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Population biology of *Hirondellea* sp. nov. (Amphipoda: Gammaridea: Lysianassoidea) from the Atacama Trench (south-east Pacific Ocean)

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A new species of *Hirondellea* was trapped in large numbers (N=441) in the Atacama Trench (Pacific Ocean) at 7800 m depth. The species accounted for 47% of the total number of amphipods collected and was the second most abundant amphipod after *Eurythenes gryllus*. Adult males and females reached maximum lengths of 13.5 and 14.1 mm. Length–frequency histograms showed no clear evidence of growth classes, but instars could be determined by using a combination of morphological criteria and size–frequency data. Growth factors based on mean lengths of successive instars ranged from 1.09 to 1.24 except at moults immediately prior to maturity when factors were in the range 1.02–1.04. Females moult from the pre-adult to the adult instar, without body growth. Moulting modalities of immature males are unclear. Equations obtained from regression analysis between wet weight and total body length indicate an allometric growth. Females grow at a rate of 10% higher than males, and both females and males display growth rates lower than those observed for juveniles, but growth increments at each instar of females are not significantly higher than those of males. The relationship between total body length (L) and wet weight (W) of all instars of *Hirondellea* sp. nov. is expressed by the power curve $W=0.012\ L^{3.279}$ (W in mg and L in mm).

INTRODUCTION

Although baited traps have been used for many years (e.g. Chevreux, 1900), it is only in recent decades that baited cameras have revealed the abundance and diversity of megafaunal necrophages in the deep sea (Hessler et al., 1972; Thurston et al., 1995). Amphipods form an important element of this fauna (Hessler et al., 1972; Thurston, 1979; Ingram & Hessler, 1983; Baldwin & Smith, 1987; Charmasson & Calmet, 1987; Janssen et al., 2000). Lysianassoid amphipods such as *Eurythenes gryllus* are pan-oceanic and are considered possible vectors for upward transport of material from the deep-sea floor (Bowman & Manning, 1972; Charmasson & Calmet, 1990; Thurston, 1990).

A clearer picture of necrophagous amphipod faunas at abyssal depths is emerging, but knowledge of the biology of benthic and bentho-nektonic organisms at hadal depths (>6000 m) is still extremely limited (Angel, 1982). This is due largely to technical difficulties in obtaining reliable and quantitative samples. Available information from investigations at hadal depths indicates that amphipods form an important and diversified component of the benthic boundary layer fauna. Studies carried out in the Philippine Trench at 9800 m depth found *Hirondellea gigas* to be the dominant necrophage on the trench floor (Hessler et al., 1978). The 34 species of gammaridean amphipods collected in Pacific Ocean trenches showed wide trophic diversity, and at least 24 of these species appear to be confined to depths greater than 6000 m (Kamenskaya, 1995). Differences in species composition among hadal environments suggests that each trench system has been isolated over geological time-scales and has developed different ecological features and different key species. The poorly investigated Peru–Chile Trench system is distant from the trench systems of the western Pacific Ocean. *Eurythenes gryllus* has been reported from the Atacama Trench, part of the Peru–Chile system (Ingram & Hessler, 1987), while the presence of other smaller species can be inferred from the photograph in Hessler et al. (1978, their figure 11). Recent investigations in the Atacama Trench, of which the present contribution forms a part, have indicated that most of the amphipod species from hadal depths are undescribed or show differences from species already in the literature (Thurston, 1999).

During the Atacama Trench International Expedition (ATIE), baited traps were set at a depth of 7800 m in the Atacama Trench (Della Croce et al., 1998). Most of the specimens caught were amphipods. *Eurythenes gryllus* was the most abundant species present (Thurston et al., 2002), but an undescribed species of the genus *Hirondellea* was co-dominant (Thurston, 1999). In the present study the population biology of this undescribed species has been investigated, with the specific aim of identifying morphological criteria for describing different instars and the state of maturity, and providing growth increments and growth equations.

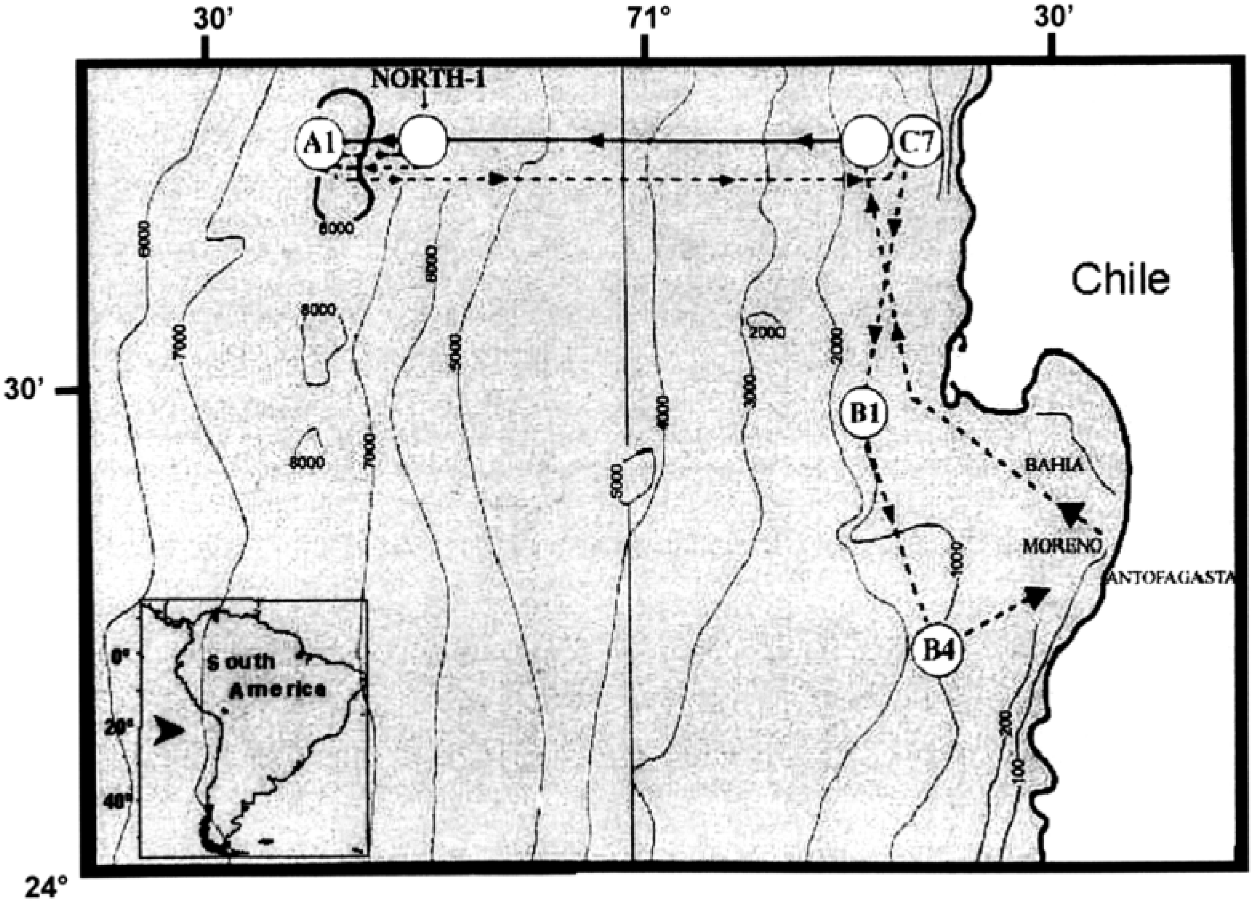

Figure 1. Sampling area and station location.

MATERIALS AND METHODS

Study area and sampling

Amphipod specimens were collected in September 1997 during the ATIE oceanographic cruise from a depth of 7800 m at 23°15′S 71°21′W (Figure 1). The Peru–Chile Trench is the largest trench system in the world, extending for about 5900 km with a mean width of 100 km (Angel, 1982). The Atacama Trench is that part of this system that lies off northern Chile. In 23–24°S the 6000 m isobath is about 50 km from land, and the trench axis, with depths in excess of 8000 m, is less than 80 km from the shoreline. The Peru–Chile Trench is located in an area characterized by important up-welling events, which can generate very high primary production values (Fossing et al., 1995). There are no rivers in the adjacent continental desert, and winds play a major role in transferring terrigenous material from land to ocean. The hydrography of the area has been reviewed recently by Sievers et al. (1999).

Amphipods were collected using six traps lying on the bottom sediments along a single mooring line. The trap line was deployed manually using a special neutrally buoyant polypropylene rope (16 mm diameter, 10,000 m). Five units of ballast (for a total of about 420 kg) were distributed at the end of the line, in between the baited traps, and in front of the first trap to ensure that all traps reached the bottom. The traps were constructed of 2-mm metallic mesh and were of three different patterns: (i) cylindrical (TI and TIV), 1500 mm in length and 750 mm in diameter with a single funnel opening of 230 mm in diameter at one end; (ii) cylindrical (TIII and TVI), 1000 mm in length and 500 mm in diameter with a funnel opening of 100 mm in diameter at one end; and (iii) truncated-conical (TII and TV), 1000 mm in length and 500 mm in diameter tapering to 260 mm at the smaller end, and with a single funnel opening of 100 mm diameter in the larger base. Each of the traps TI–TIV was equipped with a food dispenser enclosing bait and an artificial starlight (30 mm in length), and a pressure sensor programmed to deliver bait and light into the trap below 6000 m depth. Bait consisted of squid, horse-mackerel, and commercial fish food enriched with blood. Traps TV and TVI were not baited, nor were they supplied with light sources. In order to increase catching efficiency of smaller organisms, three micro-traps, oriented at 120° one from the other, were placed inside each large trap. Micro-traps were of 1.5-l capacity (200 mm high and 90 mm in diameter and with a funnel entrance of 20 mm) and made of transparent plastic. Immediately after collection all organisms were fixed in a 10% formalin solution buffered with sodium borate (20 g l^{-1}).

Biometric analysis

Body length was determined to the nearest 0.1 mm, based on the average of three repeated measurements, by straightening the dorsal curvature and measuring from the anterior portion of the head to the tip of the telson.

Table 1. *Criteria used to separate instars of the amphipod* Hirondellea *sp. nov. Oostegite lengths refer to the length of the oostegite on coxa 4.*

Instar	Criteria
Juveniles	Total body length <6.8 mm. Penile papillae and oostegites absent
Females	
Juvenile I	Oostegites are visible as minute internal buds and do not form distinct protuberances
Juvenile II	Oostegites are visible and form a small rounded dot at the base of the pereopods, protruding slightly from the point of attachment on the coxa
Immature I	Oostegites are elongate and straight with a relatively uniform diameter
Immature II	Oostegites are larger, distally broadest and slightly hooked with smooth margins
Pre-adult	Oostegites with serrate margins and one or two short setae distally
Adult	Oostegites with long setae on the tip and sides of the oostegites
Males	
Immature I	Calceoli not present on article segments of antenna 2 flagellum; penile papillae are present on the surface of teguments as little dots without protruding from the ventral septa of 7th pereionite
Immature II	Calceoli not present; penile papillae increase in size and protrude slightly from the ventral sternite
Immature III	Calceoli still absent on the flagellum of antenna 2; penile papillae are larger, well developed and become flexed toward each other at the mid-line
Adult I	Antenna 2 flagellum generally shorter than 1.33 length of antenna 1 flagellum; calceoli present on 30–40% of articles of antenna 2
Adult II	Antenna 2 flagellum generally longer than 1.32 length of antenna 1 flagellum; calceoli present on 60–70% of articles of the proximal portion of flagellum of antenna 2

Individuals were sexed by the presence of penile papillae (males) or oostegites (females). Specimens lacking these secondary sexual characters were considered to be juveniles. As males showed allometric growth of the flagellum of antenna 2, the lengths of the flagella of antenna 1 and 2 were measured and the number of articles in the flagellum of antenna 2 counted. The wet weight of each individual was determined using a Mettler balance (accuracy ±0.1 mg).

Crustaceans increase in size only by moulting, because of their rigid exoskeleton, and individuals pass through a series of instars as they grow. Instars were separated using a combination of size–frequency distribution and morphological changes associated with sexual maturation following the criteria used by Hessler et al. (1978) and Ingram & Hessler (1987) (Table 1).

Growth factors, used to obtain size changes, were calculated as the ratio between mean total lengths of successive instars.

RESULTS

The traps collected a wide range of benthic and benthonekton organisms belonging to 11 taxa (Table 2; summarized from Della Croce et al., 1998). Amphipods dominated both in terms of abundance and biomass. Of the 945 amphipods collected 441 (46.7%) were *Hirondellea* sp. nov. which represented the second most abundant species after *Eurythenes gryllus*. All but one specimen were obtained from traps that had been baited (Thurston, 1999). Of the 441 specimens collected, 420 were analysed, including 254 females identified by the presence of oostegites, 134 males with genital papillae, and 32 juveniles. Instars were identified using morphological criteria reported by Hessler et al. (1978; Table 2). Juveniles measured from 3.1 to 6.7 mm in length, and could be separated into a minimum of four instars (Table 3; Figure 2). Females measured from 7.0 to 14.1 mm in length, and instar separation was based on

Table 2. *Organisms collected in the traps deployed at 7800 m in the Atacama Trench.*

	Baited traps containing artificial light				Non-baited traps without artificial light		
Taxa	TI	TII	TIII	TIV	TV	TVI	Total
Copepoda	21	93	37	25	40	6	222
Isopoda	6	7	5	2	6	7	33
Amphipoda	270	326	94	241	7	7	945
Other Crustacea	2	1	3	0	1	0	7
Crustacea	299	427	139	268	54	20	1207
Osteichthyes	1	0	0	0	0	0	1
Echinodermata	0	0	1	0	0	0	1
Annelida Polychaeta	0	2	2	15	13	9	41
Nematoda	0	0	1	3	7	38	49
Chaetognatha	0	0	0	0	3	0	3
Mollusca Bivalvia and Gastropoda	0	0	0	0	0	2	2

Table 3. *Number, size and growth factors of juvenile, female and male* Hirondellea *sp. nov.*

Female instars	Number	Mean body length (mm)	Range (mm)	Growth factor
Juveniles a*	2	3.9	3.9	1.17
Juveniles b	4	4.55	4.4–4.7	1.20
Juveniles c	9	5.44	5.2–5.9	1.18
Juveniles d	15	6.44	6.1–6.7	1.15
Females, juvenile I	5	7.38	7.0–7.7	1.16
Females, juvenile II	18	8.56	7.9–9.4	1.18
Females, immature I	64	10.09	8.6–11.33	1.18
Females, immature II	57	11.92	10.2–13.4	1.04
Females, pre-adult	15	12.37	11.5–13.3	1.02
Females, adult	95	12.61	11.3–14.1	

Male instars	Number	Mean body length (mm)	Range (mm)	Growth factor
Juveniles a*	2	3.9	3.9	1.17
Juveniles b	4	4.55	4.4–4.7	1.20
Juveniles c	9	5.44	5.2–5.9	1.18
Juveniles d	15	6.44	6.1–6.7	1.20
Males, immature I	7	7.71	7.1–8.2	1.24
Males, immature II	32	9.59	8.6–11.0	1.14
Males, immature III	28	10.95	9.7–11.9	1.09
Males, adult I	16	11.91	10.9–13.2	1.04
Males, adult II	51	12.38	11.7–13.5	

*, Specimens of 3.1–3.5 mm were excluded.

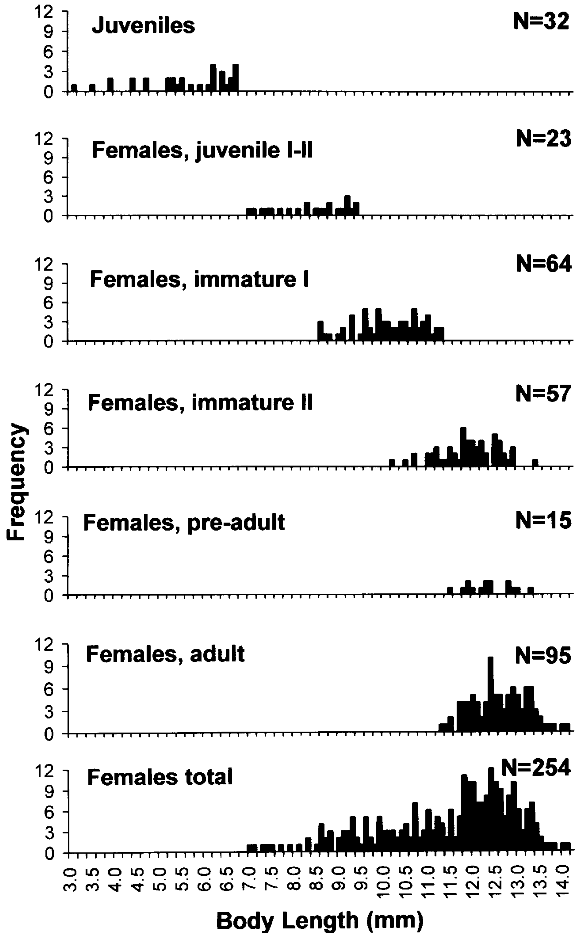

Figure 2. Numbers and size–frequency data of juvenile and female *Hirondellea* sp. nov.

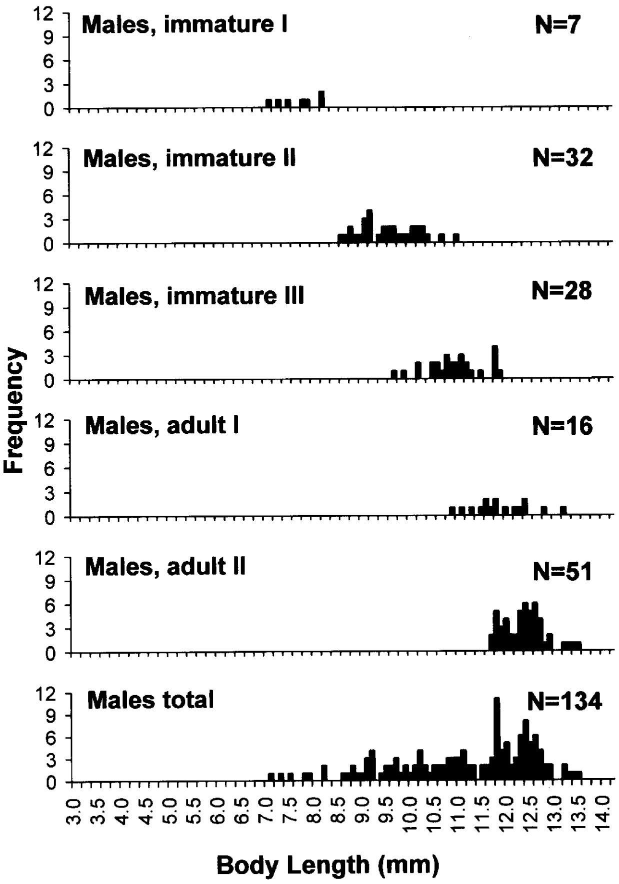

Figure 3. Numbers and size–frequency data of male *Hirondellea* sp. nov.

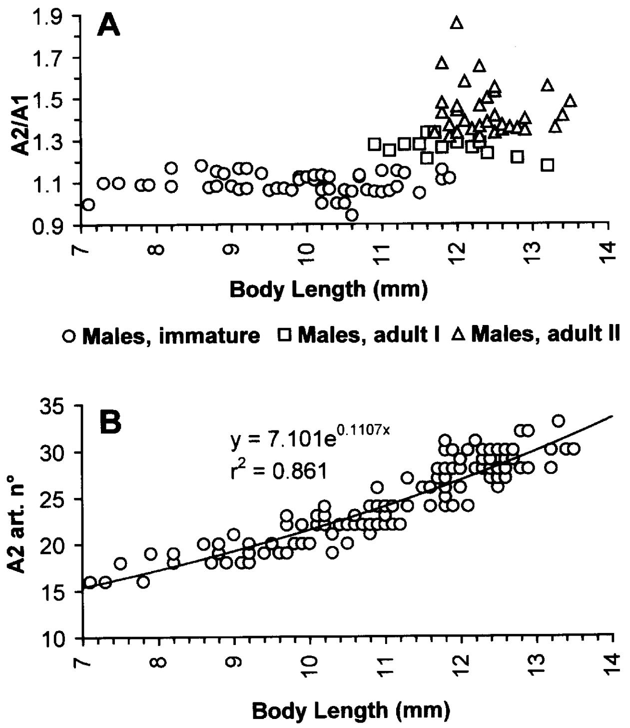

Figure 4. Ratio of the length of antenna 2 flagellum to the length of antenna 1 flagellum (A2:A1) against body length of males (A) and relationship (B) between the number of articles in antenna 2 flagellum (A2 art. no.) and male body length.

development of the oostegites on the coxa of peraeopod 4 (Table 3; Figure 2). Females pass through five instars before attaining sexual maturity, marked by fully setose oostegites. None of the specimens was ovigerous. Male lengths fell into the range 7.1–13.5 mm (Table 3; Figure 3).

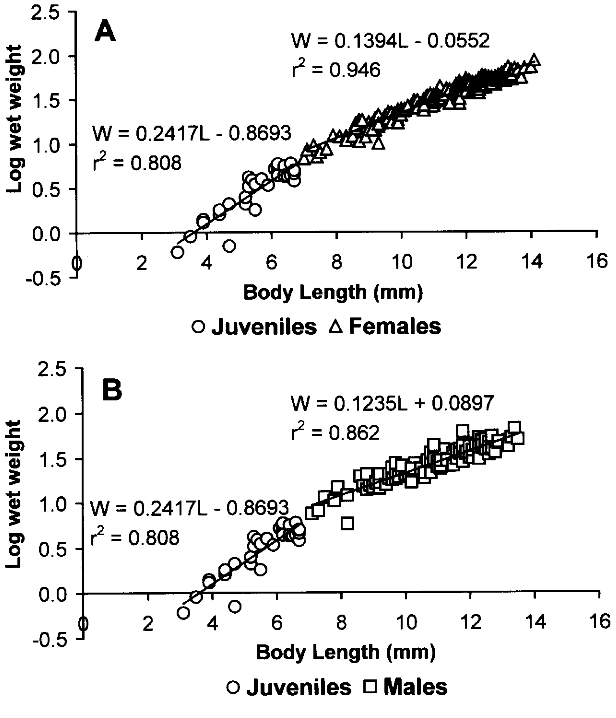

Figure 5. Relationship between body length and log-transformed wet weight of *Hirondellea* sp. nov. (A) Juveniles and females; (B) juveniles and males.

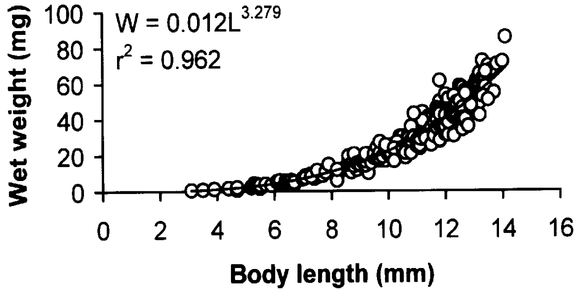

Figure 6. Relationship between total body length and wet weight of *Hirondellea* sp. nov. (N=420).

Instars were separated by the size of the genital papillae, the relative elongation of the flagellum of antenna 2, and the appearance of calceoli on the antennae. The last two male instars, Adult I and Adult II, were similar in size (mean lengths 11.91 and 12.38 mm respectively) but could be separated by the relative length of antenna 2. The ratio of the length of the flagellum of antenna 2 to the length of the flagellum of antenna 1 in males was rather constant for each instar, with values of 0.94–1.18 in immature individuals, 1.17–1.33 in Adult I instar, and 1.32–1.86 in the Adult II instar (Figure 4A). Ranges of the number of flagellum articles on antenna 2 for the same three categories of males were 16–26, 21–30 and 24–33 respectively. The number of articles in antenna 2 flagellum was significantly correlated to body length (Figure 4B). The relative elongation of antenna 2 arises from an increase in the number of articles, rather than an increase in the length of individual articles.

Body length and log-transformed data of body weight were plotted in linear regression to identify the characteristic growth curves for females and males, respectively (Figure 5A,B). In both females and males there is a relative increase in weight against length at the onset of development of the secondary sexual characteristics.

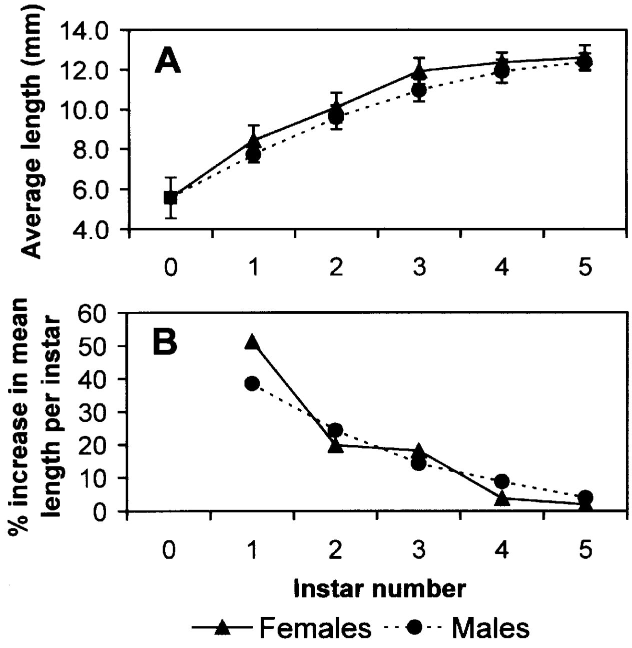

Figure 7. Growth of female and male *Hirondellea* sp. nov. (A) Change in length with instar number (with standard deviations); (B) per cent increase in length per instar.

DISCUSSION

Although benthic traps have been used widely in the deep sea (see above), most information on hadal amphipods has been derived from grabs or towed gear (Dahl, 1959; Wolff, 1980; Kamenskaya, 1995). There is some evidence to suggest that deep trench species shows a high degree of endemism, and that many appear to be confined to a single trench or trench system (Belyaev, 1966; Kamenskaya, 1995). Hessler et al. (1978) found only a single species, *Hirondellea gigas*, in traps set at 9600 m depth in the Philippine Trench. However, hadal faunas are not well known, and baited traps attract only a narrow spectrum of species, mostly necrophages and perhaps some predators. Physical constraints imposed on sampling at great depths are such that mobile organisms may easily evade capture (Hessler et al., 1978), perhaps resulting in over-estimates of endemism. In contrast, our trap samples contained 11 species of amphipods, most of which are undescribed or which cannot be identified unequivocally with known species (Thurston, 1999). This is a higher number than has been recorded previously at hadal or abyssal depths (Bowman & Manning, 1972; Hessler et al., 1978; Thurston, 1979, 1990; Ingram & Hessler 1983; Christiansen, 1996; Janssen et al., 2000), and indicates that the Atacama Trench may be distinct from the somewhat better known trenches of the western Pacific Ocean. In this regard, it is not surprising that an undescribed species should be present in such high numbers, accounting for nearly 50% of the total number of amphipods collected. The biology of this species is of interest for several reasons including novelty, geographical isolation, and depth of occurrence.

Gammaridean amphipods display clear morphological changes associated with the development of sexual characters, allowing the identification of maturity stages (Sexton, 1924; Bowman & Manning, 1972; Hessler et al., 1978; Ingram & Hessler, 1987). Instars can be separated by a combination of morphological criteria and size–frequency. Within each instar, measurements typically are distributed normally around a mean value (Hessler et al., 1978). In the present study, length–frequency histograms showed evidence of incremental growth among juveniles, females and, to a lesser extent, males of this new species (Figures 2 & 3). Growth factors, based on mean lengths of successive instars, ranged from 1.09 to 1.24, except for moults after the Immature II stage in females and the moult to maturity in males where values were much lower (1.02–1.04) (Table 3). These values are comparable to those reported by Hessler et al. (1978) for *H. gigas*, the only other amphipod species typical of ocean trenches for which similar information is available. Values fall within the expected range (e.g. Thurston, 1979), and lie below 1.26, the linear factor representing a doubling of body volume.

The moult to maturity in females is accompanied by minimal growth, with energy reserves diverted from somatic growth and invested into reproductive products. This pattern of development is widespread among Peracarida where moulting is a necessary precursor to spawning (Charniaux-Cotton, 1985). The length–frequency distribution of 95 adult females (Figure 2) could not be resolved into Gaussian components (cf. Ingram & Hessler, 1987), despite the relatively wide length range (11.3–14.1 mm). Therefore, it is not clear whether this development class represents more than one instar, and whether this species is semelparous or iteroparous. The overall length–frequency distribution, with most individuals close to the maximum size, is a pattern found widely among deep-sea invertebrates, and is indicative of a relatively long adult existence and possible multiple spawning (Gage & Tyler, 1991). Sainte-Marie (1991) defined the 'half range of mature female body length ratio' as $(BL_{max}-BL_{mean}):BL_{mean}$. Based on an extensive database, in cold waters this ratio ranged from 0.0110 to 0.3478 in semelparous species, and from 0.1304 to 0.7846 in iteroparous species. The value of the ratio in *Hirondellea* sp. nov. is 0.1190 a strong indicator of semelparity. In common with most lysianassoids, females are larger than males (Table 3). Equations based on data from deep-water species and from lysianassoids (Sainte-Marie, 1991, tables 8 & 9) predict brood sizes of 17.69 and 26.57 mm respectively.

The absence of ovigerous females, from samples collected in this study, parallels previous observations of trap-caught amphipods from abyssal and hadal depths, and is interpreted as a strategy to avoid cannibalism and predation (Hessler et al., 1978; Thurston, 1979; Ingram & Hessler, 1983; Lampitt et al., 1983; Baldwin & Smith, 1987).

The relationship between body length and wet weight in *Hirondellea* sp. nov. was expressed by a power curve (Figure 6), the standard form for allometric growth (Teissier, 1960). The equation, $W=0.012L^{3.279}$ (W=wet weight in mg, L=body length in mm) (N=420) gives the best fit to the data ($r^2=0.962$). This equation gave a higher weight to length ratio than was found for *Eurythenes gryllus* by Ingram & Hessler (1987). However, that study dealt with a much larger species, and with specimens that had been denied access to bait, in contrast with the present case.

Regressions of log-transformed wet weight on length were highly significant for juveniles, females and males (Figure 5A,B). Females and males display growth rates lower than those observed for juveniles, with females growing at a rate about 10% higher than males. The change in growth rates occurred at a length of about 7 mm, the size at which secondary sexual characters became macroscopically apparent. Juvenile growth is described by the expression $W=0.2417L-0.8693$ ($r^2=0.808$). Corresponding expressions for females and males are $W=0.1394L-0.0552$ ($r^2=0.946$) and $W=0.1235L+0.0897$ ($r^2=0.862$) respectively.

Despite the difference in growth rates, an analysis of mean length per instar against instar number indicated that female growth increments at each instar were not significantly higher than those of males (analysis of variance, ns; Figure 7). A reduction in growth rate and a divergence of rates between sexes also occurs in *E. gryllus* (see Ingram & Hessler, 1987). As in the present species, the point of change occurs at a body length close to half the maximum attained by adult females.

Opportunities for studies of abyssal and hadal amphipods are limited, and are confined to necrophagous species that can be trapped in sufficient numbers for analysis. Despite belonging to an undescribed trench species, the reproductive bionomics of the present species appear to conform to those of the limited number of cold- and deep-water lysianassoids that have been studied to date (Sainte-Marie, 1991).

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