Population structure, growth and production of a recent brachiopod from the Chilean fjord region

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Abstract

Magellania venosa, the largest recent brachiopod (Davidson 1886, McCammon 1973), occurs in clusters and banks in population densities of up to 416 ind m^{-2} in the fjord Comau, northern Chilean fjord region. Below 15 m depths, it co-occurs with the mytillid *Aulacomya atra* and dominates the benthic community below 20 m. To determine the question why *Magellania venosa* is a successful competitor, the brachiopod's *in situ* growth rate was studied and its overall growth performance was compared with that of other brachiopods and mussels. The length growth was measured between Februay 2011 and March 2012 after mechanical tagging and Calcein staining. Settlement and juvenile growth were determined from recruitment tiles installed in 2009 and from subsequent photocensus. Growth of *Magellania venosa* is best described by the general von Bertalanffy growth function, with a maximum shell length (L_∞) of 71.53 mm and a Brody growth constant (K) of 0.336 yr^{-1}. The overall growth performance (OGP index = 5.1) is the highest recorded for a rynchonelliform brachiopod and in the range of that for *Mytilus chilensis* (4.8 – 5.27), but lower than that of *Aulacomya atra* (5.74). Maximal individual production (P_{Ind}) is 0.29 g AFDM ind^{-1} yr^{-1} at 42 mm shell length and annual production ranges from 1.28 – 89.25 g AFDM yr^{-1} m^{-2} (1 – 57% of that of *Aulacomya atra* in the respective fjord). The high shell growth rate of *Magellania venosa,* together with its high overall growth performance may explain the locally high population density of this brachiopod in the fjord Comau. However, the production per biomass of the population ($P/\bar{B}$-ratio) is low (0.535) and *Magellania venosa* may play a minor role in the food chain. Settling dynamics indicates that *Magellania venosa* is a pioneer species with low juvenile mortality. The brachiopod-bivalve coexistence suggests that neither the presence of potential brachiopod predators nor space competitors (i.e. mytiilids) affect the survival of the brachiopod population.

Keywords:

Brachiopoda; *Magellania venosa;* growth function; growth performance; productivity; zonation; Comau Fjord; Chilean Patagonia

Introduction

Brachiopods dominated global benthic habitats in the Palaeozoic period and have disappeared from most modern marine ecosystems. Their ecological niche seems to be almost taken over by a far more diverse bivalve fauna (James 1992; Peck 1992; Walsh 1996;

Försterra *et al*. 2008). Different scenarios are proposed for this community shift: Gould & Calloway (1980) proposed that brachiopods were not sequentially and gradually replaced by bivalves but more or less stochastically after the end-Permian mass extinction event which heavily affected brachiopods. On the other hand, there is strong evidence for local space competition, differences in predation pressure and filter-feeding efficiency between brachiopods and bivalves (Simoes *et al*. 2007; Thayer 1985; Rhodes & Thompson 1993).

The two recent brachiopod subphyla, the Linguliformea and Craniiformea, are mainly found in the tropics (Kowalewski *et al*. 2002; Bitner 2007, 2008). The most diverse recent brachiopod subphylum Rynchonelliformae—formerly classified as the Articulata or articulate brachiopods (Williams *et al*. 2000, 2002, 2006)—shows increasing diversity and population density towards higher latitudes. High population densities of rynchonelliform brachiopods only occur regionally and mainly in upwelling areas with nutrient-rich waters such as off the west coast of south Africa (Hiller 1991, 1994) or the south east coast of Brazil (Kowalewski *et al*. 2002). Numerically dominant brachiopods are also reported from New Zealand (Doherty 1979; Thayer *et al*. 1992), the west coast of North America (Thayer 1977; Pennington *et al*. 1999) and Antarctica (Foster 1974, 1989).

For a sessile suspension-feeder rapid growth is essential to successfully compete for space and to reach a certain size to avoid overgrowth and predation (Paine 1976). The large cavity needed for the lophophore of rynchonelliform brachiopods seems to be disadvantageous for rapid growth: the mantle cavity in which this respiration and filtration apparatus is located requires up to 75% of the total body volume. Despite the large lophophore, rynchonelliform brachiopods are still considered to be low in metabolic activity (Peck *et al*. 1997) and filter-feeding ratios compare to associated bivalves (Rhodes & Thompson 1993).

Even though the individual growth rate often determines the relative success in a benthic community (Sebens 1982), few attempts have been undertaken to describe brachiopod growth as one of the essential features of population dynamics. Former studies estimated rynchonelliform brachiopod growth from length-frequency distributions (Paine 1963, 1969) and shell growth lines (Curry 1982; Brey *et al.* 1995). Doherty (1979) used newly settled brachiopods on recruitment tiles for repeated size measurements. Exact measurements of growth rates are also achieved when using *in situ* tag-recapture experiments. To date this method has only been applied on the Antarctic, rynchonelliform brachiopod *Liothyrella uva* (Peck *et al*. 1997).

In many benthic communities brachiopods are restricted to cryptic habitats such as caves and crevices (Jackson *et al*. 1971; Tunnicliffe & Wilson 1988; Wilson 1998). This has been suggested to be an evolutionary response to space competition with bivalves (Walsh 1996). In some northern Chilean fjords however, mass occurrences of the largest recent brachiopod *Magellania venosa* (Solander, 1789) have been reported (Försterra *et al*. 2008). This rynchonelliform brachiopod is described from vertical rock faces and overhangs below 15 m depths in the fjords Comau, Reñihué and Pitipalena, competing for space mainly with the mussel *Aulacomya atra*.

This study aimed to determine the *in situ* growth rate of *Magellania venosa* and its overall growth performance compared with that of other brachiopods and mussels to address the question why this largest living brachiopod species is a successful competitor. To understand the population dynamics, its production and productivity was estimated.

Material and Methods

Study Site

The fjord Comau is located in the northern Chilean fjord region (42°20’S, 72°27’W, Fig. 1). It is characterized by a typical U-shaped cross section profile with near vertical basaltic littoral-walls. It has no sill at its mouth and is connected to the Gulf of Ancud across the Marilmo and Comau passes (250 – 350m deep) and to the Hornopiren channel, across the Cholgo channel. Along its axis, the depth decreases from a maximum depth of 487 m at its mouth to less than 50 m near its head (Häussermann & Försterra 2009). It has a maximal width of 8.5 km, and a length of ~ 45 km from its mouth at Lilihuapi Island to its head at Leptepu (Häussermann *et al*. 2012). The basin of the fjord is dominated by Modified Sub-Antarctic Water (MSAAW) (Pantoja *et al*. 2011).

The fjord is characterized by a strong vertical stratification, typical for the fjords of the Northern Patagonian Zone (Sievers & Silva 2008): a well-oxygenated superficial low salinity layer with a higher pH and nutrient content, and a more homogeneous water body below 20-30 m characterized by higher salinity, lower pH and lower nutrient concentrations (Sievers & Silva 2008). The high annual precipitation of approximately 6600 mm m^{-2} yr^{-1} and large diffuse freshwater run-offs contribute to the low salinity layer, with minimum salinities close to two. Sea surface temperatures reach 22°C in summer and decrease to 5°C in winter. Temperatures below the surface layer are fairly homogenous at 8°C –12°C all year round (own observations; Montero *et al*. 2011).

Key features of the Northern Patagonian fjord region are its high primary production rates in the spring and aestival months. Aracena *et al.* (2011) calculated a primary production of up to 2.3 g C m^{-2} d^{-1} for the fjord Comau and average primary production for the Inner Sea of Chiloé ranged from 1.8 g C m^{-2} d^{-1} to 5.4 g C m^{-2} d^{-1} (González *et al.* 2010). Maximum primary production was measured at 9.4 g C m^{-2} d^{-1} in the Reloncaví fjord, whereas values from Central and South Patagonia hardly reach 1 g C m^{-2} d^{-1} (Aracena *et al.* 2011).

Population structure and length-mass relation

The population density of *Magellania venosa* was measured from 78 pictures taken in 2011 at the stations Punta Gruesa (n = 38) and SWALL (n = 40). Following three line transects (15, 20 and 25 m water depth), SCUBA divers placed a counting square of 50 cm side length blindfolded (to prevent selection) at the vertical wall and took photographs with a Canon PowerShot G11 camera placed in a WP-DC34 housing. This resulted in 12 pictures taken at 25 and 20 m water depth at both study stations and 14 and 16 pictures at 15 m water depth at Punta Gruesa and SWALL, respectively.

To estimate high-end population density, pictures were also taken using the same method at Cahuelmó (n = 4) were the highest densities of *M. venosa* had already been observed.

In 2011, length-frequency distributions were determined at the stations Cahuelmó (n = 1), Huinay Dock (n = 2) and CrossHuinay (n = 1). The maximal anterior-posterior length of the ventral shell was measured *in situ* on random samples found along the respective isobar to the lower millimetre using vernier callipers. The measurements were immediately classified in 2 mm-length classes from 0 mm to 80 mm. To calculate production, all length-frequency distributions for the four stations were pooled. The mean individual length was then calculated from the length classes by weighted average.

$$\bar{L} = \frac{\sum_1^n N_c L_c}{\sum_1^n N_c} \quad (c = 1, 2, 3, \ldots n) \qquad [\mathrm{mm}] \qquad [1]$$

Where N_c is the number of individuals in length class c and L_c the mean length in the respective length class.

The length-mass relationship (n = 21) was determined for the entire size range of the brachiopod population. The tissue remained within the shells during all states of drying and burning to ensure that the shell-connected and integrated tissues were included in the calculation. Individuals were collected at CrossHuinay (n = 7), Punta Gruesa (n = 7) and Cahuelmó (n = 7) in 2011 at 15 to 25 m water depth. Individuals were subsequently dried at 50°C for 48 h to record the dry mass (DM) values. To determine ash mass, the samples were burned in a muffle furnace for 7 hrs at 550°C. Both, ash mass and shell mass were measured subsequent to burning and subtracted from DM, resulting in shell-free, ash-free dry mass (AFDM). Regression of AFDM to shell length followed the power function (Brey 1999, 2001):

$$M = a * L^b \qquad [2]$$

where M is the mass [g AFDM], L the anterior-posterior length of the ventral shell [mm], a the intercept and b the slope of the function.

In situ Growth

Mechanical tag

To measure size increments, individuals with a ventral shell length of 14 – 70 mm (anterior-posterior) were mechanically tagged with an electric underwater rotary drill (Dremel 8200 12V$^{\mathrm{Max}}$, Racine, Wisconsin, USA) sealed in a custom-made underwater housing. Two notch marks were engraved with parallel mounted cut-off wheels (Dremel cut-off wheel No. 409, Ø 24 mm, 0.6 mm thick, distance between parallel wheels: 2 mm) along the ventral shell, perpendicular to the shell edge (Laudien *et al*. 2003). The individuals were harvested one year later in February 2012 and the respective size increment on the ventral shell was measured from the end of the parallel notch marks to the new shell edge (Fig. 2) using digital vernier callipers (resolution: 0.01 mm).

Staining

Clusters of brachiopods with up to 25 individuals were stained with Calcein (3,6 Dihydroxy-2,4-bis-[N,N' di(carboxymethyl)-aminomethyl] fluoran, $C_{30}H_{26}N_2O_{13}$, CAS ID: 1461-15-0) in February 2011. Calcein has been shown to be incorporated passively into growing calcium carbonate structures in various taxa (e.g. Moran & Marko 2005; Riascos *et al*. 2007; Herrmann *et al*. 2009), including brachiopods (Rowley & Mackinnon 1995). None of the authors reported enhanced mortality or other negative influences on life histories. Twelve brachiopod clusters (Punta Gruesa: six clusters, CrossHuinay: five clusters and Cahuelmó: one cluster,) were covered with a 2-l seawater filled plastic bag at 20 m (Punta Gruesa, CrossHuinay) and at 23 m (Cahuelmó). A Calcein-seawater stock-solution was injected into the bag with a syringe, resulting in a final calcein concentration of 90 mg l^{-1}. The bags were removed after 10 hrs and the treated clusters marked with cable ties.

After harvest in February 2012, ventral shells were bleached with sodium hypochlorite (13% concentration; CAS ID: 8007-59-8) for 20 min to reduce confounding organic background fluorescence. A dissecting microscope (Olympus SZX12, magnification: 7×; SZX-RFL

GFP filter set DM505; excitation filter BP460-490; emission filter BA510IF, Olympus, Tokyo, Japan), equipped with an external light source (Olympus USH 102D) was used to detect shell fluorescence. Pictures of the stained growth line to the shell edge were taken with a connected life-view camera (camera: Olympus DP72; 2150 ms exposure time; ISO 400; 1% spot metering; 4140 × 3096 effective image resolution:). Size increment measurements were conducted digitally (analySIS doku software, Olympus, Tokyo, Japan).

Juvenile growth

Recruitment tiles were installed at ~18 m depth at CrossHuinay and Lilihuapi in 2009. The backs of stoneware tiles ("Radica", Zirconio, Vila-real (Castellón), Spain) were used as settling substrates. The tiles were cut to 15 cm×15 cm edge length and fixed in plastic bases.

Core holes were drilled in the rock using a pneumatic drill-hammer (Atlas Copco DKR 36; Ø bit: 10 mm, Atlas Copco, Nacka, Stockholm, Sweden) and the plastic bases subsequently fixed with stud bolts. The tiles were attached on overhangs in angles from 11° to 61°, simulating the preferred habitat structure of *Magellania venosa* (Försterra *et al*. 2008). *In situ* photographs (Canon 5D Mark II; 50mm focal length, Canon, Tokyo, Japan) of the recruitment tiles were taken at different time intervals from 2010 to 2012 (22. April 2010, 12.11.2010, 24.02.2011, 08.07.2011, 10.12.2011, 31.01.2012).

The successive width increment of each settled individual of *Magellania venosa* was measured on the distinct images with the GNU Image Manipulation Software (GIMP) 2.6. As brachiopod individuals were attached on the substrate and their shell grows in the third dimension and they were not covered by the two-dimensional pictures (which were taken in the plane of the substrate) it was easy to measure shell width accurately but not shell length. Therefore the width of the individuals was converted to length data using the empirical length-width relation calculated from 162 individuals collected in 2012

$$L = a * W \text{ [mm]} \qquad [3]$$

where L is the ventral anterior-posterior shell length and W is the maximal shell width of the ventral shell.

Table 1 shows where data on population structure and growth were collected.

Growth

The length growth of the shell was described by the general von Bertalanffy growth function (Bertalanffy 1938),

$$L_t = L_\infty(1 - e^{-K(t-t_0)}) \quad [4]$$

where L_t is the length at age t, L_∞ is the potential maximum length, i.e. the asymptotic length, reached after an infinite time of growth, K is the Brody growth constant, defining the speed of growth, and t_0 is the age at which length would have been zero.

The age of the individual brachiopods is not known and the only measured variables are the length of the shellsat the time of tagging (t_1) and collection (t_2). Thus, the rearranged form of the general von Bertalanffy growth function

$$L_2 = L_1 + (L_\infty - L_1)\left(1 - e^{-K(t_2-t_1)}\right) \quad [5]$$

was fitted to the length-increment data from the mechanical tagging, the staining and the successive length measurements from the pictures of the recruitment tiles (Fabens 1965). Iterative fitting was achieved by the non-linear Newton algorithm (GRG-nonlinear method, Solver, Microsoft Excel 2011) (Brey 2001).

Production

Production was computed with the mass-specific growth rate method (Crisp 1984; Brey 2001). Data required for this method are (i) the length-frequency distribution, (ii) the length-mass relation and (iii) the general von Bertalanffy growth function. The individual production [g AFDM yr^{-1}] in size class c is calculated with

$$P_{Ind} = M_c G_c \text{ [g AFDM yr}^{-1}\text{]} \quad [6]$$

where M_c corresponds to the mean individual biomass in length class c and G_c is the respective annual mass-specific growth rate:

$$G_c = b * K((L_\infty / L_c) - 1) \text{ [yr}^{-1}\text{]} \quad [7]$$

where b is the exponent of the length-mass relation, L_∞ and K correspond to the VBGF parameters and L_c is the mean length in length class c.

The population production of the sample (P_s) also takes into account the number of individuals in length class c and the sum of all length classes.

$$P_s = \sum_1^n N_c \, M_c G_c (c = 1, 2, 3, \ldots n) \text{ [g AFDM yr}^{-1}\text{]} \qquad [8]$$

The biomass of the sample is further calculated by:

$$B = \sum_1^n M_c \, N_c (c = 1, 2, 3, \ldots n) \text{ [g AFDM]} \qquad [9]$$

The mean biomass of the population (M_{mean}) was derived from the mean shell length of the population ($\bar{L}$) and the length-mass relation. With the mean population density N_{mean} [ind m^{-2}] at the respective site and the ratio of P_S to mean B $(P/\bar{B})$, the annual population production P_A per square meter (Brey *et al.*1995) is

$$P_A = P/\bar{B} * M_{mean} N_{mean} \text{ [g AFDM yr}^{-1}\text{ m}^{-2}\text{]} \qquad [10]$$

Results

Population structure and length-mass relation

The population density averaged at 8 ind m^{-2} (SWALL) and 6 ind m^{-2} (Punta Gruesa) at all three depths. At Punta Gruesa, lowest and highest mean population densities were found at 15 m and 25 m depth, respectively. At SWALL, the lowest mean population density was determined at 25 m depth and peaked at 20 m water (Table 2). The highest overall population density was found at Cahuelmó (416 ind m^{-2}) on an isolated boulder (~10 m^{-2}). This estimate cannot be considered to be the mean population density within the entire Cahuelmó Fjord, but represents the observed maximum population density of *Magellania venosa* (Fig. 3).

A mean length ($\bar{L}$) of 34.33 mm was calculated (n = 226) using the pooled length-frequency distributions. The length-mass relation with $a = 6 \times 10^{-5}$ and $b = 2.43$ (n = 21, $r^2 = 0.84$), corresponded to a body mass M_{mean} of 0.323 g AFDM ind^{-1} (Fig. 4).

Growth

A total of 59 mechanically tagged individuals was recaptured in 2012 (Lilihuapi: n = 8; Cahuelmó: n = 3; Huinay Dock: n = 11; CrossHuinay: n = 20; Punta Gruesa: n = 17); ten of those were also stained with Calcein and one was only stained with Calcein.

In all, 170 size-increment measurements were derived from the picture analyses of 63 juvenile brachiopod recruits on the tiles. The length-width relation for conversion of measured recruit shell width to length is as follows:

$$L = 1.07 * W \text{ [mm] } (r^2=0.92) \qquad [11]$$

To reflect the growth performance of all length classes these data were pooled with the length increment data derived form the mechanically tagged individuals of all stations. Fitting a general von Bertalanffy growth function to this pooled data resulted in a Brody growth constant (K) of 0.336 yr^{-1} and an asymptotic shell length (L_∞) of 71.53 mm ($r^2 = 0.99$; n = 229) (Fig. 5a).

The brachiopods which settled on recruitment tiles ranged in length between 1.96 mm (22.04.2010) to 58.32 mm (31.01.2012); they were observed as pioneers on all tiles.

The largest individual considered in the general von Bertalanffy growth function was 70.03 mm at the time of harvest with an estimated age of ~ 11 yrs. Comparison of the mean residuals from length-increment (i.e. individuals from recruitment tiles) and tagging-recapture data (i.e. mechanically tagged and calcein tagged individuals) (Fig. 5b) did not show significant differences between the five study stations (Kruskal-Wallis; $\chi^2 = 6.0253$; df = 4; $p = 0.1973$). This was reflected by the good overall fit of the growth model ($r^2 = 0.99$). No significant difference of residuals from the general von Bertalanffy growth function model were detected between data pairs obtained from the recruitment tiles in comparison to those derived from mechanical tagging (Wilcoxon test; Z = -1.59; $N_{picture} = 170$; $N_{mechanical} = 59$; $p = 0.11$).

Production

The annual individual production (P_{ind}) increased to 0.29 g AFDM Ind^{-1} yr^{-1} at 42 mm shell length before decreasing continuously.

Total annual population production (P_S) is 49.59 g AFDM yr^{-1} and the corresponding biomass of the population was 92.67 g AFDM, resulting in a productivity ($P/\overline{B}$ ratio) of 0.535 (Fig. 6).

The annual population production per square meter (P_A) for the mean population densities from 15 m to 25 m was 1.03 g AFDM yr^{-1} m^{-2} (Punta Gruesa) and 1.38 g AFDM $yr^{-1} m^{-2}$ (SWALL), respectively. Values for maximum population densities ranged from 7.6 g

AFDM yr^{-1} m^{-2} (Punta Gruesa, n = 44 ind m^{-2}) to 8.98 g AFDM yr^{-1} m^{-2} (SWALL, n = 52 ind m^{-2}) and peaked at 71.88 g AFDM yr^{-1} m^{-2} (Cahuelmó, n = 416 ind m^{-2}).

Discussion

Population structure and length-mass relation

The high primary production in the northern Chilean fjord region (González *et al.* 2010, Aracena *et al.* 2011) may contribute to the overall rich benthic invertebrate communities found along the Northern Chilean fjords and favour the occurrence of *Magellania venosa* in the fjord Comau (Försterra *et al*. 2008).

Analyses of the length-frequency distribution did not detect cohorts, suggesting that recruitment is either not peaking seasonally or variations in juvenile growth may be blurring any cohort structure in the size-frequency plot. However, McCammon (1973) reports that the main gonad maturity of *Magellania venosa* from December to January. This is in agreement with observations on the present recruitment tiles; newly settled brachiopods were only found during the aestival months in 2010 and 2011. The missing recruitment cohorts in the length-frequency distribution might therefore be due to variations in post-settlement and juvenile growth. Unfortunately, there is no information on larval dispersal of *Magellania venosa* available.

The presently recorded large range of maximal brachiopod population densities (4 ind m^{-2} – 416 ind m^{-2}) may reflect specific local conditions that benefit brachiopod recruitment success and growth. Patchy recruitment, which is also known from other rynchonelliform brachiopods (Valentine & Jablonski 1983; James 1992), may be due to influences of the prevailing current regime. In general, in the fjord Comau highest population densities were recorded on almost vertical substrate slopes.

In situ growth methods

All individuals (n = 59) exhibited disturbance lines at the former shell edge where mechanical tags were applied. Some recaptured individuals (n = 8) showed no growth increment after the mechanical tagging. This may suggest that growth in other individuals with mechanical tags had slowed down over time, and the estimated growth function is therefore conservative.

Only 11 of the approximately 100 individuals stained in 2011 were collected in 2012. Ten of them were also mechanically tagged and the size-increment data obtained using the two methods did not differ . Hence, it was not necessary to make separate computations of the growth function for the distinct tagging methods. Due to the loss of cable tie marks Even though the recapture rate of the stained individuals remained low (e.g, clusters may be lost as in many cases the specimens grew on the shell of one single large individual, resulting in the loss of the entire cluster if it dies, possibility that only some individuals incorporated the stain), the method itself has to be considered applicable. On one specimen that was stained without mechanical tag, no disturbance line was visible suggesting staining to be less invasive.

Rowley & McKinnon (1995) used five times higher Calcein concentrations (500 mg l^{-1}) and twice as long incubation times (24 h) for Calcein marks in brachiopods under laboratory conditions. However, this concentration is not applicable for the present *in situ* experimental setup since it would lead to oversaturation of the stock solution in the syringe and diminished oxygen concentration within the incubation bags during such a long exposure time. The detection of fluorescent growth marks in the present study shows that the lower concentration and incubation time are sufficient for *in situ* growth studies on brachiopods. This is in line with studies on bivalves, where no differences of Calcein mark quality were reported for different concentrations (50 mg l^{-1} and 100 mg l^{-1}) and incubation times (3 h and 6 h) (Riascos *et al*. 2007; Herrmann *et al*. 2009).

Growth

The calculated parameters of the general von Bertalanffy growth function (K = 0.336 yr^{-1}, L_∞ = 71.53 mm) are applicable for the entire fjord population and comparable study sites since the length-increment data (n = 229) from six stations were pooled. Nevertheless, local differences in growth rate and production may occur due to vertical gradients in water parameters such as pH, temperature and salinity (Sievers & Silva 2008; Jantzen *et al*. 2013) and calculations of the very exact age by the general von Bertalanffy growth function might be difficult.

Some length classes of both data sets (recruitment tile experiment, mechanical tagging) coincide. This allowed analysis of a continuous length-increment dataset reflected in a good overall fit of the calculated general von Bertalanffy growth function (r^2 = 0.99).

A similar fit of the dataset was found when the Gompertz growth function was used, but with a much smaller maximal shell length (L_∞ = 62.34mm). Because of this divergence to the observed maximal shell length of *Magellania venosa* in the fjord Comau (L = 70.03 mm), the von Bertalnffy growth function was used for further production calculations. Sigmoidal growth curves (e.g. Gompertz growth curve) with lower growth rates in smaller length classes or a lag-phase in growth of newly settled individuals were determined for other rynchonelliform brachiopod (Doherty 1979; Collins 1991). Logarithmically declining growth curves were reported from other rynchonelliform brachiopods, e.g. *Liothyrella uva (*Peck *et al.* 1997*)* and *Magellania fragilis* (Brey *et al.* 1995).

Overall Growth Performance

Non-linear growth functions are difficult to compare; the parameters *K* and L_∞ have been shown to vary significantly between populations and habitats of the same taxon. Several authors (e.g. Pauly 1979; Vakily 1992; Laudien *et al*. 2003; Herrmann *et al*. 2009) demonstrated the suitability of composed indices for overall growth performance (OGP) for intra- and interspecific comparisons. The OGP index is proportional to the maximum rate in body mass increase during lifetime, i.e. the mass increase at the inflexion point of the sigmoid mass growth curve $(\mathrm{OGP} = \mathrm{Log}(\mathrm{K}^*\mathrm{M}_\infty))$.

Statistical analysis of data sets among various macrobenthic invertebrate taxa revealed that OGP is a robust, taxon-specific feature. This underlines that OGP may successfully be used for ecological characterization of species as growth reflects environmental conditions (i.e. temperature, nutrition, disturbances etc.). OGP is less affected by external factors than *K* and L_∞ (Brey *et al*. 1999). Since values of maximum body mass are scarce in the literature, the maximal mass M_∞ can be approximated by $M_\infty = L_\infty^3$. Inferring the maximal mass by length according to $M_\infty = L_\infty^3$ can be used for a variety of benthic invertebrates (Brey 1999, 2001; Laudien *et al.* 2003), but different shell shapes might lead to variations in size-mass relation aand thus in OGP (Vakily 1992). Size-mass relations comparable to the one of *Magellania venosa* ($M = 6 * 10^{-5} * L^{2.43}$) were calculated for *Mytilus chilensis* ($M = 3 * 10^{-6} * L^{3.04}$) and *Aulacomya atra* ($M = 4 * 10^{-6} * L^{2.95}$) from the fjord Comau (Müller 2012). An OGP that is comparable between mytilids and brachiopods might then be calculated by:

$$\mathrm{OGP} = \log(\mathrm{K} * [\mathrm{L}_\infty]^3) \qquad [12]$$

For *Magellania venosa* from the fjord Comau, an OGP-index of 5.1 was calculated. Lower OGP-indices are known from antarctic, rynchonelliform brachiopods, ranging from 4.44 for *Magellania fragilis* (Brey *et al.*1995), 3.9 for *Liothyrella uva*, that also displays significant seasonal growth (Peck *et al*. 1997) to 3.4 for *Neorhynchia strebeli* (Barnes & Peck 1997). The only growth function (OGP-index = 4.9) for a tropical, linguliform brachiopod

(*Lingula unguis*) is provided by Park *et al*. (2000). Thus, *Magellania venosa* has the highest OGP-index known for recent brachiopods. This OGP-index is comparable to OGP-indices of the abundant mytilids from the fjord Comau, *Mytilus chilensis* and *Aulacomya atra* (Fig. 7).

VBGF for both mussels were investigated at the fjord Comau (Müller 2012) and the Falkland Islands (Gray *et al.*1997). The OGP-index for *Mytilus chilensis* ranges between 4.8 and 5.27, depending on the study station, whereas *Aulacomya atra* reaches a OGP-index of 5.74 (Table 3).

Production

While *Magellania venosa* shows highest individual production at 42 mm (0.29 g AFDM ind^{-1} y^{-1}), *Mytilus chilensis* of similar size already reaches twofold higher values (0.713 g AFDM ind^{-1} yr^{-1}) and a more than tenfold higher maximal production (3.475 g AFDM ind^{-1} yr^{-1} at 78 mm; Navarro & Winter 1982; data was processed by converting shell-free dry mass to ash-free dry mass according to Ricciardi & Bourget 1998).

The steady increase of cumulative annual population production indicates that all size classes contribute equally to the total annual population production and refers to the equally distributed length-frequency distribution of the population.

Despite the locally high population density of *Magellania venosa* in the fjord Comau and the high OGP, the low $P/\bar{B}$ ratio (0.535) suggests that this brachiopod species may play only a minor role in the energy flow of the benthic system.

Biotic interactions and zonation patterns

Under laboratory conditions brachiopods showed significantly higher mortality rates, when bivalves were transplanted in close proximity (Thayer 1985). Patches of the brachiopod *Terebratalia transversa* were trapped and overgrown by the mussel *Mytilus edulis* within hours and even mussel faeces raised the mortality rate of brachiopods (Thayer 1985). The latter may not hold true under *in situ* conditions due to higher rates of water exchange.

In contrast brachiopods are not outcompeted by mussels in the fjord Comau; the upper distribution limit of *Magellania venosa* (15 m to 20 m water depth) overlaps with the lower occurrence limit of the mussel *Aulacomya atra.* The mytilid dominates the tidal and subtidal benthic habitats in the fjord Comau with highest population densities found at 5 m water depth (mean = 369 ind m^{-2}) and decreasing population densities with increasing depth (10m: mean = 69 ind m^{-2}; 15 m: mean = 35 ind m^{-2}; 20 m: mean = 18 ind m^{-2}) (Müller 2012). In the zone of overlapping occurrence, the brachiopods occur between and on *Aulacomya* *atra*, suggesting an oppotunistic settlement dynamic (Fig. 8a). In depth of lower *Aulacomya atra* population densities (~18 m), individuals of *Magellania venosa* were also found as pioneers on the recruitment tiles, supporting this settlement dynamic (Fig. 8b).

The well accepted concept of zonation patterns in rocky shore communities exposed to high tidal amplitudes (Boaden & Seed 1985; Suchanek 1985; Seed & Suchanek 1992) helps to explain the observed zonation pattern. The concept states that the upper limit of a species distribution is controlled by abiotic factors, whereas biotic interactions limit the expansion to the lower end. One of the major biotic drivers are apparently mussel predators such as the highly abundant sea stars (e.g. *Cosmasterias lurida*), and carnivorous gastropods. These predators seem to be restricted to depths below 10 m, avoiding the upper, low salinity water layer with its varying environmental parameters (Jantzen *et al.* 2013). Thus, the Asteroidae seem to determine the lower distribution limit of *Aulacomya atra* with the low salinity layer creating a refuge for the mussel.

One indication for the survival of the brachiopod population might be that no signs of predation (e.g. sea stars sitting on *Magellania venosa* or their shells drilled by carnivorous gastropods) were observed during the photocensus of the recruitment tiles. Additionally, only five of the 63 juvenile brachiopods were lost from the recruitment tiles during the observation period and the comparatively high age reached by a sampled individuum (~11 yrs) may be a sign that natural mortality is rather low.

Caging and transplantation experiments indicated that predators prefere bivalves rather than brachiopods as food source (Thayer 1985). This may be due to differences in tissue densities: Bivalve tissue densities (120 mg cm^{-3} tissue) reach 7.5 times higher values than those of brachiopods (16 mg cm^{-3} tissue) (Peck 1993). This low energetic value, together with repellent chemicals within the shell and tissue, as proposed by several authors (Thayer 1985; Thayer & Allmon 1991; McClintock *et al*. 1993), may protect brachiopods. In modern ecosystems, frequencies of drilling holes produced by carnivorous gastropods are found to be 10 to 50 times lower in brachiopod shells than in associated bivalves (Baumiller *et al*. 2003; Harper & Peck 2003; Delance & Emig 2004; Simoes *et al*. 2007). Comparisons of fossil records and recent findings on rynchonelliform brachiopods suggest that drilling and predation were present throughout the geological history, but always remained at a low level, regardless of the associated fauna and habitat (Simoes *et al*. 2007).

With the potentially lower predation pressure on *Magellania venosa* and the restricted habitat of *Aulacomya atra*, the brachiopod seems to find a preferable settlement substrate. With stable water conditions in the subtidal and lower population density of the mussels, it is able to populate the benthic habitat with locally high population densities down to ~50 m (own observations with a remotely operated vehicle). The lower distribution limit of *Magellania venosa* might be limited by the insufficient abundance of phytoplankton food supply from ~50 m downwards where an increase in population densities of the mussel *Acesta patagonica* was recorded.

Conclusions

Magellania venosa shows the highest growth rate known for a recent brachiopod. It occurs locally in high population densities and is a pioneer species on recruitment tiles and may thrive sucessfully in the vicinity of mytilids. Neither the presence of potential benthic predators nor competition for ressources (i.e. space, food) seems to affect the survival of the brachiopod population significantly. Besides the fast growth and locally high population density of *Magellania venosa*, production is rather low and this brachiopod species plays only a minor role in the energy flow within the benthic system.

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Legends for Figures:

Figure 1: Station map of the fjord Comau; (A): Lilihuapi, (B): Cahulemo, (C): SWALL, (C): Huinay Dock, (E): CrossHuinay, (F): Punta Gruesa, (1): Gulf of Ancud, (2): Marilmo pass, (3): Comau pass, (4): Cholgo channel, (5): Hornopiren channel, (6): Leptepu

Figure 2: Under water picture of ventral valve of *Magellania venosa* taken 12 months after mechanical tagging. The notch marks (1) indicate the former valve margin (2). The distance betwenn the former and the actual valve margin (3) is the size increment (4) measured.

Figure 3: High population densities of the brachiopod *Magellania venosa* on study station Cahuelmó.

Figure 4: Length-mass relation of the brachiopod *Magellania venosa.*

Figure 5: (a) Size-at-Age plot for the size-increment dataset of tagging-recapture and recruitment tile experiments calculated by the general von Bertalanffy growth function $L_t = 71.53(1 - e^{-0.336(t-t_0)})$ (grey line). (b) Residuals of best-fitting von Bertalanffy growth function. L_2(calculated) results from the general von Bertalanffy growth function with the best-fitting parameters $K = 0.336$ yr^{-1} and $L_\infty = 71.53$ mm. L_2(measured) is the actual measured ventral shell length (anterior-posterior) at time of collection in February 2012. ΔL_2 = L_2(measured) - L_2(calculated).

Figure 6: Distribution of annual population production (P_S) and cumulative population production of the brachiopod *Magellania venosa* from the fjord Comau in 2011. Additionally, the mean population density (grey area = 100%, n = 226) for different length classes is included.

Figure 7: Auximetric grid with OGP-indices of brachiopods (○) and mytilids (◆). **1**: *Magellania venosa* (this contribution); **2**: *Waltonia inconspicua*, (Rickwood 1977); **3**: *Magellania fragilis* (Brey *et al.*1995); **4**: *Liothyrella uva*, (Peck *et al.* 1997); **5**: *Neorynchia strebeli*, (Barnes & Peck 1997); **6**: *Lingula unguis* (Park *et al.* 2000); **7**, **8**, **9**: *Mytilus chilensis* (Gray *et al.* 1997); **10**: *Aulacomya atra* (Müller, not published)

Figure 8: (a) Juvenile brachiopod *Magellania venosa* settling on shell of the mussel *Aulacomya atra.* (b) Recruitment tile at study station CrossHuinay densely populated with *Magellania venosa* 36 months after installation (depth ~18 m).

Table 1: Study stations and investigated population structure parameters.

Table 2: Population density estimates at station SWALL and Punta Gruesa. Mean and max: numbers of individuals per m^2. N: number of picutres taken per depth line transect.

Table 3: Growth rate parameters for mytilids and brachiopods used in the calculation of overall growth performance

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