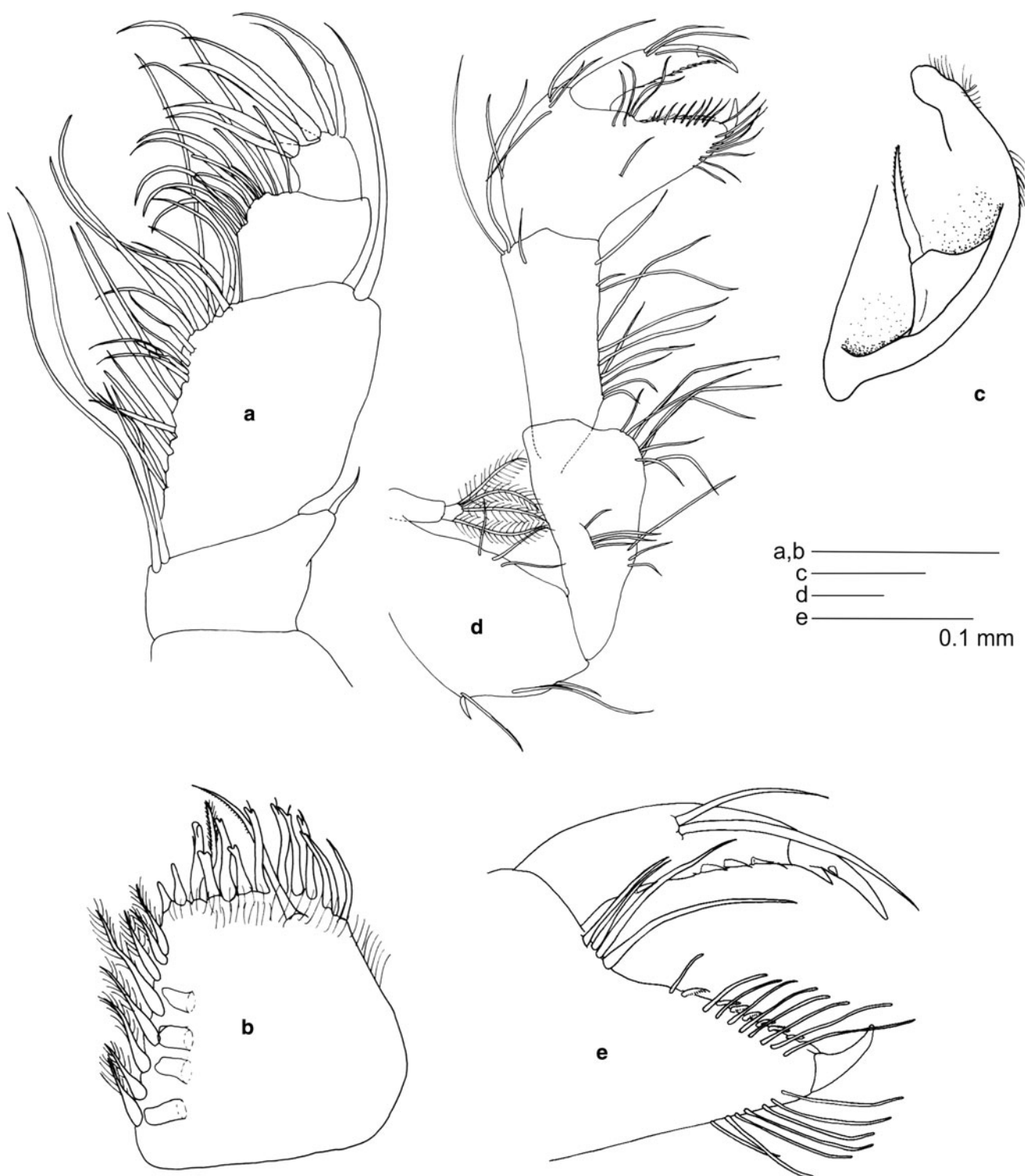


Fig. 4 *Apseudopsis adami* sp. nov. Preparatory female: **a** Maxilliped. **b** Maxilliped endite. **c** Epignath. **d** Cheliped. **e** Chela

Antennule (Fig. 2d) peduncle first article 2.7 times as long as wide, outer margin bearing three proximal and two medial penicillate setae, and subdistal tuft of simple setae and two penicillate setae, inner margin with simple setae.

Second article about half length of first, twice as long as wide, with inner and outer subdistal tufts of simple setae, and three medial subdistal penicillate setae. Third article half length of second, with inner and outer simple setae.



Fig. 5 *Apseudopsis adami* sp. nov. Preparatory female: **a** Pereopod 1. **b** Pereopod 2. **c** Pereopod 3. **d** Pereopod 4

Fourth article as long as third, naked. Main flagellum of 11 segments, with five aesthetascs. Accessory flagellum three-segmented.

Antenna (Fig. 2e) peduncle first article as long as wide, with inner lobe bearing one to three small setae. Second

article 1.5 times as long as first, 1.5 times as long as wide, bearing outer squama with long marginal setae. Third article one-third length of second, with inner-distal seta almost reaching tip of peduncle. Fourth article about twice as long as third, bearing one penicillate seta on inner

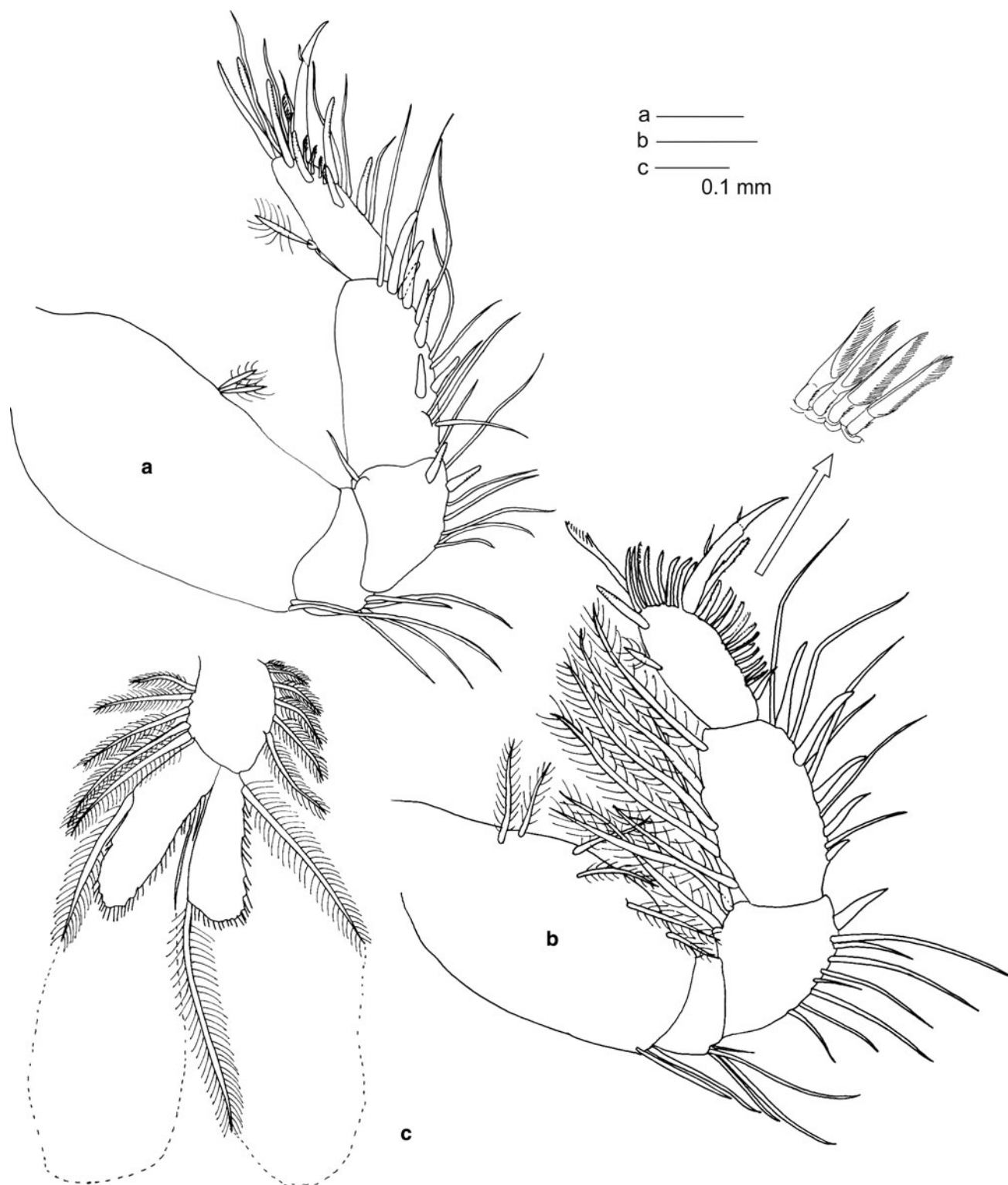


Fig. 6 *Apseudopsis adami* sp. nov. Preparatory female: **a** Pereopod 5. **b** Pereopod 6. **c** Pleopod 1

margin. Fifth article 1.3 times as long as two preceding articles together, bearing simple setae, and one medial and two subdistal penicillate setae. Flagellum of six segments, first segment bearing long simple setae on outer margin.

Mouthparts Labrum (Fig. 3a) bilobed, setulose. Left mandible (Fig. 3b, c) with strongly dentate pars incisiva, lacinia mobilis tridentate; setiferous lobe with five bifurcate and trifurcate setae; pars molaris triturative. Right

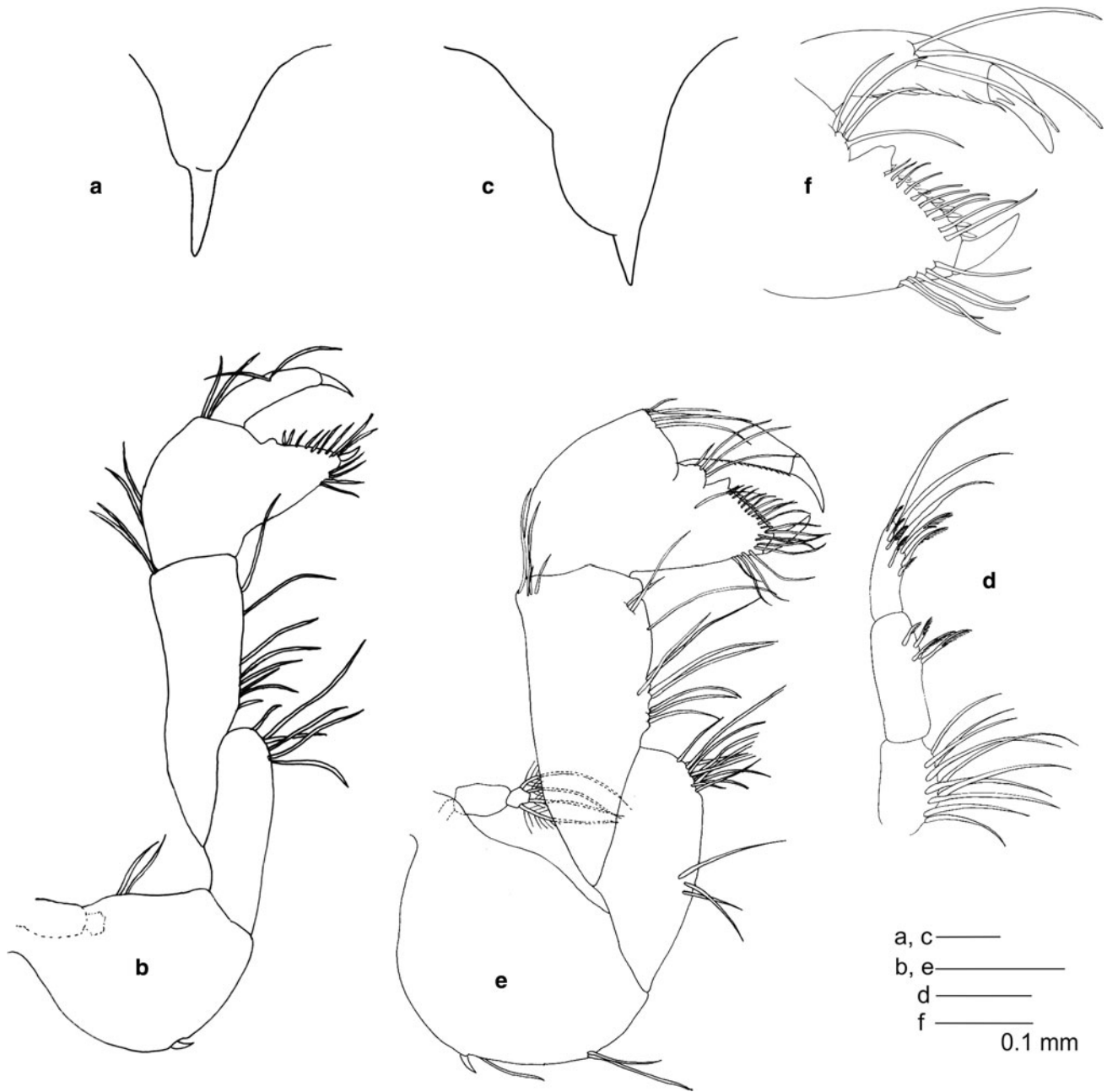


Fig. 7 *Apseudopsis adami* sp. nov. Male I: **a** Penial tubercle. **b** Cheliped. Male II: **c** Penial tubercle. **d** Mandibular palp. **e** Cheliped. **f** Chela

mandible (Fig. 3d) as left but without lacinia mobilis; distal spine trifurcate, shorter and stouter than rest. Mandibular palp (Fig. 3b, e) three-articled; first article about as long as broad, bearing numerous setae on inner margin; second article twice as long as first, bearing three pectinate setae, proximal seta significantly longer; distal article bearing subterminal pectinate spines, one pectinate seta and three terminal simple setae. Maxillule (Fig. 3f) inner endite with marginal apophysis and fine setae on outer margin, bearing five distal setulose setae; outer endite bearing 11 distal spines and two subdistal pectinate setae,

outer margin with fine setae; palp (Fig. 3g) bearing three subterminal and one terminal minutely plumose setae. Maxilla (Fig. 3h) with margins serrated, outer lobe of fixed endite with simple setae, and bifurcate, trifurcate and pectinate spines. Inner lobe of fixed endite with a row of numerous simple setae in front of four pectinate setae, and one pectinate seta on the inner corner. Outer lobe of moveable endite with serrate setae, simple setae, and two strong, pectinate setae with medial setules on the outer margin. Labium (Fig. 2i) with outer margin serrated, palp with three distal setae and marginal setae and setules.

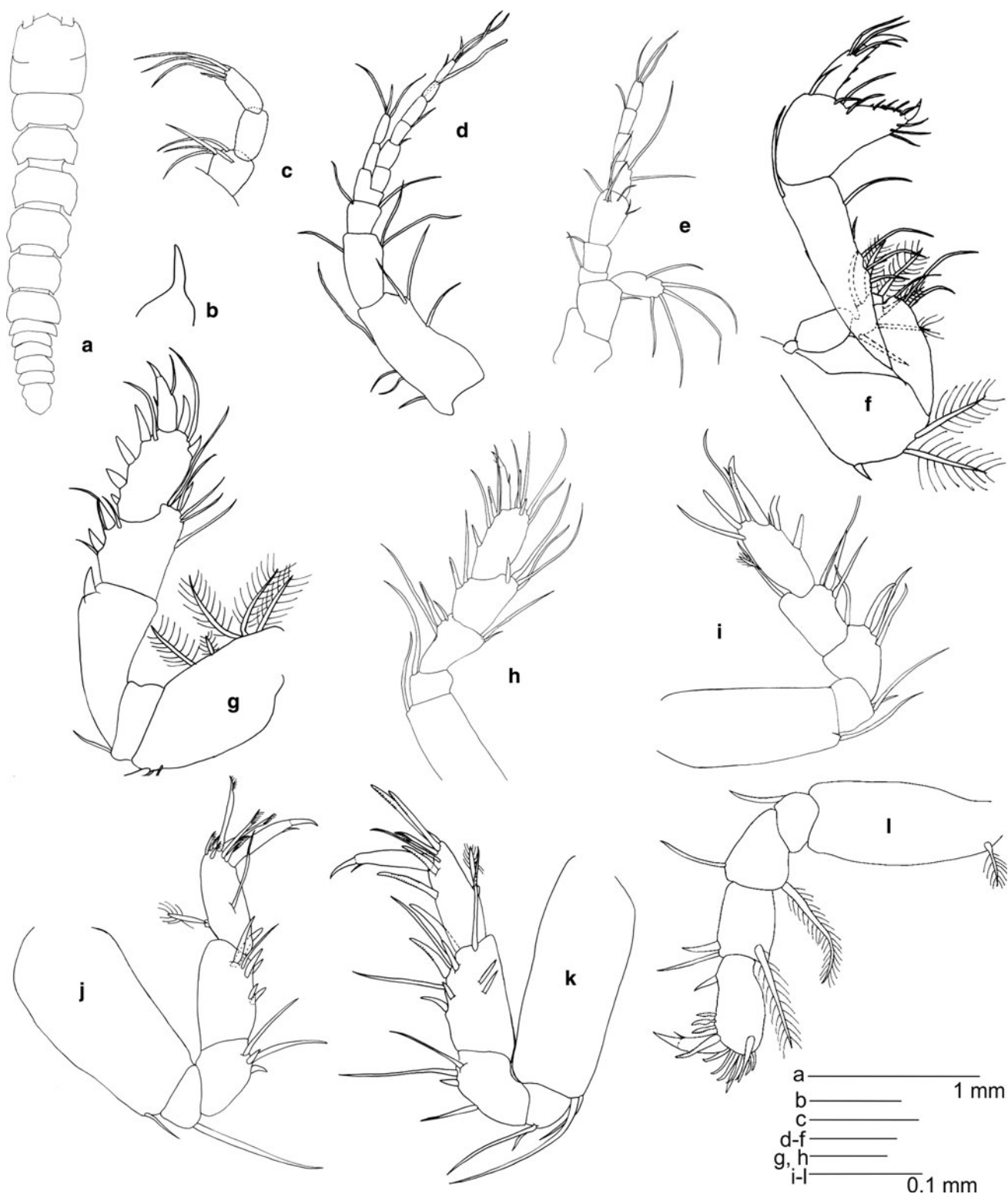


Fig. 8 *Apseudopsis adami* sp. nov. Juvenile I: **a** dorsal view, appendages not shown. **b** Undifferentiated structure on sternite 6. **c** Mandibular palp. **d** Antennule. **e** Antenna. **f** Cheliped. **g** Pereopod 1. **h** Pereopod 2. **i** Pereopod 3. **j** Pereopod 4. **k** Pereopod 5. **l** Pereopod 6

Maxilliped (Fig. 4a) basis simple: palp first article with one longer and one shorter inner setae and outer distal spine; second article inner margin with numerous setae, outer

margin with one distal seta; third article with setae along inner margin; distal article with distal setae, four setae stronger than rest. Maxilliped endite (Fig. 4b) with



Fig. 9 *Apseudopsis adami* sp. nov. Juvenile II. **a-d** Development of antennule. **e** Antenna. **f** Mandibular palp

subdistal setules; inner margin with eight setulose setae and four coupling-hooks, distal margin with simple, bifurcate, trifurcate and pectinate setae; inner caudodistal seta

slender, tapering, finely pectinate. Epignath (Fig. 3c) bearing a long, distally setulose spine; border sparsely setulose.

Cheliped slender (Fig. 4d) Basis 1.9 times as long as broad, with mid-ventral stout spine, and simple setae on ventral and dorsal margins. Exopodite present, three-articled: first article small, second article cylindrical, naked, distal article with four or five long, plumose setae. Merus elongate, narrower proximally, with medial and ventrodistal groups of setae. Carpus slender, 2.5 times as long as wide with simple setae along the ventral margin and on dorsodistal corner. Chela (Fig. 4e) twice as long as wide; palm region about as long as wide, with dorsal and lateral simple setae; fixed finger with row of ventrodistal setae; cutting edge almost straight, bearing row of pinnate spines and adjacent row of simple setae, shorter towards insertion of dactylus. Dactylus as long as fixed finger, with three medial simple setae; cutting edge with small spines.

Pereopod 1 (Figs. 1d and 5a) with oostegite Coxa with pronounced anterodistal apophysis. Basis twice as long as wide, bearing ventrodistal spine accompanied by four or five setae; exopodite as on cheliped. Ischium naked. Merus narrower proximally, 1.8 times as long as wide, bearing dorsodistal setae, ventral setae and a ventrodistal spine. Carpus 0.7 times as long as merus, bearing marginal setae, two ventral spines and one dorsodistal spine. Propodus about as long as carpus, bearing marginal setae, four ventral spines and two dorsodistal spines. Dactylus with two mid-dorsal fine setae and one mid-ventral spinule. Unguis about one-quarter of length of dactylus.

Pereopod 2 (Fig. 5b) with oostegite Basis 2.2 times as long as wide, with one dorsal penicillate seta, proximal and ventral simple setae, and a tuft of ventrodistal setae. Ischium with ventrodistal setae. Merus, carpus and propodus with long marginal setae. Merus narrower at base, 1.4 times as long as wide, with one ventrodistal, long spine. Carpus about as long as merus, bearing one ventral spine and one dorsodistal, slender spine. Propodus 2.7 times as long as wide, with two ventral, slender spines and two terminal spines. Dactylus 0.6 times as long as propodus, with one mid-dorsal fine seta and one subterminal, ventral setule. Unguis about one-quarter of length of dactylus.

Pereopod 3 (Fig. 5c) with oostegite Basis 2.4 times as long as wide, with pair of medial, long setae and tuft of long ventrodistal setae. Ischium with ventrodistal setae. Merus, carpus and propodus with long ventral and lateral setae. Merus narrower at base, about as long as wide, with one long ventrodistal spine and two shorter ventrolateral shorter spines. Carpus 1.5 times as long as wide, with one long ventrodistal spine, one long dorsodistal spine and two stouter lateral spines. Propodus slender, narrower at base, 2.7 times as long as wide and 1.3 times as long as carpus, with one dorsal penicillate seta, two long ventral spines,

two long and slender distal spines, and a row of lateral spines increasing in length distally. Dactylus very slender, 1.2 times as long as propodus, with one short setule near unguis. Unguis about one-fifth of length of dactylus.

Pereopod 4 (Fig. 5d) with oostegite Basis twice as long as broad, with paired ventrodistal setae. Ischium with ventrodistal tuft of setae. Merus, carpus and propodus with long ventral setae. Merus with one pair of ventral spines. Carpus about twice as long as merus, bearing two rows of five ventral spines becoming longer approaching propodus. Propodus 2.2 times as long as wide and 0.8 times as long as carpus, with one dorsal penicillate seta, a row of subterminal pectinate spines, and long pectinate terminal setae. Dactylus about as long as propodus, with one fine short setule near unguis. Unguis one-quarter of length of dactylus.

Pereopod 5 (Fig. 6a) Basis twice as long as broad, with two medial penicillate setae and two ventrodistal simple setae. Ischium with ventrodistal setae. Merus, carpus and propodus with ventral setae. Merus with one pair of ventral spines. Carpus twice as long as merus, with two rows of three spines, becoming longer approaching propodus. Propodus 1.7 times as long as wide and 0.8 times as long as carpus, with one dorsal penicillate seta, two pairs of ventral spines, three terminal, long spines and some subdistal and terminal pectinate setae and pectinate spines.

Pereopod 6 (Fig. 6b) Basis fusiform, twice as long as wide, with six dorsal plumose setae and ventrodistal simple setae. Ischium with a ventrodistal tuft of simple setae. Merus and carpus with ventral simple setae. Merus narrower proximally, with one ventral spine and three long plumose dorsal setae. Carpus with five ventral spines, longer towards propodus, and five long plumose dorsal setae. Propodus ovate, 0.8 times as long as carpus, with one dorsal penicillate seta, one dorsodistal spine, one long, pectinate terminal seta and row of lanceolate, pinnate spines along ventral and terminal border. Dactylus about as long as propodus, with one medial and one distal dorsal setules. Unguis about one-third of length of dactylus.

Pleopods 1 and 2, basis with six inner and five outer plumose setae; pleopods 3 and 4 (Fig. 6c) with five inner and five outer, and pleopod 5 with four inner and four outer plumose setae. Both rami with numerous distal and outer marginal plumose setae, endopod with two inner marginal setae.

Uropod (Fig. 2c) basis with one inner-distal seta. Endopod with 25 to 30 segments, some with simple or penicillate setae. Exopod three-segmented; distal segment significantly longer than the other two together, bearing three long distal setae.

Copulatory female

Adult females with complete marsupium. Total length: 3.6–4.8 mm.

Intermediate female

Adult females with neither marsupium nor oostegites. Total length: 3.5–4.7 mm.

Male I

Total length: 3.0–5.1 mm. Mostly similar to adult female, with penial tubercle on pereonite 6 (Fig. 7a). Cheliped slender (Fig. 7b), with triangular apophysis on cutting edge of fixed finger.

Male II

Total length 4.2–5.4 mm. Penial tubercle on pereonite 6 (Fig. 7c). Pereonites and limbs more setose in general than in female.

Mandibular palp (Fig. 7d) bearing four pectinate setae on second article, terminal article with two pectinate setae, five pectinate spines and three terminal simple setae. Other mouthparts as in female.

Cheliped (Fig. 7e) more robust than that of female: basis 1.2 times as long as wide, with one medial spine and simple setae on ventral margin. Merus about as long as basis, with a dense distal tuft of setae on ventral margin. Carpus 1.3 times as long as merus, 2.2 times as long as wide, with setae along ventral margin and dorsodistal corner. Chela (Fig. 6f) robust, 1.7 times as long as wide. Cutting edge of fixed finger straight, with triangular proximal apophysis; spination and ornamentation as in female.

Juvenile I

Total length 1.4–2.6 mm. Shape of pereonites as in adult (Fig. 8a). Less setose in general than adult. Cephalothorax about 1/5 of total length, rudimentary copulatory structure not differentiated (Fig. 8b).

Mouthparts as in adult, apart from mandibular palp (Fig. 8c): proximal article bearing four simple setae; second article naked; distal article bearing three terminal simple setae and one pectinate spine.

Antennular accessory flagellum two-segmented, main flagellum six-segmented, with one aesthetasc on fifth segment (Fig. 8d). Antennal flagellum four-segmented (Fig. 8e).

Cheliped (Fig. 8f) slender, similar to that of female, exopod proportionally larger, basis bearing two long, plumose setae.

Pereopods 1–6 (Fig. 8g–l) sparsely setose by comparison with adult. Pereopod 1 (Fig. 8g) spination as in adult; exopodite (not figured) proportionally larger; basis bearing long, plumose setae on dorsal margin.

Pereopod 2 (Fig. 8h) spination similar to adult. Pereopod 3 (Fig. 8i) merus with one long ventral spine; carpus bearing one long, ventral spine; propodus bearing two ventral and two long terminal spines.

Pereopod 4 (Fig. 8j) merus with two ventral spines; carpus with three pairs of ventral spines, distal pair longest; propodus as in adult, but with fewer spines and setae. Pereopod 5 (Fig. 8k) merus with one ventral spine; carpus with two pairs of ventral spines and one subterminal, long spine; propodus with two ventral and two long, distal spines, and one distal pectinate seta.

Pereopod 6 (Fig. 8l) basis with one proximal plumose seta; merus with one dorsal and one ventral plumose setae; carpus with one ventral spine and one dorsal plumose seta; propodus with one ventroproximal spine, one dorsal subdistal spine, and row of lanceolate pinnate spines around terminal border.

Pleopods similar to those of adult, but basis with two plumose setae on outer margin and one plumose seta on inner margin, and fewer plumose setae on rami than adult.

Uropod endopod of 15–18 segments.

Juvenile II

Total length: 2.0–4.2 mm. Males differing from females by the presence of penial tubercle on pereonite 6. Setation of appendages variable, spination as in adults.

Antennular accessory flagellum three-segmented, main flagellum seven- to nine-segmented (Fig. 9a–d). Antennal flagellum generally five-segmented, six-segmented in largest specimens with nine-segmented outer antennular flagellum (Fig. 9e).

Mandibular palp (Fig. 9f) proximal article with about seven simple setae, medial article with one pectinate seta, distal article with one pectinate seta and three terminal simple setae. Cheliped as in adult female.

Pleopod setation variable.

Uropod endopod of 22–28 segments.

Other appendages and mouthparts as in adult.

Remarks

Apseudopsis adami sp. nov. differs from the sympatric *A. latreillii* (co-occurring in some samples) in having posterolateral apophyses on pereonites 2–6, and pereopod 1 with four ventral spines on the propodus (three in *A. latreillii*) and no dorsal spine on the merus. It mostly resembles *A. mediterraneus*, but that species has

posterolateral apophyses on pereonites 1–6, while *A. adami* lacks apophyses on pereonite 1; additionally, the number of segments of the antennular main flagellum is higher in the new species (ten) than in *A. mediterraneus* (seven).

Apseudopsis adami resembles other Mediterranean species of the genus which share the shape of the rostrum and four ventral spines on the pereopod 1 propodus, such as *Apseudopsis bacescui* (Guțu 2002) and *Apseudopsis ostroumovi* (Bacescu and Carausu 1947), but these have apophyses on the first pereonite, a maximum of eight segments on the antennular main flagellum and hyposphenia on several sternites, *inter alia*.

Other species with ten segments on the main flagellum of the antennule include: *Apseudopsis tridens* (Guțu 2002), but this species has a characteristic trident-shaped rostrum, hyposphenia on pereonites 3–6 and apophyses on pereonite 1; *Apseudopsis apocryphus* (Guțu 2002), but this species has only three ventral propodal spines on pereopod 1 and no apophyses on the pereonites; *Apseudopsis caribbeanus* Guțu 2006, but this has four articles on the accessory flagellum, as well as lateral invaginations on the pereonites, a cephalothorax distinctly longer than wide, and angular shoulders on the rostrum.

A summary of the principal diagnostic characters of the North Atlantic and Mediterranean species of the genus is detailed on Table 1.

Etymology

The new species is named after “ADAM”, the acronym of the “Adaptaciones de Animales Marinos” (Marine Animals Adaptations) laboratory of the University of Vigo, past and present team members from which have collaborated with sampling, sorting and preserving of the specimens examined for this work.

Development

Three developmental stages (juveniles I, juveniles II and adults) and five types of adults (preparatory, copulatory and intermediate females, males I and II) were distinguished in the studied population. No postmarsupial manca stages were found in the samples, although mancas I (*sensu* Messing 1981: individuals with neither pleopods nor pereopod 6) were found inside the marsupium of several copulatory females.

Besides a general increase in setation and spination of the appendages, meristic changes through the life history of *Apseudopsis adami* include an increase in the number of articles of the antennular and antennal flagella and of the endopod of the uropod. Notable morphometric changes (as described above) include the size of the cephalothorax in relation to the total length, and of the exopodites of the

cheliped and pereopod 1. Although the mouthpart ornamentation is in general stable and characteristic of the genus, an increase in the setation and spination of the mandibular palp occurs in a stable way from the juveniles I to the adults; in addition, the palp morphology differs among stages of development and shows sexual dimorphism. Conversely, a number of characters that show interspecific variation within the genus remain stable from the early stages to the largest adults, namely: the shape of the rostrum, the apophyses of the pereonites, the ornamentation of the mouthparts (with the exception of the mandibular palp) and the spination of the first pereopod.

Size-frequency distribution

Total body length of juvenile stages ranged from 1.46 to 4.18 mm; adult females ranged from 3.09 to 4.87 mm, and males were generally slightly larger (Table 2; Fig. 10). Separation into the two juvenile stages and the adults demonstrates that these age classes form single normal distributions (Fig. 11).

Fecundity

Fecundity ranged from 7 to 18 potential offspring per brood (mean: 11.5; standard deviation: 3.2).

Ecology

Apseudopsis adami has been found in sandy and muddy bottoms with the seagrasses *Zostera marina* and *Z. noltii*, and in sandy bottoms with shell fragments, at 3–7 m depth.

In O Grove inlet, salinity values were relatively low, ranging from 20 to 33‰, and the temperature of the bottom water ranged from 13.0 to 16.7°C during the sampling period (winter). Sediments were composed mainly of muddy sand (Q_{50} : 0.11–0.19 mm; S_0 : 1.52–1.61), with relatively high percentages of fine and very fine sand (up to 64.6 and 47.9%, respectively) and silt/clay (up to 61.6%). Although total organic matter content was high (up to 15.5%), *A. adami* was present only in sites with values between 1.32 and 3.39%. Carbonate content was relatively low (7.58–10.46%). For detailed information on environmental variables see Esquete et al. (2010).

In Baiona inlet, *Apseudopsis adami* was found in sandy bottoms with scattered mats of *Z. marina* and in a sandy bottom with shell fragments, near the harbour of Baiona. Previous studies (Moreira et al. 2008) showed values of 89.9% of sand in the *Zostera* bed, and 84.2% of sand in the site near the harbour. Values of total organic matter content in these sites were similar to those found in O Grove (1.91 and 3.18%, respectively), and carbonate content was comparatively higher (32.39 and 72.35%, respectively).

Table 1 Relevant taxonomic characters of the North Atlantic and Mediterranean species of the genus *Apeuldopsis*

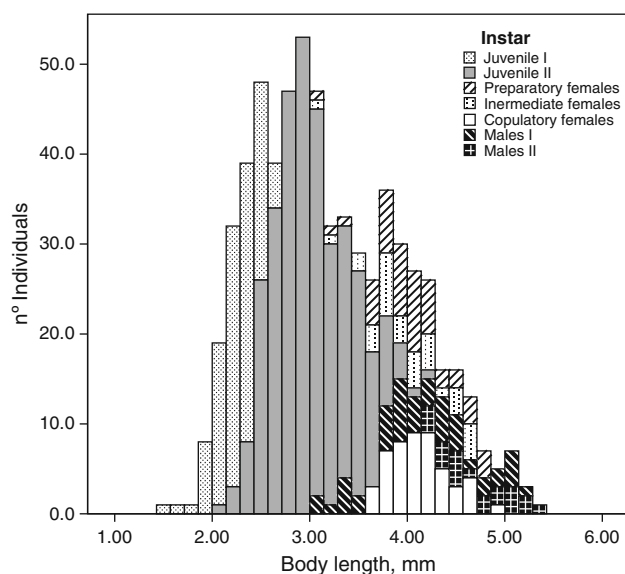
	Rostrum	Pereonites with apophyses	PI propodus ventral spines	PI merus dorsal spine	Antennular flagella (adults)	Pereonites with hyosphenia (females)
<i>A. adami</i> sp. nov.	Pointed, rounded shoulders	2–6: Posterior corners	4	No	Inner: 3 Outer: 10	6
<i>A. acutifrons</i> (Sars 1882)	Long, acute	1, 2: Posterior corners. 3–6: Anterior and posterior corners	4	No	Inner: 3 Outer: 6–7	2, 3, 5, 6
<i>A. amabensis</i> (Guțu 2002)	Pointed, rounded shoulders	1–6: Posterior corners	5	No	Inner: 3 Outer: 6–7	6
<i>A. apocryphus</i> (Guțu 2002)	Pointed, rounded shoulders	No	3	No	Inner: 3 Outer: 8–10	3, 6
<i>A. arguinensis</i> (Guțu 2002)	Short, acute	2–6: Posterior corners	6	No	Inner: 3 Outer: 7–8	2, 6
<i>A. bacescui</i> (Guțu 2002)	Pointed, rounded shoulders	1–6: Posterior corners	4	No	Inner: 3 Outer: 6–7	2, 3, 6
<i>A. elisae</i> (Băcescu 1961)	Pointed, rounded shoulders	1–2: Posterior corners. 3–6: Anterior and posterior corners	5	Yes	Inner: 4 Outer: 8	2–6
<i>A. hastifrons</i> (Norman and Stebbing 1886)	Pointed, rounded shoulders	1: Posterior corners. 3–6: Anterior and posterior corners	6	No	Inner: 3 Outer: 7	2, 3, 5, 6
<i>A. latreillii</i> (Milne-Edwards 1828)	Pointed, rounded shoulders	No	3	Yes	Inner: 4 Outer: 10	2–6
<i>A. mediterraneus</i> (Băcescu 1961)	Pointed, rounded shoulders	1–6: Posterior corners	4	No	Inner: 3 Outer: 6–8	2, 6
<i>A. minimus</i> (Guțu 2002)	Pointed, rounded lobes	1–6: Posterior corners	3	No	Inner: 3 Outer: 6	n. d.
<i>A. ostroumovi</i> Băcescu and Carausu 1947	Pointed, rounded shoulders	1–6: Posterior corners	4	No	Inner: 3 Outer: 7–8	1–6
<i>A. robustus</i> (Sars 1882)	Pointed	No	4	Yes	Inner: 7–9 Outer: 15–16	1–6
<i>A. tridens</i> (Guțu 2002)	Long, with pointed shoulders	1–6: Posterior corners	4	No	Inner: 3 Outer: 10	3–6
<i>A. uncidigitatus</i> (Norman and Stebbing 1886)	Small, rounded	4, 5: Posterior corners	4	No	Inner: 5 Outer: 9	6

nd no data available

Table 2 Body lengths (mean and standard deviation, maximum and minimum) for every developmental stage of *Apseudopsis adami* sp. nov.

	N	Minimum	Maximum	Mean	Standard deviation
Juvenile I	79	1.46	2.59	2.24	0.2
Juvenile II	326	2.04	4.18	3.03	0.38
Preparatory female	48	3.14	4.78	4.03	0.38
Copulatory female	49	3.63	4.87	4.13	0.29
Intermediate female	33	3.09	4.7	4	0.41
Males I	47	3.01	5.16	4.14	0.57
Males II	21	4.18	5.36	4.69	0.37

Values in mm

**Fig. 10** Size/frequency histogram of total body length of the specimens of *Apseudopsis adami* sp. nov. found in one sample from O Grove

In both inlets, the new species is sympatric with the congeneric species *Apseudopsis latreillii*, and in O Grove also with the apseudomorph *Apseudes talpa* (Montagu 1808).

Discussion

Species identification

The relevance of different morphological characters in distinguishing species of the genus *Apseudopsis* has been largely discussed. Norman (1899) proposed the spination of the pereopod 1 as a stable, diagnostic character. Lang

(1955) agreed on the stability of this character, but considered the shape and armature of the pereonites as highly variable within individuals of the same species, thus invalidating *A. hastifrons* and *A. ostroumovi* and synonymizing them with *A. acutifrons*.

Guțu (2002) proposed a number of characters as useful for identification of species of the genus *Apseudopsis* (as *Apseudes* Leach 1814), revalidating species synonymized with *A. acutifrons* by Lang (1955), but included characters that vary intraspecifically between instars (see above, and Esquete et al. 2011), and thus are valid solely for adults. Among the characters that remain stable throughout the life history of *A. adami* sp. nov. we have selected those that show interspecific variation, namely: the shape of the rostrum, the number and position of pereonite apophyses, and the spination of pereopod 1. These characters are stable in other species of the genus where sufficient material has been studied, e.g., *A. mediterraneus*; *A. latreilli* (pers. obs.; Esquete et al. 2012) and their combination allows the positive identification of these species, regardless of the developmental stage of the individual. Other characters considered reliable for identification in previous studies (i.e. the number of segments of the antennular main flagellum and the number and position of hyposphenia) are useful for adults and/or preparatory females (see Table 1).

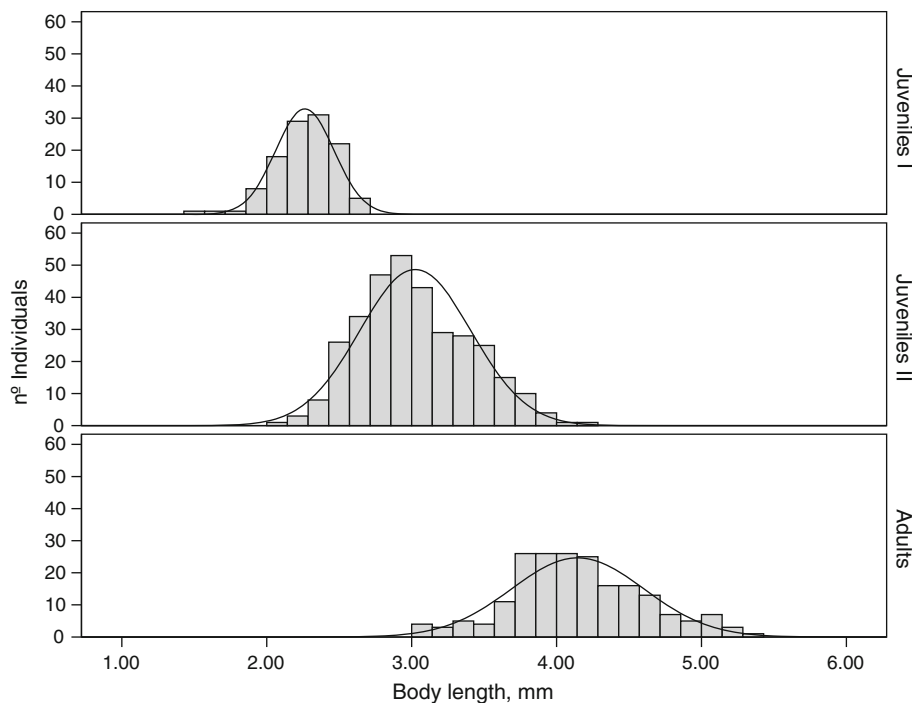
Size-frequency distribution

In Crustacea, the existence of several normal distributions in a length-frequency histogram usually indicates different age groups within the samples (Schmidt et al. 2002). The existence of three normal distributions supports the separation of the population in three developmental stages (juveniles I, juveniles II and adults) and the inclusion of the males I within the adults. On the other hand, the large size ranges suggest several moults are involved (Schmidt et al. 2002; Blazewicz-Paszkowycz 2001); in juveniles II, subsequent moults involve meristic changes (addition of segments in antennal flagella and uropodal rami), while in adult males, several moults lead to an increase in the body size, without the occurrence of significant meristic changes. In the adult females, every copulatory instar implies one moult (Lang 1953).

Life history and development

Several characters have been proposed as indicative of the developmental stage of an individual in tanaidacean species, e.g., the number of segments of the antennular and uropodal flagella (Vengayil et al. 1988), the presence of hyposphenia (Guțu 2002, 2006) and the ornamentation of the mandibular palp (Esquete et al. 2011). Although the number of segments and the type of ornamentation in each

Fig. 11 Size/frequency distribution of total body length of the developmental stages of *Apseudopsis adami* sp. nov. found in one sample from O Grove



stage varies from one species to another, these characters are stable within each developmental stage. Nevertheless, such characters might be different depending on the family. For instance, Messing (1983) found in *Pagurotanais largoensis* (McSweeney 1982) that most of the above-mentioned characters remained stable from the first manca stage. In *Apseudopsis adami*, the number of segments of the antennule, the ornamentation of the mandibular palp, and the presence of penial tubercle, oostegites or marsupium allow the identification of the developmental stage.

Although mancas I were found inside the marsupium of several copulatory females, no manca II appeared in the population. This absence might be due to: (1) the absence of a manca II stage; (2) seasonality in the manca release, such that mancas II appeared before or after sampling was done; (3) the moult from manca II to juveniles occurs immediately, so manca II is never found in the population. The presence of at least one postmarsupial manca stage (sensu Messing 1981) is generalized not only among tanaidaceans but in all peracaridans (see Gardiner 1975). On the other hand, the presence of females carrying eggs and mancas I in the marsupium as well as juveniles and adults of all sizes and developmental range discards reproductive seasonality as an explanation. Experimental work would be needed to solve this question definitely.

Male dimorphism is common among tanaidaceans (see for example Gardiner 1973; Sieg 1978; Messing 1983; Vengayil et al. 1988; Pereira Leite and Pereira Leite 1997; Schmidt et al. 2002; Pennafirme and Soares-Gomes 2009). Secondary males have been shown to derive from protogynous development in some cases (Lang 1958; Gardiner

1975), while in other species, they derive from males I which are simply subadults (Bamber 2010), and in other cases, all types of males are reproductive (Hamers and Franke 2000; Fonseca and D’Incao 2003). In *Apseudopsis adami* the penial tubercle is differentiated in the juvenile stage, and there is no particular reason to consider protogyny. Males I can be considered subadults on the basis of their adult-like morphology together with a penial tubercle that is rudimentary by comparison with that of the males II. This is supported by the size range of males I (Fig. 10), within the range of the adults but not reaching the size of the largest males II. Nevertheless, experimental rearing or histological analyses would be needed to demonstrate whether males I are reproductive or not and to discard protogyny.

The occurrence of intermediate females in a wide range of sizes indicates that there is a stage after every manca release in which the female is without marsupium or oostegites that may involve a moult. This sequence (preparatory-copulatory-intermediate) was proposed by Lang (1953) for the Apseudidae, and Shiino (1937), Blazewicz-Paszkowycz (2001) and Johnson and Attramadal (1982) related the intermediate instar with parental care in *Apseudes nipponicus* (Shiino 1937), *Nototanais antarcticus* (Hodgson 1902) and *Tanais dulongii* (Audouin 1826), respectively, the last through experimental research.

A proposed life history sequence for *Apseudopsis adami* based on the results obtained from this study is presented in Fig. 12. Within the general life history scheme common to the peracaridans, species of tanaidaceans present different strategies (Gardiner 1975; Hamers and Franke 2000).

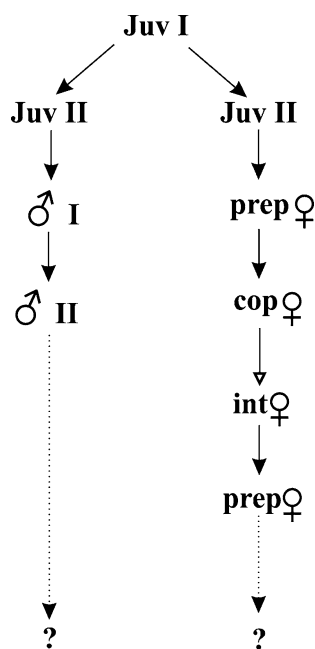


Fig. 12 Proposed life history diagram for *Apseudopsis adami* sp. nov. Juv I, Juveniles I. Juv II, Juveniles II. prep♀, preparatory females. int♀, intermediate females, cop♀, copulatory females. ♂I, males I. ♂II, males II. White arrow indicates no moult necessarily involved

Furthermore, experimental and field work has proved that sequence of instars in one species might vary depending on the environmental conditions (Schmidt et al. 2002), especially sex reversal (Lang 1958; Bückle-Ramírez 1965; Highsmith 1983; Blazewicz-Paszkwyc 2001). Interestingly, Stoner (1986) indicated that sex reversal, ratios and distributional patterns of two sympatric species of *Leptochelia* Dana 1849 were influenced by interspecific interactions between them. Considering that *A. adami* was found in a estuarine ecosystem where it was sympatric with *A. latreilli*, we can expect that both species influence each other depending on the changing environmental conditions of the estuary. Consequently, the scheme proposed here and the population structure of both species would experience seasonal variations within the inlet.

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III. Discusión General

1. DISCUSIÓN GENERAL

Distribución espacial y temporal de la fauna

Los resultados de este estudio muestran que las praderas de *Zostera* L. de la ensenada de O Grove albergan una fauna de peracáridos y picnogónidos abundante y diversificada, con un total de 21291 ejemplares pertenecientes a 116 taxones de peracáridos y 529 pertenecientes a 9 especies de picnogónidos identificados en el desarrollo de este estudio. Quintas (2005), utilizando la misma metodología, también obtuvo valores altos de diversidad y abundancia para poliquetos, y en menor medida para moluscos, en las mismas estaciones de muestreo; en su estudio, los poliquetos constituyeron un grupo con una riqueza específica equiparable a la obtenida aquí para los peracáridos, aunque alcanzando valores de abundancia muy superiores (ver tabla 1). Los moluscos, por el contrario, son un grupo menos diverso y abundante en la ensenada, y los picnogónidos en comparación pueden considerarse un grupo minoritario.

	nº taxones	% taxones	nº individuos	% individuos
Poliquetos*	91	32.4	36131	60.7
Moluscos*	68	24.2	7641	12.8
Peracáridos	116	40.2	15523	26.1
Picnogónidos	9	3.2	232	0.4
Total	281		59527	

Tabla 1. Número, abundancia y dominancia (%) de los cuatro taxones estudiados durante la fase cartográfica de la ensenada de O Grove. *Datos extraídos de Quintas (2005).

Estudios previos han mostrado que en el conjunto de los fondos submareales de la ría de Arousa los poliquetos son el grupo dominante seguido de los moluscos, tanto en términos de biomasa (López-Jamar, 1892) como de densidad y riqueza específica (Mora, 1980), siendo los crustáceos de menor importancia, si bien este hecho podría ser debido a diferencias en las metodologías de muestreo empleadas.

Los picnogónidos sólo habían sido citados previamente en densidades muy bajas, precisamente en las inmediaciones de la ensenada de O Grove (Mora, *opus cit.*). En cualquier caso, estas diferencias sugieren que las condiciones dentro de la ensenada son particularmente favorables a peracáridos y picnogónidos. Esto puede deberse a la presencia de fanerógamas, que proveen de recursos alimenticios a la vez que refugio a organismos de un amplio rango de grupos funcionales (Alfaro *et al.*, 2006), que pueden ser explotados y colonizados por un grupo tan diversificado taxonómica y funcionalmente como son los peracáridos. Los picnogónidos, como se ha discutido en el capítulo 2, se ven beneficiados por los recursos alimenticios adicionales asociados a la planta. En áreas protegidas de las rías de Galicia, donde prevalecen los fondos sedimentarios, el grupo más diverso de los que aquí consideramos es, de forma generalizada, la clase Polychaeta. No obstante, los peracáridos pueden ser localmente dominantes en número de especies y/o individuos, como muestran los estudios de Moreira (2003) en la ensenada de Baiona, Cacabelos (2005) en San Simón o Lourido (2009) en la ría de Aldán. En praderas de fanerógamas de latitudes medias, la diversidad y abundancia relativa de los diferentes grupos es variable (e. g. Böstrom & Bonsdorff, 1997; Çinar *et al.*, 1998; Sfriso *et al.*, 2001; Blanchet *et al.*, 2004), lo que indica la dependencia de éstas de factores oceanográficos o medioambientales tanto regionales como locales.

Los fondos sedimentarios de las rías de Galicia albergan una fauna de especies bentónicas en general, y de peracáridos en particular, que muestra valores de abundancia y/o diversidad mayores que en otras zonas del Nordeste Atlántico con condiciones similares (e. g. Moreira *et al.*, 2008a, b; Lourido *et al.*, 2008; Cacabelos *et al.*, 2010). Los valores observados en este estudio confirman este hecho (Tabla 2). Lourido *et al.* (2008) y Moreira *et al.* (2008b) sugieren que la alta diversidad de peracáridos halladas en la ría de Aldán y en la ensenada de Baiona, respectivamente, están relacionadas con la heterogeneidad de sedimentos que constituyen sus fondos, debido a la diversidad de hábitats que éstos proveen. Sin embargo, los fondos estudiados en este trabajo son relativamente homogéneos, correspondientes a fango arenoso y arena fangosa. En este caso, la diversidad de microhábitats responsable en

parte de una mayor diversidad biológica es aportada por las propias fanerógamas. El elevado número de especies de peracáridos encontrados en O Grove puede ser explicado por una combinación de las particularidades propias de las rías de Galicia (i. e. elevada productividad primaria, diversidad de nichos ecológicos; Figueiras *et al.*, 2002) junto con las propiedades intrínsecas de estas fanerógamas. Estudios previos llevados a cabo en la ensenada han mostrado la importancia de la presencia de estas praderas (Quintas, 2005). Igualmente, es de destacar los efectos del cultivo de bivalvos en las características fisicoquímicas del fondo (Romero *et al.*, 1982), incrementando el aporte de recursos alimentarios para especies bentónicas, así como en la introducción y subsiguiente asentamiento de especies foráneas (Bañón *et al.*, 2008).

	Amp	Iso	Mys	Tan	Cum	Total
Ensenada de O Grove (este estudio)*	84	14	0	7	11	116
Ensenada de San Simón (Cacabelos <i>et al.</i> , 2010)*	60	9	3	7	4	83
Ensenada de Baiona (Moreira & Troncoso, 2007)*	74	11	2	3	2	92
Ría de Aldán (Lourido <i>et al.</i> , 2008)	79	20	7	5	14	125
Ría del Eo (Penedo, 1999)*	24	4	0	4	2	36
Ría de Ares-Betanzos (Garmendia <i>et al.</i> , 1998)	73	9	0	2	13	97
Canal Ovar, Ría de Aveiro (Cunha <i>et al.</i> , 1999)*	26	6	9	2	1	44
Canal Mira, Ría de Aveiro (Cunha <i>et al.</i> , 1999)*	30	9	12	2	3	56
Plataforma continental vasca (Martínez & Adarraga, 2001)	40	5	3	1	18	67
Playa Hendaya (San Vicente & Sorbe, 2001)	19	3	12	0	5	39
Exterior del Delta del Ebro (Cartes <i>et al.</i> , 2007)	31	5	10	2	10	58
Bahía de Cádiz (Drake <i>et al.</i> , 1997)	30	22	10	1	2	75
Mar Tirreno (Scipione <i>et al.</i> , 2005)	82	3	2	5	10	102
Mar Negro (Ersoy Karaçuha <i>et al.</i> , 2009)*	35	6	1	2	2	46

Tabla 2. Número de taxones de peracáridos determinadas en diferentes medios sedimentarios del Atlántico Nordeste (datos de O Grove relativos al estudio cartográfico). *Áreas con fanerógamas. Amp, Amphipoda. Iso, Isopoda. Mys, Mysida. Cum, Cumacea. Tan, Tanaidacea.

La composición específica de los peracáridos de la ensenada de O Grove es muy similar a la encontrada en otras zonas de las rías de Galicia antes mencionadas (i. e. Moreira *et al.*, 2008a, b; Lourido *et al.*, 2008; Cacabelos *et al.*, 2009, 2010), así como a

la presente en otros medios estuarinos similares del Nordeste Atlántico (Cunha *et al.*, 1999; Dauvin *et al.*, 2000, 2009; Dauvin & Vallet, 2006). Estudios llevados a cabo en fondos con praderas muestran también similitudes en la composición faunística (e. g. Cunha *et al.*, 1999; Sfriso *et al.*, 2001; Ersoy Karaçuha *et al.*, 2009). Si bien es ampliamente reconocido que los valores de abundancia y diversidad de especies bentónicas en general, y peracáridos en particular, son mayores en praderas de fanerógamas que en fondos no vegetados (Sfriso *et al.*, *opus cit.*; Whitlow & Grabowski, 2012) existen diferencias en cómo éstas influyen en la composición específica (Blanchet *et al.*, 2004). Así, por ejemplo, los atributos faunísticos en las praderas de fanerógamas se relacionan con la especie o especies de plantas que las conforman (Stoner, 1983; Scipione & Zupo, 2010). Los datos presentados por Scipione & Zupo (*opus cit.*) muestran que los lechos monoespecíficos de *Zostera marina* L. en el Adriático presentan una comunidad de anfípodos bien diferenciada con respecto a lechos de otras especies como *Cymodocea nodosa* (Ucria) y *Posidonia oceanica* (L.). Estos autores señalan como las especies más abundantes y que más contribuyen a la diferenciación de las comunidades a *Dexamine spinosa* (Montagu, 1813), *Perioculodes aequimanus* (Korssman, 1880) y *Gammarus insensibilis* Stock, 1966, las cuales se encuentran entre las numéricamente dominantes en las praderas de *Z. marina* de la ensenada de O Grove. No obstante, a pesar de que Cacabelos *et al.* (2010) encuentra en el conjunto de la ensenada de San Simón (ría de Vigo) una composición específica similar a la que encontramos en O Grove, resulta destacable que es en los puntos de muestreo situados en praderas de *Zostera* en los que la fauna de peracáridos tiene menos especies en común con este estudio. Estas diferencias pueden achacarse a que las praderas de O Grove son submareales, mientras que las de San Simón son fundamentalmente intermareales. De hecho, los resultados de Cacabelos *et al.* (*opus cit.*) muestran que la distribución de la fauna de crustáceos en dicha ensenada varía fundamentalmente en función de la profundidad, presentando las estaciones intermareales, además, una elevada similitud en cuanto a su composición faunística. Moreira *et al.* (2008b) incluyen en su estudio de la ensenada de Baiona una estación submareal con *Z. marina*, en la que la fauna de peracáridos es similar a la que encontramos en O Grove, siendo dominantes entre los crustáceos el tanaidáceo

Apseudopsis latreillii (Milne-Edwards, 1828) y los anfípodos *Gammarella fucicola* (Leach, 1814), *Photis longipes* (Della Valle, 1893) y *Microdeutopus* spp. Dicho estudio indica que los crustáceos alcanzan, como en O Grove, sus máximas densidades en otoño y que la fauna bentónica es, en general, más abundante y diversa en este punto de muestreo que en fondos adyacentes de granulometría y batimetría semejantes. Además, los valores de riqueza específica y diversidad se encuentran entre los más elevados de la ensenada. Los resultados de Penedo (1999) en un estudio llevado a cabo en las praderas de *Zostera* de la ría del Eo también muestran valores menores de diversidad y abundancia de especies bentónicas en estaciones con *Zostera noltii* Hornem. y aportes fluviales estacionales que en praderas de *Z. marina* con condiciones más estables. En el área sureste de O Grove, con fondos de *Z. noltii* y praderas mixtas, donde desembocan corrientes estacionales de agua dulce, los valores de diversidad, abundancia y riqueza específica son los menores de la ensenada. Además, abundan especies consideradas eurihalinas, (e. g. *Idotea chelipes* (Pallas, 1776), *I. baltica* (Pallas, 1776), *Monocorophium acherusicum* (Costa, 1851), *M. insidiosum* (Crawford, 1937), *Gammarus* spp.) confirmando la importancia en la composición de la comunidad que tienen los cambios abruptos de salinidad debidos a los aportes de agua dulce que se producen en la zona. Penedo (*opus cit.*) destaca también la influencia del ciclo vital de las fanerógamas en la densidad poblacional de las especies de peracáridos, aunque al contrario de lo que muestran otros estudios indica que éstos están mejor representados en los meses de primavera-verano.

No obstante, y a pesar de la evidente influencia de la presencia de *Zostera*, el análisis multivariante de los datos faunísticos indica que en el conjunto de las praderas de O Grove la distribución de los peracáridos se relaciona de manera significativa con la granulometría del sedimento, concretamente con la fracción más fina, i. e. arcillas y limos. Estudios llevados a cabo en otros puntos de la ría de Arousa (Mora, 1980; Penas & González, 1983) encuentran una mayor relación entre la distribución de las comunidades bentónicas con las variables granulométricas respecto a otros factores ambientales. Sus resultados muestran importantes similitudes en la composición específica de peracáridos, aunque con densidades y valores de diversidad menores.

Ciclos de vida y estructuras poblacionales

El ciclo de vida y las estrategias reproductivas de las especies pueden determinar importantes fluctuaciones en las densidades poblacionales de las especies bentónicas, resultando en variaciones estacionales en las características faunísticas de la comunidad (Dauvin *et al.*, 1994; Cunha *et al.*, 1999; Moreira *et al.*, 2008a). Por todo ello, el estudio del ciclo de vida y la estructura poblacional de las especies puede ayudarnos a entender el papel que juega una especie dentro del ecosistema, su relación con otras y cómo influyen unas poblaciones en otras.

En el caso de la dinámica poblacional del picnogónido *Achelia echinata* Hodge, 1864 en la pradera de *Zostera marina* que ocupa la parte central de la ensenada de O Grove, se observa una mayor proporción de juveniles en julio. En septiembre, se produce un incremento significativo en la proporción de adultos y el número total de individuos, lo cual sugiere una alta supervivencia de juveniles durante el verano. El otoño, tiene lugar un descenso del número total de individuos, pero el reclutamiento se mantiene hasta el invierno. Sin embargo, estudios anteriores (Munilla León, 1980) mostraron resultados diferentes, indicando una dinámica estacional distinta en la población estudiada de la misma especie. Es bien sabido que las especies bentónicas que denominamos “ingenieros del ecosistema” son capaces de hacer disponibles recursos bióticos y/o abióticos para otras especies (Jones *et al.*, 1994), de manera que influyen en la supervivencia y/o desarrollo de éstas. En este caso, la fanerógama sirve tanto de sustrato para los propios individuos como para las especies de las que se alimentan, por lo que resulta muy probable que sea el factor que determine el ciclo vital y la dinámica poblacional de *A. echinata* en la pradera de *Z. marina* de O Grove.

Las dos especies estudiadas del género *Apseudopsis* Norman, 1899 comparten un ciclo de vida similar, que puede incluirse dentro de la estrategia general mostrada mayoritariamente por los peracáridos, y en particular por los tanaidáceos apseudomorfos (Gardiner, 1975; Schmidt *et al.*, 2002). No obstante, existen algunas diferencias destacables: por un lado, los individuos de *Apseudopsis latreillii* no presentan una estructura copulatoria diferenciada hasta que están morfológicamente

desarrollados, mientras que en los ejemplares de *Apseudopsis adami* que todavía no han desarrollado completamente algunos apéndices (e. g. antenas, palpo mandibular) ya se aprecian estructuras diferenciadas, aunque no totalmente desarrolladas. Otro rasgo destacable es la ausencia de manchas extramarsupiales de *A. adami* en el periodo de estudio. Por otro lado, el histograma de frecuencias de tamaños también presenta algunas diferencias para las dos especies; así, no sólo *A. latreilli* alcanza tamaños mayores, sino que el rango de tamaño también es mayor que el de *A. adami*. Además, el rango de tamaños de los dos tipos de machos está perfectamente segregado en *A. adami*, mientras que en *A. latreilli* se superponen completamente. Como otros autores han sugerido para diversas especies bentónicas, los ciclos de vida y las estrategias de desarrollo pueden verse afectadas tanto por factores ambientales (Cane, 1979; Highsmith, 1983; Schmidt *et al.*, 2002; Pennafirme & Soares-Gomes, 2009) como por la presencia de otras especies próximas, permitiendo así su coexistencia (Stoner, 1986; Da Silva Castiglioni & Buckup, 2008). Estudios basados en experimentos de laboratorio han mostrado que especies congénéricas de tanaidáceos que comparten un mismo hábitat influyen unas en las otras, acomodando su estrategia de desarrollo, comportamiento o ciclo vital (Stoner, 1986). De este modo, los esquemas mostrados en los capítulos 4 y 5 de esta memoria podrían ser fruto de la influencia mutua experimentada por ambas poblaciones, y no se puede descartar que puedan presentar variaciones en otros medios o en presencia de otras especies.

Estudio taxonómico

En estudios de ecología del bentos es frecuente que el número de especies de ciertos grupos (particularmente cumáceos, tanaidáceos y picnogónidos) sea subestimado debido a dificultades taxonómicas (Cunha *et al.*, 1999). Algunos ejemplos pueden extraerse de este estudio, además del ya discutido *Perioculodes aequimanus* (ver Capítulo 3): *Cumella limicola* Sars, 1879 es considerada especie endémica del mar Mediterráneo (Izquierdo & Guerra-García, 2011), aunque ha sido citada en el oeste de África y Madagascar (Radhadevi & Kurian, 1980), y recientemente encontrada como único representante de los cumáceos en un estudio llevado a cabo en las islas Azores (Bamber & Robbins, 2009). Por su parte, este trabajo amplía el límite de distribución

de *Cumella africana* Băcescu, 1972 hacia el Norte, ya que previamente sólo había sido documentada en la costa atlántica africana y en las islas Canarias (Corbera *et al.*, 2002; Bochert & Zettler, 2011). El tanaidáceo *Akanthophoreus gracilis* (Krøyer, 1842) era considerado una especie nórdica hasta la cita de Bamber (2011) en las islas de Scilly; este trabajo amplía su rango latitudinal aún más hacia el Sur. Por último, y a pesar de que la distribución de los picnogónidos de la península Ibérica ha sido estudiada por Munilla (1987, 1993, 1997), los picnogónidos *Callipallene brevis* (Johnston, 1837) y *C. tiberi* (Dohrn, 1881) no habían sido citados hasta el momento en costas atlánticas ibéricas más allá del estrecho de Gibraltar.

La descripción de nuevas especies en las últimas décadas ha puesto de manifiesto que la fauna bentónica de aguas someras de las costas del nordeste Atlántico y Mediterráneo dista mucho de ser completamente conocida. Por el contrario, estudios faunísticos centrados en hábitats bentónicos concretos han traído consigo la descripción de nuevas especies pertenecientes a todos los grupos zoológicos. Concretamente, en los últimos diez años se han descrito en las costas de Europa y norte de África especies nuevas de poríferos (Goodwin & Picton, 2009), platelmintos (Lanfranchi *et al.*, 2010), gastrotricos (Hummon & Kelly, 2011), oligoquetos (Parapar *et al.*, 2008), poliquetos (Moreira *et al.*, 2004; Tovar Hernández *et al.*, 2007; Palmero *et al.*, 2008), picnogónidos (Bamber & Costa, 2009a) y, en lo que se refiere a crustáceos en particular, se han descrito nuevas especies de leptostráceos (Moreira *et al.*, 2003a, b, 2007, 2009), misidáceos (Vilas-Fernández *et al.*, 2008), anfípodos (Guerra-García *et al.*, 2001, 2002; Guerra-García & Takeuchi, 2002; Myers *et al.*, 2010; Sturaro & Guerra-García, 2012; Tato *et al.*, en prensa) y tanaidáceos (Guțu, 2002; Bamber & Costa, 2009b; Bamber *et al.*, 2009), por citar algunos ejemplos.

Los tanaidáceos son un grupo cuyo desarrollo larvario ocurre fundamentalmente dentro del marsupio, siendo los reclutas liberados en forma de juveniles (postlarvas) epibentónicos. Al no existir una fase larvaria obligatoriamente dispersiva, y ser especies de pequeño tamaño que no realizan grandes desplazamientos, es un grupo proclive a la aparición de endemismos y tendencia a la especiación (Bamber, 2010; Blazewicz-Paszkowycz *et al.*, 2012). La presente memoria

incluye trabajos taxonómicos centrados en el estudio de la morfología y caracteres taxonómicos de tanaidáceos del género *Apseudopsis* y anfípodos del género *Perioculodes* Sars, 1895, ambos abundantes en los fondos sedimentarios de las rías de Galicia y con especies numéricamente dominantes en la ensenada de O Grove, con el objetivo de facilitar la identificación de las especies en futuros estudios de carácter ecológico y faunístico en el nordeste atlántico.

El suborden Apseudomorpha se considera el más plesiomórfico dentro de los tanaidáceos (Blazewicz-Paszcowycz *et al.*, 2012). La relevancia de los caracteres morfológicos para discriminar taxones a nivel supraespecífico es desconocida (Blazewicz-Paszcowycz *et al.*, *opus cit*), y es objeto de constante revisión (e. g. Guțu, 2006; Larsen *et al.*, 2011). El género *Apseudopsis* fue propuesto por Norman (1899) para distinguir aquellas especies de tanaidáceos apseudomorfos cuyos lóbulos oculares están fusionados con el caparazón, diferenciándolas de las pertenecientes al género *Apseudes* Leach 1814. Guțu (2006) aportó una diagnosis completa, destacando una serie de caracteres útiles para distinguir el género: tres (raramente cuatro) segmentos en el flagelo interno de las anténulas, así como en el exopodito de los urópodos; presencia de largas setas simples en el margen dorsal de la basis de los quelípedos en ambos sexos; presencia de una protuberancia anteroproximal con algunas setas simples largas en el segundo pereópodo; y la ausencia de espina dorsodistal en el mero del primer pereópodo. De estos caracteres, los tres primeros están presentes en las especies examinadas en este estudio. No obstante, *Apseudopsis acutifrons* (Norman, 1899), la especie tipo, y *Apseudopsis latreillii*, redescrita y discutida en esta memoria, así como en la mayoría de las especies del género presentan espina dorsodistal en el mero del primer pereópodo (ver tabla 1 del capítulo 5 de esta memoria). Es necesaria, por tanto, una revisión en profundidad del género *Apseudopsis* y de la familia Apseudidae para confirmar su validez y determinar los caracteres que lo definen.

Los caracteres válidos para identificar especies del género *Apseudopsis* han sido discutidos esta memoria en los capítulos 4 y 5. Algunos de estos caracteres han sido propuestos con anterioridad para distinguir especies tanto del género *Apseudes* como

Apseudopsis por su estabilidad en las diferentes etapas del desarrollo y entre géneros. Así, Norman (1899), por ejemplo, propuso el número y distribución de espinas en el primer pereópodo, mientras que Guțu (2002) propone, entre otros, la forma de los pereonitos y, para identificar hembras adultas, el número y disposición de hiposfenias. En la misma línea, Guțu (1998, 2001) propone el estudio y el uso de microestructuras distinguibles en los pereópodos (tales como el número exacto de setas en ciertos puntos, o la morfología de ciertas espinas) para identificar las especies del suborden Apseudomorpha. En las especies de *Apseudopsis* presentes en O Grove no hemos encontrado diferencias significativas en este tipo de estructuras, que sin embargo si son más complejas en los individuos de mayor tamaño que en los juveniles, por lo que podría dar lugar a confusión. No obstante, la falta de ilustraciones detalladas en la literatura del grupo dificulta la valoración de estos y otros caracteres; un ejemplo ilustrativo de esta situación es la escasa atención que se ha prestado a las piezas bucales: a pesar de que hasta el momento los caracteres estudiados eran escasos para apseudomorfos, recientemente se ha descubierto que su morfología contiene caracteres críticos para distinguir especies y evaluar la validez de un determinado género (Larsen *et al.*, 2011).

Si bien los peracáridos son un grupo con tendencia a la especiación y escasos ejemplos de distribución cosmopolita, la variabilidad intraespecífica de los caracteres morfológicos es frecuente entre individuos o poblaciones expuestas a diferentes condiciones ambientales (Berezina, 2007). Un ejemplo lo encontramos en las diferencias halladas en los ejemplares de *Periculodes aequimanus* de O Grove con ejemplares mediterráneos. Por otro lado, estudios cuantitativos como los desarrollados en los capítulos 4 y 5 de esta memoria muestran una variabilidad intraespecífica en dos especies de *Apseudopsis* que se sustenta con variaciones de tamaño y, por ende, estadios de desarrollo. Dada esta variabilidad, y a la vista de los resultados de este estudio, se hace patente la necesidad de estudios taxonómicos que incluyan no sólo la descripción de caracteres morfológicos identificativos, sino también datos ecológicos y biogeográficos. De este modo, las especies descritas y los caracteres estudiados podrán ser integrados tanto en el conocimiento taxonómico, la sistemática

del grupo, y su biogeografía, contribuyendo, a la postre, a un mejor entendimiento de la diversidad del sistema bentónico de las costas atlánticas.

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IV. Conclusiones generales

General conclusions

SPATIAL DISTRIBUTION AND TEMPORAL DYNAMICS:

- **The *Zostera* meadows in O Grove inlet host a much diversified peracarid faunas**, reaching levels of diversity and abundance that are greater than in other similar environments of the Northeast Atlantic.
- **The Pycnogonid taxocoenosis is highly diversified** by comparison with other sedimentary bottoms in the Galician rias.
- **The Peracarid biocoenosis in O Grove seagrass meadows presents a definite spatial distribution.** The assemblage located in the *Zostera marina* L. meadows of the centre of the inlet constitute a definite group, and differ significantly from those meadows located on the south-east, composed by *Z. noltii* Hornem. or both species, where frequent salinity and temperature fluctuations due to freshwater discharge take place.
- **The main factor determining the spatial distribution and temporal variation of the peracarid assemblages is the sediment granulometry.** Nevertheless, the presence of the seagrasses should influence in a major way the hydrodynamic and sedimentary features of the habitat, and utterly the spatial and temporal patterns observed.
- **Seasonal variations of both Peracarida and Pycnogonida are coupled with the *Z. marina* life cycle.** Thus, while most of the species show the highest abundances in September, after the enlargement of the leaves and summer bloom of epiphytes, others reach the highest values in late autumn, probably because of benefiting from the detritus due to leave decay and decomposition.

TAXONOMY AND BIOGEOGRAPHY:

- **The oedicerotid amphipod *Periocolodes aequimanus* (Kossmann, 1880) is present in Atlantic waters, and is a well-established species in O Grove.**
- ***P. aequimanus* can be distinguished from the sympatric *P. longimanus* (Bate & Westwood, 1868) mainly for the oval shape of the first gnathopod propodus.** Other diagnostic features are: the length of the segments of the antennal peduncle, the first coxa and the seventh pereopod basis frontal anterior margin.

- **The species of the apseudomorph tanaidacean genus *Apseudopsis* Norman, 1899 can be diagnosed, regardless the developmental stage of the specimen, by a combination of the following characters:** the shape of the rostrum, the presence/absence of apophyses on pereonites and the spination of the first pereopod.
- ***Apseudopsis latreillii* (Milne-Edwards, 1828) can be identified from the following combination of morphological characters:** pointed and downturned rostrum, pereonites without apophyses, three ventral spines on the pereopod 1 propodus, and one dorsodistal spine on the merus.
- ***Apseudopsis adami* Esquete & Bamber, sp. nov. is described and differs from other species of the genus in the following combination of morphological characters:** pointed and downturned rostrum, posterolateral apophyses on pereonites 2-6, four ventral spines on the propodus and no dorsodistal spine on the merus.
- **The developmental stage of a specimen of *Apseudopsis* can be determined observing the following characters:** the number of segments on the antennal and antennular flagella, the ornamentation of the mandibular palp and the presence of hyposphenians.

V. Anexos

Anexo 1. Relación sistemática de los taxones encontrados en las praderas de fanerógamas de la ensenada de O Grove durante la realización de este estudio.

Filo **ARTHROPODA**

Subfilo CRUSTACEA

Clase **MALACOSTRACA**

Subclase EUMALACOSTRACA

Superorden PERACARIDA

Orden **AMPHIPODA**

Amphipoda indet.

Suborden GAMMARIDEA

Familia **Lysianassidae** Dana, 1849

Lysianassa ceratina (Walker, 1889)

Tryphosites longipes (Bate & Westwood, 1861)

Familia **Ampeliscidae** Costa, 1857

Ampelisca spp.

Ampelisca brevicornis (Costa, 1853)

Ampelisca gibba Sars, 1882

Ampelisca serraticaudata Chevreux, 1888

Ampelisca spinifer Reid, 1951

Ampelisca spinipes Boeck, 1861

Ampelisca tenuicornis Lilljeborg, 1855

Ampelisca typica (Bate, 1856)

Familia **Ampilochidae** Boeck, 1871

Ampilochus spencebatei (Stebbing, 1876)

Familia **Cyproideidae** Barnard, 1974

Peltocoxa marioni Catta, 1875

Familia **Leucothoidae** Dana, 1852

Leucothoe incisa Robertson, 1892

Leucothoe lilljeborgi Boeck, 1861

Leucothoe spinicarpa (Abildgaard, 1879)

Familia **Stenothoidae** Boeck, 1871

Stenothoe monoculoides (Montagu, 1815)

Familia **Gammaridae** Leach, 1814

Gammaridae indet.

Gammarus spp.

Gammarus crinicornis Stock, 1966

Gammarus insensibilis Stock, 1966

Gammarus tigrinus Sexton, 1939

Familia **Melitidae** Bousfield, 1973

Gammarella fucicola (Leach, 1814)

Abludomelita gladiosa (Bate, 1862)

Melita dentata (Kroyer, 1842)

Melita hergensis Reid, 1939

- Melita palmata* (Montagu, 1804)
- Familia **Urothoidae** Bousfield, 1978
- Urothoe elegans* (Bate, 1857)
- Urothoe grimaldii* Chevreux, 1895
- Urothoe pulchella* (Costa, 1853)
- Familia **Oedicerotidae** Lilljeborg, 1865
- Periocolodes aequimanus* (Kossmann, 1880)
- Periocolodes longimanus* (Bate & Westwood, 1868)
- Familia **Phoxocephalidae** Sars, 1895
- Harpinia* spp.
- Harpinia antennaria* Meinert, 1890
- Harpinia crenulata* (Boeck, 1871)
- Harpinia delavallei* Chevreux, 1910
- Harpinia laevis* Sars, 1891
- Harpinia pectinata* Sars, 1891
- Familia **Calliopiidae** Sars, 1895
- Apherusa bispinosa* (Bate, 1856)
- Apherusa henneguyi* Chevreux & Fage, 1925
- Apherusa jurinei* (Milne-Edwards, 1830)
- Familia **Dexaminidae** Leach, 1814
- Dexamine spinosa* (Montagu, 1813)
- Familia **Ampithoidae** Stebbing, 1899
- Ampithoe* spp.
- Ampithoe gammaroides* (Bate, 1856)
- Ampithoe helleri* Karaman, 1975
- Ampithoe ramondi* Audouin, 1826
- Ampithoe rubricata* (Montagu, 1808)
- Sunamphitoe pelagica* (Milne-Edwards, 1830)
- Familia **Aoridae** Stebbing, 1899
- Aoridae indet.
- Lembos* spp.
- Lembos websteri* Bate, 1857
- Leptocheirus pilosus* Zaddach, 1844
- Microdeutopus* spp.
- Microdeutopus anomalus* (Rathke, 1843)
- Microdeutopus chelifera* (Bate, 1862)
- Microdeutopus damnoniensis* (Bate, 1856)
- Microdeutopus gryllotalpa* Costa, 1853
- Microdeutopus stationis* Della Vale, 1893
- Microdeutopus versiculatus* (Bate, 1856)
- Familia **Microprotopidae** Myers & Lowry, 2003
- Microprotopus maculatus* Norman, 1867
- Familia **Colomastigidae** Stebbing, 1899
- Colomastix pusilla* Grube, 1861
- Suborden COROPHIIDEA
- Familia **Photidae** Boeck, 1871
- Gammaropsis maculata* (Johnston, 1827)

Gammaropsis sophiae (Boeck, 1861)

Gammaropsis palmata (Stebbing & Robertson, 1891)

Photis longipes (Della Valle, 1893)

Familia **Corophiidae** Leach, 1814

Monocorophium spp.

Monocorophium acherusicum (Costa, 1851)

Monocorophium insidiosum (Crawford, 1937)

Monocorophium sextonae (Crawford, 1937)

Familia **Ischyroceridae** Stebbing, 1899

Ischyrocerus anguipes Krøyer, 1838

Siphonocetes kroyeranus Bate, 1856

Siphonocetes striatus Myers & McGrath, 1979

Siphonocetes sabatieri de Rouville, 1894

Erichthonius punctatus (Bate, 1857)

Jassa falcata (Montagu, 1808)

Familia **Caprellidae** Leach, 1814

Caprellidae indet.

Caprella sp.1

Caprella sp.2

Caprella acanthifera Leach, 1814

Caprella equilibra Say, 1818

Caprella penantis Leach, 1814

Pariambus typicus (Krøyer, 1884)

Phtisica marina Slabber, 1769

Pseudoprotella phasma Montagu, 1804

Orden **ISOPODA**

Suborden VALVIFERA

Familia **Idoteidae** Milne-Edwards, 1840

Idotea spp.

Idotea baltica (Pallas, 1772)

Idotea chelipes (Pallas, 1776)

Idotea granulosa Rathke, 1843

Idotea neglecta Sars, 1897

Familia **Arcturidae** Sars, 1899

Arcturidae indet.

Astacilla sp.

Astacilla longicornis (Sowerby, 1806)

Suborden CYMOTHOIDA

Familia **Anthuridae** Leach, 1814

Cyathura carinata (Krøyer, 1847)

Suborden ASELLOTA

Familia **Janiridae** Sars, 1897

Jaera albifrons Leach, 1814

Janira maculosa Leach, 1814

Janiropsis sp.

Familia **Munnidae** Sars, 1897

Munna spp.

Uromunna spp.

Suborden SPHAEROMATIDEA

Familia **Sphaeromatidae** Latreille, 1825

Lekanesphaera levii (Argano & Ponticelli, 1981)

Orden **CUMACEA**

Familia **Bodotriidae** Scott, 1901

Bodotria pulchella (Sars, 1879)

Iphinoe tenella Sars, 1878

Iphinoe trispinosa (Goodsir, 1843)

Familia **Nannastacidae** Bate, 1866

Nannastacus spp.

Cumella limicola Sars, 1879

Cumella africana Băcescu, 1972

Cumella pygmaea Sars, 1865

Pseudocuma longicorne (Bate, 1858)

Pseudocuma simile G.O. Sars, 1900

Orden **TANAIDACEA**

Suborden APSEUDOMORPHA

Familia **Apseudidae** Leach, 1814

Apseudes talpa (Montagu, 1808)

Apseudopsis latreillii (Milne-Edwards, 1828)

Apseudopsis adami Esquete & Bamber, sp. nov.

Suborden TANAIDOMORPHA

Familia **Tanaidae** Dana, 1849

Tanais dulongii (Audouin, 1826)

Zeuxo holdichi Bamber, 1990

Familia **Leptocheliidae** Lang, 1973

Leptochelia savignyi (Krøyer, 1842)

Familia **Akanthophoreidae** Sieg, 1986

Akanthophoreus gracilis (Krøyer, 1842)

Subfilo CHELICERATA

Clase **PYCNOGONIDA**

Orden **Pantopoda**

Familia **Ammotheidae** Dohrn, 1881

Achelia echinata Hodge, 1864

Familia **Nymphonidae** Wilson, 1878

Nymphon gracile Leach, 1814

Familia **Callipallenidae** Hilton, 1942

Callipallene brevirostris (Johnston, 1837)

Callipallene emaciata (Dohrn, 1881)

Callipallene spectrum (Dohrn, 1881)

Callipallene tiberi (Dohrn, 1881)

Familia **Phoxichilidiidae** Sars, 1891

Anoplodactylus petiolatus (Hodge, 1864)

Anoplodactylus pygmaeus (Hodge, 1864)

Familia **Endeidae** Norman, 1908

Endeis spinosa (Montagu, 1808)

Anexo 2. Abundancias (individuos/0.28 m²) de los taxones encontrados en las estaciones de muestreo en el estudio de variabilidad espacial.

	D24	D26	D27	D31	D34	D35	D37	D38	D39	D40	TOTAL
<i>Amphipoda</i> indet.	0	0	0	0	3	0	0	0	0	0	3
<i>Abludomelita gladiosa</i>	0	0	1	0	0	0	0	0	0	0	1
<i>Ampelisca</i> spp.	0	0	1	1	0	0	0	0	0	0	2
<i>Ampelisca brevicornis</i>	6	6	3	0	0	6	0	4	3	0	28
<i>Ampelisca gibba</i>	0	0	13	2	0	0	0	0	0	0	15
<i>Ampelisca serraticaudata</i>	0	0	0	0	0	0	0	0	0	0	0
<i>Ampelisca spinifer</i>	3	17	0	0	0	0	0	0	1	0	21
<i>Ampelisca spinipes</i>	1	0	0	0	0	0	0	0	0	0	1
<i>Ampelisca tenuicornis</i>	3	0	6	0	0	0	0	0	0	0	9
<i>Ampelisca typica</i>	0	2	0	2	0	0	1	0	0	0	5
<i>Ampilochus spencebatei</i>	4	24	6	3	1	2	0	0	0	0	40
<i>Ampithoe</i> spp.	0	0	0	0	0	0	0	0	4	0	4
<i>Ampithoe gammaroides</i>	0	1	0	0	2	2	0	2	0	0	7
<i>Ampithoe helleri</i>	0	0	0	0	0	8	0	0	0	0	8
<i>Ampithoe neglecta</i>	0	0	0	1	2	11	0	0	2	0	16
<i>Ampithoe ramondi</i>	3	8	2	0	0	1	0	2	4	0	20
<i>Ampithoe rubricata</i>	10	0	0	3	1	0	0	0	0	0	14
Aoridae indet.	0	1	0	1	12	0	0	246	16	4	280
<i>Apherusa bispinosa</i>	2	1	2	3	0	1	0	2	2	0	13
<i>Apherusa henneguyi</i>	0	0	0	0	0	0	0	0	0	2	2
<i>Apherusa jurinei</i>	3	1	0	0	0	0	0	0	0	46	50
<i>Colomastix pusilla</i>	0	0	16	0	0	0	0	0	1	0	17
<i>Dexamine spinosa</i>	25	5	28	12	0	0	0	74	34	0	178
<i>Erichthonius punctatus</i>	11	44	1	7	6	3	0	2	7	0	81
Gammaridae indet.	0	0	0	0	4	0	0	0	0	0	4
<i>Gammarella fucicola</i>	17	22	516	18	0	1	2	170	69	5	820
<i>Gammaropsis maculata</i>	1	0	0	0	0	5	0	0	0	0	6
<i>Gammaropsis sophiae</i>	0	3	0	0	0	0	0	0	0	0	3
<i>Gammaropsis palmata</i>	3	5	1	0	0	0	0	0	1	0	10
<i>Gammarus</i> spp.	0	0	0	0	110	0	0	1	0	0	111
<i>Gammarus crinicornis</i>	0	0	1	0	60	0	1	0	2	1	65
<i>Gammarus insensibilis</i>	0	0	1	0	56	0	1	1	0	4	63
<i>Gammarus tigrinus</i>	0	1	1	0	213	0	1	10	0	1	227
<i>Harpinia</i> spp.	6	1	50	4	0	0	0	34	24	0	119
<i>Harpinia antennaria</i>	0	4	4	0	0	0	0	24	22	0	54
<i>Harpinia crenulata</i>	0	4	6	0	0	0	0	32	16	1	59
<i>Harpinia delavallei</i>	0	4	11	0	0	0	0	1	0	1	17
<i>Harpinia laevis</i>	2	0	10	1	0	0	0	0	7	0	20
<i>Harpinia pectinata</i>	12	55	78	16	0	11	0	33	39	0	244
<i>Jassa falcata</i>	0	0	0	26	0	11	0	1	0	0	38
<i>Lembos</i> spp.	0	1	2	0	9	0	1	79	24	3	119
<i>Lembos websteri</i>	0	4	0	0	0	0	0	55	4	0	63
<i>Leptocheirus pilosus</i>	4	70	1	5	0	0	0	1	0	0	81
<i>Leucothoe incisa</i>	16	27	14	9	0	1	0	0	0	0	67
<i>Leucothoe lilljeborgi</i>	9	0	1	4	0	0	0	0	0	0	14
<i>Leucothoe spinicarpa</i>	0	0	18	0	0	0	0	0	0	0	18
<i>Lysianassa ceratina</i>	0	1	0	0	0	0	0	0	0	0	1
<i>Melita dentata</i>	0	0	0	0	1	0	0	0	0	1	2
<i>Melita hergensis</i>	0	0	0	0	0	1	0	0	0	4	5

	D24	D26	D27	D31	D34	D35	D37	D38	D39	D40	TOTAL
<i>Melita palmata</i>	0	0	1	0	0	6	6	0	0	157	170
<i>Microdeutopus</i> spp.	13	9	17	30	60	6	3	166	81	27	412
<i>Microdeutopus anomalus</i>	0	0	2	0	0	0	0	54	7	0	63
<i>Microdeutopus chelifer</i>	0	0	0	0	3	0	0	0	0	4	7
<i>Microdeutopus damnoniensis</i>	0	0	0	0	2	0	0	7	2	5	16
<i>Microdeutopus gryllotalpa</i>	0	4	3	3	52	7	0	16	7	6	98
<i>Microdeutopus stationis</i>	2	1	2	2	1	0	0	0	1	0	9
<i>Microdeutopus versiculatus</i>	2	64	1	0	96	0	1	0	1	0	165
<i>Microprotopus maculatus</i>	59	0	1	1	0	0	0	0	0	0	61
<i>Monocorophium</i> spp.	4	1	2	0	4	0	0	2	2	0	15
<i>Monocorophium acherusicum</i>	1	0	3	0	14	1	6	7	5	0	37
<i>Monocorophium insidiosum</i>	2	0	0	0	101	3	31	2	3	6	148
<i>Monocorophium sextonae</i>	5	1	13	2	18	7	13	12	6	11	88
<i>Peltocoxa marioni</i>	3	1	0	0	0	0	0	0	0	0	4
<i>Periculodes aequimanus</i>	28	5	7	8	1	11	0	55	105	68	288
<i>Periculodes longimanus</i>	45	3	4	4	3	0	0	0	0	0	59
<i>Photis longipes</i>	40	25	1	2	0	6	1	0	2	0	77
<i>Siphonoecetes kroyeranus</i>	1	3	0	0	0	0	0	0	2	0	6
<i>Siphonoecetes striatus</i>	2	1	0	0	0	0	0	0	0	0	3
<i>Siphonoecetes sabatieri</i>	0	0	0	0	0	7	0	0	149	0	156
<i>Stenothoe monoculoides</i>	21	9	6	3	23	3	0	10	4	87	166
<i>Sunampithoe pelagica</i>	5	8	0	0	0	0	0	4	1	0	18
<i>Tryphosites longipes</i>	0	9	0	0	0	0	0	0	0	0	9
<i>Urothoe elegans</i>	1	0	0	0	0	0	0	0	0	0	1
<i>Urothoe grimaldii</i>	0	0	0	24	0	0	0	0	0	0	24
<i>Urothoe pulchella</i>	0	1	0	0	0	0	0	0	0	0	1
Caprellidae indet.	0	0	2	0	0	0	0	0	0	0	2
<i>Caprella</i> sp.1	1	0	0	0	0	0	0	0	0	0	1
<i>Caprella</i> sp.2	0	0	3	0	0	0	0	0	0	0	3
<i>Caprella acanthifera</i>	27	43	16	23	0	2	0	6	8	0	125
<i>Caprella equilibra</i>	0	0	0	4	0	0	0	0	0	0	4
<i>Caprella penantis</i>	0	0	0	0	0	1	0	0	0	0	1
<i>Pariambus typicus</i>	22	17	178	25	0	0	0	0	1	0	243
<i>Phtisica marina</i>	12	3	8	18	0	0	0	1	2	0	44
<i>Pseudoprotella phasma</i>	0	0	0	0	0	2	0	0	0	0	2
Arcturidae indet.	0	2	0	0	0	0	0	0	0	0	2
<i>Astacilla longicornis</i>	1	0	4	0	0	0	0	0	0	0	5
<i>Cyathura carinata</i>	0	74	2	0	1	6	3	15	6	68	175
<i>Idotea</i> spp.	0	0	0	0	2	2	94	0	0	44	142
<i>Idotea baltica</i>	0	0	0	0	27	0	94	2	0	9	132
<i>Idotea chelipes</i>	0	0	0	0	13	0	84	2	0	51	150
<i>Idotea granulosa</i>	0	0	0	0	5	0	18	0	0	1	24
<i>Idotea neglecta</i>	0	0	0	0	4	0	19	0	0	15	38
<i>Jaera albifrons</i>	0	0	0	0	0	0	137	0	0	2	139
<i>Janira maculosa</i>	0	0	59	0	0	0	0	0	0	0	59
<i>Janiropsis</i> sp.	0	0	11	0	0	0	0	0	0	0	11
<i>Munna</i> sp.	0	0	14	3	0	1	0	0	0	0	18
<i>Uromunna</i> sp.	12	0	10	57	2	16	0	180	87	4	368
<i>Lekanesphaera levii</i>	1	0	0	0	1	1	0	0	1	0	4
<i>Bodotria pulchella</i>	0	1	1	0	0	0	0	0	0	0	2
<i>Cumella limicola</i>	0	0	0	0	0	1	0	1	4	0	6
<i>Cumella africana</i>	0	0	2	7	0	11	0	19	26	0	65
<i>Iphinoe tenella</i>	21	7	61	10	0	5	0	22	20	0	146

	D24	D26	D27	D31	D34	D35	D37	D38	D39	D40	TOTAL
<i>Iphinoe trispinosa</i>	173	2	30	8	0	5	0	9	10	3	240
<i>Nannastacidae</i> indet.	0	0	2	1	0	0	0	5		0	8
<i>Nannastacus</i> spp.	0	0	0	1	0	1	0	0	0	0	3
<i>Pseudocuma longicorne</i>	1	0	0	0	0	0	0	1	0	0	2
<i>Pseudocuma simile</i>	1	0	0	0	0	0	0	0	0	0	1
<i>Apseudes talpa</i>	0	530	0	0	0	15	0	61	117	3	726
<i>Apseudopsis latreillii</i>	226	141	2699	637	0	12	0	30	24	0	3769
<i>Apseudopsis adami</i>	928	570	0	576	0	25	0	0	104	0	2203
<i>Akanthophoreus gracilis</i>	0	0	0	0	0	0	0	0	33	0	33
<i>Leptochelia savignyi</i>	0	0	0	1	0	12	0	400	51	1	465
<i>Tanais dulongii</i>	3	5	6	0	0	0	0	0	0	22	36
<i>Zeuxo holdichi</i>	59	70	6	173	0	194	0	171	23	4	700
<i>Achelia echinata</i>	6	0	73	11	0	3	7	2	6	0	72
<i>Anoplodactylus petiolatus</i>	2	0	0	0	0	0	0	0	0	0	2
<i>Anoplodactylus pygmaeus</i>	5	0	7	6	5	22	2	2	7	0	57
<i>Callipallene brevirostris</i>	0	0	0	0	1	0	0	0	0	0	1
<i>Callipallene emaciata</i>	0	0	0	0	3	0	0	0	3	3	9
<i>Callipallene spectrum</i>	0	0	0	0	2	0	0	2	0	0	4
<i>Callipallene tiberi</i>	0	0	10	2	40	1	0	14	10	8	85
<i>Endeis spinosa</i>	1	0	0	0	0	0	0	0	0	0	1
<i>Nymphon gracile</i>	0	0	0	1	0	0	0	0	0	0	1

Anexo 3. Abundancia (individuos/0.0625 m²) de los taxones encontrados en los meses de muestreo en el estudio de variación estacional.

	May 98	Jul 98	Sep 98	Nov 98	Ene 99	Mar 99	Total
<i>Ampelisca</i> spp.	0	0	0	1	0	0	1
<i>Amphilocheus spencebatei</i>	1	0	0	0	1	0	2
<i>Ampithoe gammaroides</i>	0	0	13	0	0	0	13
<i>Ampithoe neglecta</i>	1	3	5	9	0	0	18
<i>Ampithoe ramondi</i>	0	0	9	29	6	3	47
<i>Ampithoe rubricata</i>	0	0	1	0	0	0	1
<i>Aora typica</i>	1	1	0	0	0	0	2
Aoridae indet.	5	46	27	0	0	0	78
<i>Apherusa bispinosa</i>	0	1	0	2	0	2	5
<i>Apherusa clevei</i>	0	0	0	0	0	1	1
<i>Apherusa henneguyi</i>	0	1	0	0	0	1	2
<i>Colomastix pusilla</i>	0	0	0	0	1	0	1
<i>Monocorophium</i> spp.	1	0	0	0	0	0	1
<i>Monocorophium acherusicum</i>	11	3	3	0	0	0	17
<i>Monocorophium insidiosum</i>	1	0	0	1	1	0	3
<i>Monocorophium sextonae</i>	11	14	4	5	3	0	37
<i>Dexamine spinosa</i>	19	36	73	38	3	6	175
<i>Elasmopus rapax</i>	0	0	0	0	1	0	1
<i>Erichtonius punctatus</i>	0	4	8	41	15	3	71
<i>Gammarella fucicola</i>	208	19	706	298	49	82	1362
<i>Gammaropsis maculata</i>	5	0	2	0	0	0	7
<i>Gammaropsis nitida</i>	1	2	0	0	0	0	3
<i>Gammaropsis palmata</i>	1	10	0	3	7	11	32
<i>Gammarus crinicornis</i>	1	1	35	0	0	0	37
<i>Gammarus insensibilis</i>	0	0	2	0	0	1	3
<i>Gammarus tigrinus</i>	1	2	20	2	0	0	25
<i>Harpinia</i> spp.	0	0	0	1	0	0	1
<i>Harpinia crenulata</i>	0	0	0	1	0	0	1
<i>Harpinia laevis</i>	0	0	0	1	0	0	1
<i>Harpinia pectinata</i>	0	0	0	12	0	0	12
<i>Ischyrocerus anguipes</i>	0	0	3	3	0	0	6
<i>Jassa falcata</i>	0	4	2	0	0	1	7
<i>Lembos</i> spp.	11	3	10	4	1	1	30
<i>Lembos denticarpus</i>	0	0	0	0	2	1	3
<i>Lembos websteri</i>	0	0	1	0	0	1	2
<i>Leptocheirus pilosus</i>	0	0	0	0	3	1	4
<i>Leptochelia savignyi</i>	5	1	0	1	0	3	10
<i>Leucothoe spinicarpa</i>	0	0	0	1	0	0	1
<i>Melita hergensis</i>	0	0	0	1	0	0	1
<i>Leucothoe incisa</i>	0	0	0	0	1	0	1
<i>Melita palmata</i>	0	0	0	0	1	0	1
<i>Microdeutopus</i> spp.	38	41	78	24	19	9	209
<i>Microdeutopus anomalus</i>	11	11	16	5	1	1	45
<i>Microdeutopus chelifera</i>	0	0	0	1	0	0	1
<i>Microdeutopus damnoniensis</i>	3	1	3	2	0	0	9
<i>Microdeutopus gryllotalpa</i>	18	16	11	0	0	0	45
<i>Microdeutopus stationis</i>	0	0	0	0	0	1	1
<i>Microdeutopus versiculatus</i>	4	3	1	3	14	3	28

	May 98	Jul 98	Sep 98	Nov 98	Ene 99	Mar 99	Total
<i>Microprotopus maculatus</i>	52	9	1	0	0	0	62
<i>Peltocoxa marioni</i>	0	0	0	1	1	0	2
<i>Photis longipes</i>	4	0	3	0	0	0	7
<i>Stenothoe monoculoides</i>	72	70	82	93	61	59	437
Caprellidae indet.	0	0	8	0	0	0	8
<i>Caprella acanthifera</i>	0	0	63	3	0	0	66
<i>Caprella</i> sp.1	0	0	4	0	0	0	4
<i>Caprella</i> sp.2	7	0	13	21	12	3	100
<i>Pariambus typicus</i>	4	5	1	2	2	0	14
<i>Phtisica marina</i>	10	91	632	128	88	7	956
<i>Pseudoprotella phasma</i>	0	0	2	0	0	0	2
<i>Cumella</i> spp.	12	0	0	1	3	5	21
<i>Cumella pygmaea</i>	0	1	0	0	1	0	2
<i>Iphinoe tenella</i>	2	3	0	0	2	10	17
<i>Iphinoe trispinnosa</i>	0	3	0	0	0	0	3
Nannastacidae indet.	1	0	1	0	0	0	2
<i>Astacilla</i> sp.	0	0	0	1	7	8	17
<i>Astacilla longicornis</i>	0	0	3	0	0	1	4
<i>Cyathura carinata</i>	0	0	1	0	0	0	1
<i>Idotea</i> spp.	2	0	0	0	0	0	2
<i>Idotea chelipes</i>	2	0	0	0	0	0	2
<i>Jaera albifrons</i>	2	4	0	0	0	1	7
<i>Janira maculosa</i>	4	0	1	0	0	0	5
<i>Munna</i> spp.	3	0	0	0	0	0	3
<i>Uromunna</i> spp.	283	69	7	41	9	12	421
<i>Apseudes talpa</i>	0	0	0	0	3	0	3
<i>Apseudopsis latreillii</i>	19	15	1	4	43	86	168
<i>Zeuxo holdichi</i>	87	653	55	79	124	78	1076
<i>Achelia echinata</i>	14	36	63	42	34	25	214
<i>Anoplodactylus pygmaeus</i>	6	0	13	7	11	2	39
<i>Callipallene emaciata</i>	0	0	3	1	5	0	9
<i>Callipallene spectrum</i>	0	0	3	4	0	0	7
<i>Callipallene tiberi</i>	4	1	2	1	0	3	11
<i>Endeis spinosa</i>	0	1	2	1	1	0	5

Anexo 4. Parámetros faunísticos obtenidos en el estudio de variabilidad espacial (A) y en el estudio de variabilidad estacional (B). S, número de especies. N, número de individuos. H', índice de diversidad de Shannon-Wiener. J', equidad de Pielou.

A

	S	N	J'	H'(log₂)
D24	51	2103	0,42	2,38
D26	53	2017	0,54	3,07
D27	60	3971	0,35	2,05
D31	42	1777	0,38	2,04
D34	35	913	0,72	3,72
D35	42	436	0,67	3,62
D37	20	517	0,68	2,94
D38	46	2035	0,74	4,07
D39	52	1083	0,78	4,48
D40	34	671	0,73	3,74

B

	S	N	J'	H'(log₂)
Mayo	40	925	0,64	3,39
Julio	33	1146	0,52	2,63
Septiembre	42	1911	0,52	2,82
Noviembre	38	876	0,64	3,37
Enero	35	499	0,70	3,59
Marzo	33	411	0,68	3,41

Anexo 5. Criterios de calidad de las publicaciones incluidas en la presente memoria.

- **Helgoland Marine Research** (ISSN: 1438-387X) es una revista de prestigio internacional, que emplea un proceso de revisión por medio de revisores externos. Se encuentra indexada en bases de datos electrónicas como Science Citation Index, Science Citation Index Expanded (SciSearch), SCOPUS, Astrophysics Data System (ADS), CSA, CAB International, Academic OneFile, ASFA, Biological Abstracts, BIOSIS, BIOSIS Previews, CAB Abstracts, Current Abstracts, Current Contents-Agriculture, Biology & Environmental Sciences, EBSCO, EMBiology, Gale, Geobase, Global Health, Journal Citation Reports/Science Edition, OCLC, SCImago, Summon by Serial Solutions, y Zoological Record. Factor de impacto (2010): 1.671
- **Journal of the Marine Biological Society of the United Kingdom** (ISSN: 0025-3154) es una revista de prestigio internacional, publicada por The Marine Biological Association of the United Kingdom, que emplea un proceso de revisión por medio de revisores externos. Se encuentra indexada en bases de datos electrónicas como Science Citation Index, Science Citation Index Expanded (SciSearch), Current Contents-Agriculture, Biology & Environmental Sciences, EBSCO, BIOSIS Previews, CSA, SCOPUS y Zoological Record. Factor de impacto (2010): 0.933
- **Marine Biodiversity Records** (EISSN: 1755-2672) es una revista de prestigio internacional, publicada *online* por The Marine Biological Association of the United Kingdom, que emplea un proceso de revisión por medio de revisores externos. Se encuentra indexada en bases de datos electrónicas como CSA, EBSCO y SCOPUS.
- **Thalassas-An International Journal of Marine Science** (ISSN: 0212-5919) es una revista de prestigio internacional, publicada por la Universidad de Vigo, que emplea un proceso de revisión por medio de revisores externos. Se encuentra indexada en bases de datos electrónicas como Science Citation Index Expanded (SciSearch), BIOSIS Previews, CSA, FAO-Fishery Information, GMBH, SCOPUS y Zoological Record. Factor de impacto (2010): 0.067

