

Growth and size-structure of *Stegophiura* sp. (Echinodermata: Ophiuroidea) on the continental slope off central Chile: a comparison between cold seep and non-seep sites

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The growth and size-structure of the bathyal ophiuroid brittle star, Stegophiura sp., were analysed from skeletal growth bands and disc diameter frequencies. Specimens were collected in trawl samples taken on the continental slope off central Chile (~36°S) at two sites within the recently discovered Concepción Methane Seep Area (CMSA) and at two control non-seep sites. Growth bands were measured as radii of vertebral ossicles from scanning electron microscope (SEM) micrographs and used to provide size-at-age data. The von Bertalanffy and the Gompertz growth models provided good fit to size-at-age data. The size-structure distributions observed in the study area suggest that small-bodied (<10 mm disc diameter) individuals of Stegophiura sp. are more abundant near seep sites, probably attracted there by the presence of methane-derived authigenic carbonates, which provide a preferred habitat for ophiuroids and benthic fauna in general. Furthermore, size-at-age data from measurements of the ossicle growth bands indicate relatively rapid growth of Stegophiura sp. populations at seep sites. Assuming that the growth rings are annual, the maximum Stegophiura sp. age was estimated to be 15 years. The growth performance of this species falls within the range of values reported for sub-Antarctic and bathyal species.

Keywords: bathyal ophiuroid, cold seep, growth, Chile

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INTRODUCTION

Communities of benthic animals associated with methane seeps (also known as cold seeps) have been reported at several locations on active and passive continental margins of the world oceans (e.g. Olu *et al.*, 1996; Sibuet & Olu-LeRoy, 2002). Chemosymbiotic megafauna at cold seep communities are often dominated by siboglinid polychaetes, largely non-overlapping populations of vesicomyid clams and/or bathymodiolid mussels, and many other taxa (e.g. Olu *et al.*, 1996; Van Dover *et al.*, 2003; Levin, 2005). A rich assemblage of non-chemosymbiotic species, including grazers, suspension feeders, deposit feeders, predators, and decomposers, is often present at seep sites. Although some of these species are seep endemics, the majority is just attracted by local organic enrichment and/or increased habitat heterogeneity (Carney, 1994). This accompanying fauna is often dominated by suspension and deposit feeders (see Olu *et al.*, 1996; Van Dover *et al.*, 2003). Among the

deposit-feeding species, ophiuroids are one of the most important animal groups observed (Van Dover *et al.*, 2003; Stöhr & Segonzac, 2005).

The occurrence of cold seepage and gas hydrates in central Chile has been investigated since 2003 (Morales, 2003; Sellanes *et al.*, 2004). Among the chemosymbiotic fauna identified at the Concepción Methane Seep Area (CMSA) are several families of bivalves (e.g. vesicomyids, thyasirids, lucinids and solemyids) and a siboglinid tubeworm (*Lamellibrachia* sp.; Sellanes & Krylova, 2005). Non-chemosymbiotic species in this zone comprise more than one hundred taxa (Sellanes *et al.*, 2008).

Bathyal megabenthic communities of the Chilean margin have been also recently investigated by Quiroga *et al.* (in press). Many species are currently being described; nonetheless, the taxonomy of some important groups still remains problematic. In this region, sixteen species of bathyal benthic ophiuroids belonging to the families Gorgonocephalidae, Asteronychidae, Ophiomyxidae, Ophiocanthidae, Ophiuridae, Amphiuridae and Ophiolepididae have been identified. The bathyal ophiuroid *Stegophiura* sp. is one of the most conspicuous species observed on the continental slope off central Chile (Quiroga *et al.*, in press); this species is abundant at the CMSA

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as well (Sellanes *et al.*, 2008). However, in spite of its potentially important role in the functioning of the benthic system along the Chilean margin, information about its basic biological parameters, such as individual growth rates, reproduction, and population dynamics, is still lacking.

One of the approaches used to determine growth and age in ophiuroids is the study of natural growth bands at the vertebral ossicles (Dahm, 1996, 1999; Dahm & Brey, 1998; Gage *et al.*, 2004). These growth bands are produced by the deposition of calcareous skeletal material with different densities and structures (Gage, 2003). Environmental conditions and internal factors such as temperature, reproduction, and food supply can produce changes in skeletal growth (see Dahm & Brey, 1998). Individual growth rates and age are key parameters for establishing population dynamics and are required to determine the significance of each animal population in the energy flow through an ecosystem.

Hence, this paper aims: (1) to describe the growth parameters and size-structure of the ophiuroid *Stegophiura* sp. at both seep and non-seep sites; and (2) to assess if there are any differences in these parameters between seep and non-seep populations of this species on the continental slope off central Chile.

MATERIALS AND METHODS

Study area and field sampling

The cold seep site is located 72 km north-west off Concepción Bay, Chile ($36^{\circ}22'S$ $73^{\circ}73'W$), in the upper slope zone (750 to 900 m water depth; Figure 1). The presence of abundant carbonate-cemented mud, carbonate blocks, and shell fragments of several clams known to harbour chemosynthetic endo-symbiotic bacteria (vesicomyids, lucinids, thyasirids and solemyids) has been reported for this site (Sellanes *et al.*, 2004; Sellanes & Krylova, 2005). In addition, high concentrations of pore water methane and sulphide and a

widespread occurrence of authigenic carbonates and sub-surface gas hydrates were also documented in core material from the study area (Coffin *et al.*, 2006).

Samples were obtained during the SeepOx cruise (31 August–4 September 2006) onboard the AGOR R/V 'Vidal Gormáz'. Megafaunal specimens were collected by means of a modified Agassiz trawl (AGT) with a beam width of 1.5 m and a codend mesh size of 10 mm. Four successful hauls were used for this study: two performed under active seep conditions (indicated by the presence of living chemosymbiotic clams) and two at control sites (without evidence of seep activity, i.e. no living chemosymbiotic clams or authigenic carbonates; Table 1). Sampling depths varied from 732 to 893 m and, from each haul, *Stegophiura* sp. specimens were picked out and preserved onboard in buffered 4% seawater–formaldehyde. Disc diameter (DD) was measured from the disc edge above the base of an arm across the opposite interradius.

Specimens of *Stegophiura* sp. were identified according to Lara de Castro *et al.* (in preparation), who is describing the species as new. However, it is also described herein to avoid any problems with its future taxonomic identification. The species is easily distinguished by its orange colour and large disc with rounded borders, slightly pentagonal, covered with large, irregular, slightly granulated and inflated scales (Figure 2A, B). Central plate semi-pentagonal, slightly convex with the same size or larger than the primaries and separated from those by five small irregular scales. Primaries followed on the radial area by large subpentagonal scales, with distal border rounded, positioned on the proximal zone between the radial shield scales. Radial shields longer than they are wide, inflated, and united on the distal medium area. Dorsal arm plates strongly convex wider than they are long until approximately mid-arm, where they become as long as they are wide. Lateral arm plates as wide as the dorsal ones, each plate bearing from zero to two spines. Ventral interradiar surface covered with five to six large irregular scales. Bursal slits narrow and long, with borders

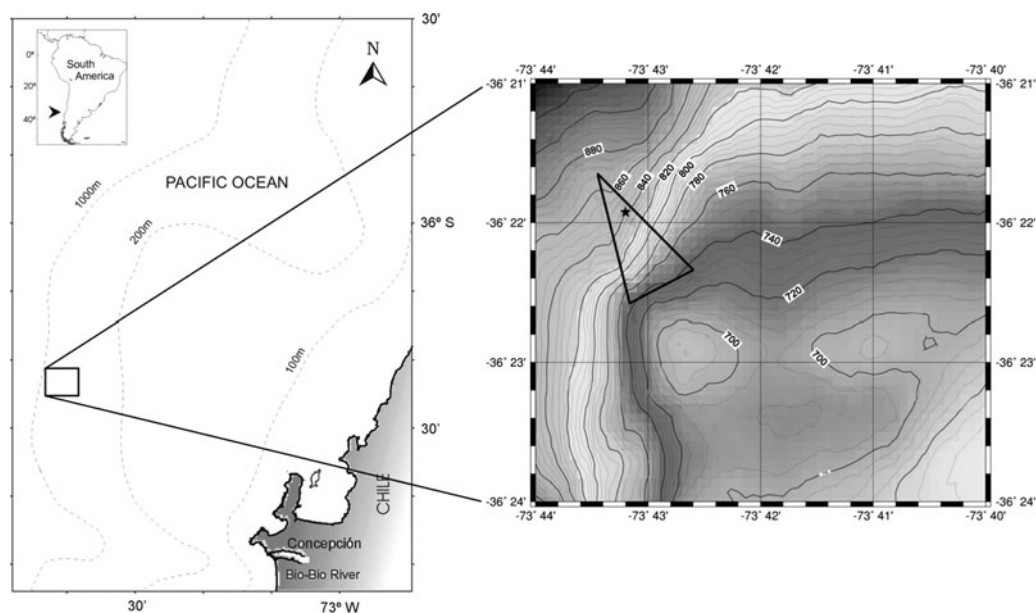


Fig. 1. Study site, located on the slope zone off central Chile ($36^{\circ}S$). The triangle indicates trawls that successfully collected evidence of active methane seepage (carbonate blocks, live chemosymbiotic clams and shell fragments).

Table 1. Station information and number of *Stegophiura* sp. individuals collected at each location. Samples were taken between 1 and 4 September 2006.

Station	Depth (m)	Date	Haul duration	Latitude (S)	Longitude (W)	Individuals	Site
VGo6-06-4	865–893	01.09.06	12:55–13:18 h	36°21'67	73°43'52	104	Non-seep
VGo6-06-7	878–847	01.09.06	02:40–02:51 h	36°21'65	73°43'38	70	Non-seep
VGo6-06-8	843–795	02.09.06	07:33–07:53 h	36°21'93	73°43'26	101	Seep
VGo6-06-11	732–746	04.09.06	09:07–09:27 h	36°22'41	73°42'56	64	Seep

Note: Seep sites are indicated by the presence of live clams *Calyptogena gallardoii*.

covered by plane, rectangular, and continuous genital scales that extend to the dorsal surface of the disc, where they become narrower and pointed forming the brachial comb. Jaws longer than they are wide, formed by strong and inflated plates. Two pointed infradental papillae present on the apex of the jaw. First oral tentacle pore communicating with the oral slit, and also with four to five papillae connected to the jaws and adoral shields. Also four papillae connected with the first ventral arm plate. Adoral shields inflated, narrow, and continuous near each other, surrounding the anterior third of the oral shield and touching the first ventral arm plate and the first lateral arm plate. Ventral plates of the arms wider than they are long, hexagonal on the first segments. Tentacle pores present all along the arm.

Ossicle growth bands

The age of the ophiuroids was determined according to Dahm (1993, 1996), Dahm & Brey (1998), and Gage (1990), by analysing the microstructure of annually formed growth bands on the vertebral ossicles of the arms. We used the proximal-most part of the arm in order to reduce error in aging of specimens whose arm(s) might have regenerated. The arm segment was prepared for examination of the vertebral ossicles according to the procedure of Dahm & Brey (1998). The vertebral ossicles were mounted on brass stubs, sputter coated with

gold under vacuum and examined using SEM micrographs (Figure 2C, D). Growth bands were measured as radii as described by Dahm (1993). We used the von Bertalanffy (1) and Gompertz (2) functions to model individual growth:

$$\text{von Bertalanffy function: } L_t = L_\infty(1 - e^{-K(t-t_0)}), \quad (1)$$

$$\text{Gompertz function: } L_t = L_\infty e^{-e^{-K(t-t^*)}}, \quad (2)$$

where L_∞ is the asymptotic size (ossicle radius, OR in mm), K (y^{-1}) is the growth constant, t_0 (y) is the age at which disc diameter would be zero and t^* is the time of growth inflexion. Growth parameters were fitted using the Microsoft Excel computation worksheet of Brey (2001), by means of iterative non-linear regressions using Excel's Solver routine. In addition, the growth performance index was computed according to (3) Brey (1998) and (4) Moreau *et al.* (1986):

$$\varphi = \log(M_{\max}/A_{\max}), \quad (3)$$

$$\varphi' = \log K + 2 \log L_\infty \quad (4)$$

where M_{\max} is maximum body mass (Kj), A_{\max} is maximum age (y), K is the growth constant (y^{-1}) and L_∞ is the maximum asymptotic size (OR in mm).

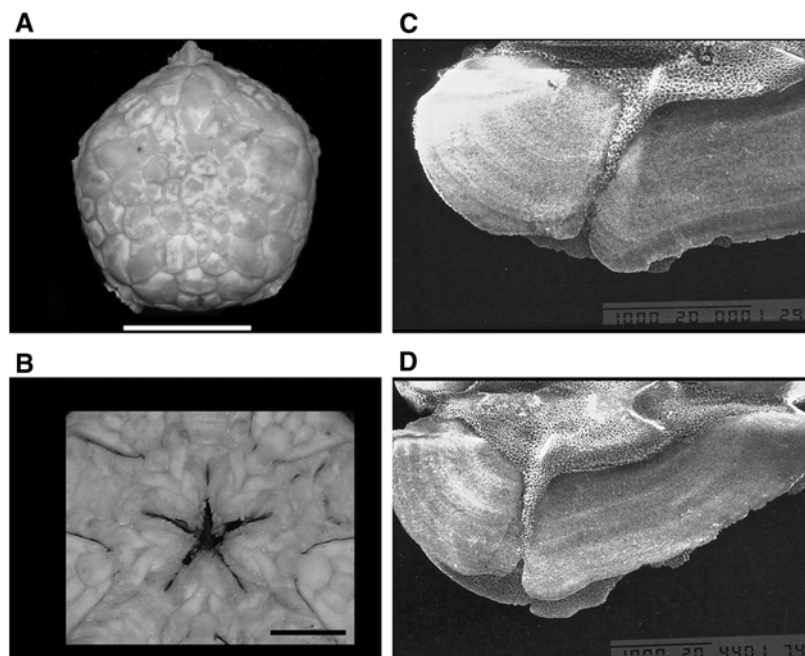


Fig. 2. (A) Photograph of an adult of *Stegophiura* sp., dorsal view; (B) ventral view (scale bars: A = 30 mm, B = 10 mm); (C) SEM microphotographs of the growth banding from a specimen of 31.8 mm disc diameter (DD) from a non-seep site; (D) specimen of 32.1 mm DD from a seep site.

RESULTS

Size-structure

Size–frequencies of disc diameter from the aggregated samples at both non-seep (Stations: VGo6-06-4 and VGo6-06-7) and seep (Stations: VGo6-06-8 and VGo6-06-11) sites are given in Figure 3A. Whereas the *Stegophiura* sp. specimens from the non-seep sites varied in size between 10.6 and 38.1 mm disc diameter (DD; 31.59 ± 4.05 mm; mean ± 1 SD), the specimens from the seep sites ranged from 8.8 to 39.6 mm DD (31.97 ± 7.28 mm). The size–frequency of this species at the non-seep sites peaked between 25 and 35 mm DD; specimens collected from the seep sites presented two peaks: major frequencies between 30 and 35 mm DD and a secondary peak between 5 and 10 mm DD. We found that small-bodied individuals (DD < 10 mm) were more frequent at the seep sites, but no significant difference in DD was detected between the non-seep and seep sites (ANOVA_{F=0.464}, N = 339, P = 0.495).

Growth and age

Growth banding is generally interpreted as reflecting zones of rapid skeletal growth during spring/summer (coarse-pore stereom), followed by a band of slower or nil growth, probably occurring in autumn/winter (fine-pore stereom). In fact, the break between fine-pore stereom and coarse-pore stereom is marked by the crest of a shallow ridge in the surface relief and provides the clearest mark of the limits of successive growth bands (Gage, 2003). Size-at-age data, expressed as the ossicle radius, was obtained from measurements of natural growth lines on the vertebral ossicles of 10 individuals (N = 120) from the non-seep sites and 9 individuals (N = 141) from the seep sites. The resulting common growth curves are shown in Figure 3. The von Bertalanffy

and the Gompertz growth functions provided a good fit to size-at-age data. In general, growth in *Stegophiura* sp. is expressed as a relatively low value of the growth constant. The von Bertalanffy growth constant for the seep sites was estimated to be $K_{VB} = 0.095$ ($r^2 = 0.92$). This value was higher than that obtained for individuals from the non-seep sites ($K_{VB} = 0.078$; $r^2 = 0.95$). In fact, based on the von Bertalanffy growth function, there was a significant difference in the elevation of the regressions of residuals versus ossicle radius (Y-intercepts) among specimens from the two sites (Table 2; Figure 3). In addition, we found a significant effect for the interaction between sites and estimated OR (ANCOVA_{F=27.366}, N = 257, P = 0.025). These results confirm the significant differences among the growth rates for specimens from seep and non-seep. On the other hand, the Gompertz function provides an estimate of the asymptotic size for the non-seep sites ($L_{\infty} = 1.4$ mm of OR) that is closer to that estimated for the seep sites ($L_{\infty} = 1.5$ mm of OR). The von Bertalanffy model provides an estimate of the theoretical growth asymptote ($L_{\infty} = 1.72$ mm of OR) higher than that derived from the Gompertz model. The oldest specimen of *Stegophiura* sp. was estimated to be 15 years old; its disc diameter was about 38.8 mm.

Table 3 summarizes growth rates and growth performance values estimated from our data set and the available literature regarding ophiuroids from various regions. In general, information on ophiuroid growth parameters is scarce in the literature; the population dynamic data collection contains the growth performance for only fourteen of the 16 species whose growth parameters are reported herein (Brey, 2001). In general, our values are higher than those reported for Antarctic species, but within the range of growth performance values reported for sub-Antarctic and boreal species.

DISCUSSION

It is known that, occasionally, non-chemosymbiotic species exhibit enhanced densities in the vicinity of deep-water seeps. In fact, dense aggregations of urchins, buccinid gastropods, cnidarians and asteroids have been described near seeps on the Oregon margin (Levin, 2005). *Stegophiura* sp. is a common ophiuroid inhabiting the continental slope off central Chile (Quiroga *et al.*, in press). Our results indicate that this species occurs in even higher densities nearby the CMSA (Sellanes *et al.*, 2008). Although the diet of this species has not been investigated, *Stegophiura* sp. specimens collected at the seep site display fairly heavy isotopic

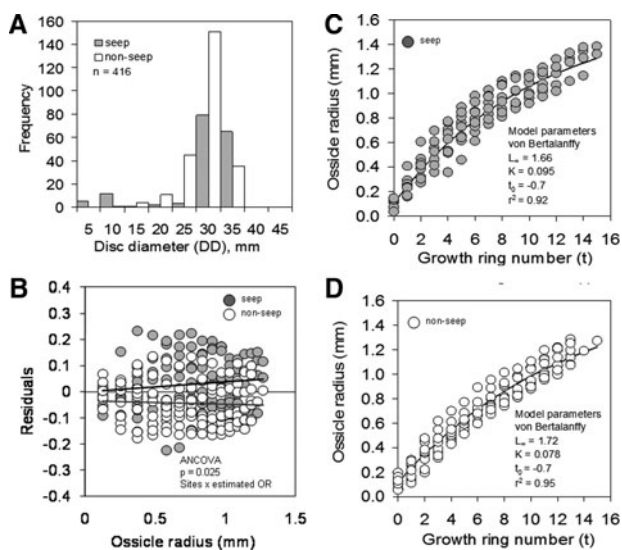


Fig. 3. (A) Disc size–frequencies of *Stegophiura* sp. individuals from the seep and control non-seep sites; (B) plot of residual versus ossicle radius (OR) estimated from the von Bertalanffy model; (C, D) von Bertalanffy functions fitted to size-at-age data for individuals from the seep and control non-seep sites, respectively.

Table 2. Analysis of covariance testing for homogeneity of regression coefficients for residuals from *Stegophiura* sp. individuals collected at seep and control non-seep sites.

Source of variation	SS	df	MS	F-ratio	P
Intercept	0.1968	1	0.1968	27.366	<0.0001
Sites (seep x non-seep)	0.0034	1	0.0034	0.4713	0.493
OR estimated	0.1793	1	0.1793	24.9231	<0.0001
Sites x OR estimated	0.0366	1	0.0366	5.0819	0.0250
Error	1.8486	257	0.0072		

OR, ossicle radius.

Table 3. Growth parameters of ophiuroids from various regions (modified from Brey, 2001).

Species	K (y^{-1})	L_{∞} (OR, mm)	L_{∞} (DD, mm)	ϕ ($\log(M_{\max}/A_{\max})$)	ϕ' ($\log K + 2\log L_{\infty}(\text{OR})$)	Model individual growth	Region	Reference
<i>Ophiura ophiura</i>	–	–	–	0.311	–	–	Celtic Sea, Bristol Channel, GB	Warwick <i>et al.</i> (1978)
<i>Ophionotus hexactis</i>	0.083	–	41.52	–0.048	–	von Bertalanffy	Southern Ocean, South Georgia Islands	Morrison (1979)
<i>Ophionotus hexactis</i>	0.079	–	43.81	0.082	–	von Bertalanffy	Southern Ocean, South Georgia Islands	Morrison (1979)
<i>Ophionotus hexactis</i>	0.160	–	27.55	–0.368	–	von Bertalanffy	Southern Ocean, South Georgia Islands	Morrison (1979)
<i>Ophiura ophiura</i>	–	–	–	0.205	–	–	Celtic Sea, Bristol Channel, GB	Warwick & George (1980)
<i>Ophiura ljungmani</i>	0.101	–	14.80	–1.711	–	von Bertalanffy	Deep Sea, Atlantic, Rockall Trough	Gage & Tyler (1981)
<i>Ophiotrix fragilis</i>	–	–	–	0.694	–	–	Celtic Sea, Bristol Channel, GB	George & Warwick (1985)
<i>Ophiocten gracilis</i>	0.380	–	8.20	–	–	von Bertalanffy	Deep Sea, Atlantic, Rockall Trough	Gage & Tyler (1982)
<i>Ophiomusium lymani</i>	0.360	–	33.79	0.870	–	von Bertalanffy	Deep Sea, Atlantic, Rockall Trough	Gage & Tyler (1982); Gage (1990)
<i>Amphiura chiajei</i>	0.373	–	9.13	0.074	–	von Bertalanffy	Atlantic, Ireland	Munday & Keegan (1992)
<i>Ophiura albida</i>	0.229	–	10.10	–1.057	–	von Bertalanffy	North Sea, German B., FRG	Dahm (1993)
<i>Ophiura ophiura</i>	0.084	–	27.70	–0.319	–	von Bertalanffy	North Sea, German B., FRG	Dahm (1993)
<i>Astrotoma agassizzi</i>	0.012	7.000	–	–	–0.23	von Bertalanffy	Southern Ocean, Weddell Sea	Dahm (1996)
<i>Ophiurolepis gelida</i>	0.066	1.989	–	–	–0.58	von Bertalanffy	Southern Ocean, Weddell Sea	Dahm (1996)
<i>Ophiurolepis gelida</i>	0.002	33.056	–	–	–	von Bertalanffy	Southern Ocean, Weddell Sea	Dahm (1996)
<i>Ophiurolepis gelida</i>	0.041	3.456	–	–	–0.31	von Bertalanffy	Southern Ocean, Weddell Sea	Dahm (1996)
<i>Ophiurolepis brevirima</i>	0.034	4.314	–	–	–0.20	von Bertalanffy	Southern Ocean, Weddell Sea	Dahm (1996)
<i>Ophioceres incipiens</i>	0.084	1.278	–	–	–0.86	von Bertalanffy	Southern Ocean, Weddell Sea	Dahm (1996)
<i>Ophionotus victoriae</i>	0.123	4.300	–	–	–	Richards function	Southern Ocean, Weddell Sea	Dahm (1996)
<i>Ophionotus victoriae</i>	0.248	3.130	–	–	–	Richards function	Southern Ocean, Weddell Sea	Dahm (1996)
<i>Ophioceres incipiens</i>	0.176	1.033	–	–	–	Richards function	Southern Ocean, Weddell Sea	Dahm (1996)
<i>Ophionotus victoriae</i>	0.248	–	32.17	–0.018	–	Richards function	Southern Ocean, Weddell Sea	Dahm (1996)
<i>Ophionotus victoriae</i>	0.123	–	44.62	0.144	–	Richards function	Southern Ocean, Weddell Sea	Dahm (1996)
<i>Ophiuroglypha lymani</i>	0.170	2.100	–	–	–	Richards function	Pacific, Magellan region	Dahm (1999)
<i>Ophiocten gracilis</i>	0.073	–	20.84	–	–	von Bertalanffy	Deep Sea, Atlantic, Rockall Trough	Gage (2003)
<i>Ophiocten gracilis</i>	0.276	–	11.93	–1.788	–	Gompertz function	Deep Sea, Atlantic, Rockall Trough	Gage (2003)
<i>Ophiocten hastatum</i>	0.632	–	14.86	–	–	Richards function	Deep Sea, Atlantic, Rockall Trough	Gage <i>et al.</i> (2004)
<i>Ophiocten hastatum</i>	0.202	–	20.35	–	–	Gompertz function	Deep Sea, Atlantic, Rockall Trough	Gage <i>et al.</i> (2004)
<i>Stegophiura</i> sp. (non-seep)	0.078	1.720	–	0.563	–0.64	von Bertalanffy	South Pacific, Central Chile	This study
<i>Stegophiura</i> sp. (seep)	0.095	1.660	–	0.446	–0.58	von Bertalanffy	South Pacific, Central Chile	This study
<i>Stegophiura</i> sp. (non-seep)	0.188	1.400	–	–	–	Gompertz function	South Pacific, Central Chile	This study
<i>Stegophiura</i> sp. (seep)	0.178	1.500	–	–	–	Gompertz function	South Pacific, Central Chile	This study

K, growth constant (y^{-1}); L_{∞} , asymptotic size; ϕ , growth performance; OR, ossicle radius (mm); DD, disc diameter (mm); M_{\max} , maximum body size (Kj); A_{\max} , maximum age (y).

signatures for C and N ($\delta^{13}\text{C} = -15.7\text{‰}$ and $\delta^{15}\text{N} = 20.1\text{‰}$), suggesting a non-chemosynthetic origin of their food sources (Sellanes *et al.*, 2008). Indeed, these isotopic signatures are close to those recorded at the same site for other ophiuroid species (i.e. secondary consumers) such as *Astrodia tenuispina* ($\delta^{13}\text{C} = -15.5\text{‰}$ and $\delta^{15}\text{N} = 18.9\text{‰}$), *Asteronyx loveni* ($\delta^{13}\text{C} = -13.5\text{‰}$ and $\delta^{15}\text{N} = 18.8\text{‰}$) and the asteroid *Ctenodiscus australis* ($\delta^{13}\text{C} = -11.0\text{‰}$ and $\delta^{15}\text{N} = 18.7\text{‰}$). Individual echinoderm growth is known to be affected by a variety of factors (temperature, food, age, competition and predation). In an ecological context, food quantity and quality have been considered to be important parameters in most studies (Bluhm *et al.*, 1998; Dahm & Brey 1998; Gage, 2003). It is clear that the relationship between primary production and benthic food availability is not direct, but is affected by a complex of coupled factors (Bluhm *et al.*, 1998). However, the relationship between low primary production and low echinoderm growth rates could indicate that the latter is limited by food availability. Therefore, the high abundance of *Stegophiura* sp. at the CMSA has to be considered as its ability to exploit this particular environment. In fact, the results obtained here suggest a size-segregated *Stegophiura* sp. distribution pattern. Indeed, juvenile forms (<10 mm of disc diameter) were found mainly at the seep sites, probably attracted to these areas by the presence of hard substrates (generating an enhanced diversity of suitable habitats) rather than the availability of food produced *in situ*.

The individual growth of benthic invertebrate species can be extremely variable, mainly due to environmental factors such as temperature and/or food supply (see Brey, 1998 and references therein). In the present study, *Stegophiura* sp. growth was investigated by analysing the microstructure of growth rings. However, the hypothesis that these rings represent annual growth marks has not been validated, although the results provide strong evidence for seasonal growth. This pattern is similar to those described for Antarctic and sub-Antarctic ophiuroid species (Dahm, 1996, 1999). In the study area, the oldest *Stegophiura* sp. specimens were estimated to be 15 years, with a disc diameter of about 38.8 mm. These values are close to those reported for Antarctic species by Dahm (1996), who determined a maximum age of 19 years for *Ophioceres incipiens*, 22 years for *Ophionotus victoriae* and 25 years for *Ophiurolepis brevirma*. However, the ages estimated for *Stegophiura* sp. are much lower than those estimated for *Ophiurolepis gelida* (33 years) and *Astrotoma agassizi* (91 years). Considering that the largest individual recorded in the study area is close to 40 mm, it is likely that the real longevity is higher than 15 years. This is reflected in the shape of the von Bertalanffy growth curve, which is not asymptotic in the analysed age-range. As proposed for Antarctic and sub-Antarctic ophiuroid species (Dahm, 1996, 1999), *Stegophiura* sp. is likely to reach asymptotic growth only after two decades. In addition, our results are similar to those estimated for sea urchins from boreal regions, which range from a maximum of 10 to 20 years (see Bluhm *et al.*, 1998 and references therein). We suggest that the growth parameters estimated in this study could be also influenced by the presence of the Antarctic Intermediate Water (AAIW) in the region. This water mass is distributed along the continental slope (400–1200 m), and is characterized by low temperatures (4–6°C) and low salinity (Palma *et al.*, 2005; Quiroga *et al.*,

in press). In fact, growth performance of *Stegophiura* sp. was relatively higher than values reported for Antarctic species, but falls within the range of those estimated for sub-Antarctic species, which are also influenced by the AAIW (see Table 3 and references cited therein).

Age-structures of hydrothermal vent and cold seep populations are still poorly understood (e.g. Schöne & Giere, 2005). The growth rates determined for *Stegophiura* sp. in the study area (von Bertalanffy $K_{\text{VB}} = 0.078\text{--}0.095$; Gompertz $K_{\text{G}} = 0.178\text{--}0.188$) are closer to those reported for other deep-sea ophiuroid species such as *Ophiura ljunghmani* ($K_{\text{VB}} = 0.06$, $K_{\text{G}} = 0.27$; Gage *et al.*, 2004) and *Ophiocten hastatum* ($K_{\text{VB}} = 0.20$, $K_{\text{G}} = 0.02$; Gage *et al.*, 2004) but lower than that of *Ophiocten gracilis* ($K_{\text{VB}} = 0.02$, $K_{\text{G}} = 0.27\text{--}0.28$; Gage *et al.*, 2004). The von Bertalanffy growth function was suggested as the most promising for ophiuroids (Dahm, 1993; Gage, 2003; Gage *et al.*, 2004). According to this growth function, size-at-age data from ossicle growth band measurements indicate a relatively rapid growth of *Stegophiura* sp. populations at methane seep sites. Therefore, we suggest that this result could be attributable to the presence of methane-derived authigenic carbonates, which provide a suitable habitat for ophiuroids, offering this heavily calcified epifaunal species some protection from predation (Gage, 1990; Gage *et al.*, 2004). On the other hand, these rates were fairly low when compared with published studies of other bathyal species. In fact, both longevity and growth patterns characterize *Stegophiura* sp. as a long-lived, slow-growing invertebrate similar to those species living in the Antarctic and sub-Antarctic regions (Dahm, 1996, 1999).

In summary, according to information published on stable isotopes for the studied sites, *Stegophiura* sp. does not benefit from extra inputs of energy derived from chemosynthetic sources at the seep sites, and this species is probably just ingesting phytodetritus and sediments, as was found for other bathyal ophiuroids (Gage & Tyler, 1982; Gage, 2003). However, although no significant differences were observed in the size-structure at both types of habitats, the higher occurrence of juveniles observed near the seep sites suggests that these areas constitute preferred breeding grounds for this species and/or represent recruitment sites as well. This preference is also reflected in the higher growth rates estimated at the seep site.

We still know little about the biochemical adaptations, trophic ecology, reproductive biology and population dynamics (e.g. secondary production and mortality) of the benthic megafauna associated with cold seep communities on the margin off Chile. In order to verify our findings, future studies should use other approaches to validate the growth models (such as stable isotope ratios $^{18}\text{O}/^{16}\text{O}$ and $^{13}\text{C}/^{12}\text{C}$; Brey, 2001).

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