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Aquatic Living Resources

Growth of *Argopecten purpuratus* (Mollusca: Bivalvia) on a natural bank in Northern Chile: sclerochronological record and environmental controls

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Abstract – Daily striae on the shell of the scallop, *Argopecten purpuratus*, were used to investigate its growth in a protected population within La Rinconada Bay, near Antofagasta (2nd Region, Northern Chile), and to determine how environmental forcings control shell growth. This sclerochronological approach was useful to describe daily shell growth *a posteriori*. Mean shell growth rates were calculated daily between February and October 1999 from shells of six specimens harvested on 15 October 1999. A multiple regression analysis performed on shell growth and environmental data shows that a temperature increase stimulates shell growth whereas particulate organic carbon concentration might be stressful above 2.5 mg L^{-1}. The lunar cycle might also have an effect on growth, most potent around New Moons, by synchronizing an endogenous oscillator. The age at commercial size (90 mm) was only 10–11 months in La Rinconada Marine Reserve and the von Bertalanffy growth parameters were $K = 2.24$ y^{-1} and $H_\infty = 117$ mm. Differences in shell growth performances between this study and previous ones dealing with *A. purpuratus* growth may be explained by the different methods used for shell growth modelling, higher growth rate on the seabed compared to suspended cultures, and particular environmental forcings (e.g. El Niño Southern Oscillation-ENSO events). Growth performance seems better during La Niña than during El Niño events, probably because of the large temperature increase (above the highest temperatures recorded in "normal" conditions) and the decline in coastal upwelling (which affects food availability) during El Niño. La Rinconada Marine Reserve appears as a very favourable site for *A. purpuratus* growth, probably because of the active upwelling zone off Antofagasta. These new insights on *A. purpuratus* shell growth confirm the importance of La Rinconada Marine Reserve as an area supporting repopulation of endangered wild stocks and scallop aquaculture in Chile.

Key words: shell growth / growth-regulating factors / *Argopecten purpuratus* / El Niño Southern Oscillation / Chile

Résumé – Croissance du pétoncle *Argopecten purpuratus* (Mollusca : Bivalvia) sur un banc naturel du nord du Chili : enregistrement sclérochronologique et facteurs environnementaux. Les stries journalières de la coquille du pétoncle chilien, *Argopecten purpuratus*, sont utilisées afin d'étudier sa croissance au sein d'une population protégée dans la réserve marine de la baie de la Rinconada, près d'Antofagasta (nord du Chili), et de déterminer de quelle manière les forçages environnementaux conditionnent la croissance coquillière. Cette approche sclérochronologique s'est avérée efficace pour décrire *a posteriori* la croissance coquillière journalière. Le taux de croissance coquillière moyen est ainsi calculé quotidiennement entre février et octobre 1999 à partir des coquilles de six spécimens pêchés le 15 octobre 1999. Une régression multiple, effectuée entre croissance coquillière d'une part et données environnementales d'autre part, indique qu'une augmentation de température stimule la croissance tandis que la concentration en carbone organique particulaire pourrait l'affecter négativement au-delà de 2,5 mg L^{-1}. Le cycle lunaire pourrait avoir un effet sur la croissance, stimulée aux environs de la nouvelle lune, en synchronisant une horloge interne. La taille commerciale (90 mm) est atteinte à l'âge de 10–11 mois, avec des paramètres de croissance de von Bertalanffy de $K = 2,24$ an^{-1} et $H_\infty = 117$ mm. Les différences de performances de croissance de ce pétoncle, entre notre étude et les études antérieures, pourraient provenir des différentes méthodes utilisées pour la modélisation de la croissance coquillière, de taux de croissance plus élevés sur le fond qu'en cultures suspendues, et de conditions environnementales particulières (telles que les phénomènes ENSO). Les performances de croissance semblent meilleures lors du phénomène La Niña que lors d'El Niño, probablement dues à l'importante augmentation de température (au-delà des températures les plus élevées enregistrées lors de conditions « normales ») et du ralentissement de l'upwelling côtier (affectant la disponibilité en

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nourriture) pendant El Niño. La réserve marine de la Rinconada apparaît comme un site très favorable à la croissance de *A. purpuratus*, vraisemblablement grâce à la présence d'une zone d'upwelling active au large d'Antofagasta ; ceci confirme l'importance de la réserve marine de la Rinconada pour le repeuplement de populations naturelles en danger ainsi que pour l'aquaculture de pétoncle au Chili.

1 Introduction

Argopecten purpuratus (Lamarck, 1819) is a large-sized scallop (Mollusca; Bivalvia; Pectinidae) living on sand bottoms in shallow bays of Peru and Chile. Its natural geographical range extends from Paita, Peru (5°S 81°W) to Bahia Vincente, Chile (37°S 73°W; Wolff and Mendo 2000). Economic exploitation of *A. purpuratus* in Chile in recent years has been primarily based on aquaculture, as harvesting of this species on natural banks was banned in 1988, due to severe overexploitation (Avendaño and Cantillánez 2005). Indeed, the annual landings dropped dramatically from 4997 tons in 1985 to 492 tons in 1987 despite identical fishing effort. Although the scallop fishery has been closed for many years, the natural scallop beds are still in jeopardy because illegal harvesting continues (Avendaño and Cantillánez 2005). Since intensive culture began in the 1980s, Chile has become the world's third largest producer of cultured scallops with 24 697 tons produced in 2004 vs. 8264 tons in 1995 (source: www.sernapesca.cl).

A better understanding of *A. purpuratus* biology appeared necessary in the late 1990s in order to characterize population dynamics within the species' geographical range and to provide the bases for sustainable exploitation (Stotz and González 1997). To this end, *A. purpuratus* shell growth has been extensively studied using various methods, i.e. length-frequency analysis, culture experiments in nets and off-bottom cages, and mark-and-recovery experiments. The specialized von Bertalanffy growth function (sVBGF), characterised by the two parameters K(Brody growth coefficient) and H_∞ (mean asymptotic shell height), was used in most of these studies to describe shell growth. Within the species' geographical range, the results varied greatly, K ranging from 0.35 (Wolff and Garrido 1991) to 2.68 y^{-1} (Wolff 1987) and H_∞ from 94.3 (Mendo and Jurado 1993) to 220 mm (Wolff and Garrido 1991). The reasons for such discrepancies have been rarely discussed. They may be partly related to different environmental forcings.

It has been demonstrated that temperature and food availability significantly influence scallop growth (Broom and Mason 1978; Wallace and Reinsnes 1985; Wilson 1987; Thouzeau 1991a; Thouzeau 1991b; Thouzeau et al. 1991; Chauvaud et al. 1998; Laing 2000; Chauvaud et al. 2001). With respect to *A. purpuratus*, growth appears to be affected by temperature (Wolff 1987; Mendo and Jurado 1993; González et al. 2002), diet composition (Navarro et al. 2000), food quantity, and dissolved oxygen concentration in bottom waters (Wolff 1987; González et al. 1999).

As many other pectinid species, *A. purpuratus* exhibits growth lines, so-called striae, on the external surface of its valves (Fig. 1). Since Clark (1968), many studies have focused on the rhythm of striae formation in scallops and have highlighted a daily periodicity for species of the genera *Argopecten* (Wrenn 1972; Clark 1975; Helm and Malouf 1983) and *Pecten* (Clark 1968; Clark 1975; Antoine 1978; Chauvaud et al. 1998; Chauvaud et al. 2005). In pectinids, this characteristic is useful to add a calendar axis to the growth record (backdating from the outer most stria, i.e. harvest date) and thus, to study the growth of a given species with accuracy. Indeed, an estimate of daily shell growth rate (i.e. dorso-ventral linear extension of the shell per unit time) can be made by measuring distances between successive striae (growth increment width). Chauvaud et al. (1998) have demonstrated the potential of daily striae to describe *a posteriori* daily shell growth of the Great Scallop, *Pecten maximus*. To our knowledge, this kind of sclerochronological approach has never been used to investigate *A. purpuratus* growth.

Our study focused on the natural scallop bed of La Rinconada Bay (2nd Region, Northern Chile), which was one of the most exploited of the country until its closure in 1986 (Avendaño and Cantillánez 1992). The objectives of this work were to establish a sclerochronological record of *A. purpuratus* shell growth in the legally protected population of La Rinconada Marine Reserve, and to determine empirically how environmental parameters, including the El Niño Southern Oscillation (ENSO) phenomenon, control shell growth.

2 Materials and methods

2.1 Study area

La Rinconada Marine Reserve (23°29'S – 70°30'W) is located in the northwest of La Rinconada Bay, an open bay south of the Mejillones Peninsula, near the city of Antofagasta (Fig. 2). This protected marine reserve was established by law in 1997 as part of management of *A. purpuratus* as a renewable resource concurrent with the conservation of wild reproductive stocks. The reserve extends ~350 ha with a maximum depth of 40 m. This region is open to the dominant southwesterly winds and presents a hyper-arid climate: the mean (1977–1991) annual rainfall in Antofagasta is 4.1 mm y^{-1} (Houston and Hartley 2003), explaining the absence of freshwater inputs in the bay. The tidal regime in La Rinconada Bay is semi-diurnal with diurnal inequality, and a maximal tidal range of 1.5 m.

Although located in the tropical zone, the coastal area near Antofagasta is characterised by cool waters because of the influence of the Humboldt Current. Coastal seawater temperature is generally highest in December-January (20–21 °C) and lowest in August-September (14–15 °C). This area is also subject to upwelling events throughout the year generating intermittent cold pulses in the seawater temperature seasonal cycle (Escribaño et al. 1995). Five water masses have been described off Northern Chile between Arica (18.5°S) and Coquimbo (30°S; see Sobarzo and Figueroa 2001 for a complete review). Between 0 and 75 m depth, the water mass near Antofagasta in "normal" conditions is the Subtropical Surface Water (SSW), characterised by temperature between 16 and 24 °C, salinity

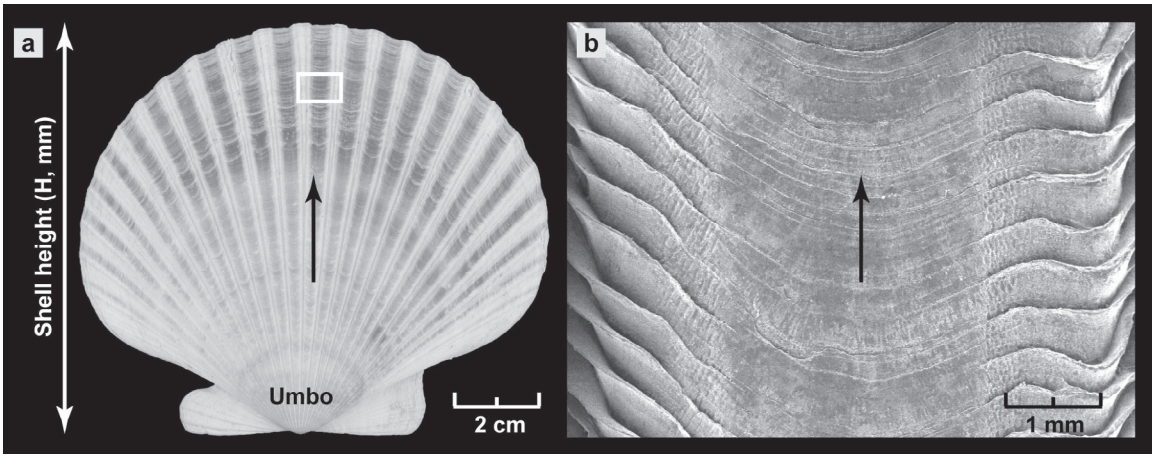

Fig. 1. (a) External view of the right valve of *Argopecten purpuratus*. The maximal growth axis is indicated by the black arrow. (b) Image (scanning electron microscopy) of daily striae taken along the maximal growth axis. Between-striae distances can be measured to reconstruct individual growth curves. Growth direction is indicated by the black arrow.

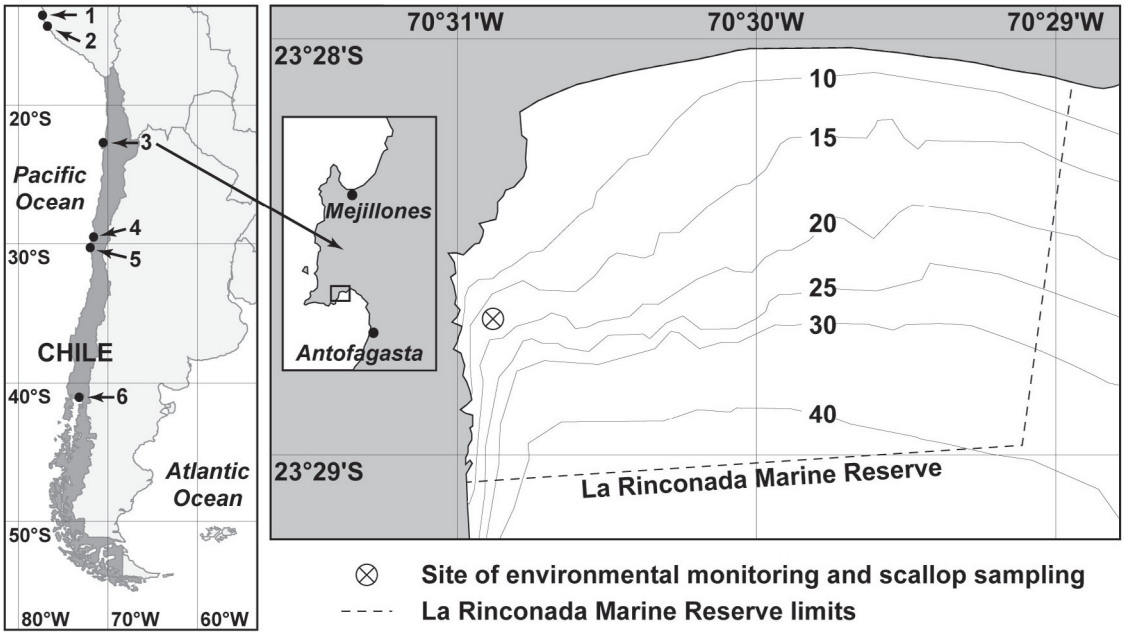

Fig. 2. Map of Chile and neighbouring countries, showing the locations where this study and previously published ones dealing with *Argopecten purpuratus* shell growth (see Table 1) were conducted. Peru: 1- Paracas Bay, 2- Tunga and Independance Bay; Chile: 3- Mejillones Pensinsula and La Rinconada Bay, 4- Herradura Bay, 5- Puerto Aldea, 6- Metri Bay. La Rinconada Marine Reserve is located in the northwestern part of La Rinconada Bay, an open bay south of the Mejillones Peninsula, near the city of Antofagasta (2nd Region of Chile).

between 34.9 and 35.3, and dissolved oxygen concentration between 6.4 and 7.9 mg L^{-1} (Silva and Konow 1975). The coastal upwelling brings Subantarctic Water (SAAW, located between 75 and 125 m depth) and Equatorial Subsurface Water (ESSW, located between 150 and 350 m depth) to the surface; the relative proportions of these two water masses depend on the strength of the upwelling (Sobarzo and Figueroa 2001). Given their physical characteristics, these two water masses will have different effects on La Rinconada Bay waters. SAAW will cause cooling, a weak salinity decrease and an increase in dissolved oxygen content throughout the water column (7.1–10.0 mg L^{-1}), whereas ESSW will induce greater cooling, a weaker salinity decrease, and an important decrease in dissolved oxygen content (0.3–4.3 mg L^{-1}; Sobarzo and Figueroa 2001). Finally, two cold (temperature < 6.5 °C) water masses, never upwelled, are found in the deeper water: Antarctic Intermediate Water (AIW) in the intermediate layer between 400 and 1000 m depth, and Pacific Deep Water (PDW) below 1000 m.

2.2 Environmental parameters

From February to October 1999, bottom water temperature was recorded daily within the Marine Reserve at a depth of 16 m. Bottom water salinity, chlorophyll *a*,

phytoplankton cell concentration, particulate organic carbon (POC) and dissolved oxygen concentrations were measured about twice a month during the study period, at the same location as the temperature recording. The mean Southern Oscillation Index (SOI) was calculated between February and October 1999, with monthly SOI provided by the Australian Governments' Bureau of Meteorology (www.bom.gov.au/climate/current/soihtm1.shtml). The SOI is calculated from monthly fluctuations in the air pressure difference between Tahiti (French Polynesia) and Darwin (Australia). Negative values of the SOI correspond to El Niño episodes whereas positive values signify La Niña events. In order to determine whether the ENSO phenomenon had an effect on shell growth, mean SOI was also calculated for seven previously published experiments dealing with *A. purpuratus* shell growth on the seabed (Wolff 1987; Mendo and Jurado 1993; Stotz and González 1997; Avendaño and Cantillánez 2005; see also Table 1).

2.3 Shell growth analysis and modelling

Six live adult scallops (mean shell height 95 mm, s.d. 3.7 mm) were collected by SCUBA divers on 15 October 1999 at 19.6 m depth, near the environmental monitoring site. Before analysis, right valves (Fig. 1a) were cleaned by soaking in acetic acid for 1 min to remove biofouling and then rinsed with distilled water and air dried. An estimate of daily shell growth rate was made for each shell by measuring distances between successive daily striae (Fig. 1b) using an image analysis technique described in detail by Chauvaud et al. (1998). Individual growth curves were used to build a mean shell growth curve for *A. purpuratus* in La Rinconada Marine Reserve. Daily growth rates are expressed in μm d^{-1}.

For all 6 specimens, it was impossible to estimate daily growth rates for portions of the shells accreted near the umbo because of striae abrasion. Therefore, this study reconstructed the mean daily growth curve for shells between 20 and 95 mm shell height. The spat data of Cantillánez (2000), obtained in collectors immersed on 16 January 1999 at 16 m depth at our sampling site, were used to reconstruct the *A. purpuratus* shell growth curve from 0.29 mm (i.e. 1 or 2 days after settlement) to 20 mm. The juxtaposition of the two datasets (0.29–20 mm and 20–95 mm) allowed reconstructing the mean daily shell growth curve of *A. purpuratus* in La Rinconada Marine Reserve beginning with settlement on the seabed.

A generalized von Bertalanffy growth function (gVBGF) was fitted to the resulting 268 size-at-age data pairs (shell height in mm – age in year) by an iterative nonlinear least-square method (Newton algorithm; see Brey 2001 for details):

$$H_t = H_\infty \left(1 - \mathrm{e}^{-K(t-t_0)}\right)^D \quad (1)$$

where H_t is shell height (mm) at time t (y), H_∞ is mean asymptotic shell height (mm), K is the Brody growth coefficient (y^{-1}), D determines the shape of the curve (inflection point if $D > 1$), and t_0 is the age (y) when shell height equals zero. Previous studies dealing with *A. purpuratus* described shell growth using a specialized von Bertalanffy growth function (sVBGF). Therefore, for comparison purpose, a sVBGF was also fitted to our size-at-age dataset using Newton algorithm:

$$H_t = H_\infty \left(1 - \mathrm{e}^{-K(t-t_0)}\right). \quad (2)$$

The shape of *A. purpuratus* growth curve was found to be strongly sigmoid so that fitting it with a sVBGF resulted in unrealistic K and H_∞ values. Therefore, the sVBGF was fitted only on the second part of the growth curve (shell height 20–95 mm), thus avoiding the early stages of development of *A. purpuratus* which made the curve sigmoid. H_∞ of the sVBGF was calculated from the gVBGF (Brey 2001).

A direct comparison of growth patterns calculated in previous studies using the two parameters K and H_∞ alone may be mathematically feasible but is not plausible biologically, as K is negatively correlated with H_∞. Several attempts have been made to solve this problem but Pauly (1979) was the first to develop a consistent concept of "Overall Growth Performance" (OGP) to make individual growth comparable. Pauly and Munro (1984) later introduced a closely related index of OGP (ϕ') which is derived from the sVBGF:

$$\phi' = \log K + 2\log(0.1 \times H_\infty) \quad (3)$$

where K is in y^{-1} and H_∞ in mm.

2.4 Statistical analysis

Spectral analysis (Fast Fourier Transformation) was performed on the mean daily shell growth rate profile in order to identify the existence of periodicities in the growth signal. Multiple forward stepwise regression analysis was performed to determine the influence of environmental forcing on the shell growth rate of *A. purpuratus* in 1999. Before performing this analysis, Pearson correlation coefficients were calculated to check multicolinearity between environmental variables ($\alpha = 0.05$). This analysis led us to exclude phytoplankton cell and dissolved oxygen concentrations from the regression analysis. Linear regression and ANOVA were also performed between the OGP indices of all studies dealing with the growth of *A. purpuratus* on the seabed, including this one, and the mean SOI during each of these studies. Statistical analyses were performed using Statistica software.

3 Results

3.1 Environmental parameters

From February to October 1999, bottom water temperature ranged from 13.4 °C to 20.4 °C (Fig. 3a), but no seasonal cycle could be identified. High-frequency variability was strong (e.g., a 4.5 °C drop between 7 and 9 March, for measurements done at the same hour). Salinity was relatively constant, ranging from 34.43 to 34.72 (Fig. 3b). Lowest values were recorded in February, April-May and at the end of August. Dissolved oxygen concentration in bottom water was variable, ranging from 1.69 mg L^{-1} to 7.47 mg L^{-1} (Fig. 3c). Important decreases were recorded in April, June and at the beginning of October.

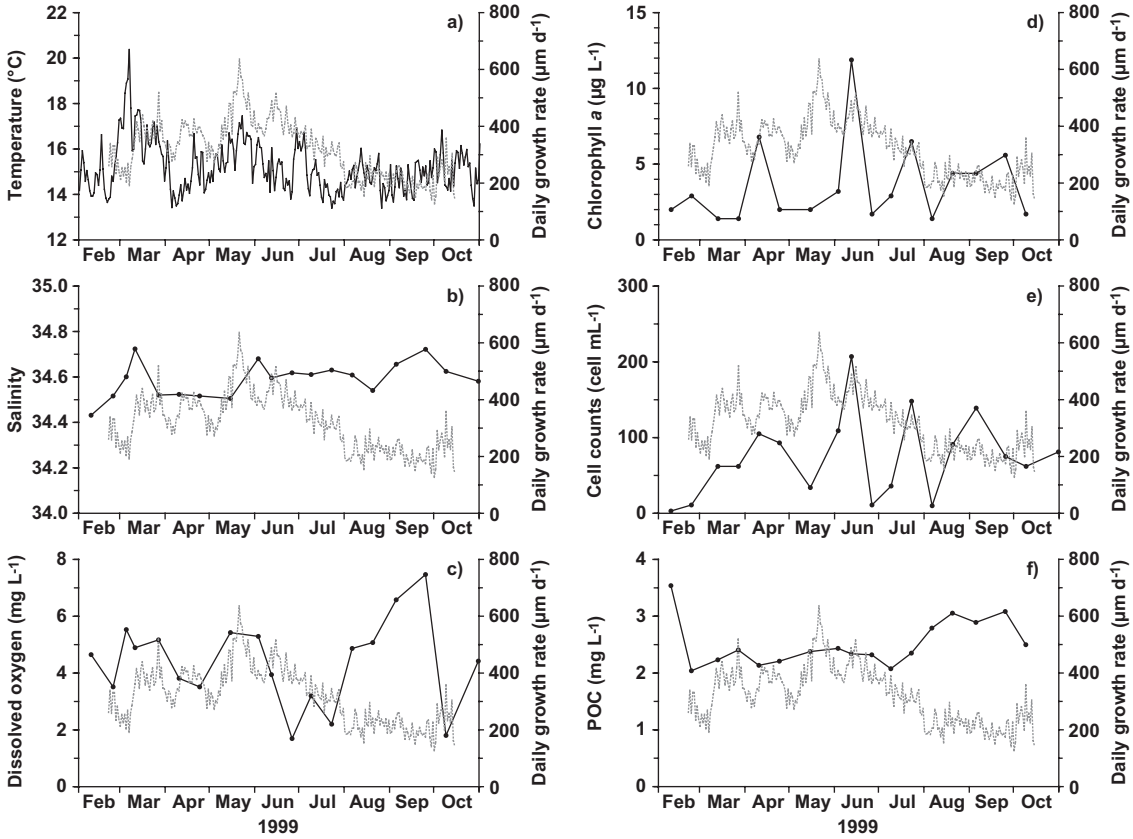

Fig. 3. Temporal variations of (a) temperature, (b) salinity, (c) dissolved oxygen concentration, (d) chlorophyll *a* concentration, (e) phytoplankton cell concentration and (f) particulate organic carbon (POC) concentration in bottom water (16 m depth) from February to October 1999. For comparison purposes, mean daily shell growth rate is superimposed on each graph (dotted grey line).

Phytoplankton blooms occurred all year long. Chlorophyll *a* concentration varied from 1.4 to 11.9 μg L^{-1} (Fig. 3d). Maximum values were measured on 10 April, 12 June and 23 July. Phytoplankton cell concentration followed a similar pattern to chlorophyll *a*, with the maximum concentration measured on 12 June (207 cell mL^{-1}; Fig. 3e). Diatoms were dominant overall, while toxic dinoflagellates were scarce (Cantillánez, unpubl.). Particulate organic carbon (POC) concentration (Fig. 3f) was high (3.54 mg L^{-1}) in early February, then it dropped at the end of this month (2.04 mg L^{-1}). From March to July, the POC concentration was mostly constant (~2.25 mg L^{-1}). From mid-July to mid-August, it increased and was about 3 mg L^{-1} until the end of September. It dropped again to 2.5 mg L^{-1} on 9 October.

Two spring tides occurred each synodic month (interval between two successive New Moon phases) from February to late October 1999. The tidal amplitude at each New Moon phase was greater than the one during the immediate preceding or following Full Moon phase. These spring tides occurred on 18 March, 18 April, 17 May, 15 June, 14 July, 11 August and 9 September 1999.

3.2 *Argopecten purpuratus* shell growth

Individual growth profiles of the six specimens presented similar shell growth rate variations from February to October 1999, allowing us to build a mean daily shell growth rate profile (February-October average relative standard deviation = 29%; Fig. 4). A succession of increases and decreases of the shell growth rate, particularly obvious from February to June, was observed for the year 1999. From mid-February to the beginning of March, the daily shell growth rate dropped from 300 to 200 μm d^{-1}. A sharp increase up to ~400 μm d^{-1} occurred within the first week of March. This increase was the first of four peaks in growth between early March and late June, leading to maximum growth rates in the 3rd week of May (640 μm d^{-1} on 21 May). There was a trend of increasing growth rate from the 1st to the 3rd growth event, while the mean growth rate was lower during the 4th event (450–500 μm d^{-1} in mid-June). The mean shell growth rate progressively decreased after the 4th event until 200 μm d^{-1} was observed on the day specimens were collected. The maximum of each of the four largest peaks in growth always occurred around spring tides of New Moon phases (Fig. 4). Moreover, the spectral analysis indicated that the mean daily shell growth rate profile exhibited a periodic oscillation with a wave-length of 31.6 days (Fig. 4).

A. purpuratus shell growth was best fitted by a gVBGF (Fig. 5):

$$H_t = 117 \times \left(1 - e^{-3.42(t+1.163)}\right)^{260.5} \quad r^2 = 0.9987. \qquad (4)$$

Table 1. Von Bertalanffy growth parameters (sVBGF), overall growth performance index (ϕ'), Southern Oscillation Index (SOI), and age at minimum catch size (90 mm) in various studies of *Argopecten purpuratus* shell growth along the Peruvian and Chilean coasts.

Study site	Study period	K (y^{-1})	H_∞ (mm)	ϕ' [a]	Age at 90 mm (months)	Mean SOI [c]	Origin of samples	Method	Authors
Paracas Bay, 13.7°	Apr. 1983 - Mar. 1984	2.02	95	2.26	17-18 [b]	−0.57	Off-bottom cages	Fortnightly measurements	Wolff 1987
-	May 1983 - Mar. 1984	2.68	95	2.38	13-14 [b]	0.93	-	-	-
-	Mar. 1983 - Mar. 1984	1.99	99.2	2.29	14-15 [b]	−2.68	Natural bank	Mark-and-recovery	-
-	May 1983 - Aug. 1983	1.26	110	2.18	16-17 [b]	−1.15	-	Length-frequency analysis	-
-	Jun. 1983 - Jan. 1984	2.10	111.5	2.42	9-10 [b]	0.53	-	-	-
-	Apr. 1983 - Aug. 1983	ND	112	ND	6-7 [b]	−4.32	-	-	Mendo and Jurado 1993
-	Feb. 1984 - Sept. 1984	2.10	95.4	2.28	16-17 [b]	−0.01	Bottom culture	Length-frequency analysis	-
Independance Bay, 14.2°S	Sept. 1987 - Sept. 1988	2.25	94.3	2.30	16-17 [b]	1.90	Lantern nets	Biannual measurements	-
Tunga, 14.2°S	Sept. 1987 - Mar. 1988	0.57	110	1.84	35-36 [b]	−3.77	Natural bank	Length-frequency analysis	-
Rinconada Bay, 23.3°S	Apr. 2001 - Apr. 2002	0.97	120.4	2.15	17.2	−1.52	-	Mark-and-recovery	Avendaño and Cantillánez 2005
-	Feb. 1999 - Oct. 1999	2.24	117	2.48	10-11	5.99	-	Striae analysis	Thébault et al. (this study)
Herradura Bay, 29.6°S	Jul. 1987 - Jun. 1988	0.35	220	2.23	18	−4.52	Pearl nets	Monthly measurements	Wolff and Garrido 1991
Puerto Aldea, 30.2°	Aug. 1992 - Nov. 1994	ND	ND	ND	18	−9.75	Natural bank	Length-frequency analysis	Stotz and González 1997
-	Dec. 1994 - Mar. 1995	0.84	124.6	2.12	18-19 [b]	−3.70	-	Mark-and-recovery	-
Metri Bay, 41.4°S	Jul. 1996 - Dec. 1997	ND	ND	ND	16-21	−6.13	Lantern nets	Bimonthly measurments	Gonzalez et al. 1999

[a] ϕ': "Overall Growth Performance" index (Pauly and Munro 1984). $\phi' = \log K + 2\log(0.1 \times H_\infty)$.
[b] Age at minimum catch size (MCS = 90 mm) estimated using sVBGF and the growth parameters cited (K and H_∞).
[c] Mean Southern Oscillation Index calculated on the study period with the data of the Bureau of Meteorology (Australia).
ND: no data.

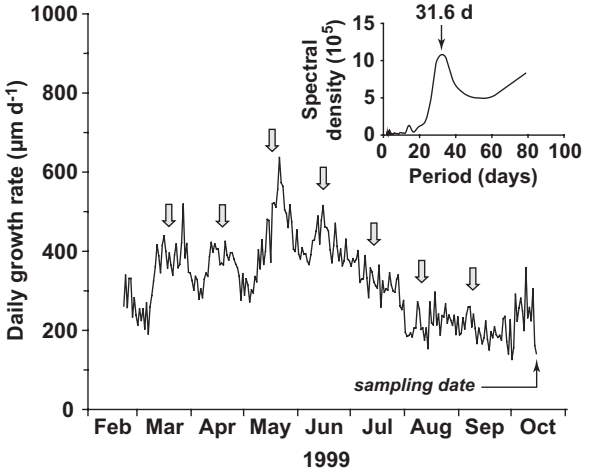

Fig. 4. Mean daily shell growth rate (μm d^{-1}) of *Argopecten purpuratus* in 1999 (n = 6). All six scallops were sampled alive by SCUBA divers on 15 October 1999 (see Fig. 2 for scallop sampling site). Arrows indicate highest spring tides (New Moon phases). Inlet: spectral analysis performed on the mean daily shell growth profile, highlighting a 31.6-day periodicity in the shell growth signal.

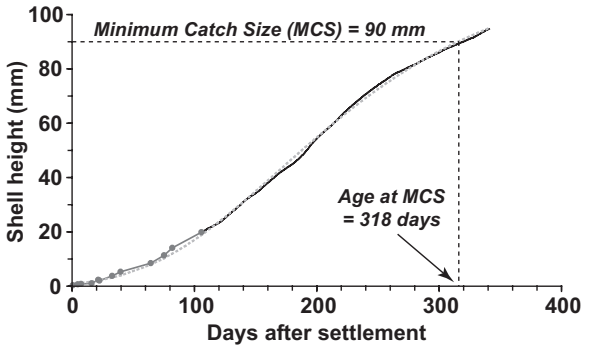

Fig. 5. Shell growth curve of *Argopecten purpuratus* in La Rinconada Bay in 1999. This curve was built from the post-larvae growth data of Cantillánez (2000; plain grey circles, 0–20 mm) and from the growth data of the six scallops sampled on 15 October 1999 (plain black line, 20–95 mm). Also represented is the gVBGF fitted to these size-at-age data pairs (dotted grey line). A 90-mm scallop, the minimum catch size (MCS), is about 318 days old.

The minimum catch size in Chile (MCS = 90 mm) would be reached after ~318 days according to this fit. An sVBGF was also fitted to our size-at-age data for comparison with previous studies, with H_∞ fixed to 117 mm (r^2 = 0.987). We found K = 2.24 y^{-1} and ϕ' = 2.48.

3.3 Environmental forcing on shell growth

Shell growth rate was significantly influenced by POC concentration (negative relationship) and temperature (positive relationship) in 1999 (multiple linear regression: r^2 = 0.5682; $p < 0.05$; Table 2), but not by salinity and chlorophyll *a* concentration variations. A significant positive relationship was also found between SOI and ϕ' ($p < 0.05$, Fig. 6) calculated

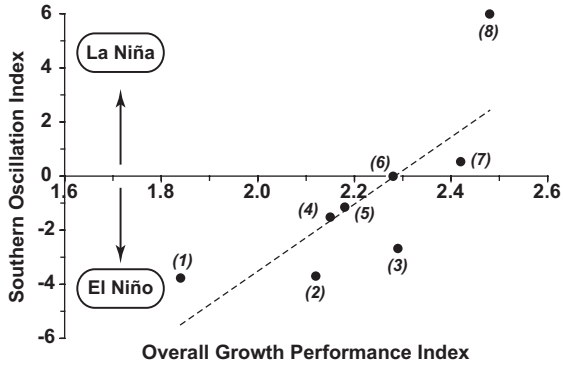

Fig. 6. Influence of the ENSO phenomenon (defined by the Southern Oscillation Index) on shell growth of *Argopecten purpuratus* on the seabed (defined by the OGP index; Pauly and Munro 1984). Data sources: (1) Tunga 1987-1988, (2) Puerto Aldea 1994–1995, (3) Paracas Bay 1983-1984, (4) La Rinconada Bay 2001-2002, (5) Paracas Bay 1983, (6) Paracas Bay 1984, (7) Paracas Bay 1983-1984, (8) La Rinconada Bay 1999.

for studies dealing with *A. purpuratus* growth on the seabed, emphasizing the influence of ENSO events on shell growth:

$$\mathrm{SOI} = -28.3 + 12.4\phi' \quad r^2 = 0.6077. \tag{5}$$

4 Discussion

4.1 Environmental variability in 1999

La Rinconada Bay, located in an area significantly impacted by ENSO events, was under the influence of La Niña in 1999 (SOI > 0; Table 1). Cantillánez et al. (2005) already highlighted the strength of this event in the bay via seawater temperature measurements (1996-2000). Temperatures below 14 °C were frequent during this cold-water episode, which started in April 1998, while annual temperature patterns in 1998 and 1999 showed no clear seasonal trends and lacked well-defined summers (see Fig. 3 in Cantillánez et al. 2005).

The La Niña event induced an intensification of cold-water upwelling episodes near shore. In February and at the beginning of April 1999, the seawater temperature, salinity and dissolved oxygen content, lower than in normal conditions, indicated two ESSW upwelling periods (Fig. 3). These nutrient-rich waters sustained the development of two phytoplankton blooms (on 23 February and 10 April). In June, decreases of temperature, salinity and especially dissolved oxygen content (down to 1.69 mg L^{-1}) indicated a third strong upwelling of ESSW (Fig. 3). The associated nutrient concentration increases sustained a major phytoplankton bloom on 12 June (11.9 μg L^{-1}). This upwelling event lasted until the end of July; the increase of temperature and oxygen concentration observed at the beginning of July was probably due to a weakening of the upwelling which strengthened again at the end of July before it collapsed. The phytoplankton bloom observed in July (6.5 μg L^{-1}; Fig. 3) was made of smaller cells (e.g., no *Chaetoceros* spp.) including more dinoflagellates (especially *Protoperidinium divergens*), compared with the June bloom

Table 2. Results of multiple stepwise regression analysis performed between shell growth rate and bottom-water environmental factors (forward procedure).

Model fitting results			Analysis of variance					r^2 "step by step" (%)
Environmental parameter	Coefficient	*p*-value	Source	Sum of square	*df*	*F*-ratio	*p*-value	
POC	−197.95	0.0035	Model	86 033	2	8.55	0.0043	39.92
Temperature	37.59	0.0420	Error	65 391	13			56.82
Constant term	266.60	0.3642						

(Cantillánez, unpubl.). From late August to late September, the important increase of dissolved oxygen concentration (up to 7.47 mg L^{-1}) highlighted a return to "normal" conditions with SSW in La Rinconada Bay (Fig. 3). SSW was sufficiently rich in nutrients to sustain another phytoplankton bloom ([Chl *a*] > 4 μg L^{-1}). At the beginning of October, the sharp decrease of dissolved oxygen content (down to 1.8 mg L^{-1}) and the weak decrease of salinity highlighted a strong upwelling of ESSW (Fig. 3). Unfortunately, the lack of pigment data in October precluded quantification of the associated pelagic primary production.

To summarize, four main periods of upwelling conditions were identified in 1999: two weak (February and April) and two strong (June-July and October) upwellings of ESSW. These results agree with the observations of Morales et al. (1996) who found that ESSW was the main source of upwelled water in the region off Northern Chile. In the following sections the effects of hydrological variability on scallop shell growth are discussed.

4.2 Environmental forcings regulating *Argopecten purpuratus* shell growth

Although performed on a limited dataset, the regression analysis showed that shell growth rate was significantly influenced by bottom-water temperature (positive relationship) and POC concentration (negative relationship). Temperature has often been described as one of the main factors controlling scallop growth (Broom and Mason 1978; Wilson 1987; Wolff 1987; Thouzeau 1991a; Thouzeau 1991b; Mendo and Jurado 1993; Chauvaud et al. 1998; González et al. 1999; Laing 2000; González et al. 2002). An increase in growth rate with temperature would be the result of an increase in metabolic rate, provided enough food is available (Broom and Mason 1978). It should be noted, however, that growth can be affected when water temperature approaches the upper thermal tolerance limit of the species, e.g. during strong El Niño events such as in 1982-83 (Urban 1994). Such a negative influence of high temperatures on shell growth has already been highlighted in the marine bivalve *Phacosoma japonicum* (see Fig. 8a in Schöne et al. 2003). The negative relationship observed between shell growth rate and POC concentration may be related to the shift observed in July, when POC concentration showed a 50% increase at the same time as a rapid decrease in shell growth rate. The latter, however, is probably related to scallop aging (ontogenetic decrease) more than to environmental forcings. Nevertheless, we cannot exclude that POC concentration might be stressful for scallops above a threshold of ~2.5 mg L^{-1}. Indeed, the negative effect of sedimentation of high amounts of particles has also been observed for *P. maximus* (Chauvaud et al. 1998; Lorrain et al. 2000; Chauvaud et al. 2001). These authors assumed that, at the end of large diatom blooms (over 5 μg Chl *a* L^{-1}; Lorrain et al. 2000), sinking aggregates of scenescent diatoms either (1) led to gill clogging, stopping scallops from ingesting food, or (2) created oxygen depletion at the sediment-water interface, thus altering scallop respiration and growth. Finally, it should be noted that, except for two major spawning events in February and late October 1999, reproductive activity in La Rinconada population was quite low during our study period (Fig. 3 in Cantillánez et al. 2005); therefore, variability of daily shell growth rates cannot be related to gametogenesis or spawnings.

Our study also highlighted a 31.6-day periodicity in the variations of daily shell growth rate (Fig. 4). In the plant and animal kingdoms, rhythmic activities are generally assumed to be controlled by endogenous oscillators, synchronized by environmental cues acting as zeitgebers ("time givers" in German; Aschoff et al. 1982). In marine bivalves, diurnal, tidal and seasonal cycles are known to be responsible for growth rhythms as a result of changes in environmental factors (Rosenberg and Jones 1975). This 31.6-day periodicity is very close to the 29.5-day cycle describing the synodic month. Therefore, we hypothesise that the synodic-month periodicity might be expressed in the variations of daily shell growth rate of *A. purpuratus*, the small difference (7%) between these two periodicities coming probably from the limited size of the dataset used to perform the Fast Fourier Transformation (n = 268 size-at-age data pairs). This influence of the lunar cycle on shell growth seems particularly obvious for juvenile scallops: from early March to late June 1999, maximal growth rate periods (middle of the four peaks in growth) occurred during the highest spring tides, i.e. at New Moon phases. The influence of the synodic month on bivalve growth was previously demonstrated for the Northern Quahog *Mercenaria mercenaria* (Pannella and MacClintock 1968; Kennish and Olsson 1975). Schöne et al. (2003) also highlighted that within a 2-week cycle, the width of lunar daily growth increments (LDGIs; formed with a 24.8h periodicity) in the shell of the bivalve *Phacosoma japonicum* is largest during the spring-tide cycle versus during the neap-tide cycle. In their study, however, the width of LDGIs was comparable at New Moon and Full Moon phases. The likely expression of the synodic month cycle in *A. purpuratus* shell growth still remains unexplained; it may be interesting to record the hydrostatic pressure variations on the seabed during

a synodic month cycle to check if they are in phase with shell growth rate variations.

A. purpuratus shell growth can thus be divided into two periods. The first one, from February to July, during the major growth episode (increasing mean growth rate overall), was mainly governed by temperature. POC ensured a baseline food supply for scallops. The variations of the daily shell growth rate might have been also partly controlled by the synodic-month cycle, which perhaps acted as a zeitgeber synchronizing an endogenous oscillator. The second phase (July-October) was primarily governed by endogenous factors (ontogenetic decrease in shell growth rate as scallops grow older). However, an increase in POC concentration above a threshold around 2.5 mg L^{-1} might have further reduced growth.

4.3 Scallop growth performance in La Rinconada Marine Reserve

Our sclerochronological approach led us to estimate that the age at minimum catch size (MCS) was about 10–11 months in La Rinconada Marine Reserve in 1999. This value is lower than those calculated in a number of previous studies within *A. purpuratus*'s latitudinal range (Table 1). Four reasons can explain this discrepancy:

• Differences may be due to the methodological biases of the various methods used to estimate shell growth (striae analysis, length-frequency analysis, mark-and-recovery experiments, or regular measurements of shell height of a given batch of scallops; see Table 1). Length-frequency data may be difficult to interpret, particularly for slow-growing adult specimens; in addition, cohort analysis is more difficult when organisms spawn all year long (Cantillánez et al. 2005). On the other hand, regular shell height measurements with a calliper can break the shell at the ventral margin, where newly-formed calcite is very thin, and thus disturb shell growth for several days. This bias has already been pointed out for other scallop species, including *Chlamys (Aequipecten) opercularis* (Broom and Mason 1978) and *Comptopallium radula* (Thébault et al. 2006). It should finally be mentioned that striae analysis is not suitable for early growth estimates because of striae abrasion near the umbo.

• Growth rates may be very different between the seabed and suspended culture devices (pearl nets, lantern nets, and off-bottom cages). Some studies pointed out that scallop shell growth rate could be increased in suspended culture (Wallace and Reinsnes 1985; Mendo and Jurado 1993; Mendoza et al. 2003), but other ones showed the limits of these rearing methods. González et al. (1999) found higher growth rates for *A. purpuratus* cultured in small pockets (1 scallop per pocket) compared with lantern nets (25 scallops per lantern net), highlighting a density-dependent effect. Higher growth rates were observed on the seabed than in suspended cultures by Kleinman et al. (1996) for *Placopecten magellanicus* in Canada and by Vélez et al. (1995) for *Euvola ziczac* in Venezuela. These differences may come from the autoecology of the species (e.g. the stress experienced by individuals of burying species being suspended), from food availability, or from the negative effect of shell epibionts on growth. The latter effect is less important on the seabed because scallops can bury partly in the sediment and thus expose a smaller area of the shell to biofoulers (Vélez et al. 1995; Lodeiros and Himmelman 2000). The examination of Wolff's results (1987) confirms the hypothesis of higher shell growth on the seabed compared with suspended cultures: over the same period, with similar environmental forcing (May 1983 – March 1984, mean SOI = 0.93; June 1983 – January 1984, mean SOI = 0.53), the age at MCS in Paracas Bay was reached 4 months earlier by specimens growing on the seabed than by those growing in off-bottom cages (Table 1).

• Climatic conditions during the studies, particularly the occurrence of El Niño or La Niña events, do influence shell growth rate. A significant relationship was found between the mean SOI and OGP indices calculated for different scallop populations in this study (Fig. 6), with better growth performances during La Niña than during El Niño events. This relationship may be due to the important water temperature increase (far above the highest temperatures recorded in "normal" conditions) and to the decline in coastal upwelling during El Niño. Indeed, increasing temperatures associated with El Niño are known to increase reproductive activity (Wolff 1987; Cantillánez et al. 2005) probably at the expense of somatic growth and more strongly at the expense of shell growth (Wolff 1987). Moreover, by bringing nutrients back to the surface, upwellings lead to the development of phytoplankton blooms, which are significant sources of organic carbon for scallops. During El Niño, food supply is strongly reduced because of the decline of coastal upwelling and the resultant decline in phytoplankton production. Therefore, taking into account that (1) under higher temperatures more metabolic energy is necessary, and (2) poor feeding conditions could increase the negative effect of high temperatures (Urban 1994), *A. pupuratus* shell growth may be significantly and negatively affected during El Niño events. We hypothesise that the presence of a very active upwelling zone around Antofagasta and the Peninsula of Mejillones (Sobarzo and Figueroa 2001) explains the high scallop shell growth rate calculated for La Rinconada Bay, compared with some of the previous studies.

• Finally, there may be a latitudinal gradient in *A. purpuratus* growth performance between the northern area of Pisco in Peru and the south of Chile (e.g. Metri Bay). Worldwide comparisons between species already highlighted that overall growth performances increase with decreasing latitude in scallops (Heilmayer et al. 2003). It was suggested that this trend is correlated with annual solar energy input and average annual water temperature. Between-species comparisons, however, probably do not reflect the more subtle differences between subpopulations of a given species in a latitudinal cline. Nevertheless, no latitudinal gradient in *A. purpuratus* growth performance can be highlighted from studies presented in Table 1, probably because they were performed in different years characterized by different environmental and meteorological forcings. The latter probably make it difficult to identify the effect of a latitudinal gradient on *A. purpuratus* shell growth.

5 Conclusion

This study concerning *A. purpuratus* shell growth provides new insights for the understanding of growth patterns in one of the main wild stocks of scallops on the southeast Pacific

coast (La Rinconada Bay). The sclerochronological approach appears as a powerful tool to characterise high-frequency variations in the shell growth of this species. This approach allowed us to conclude that temperature exerts a significant positive control on *A. purpuratus* shell growth in La Rinconada Marine Reserve. By contrast, an increase in POC concentration above a threshold of 2.5 mg L^{-1} might affect growth negatively. Our results also suggest that the lunar cycle might have an effect on juvenile scallop shell growth, strongly stimulated around New Moon phases which might act as zeitgebers synchronizing an endogenous oscillator.

This work on *A. purpuratus* growth is only the second one, following Avendaño and Cantillánez (2005), to estimate the age at commercial size in Northern Chile (the other ones were performed in Peru and in Central Chile). We found that the age at MCS in La Rinconada Marine Reserve (10–11 months) was lower than most of the other estimates calculated elsewhere. Different analytical methods, growth performance variations between on-bottom and suspended culture, and the ENSO phenomenon (strong La Niña event in 1999) may explain these results. Therefore, this study should be repeated in different areas with various environmental conditions and coincidently on the seabed and in suspended culture to confirm these trends. Nevertheless, our results highlight that La Rinconada Marine Reserve, probably due to the physical properties of the water masses around Antofagasta and the Peninsula of Mejillones (active upwelling zone), is a very favourable site for *A. purpuratus* growth. Together with the characteristics of the reproductive cycle in the bay (Cantillánez et al. 2005), this study confirms the strategic importance of this reserve as an area supporting scallop aquaculture activities in Chile and the repopulation of wild stocks to historic population levels.

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References

Antoine L., 1978, La croissance journalière chez *Pecten maximus* (L.) (Pectinidae, Bivalvia). Haliotis 9, 117–126.

Aschoff J., Daan S., Honma K.I., 1982, Zeitgeber, entrainment, and masking: some unsettled questions. In: Aschoff J., Daan S., Gross G.A. (Eds.) Vertebrate circadian system (structure and physiology), Berlin, Springer-Verlag, pp. 13–24.

Avendaño M., Cantillánez M., 1992, Colecta artificial de semilla de *A. purpuratus* (Lamarck, 1819) en la Bahia de Mejillones, Chile. II. Observaciones sobre niveles optimos de captacion. Estud. Oceanol. 11, 39–43.

Avendaño M., Cantillánez M., 2005, Growth and population structure of *Argopecten purpuratus* at La Rinconada Marine Reserve, Antofagasta, Chile. Cienc. Mar. 31, 491–503.

Brey T., 2001, Population dynamics in benthic invertebrates: A virtual handbook (version 1.2). Alfred Wegener Institute for Polar and Marine Research, Germany. http://www.awi-bremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/main.html (last access: December 19, 2007).

Broom M.J., Mason J., 1978, Growth and spawning in the pectinid *Chlamys opercularis* in relation to temperature and phytoplankton concentration. Mar. Biol. 47, 277–285.

Cantillánez M., Avendaño M., Thouzeau G., Le Pennec M., 2005, Reproductive cycle of *Argopecten purpuratus* (Bivalvia: Pectinidae) in La Rinconada marine reserve (Antofagasta, Chile): Response to environmental effects of El Niño and La Niña. Aquaculture 246, 181–195.

Chauvaud L., Thouzeau G., Paulet Y.-M., 1998, Effects of environmental factors on the daily growth rate of *Pecten maximus* juveniles in the Bay of Brest (France). J. Exp. Mar. Biol. Ecol. 227, 83–111.

Chauvaud L., Donval A., Thouzeau G., Paulet Y.-M., Nézan E., 2001, Variations in food intake of *Pecten maximus* (L.) from the Bay of Brest (France): Influence of environmental factors and phytoplankton species composition. C. R. Acad. Sci. III - Vie 324, 743–755.

Chauvaud L., Lorrain A., Dunbar R.B., Paulet Y.-M., Thouzeau G., Jean F., Guarini J.-M., Mucciarone D., 2005, Shell of the Great Scallop *Pecten maximus* as a high-frequency archive of paleoenvironmental changes. Geochem. Geophys. Geosyst. 6, doi:10.1029/2004GC000890.

Clark G.R., 1968, Mollusk shell: daily growth lines. Science 161, 800–802.

Clark G.R., 1975, Periodic growth and biological rhythms in experimentally grown bivalves. In: Rosenberg G.D., Runcorn S.K. (Eds.) Growth rhythms and the history of the earth's rotation, London, John Wiley & Sons, pp. 103–117.

Escribaño R., Rodríguez L., Irribarren C., 1995, Temporal variability of sea temperature in Bay of Antofagasta, northern Chile (1991-1995). Estud. Oceanol. 14, 39–47.

González M.L., López D.A., Pérez M.C., Riquelme V.A., Uribe J.M., Le Pennec M., 1999, Growth of the scallop, *Argopecten purpuratus* (Lamarck, 1819), in southern Chile. Aquaculture 175, 307–316.

González M.L., López D.A., Pérez M.C., Castro J.M., 2002, Effect of temperature on the scope for growth in juveniles scallops *Argopecten purpuratus* (Lamark, 1819). Aquac. Int. 10, 339–348.

Heilmayer O., Brey T., Chiantore M., Cattaneo-Vietti R., Arntz W.E., 2003, Age and productivity of the Antarctic scallop, *Adamussium colbecki*, in Terra Nova Bay (Ross Sea, Antarctica). J. Exp. Mar. Biol. Ecol. 288, 239–256.

Helm N.E., Malouf R.E., 1983, Rate of production of the external ridges in the bay scallop, *Argopecten irradians*. Am. Zool. 23, 835.

Houston J., Hartley A.J., 2003, The central Andean west-slope rainshadow and its potential contribution to the origin of hyper-aridity in the Atacama Desert. Int. J. Climatol. 23, 1453–1464.

Kennish M.J., Olsson R.K., 1975, Effects of thermal discharges on the microstructural growth of *Mercenaria mercenaria*. Environ. Geol. 1, 41–64.

Kleinman S., Hatcher B.G., Scheibling R.E., Taylor L.H., Hennigar A.W., 1996, Shell and tissue growth of juvenile sea scallops (*Placopecten magellanicus*) in suspended and bottom culture in Lunenburg Bay, Nova Scotia. Aquaculture 142, 75–97.

Laing I., 2000, Effect of temperature and ration on growth and condition of king scallop (*Pecten maximus*) spat. Aquaculture 183, 325–334.

Lodeiros C.J.M., Himmelman J.H., 2000, Identification of factors affecting growth and survival of the tropical scallop *Euvola (Pecten) ziczac* in the Golfo de Cariaco, Venezuela. Aquaculture 182, 91–114.

Lorrain A., Paulet Y.-M., Chauvaud L., Savoye N., Nézan E., Guérin L., 2000, Growth anomalies in *Pecten maximus* from coastal waters (Bay of Brest, France): relationship with diatom blooms. J. Mar. Biol. Assoc. UK 80, 667–673.

Mendo J., Jurado E., 1993, Length-based growth parameter estimates of the Peruvian scallop (*Argopecten purpuratus*). Fish. Res. 15, 357–367.

Mendoza Y., Freites L., Lodeiros C.J., López J.A., Himmelman J.H., 2003, Evaluation of biological and economical aspects of the culture of the scallop *Lyropecten (Nodipecten) nodosus* in suspended and bottom culture. Aquaculture 221, 207–219.

Morales C.E., Blanco J.L., Braun M., Reyes H., Silva N., 1996, Chlorophyll-*a* distribution and associated oceanographic conditions in the upwelling region off northern Chile during the winter and spring 1993. Deep-Sea Res. Part I 43, 267–289.

Navarro J.M., Leiva G.E., Martinez G., Aguilera C., 2000, Interactive effects of diet and temperature on the scope for growth of the scallop *Argopecten purpuratus* during reproductive conditioning. J. Exp. Mar. Biol. Ecol. 247, 67–83.

Pannella G., MacClintock C., 1968, Biological and environmental rhythms reflected in molluscan shell growth. J. Paleontol. 42, 64–80.

Pauly D., 1979, Gill size and temperature as governing factors in fish growth: a generalization of von Bertalanffy's growth formula. Ber. Inst. Meereskd. Christian-Albrechts-Univ. Kiel 63, 1–156.

Pauly D., Munro J.L., 1984, Once more on the comparison of growth in fish and invertebrates. Fishbyte 2, 21.

Rosenberg G.D., Jones C.B., 1975, Approaches to chemical periodicities in molluscs and stromatolites. In: Rosenberg G.D., Runcorn S.K. (Eds.) Growth rhythms and the history of the earth's rotation, London, John Wiley & Sons, pp. 223–242.

Schöne B.R., Tanabe K., Dettman D.L., Sato S., 2003, Environmental controls on shell growth rates and δ^{18}O of the shallow-marine bivalve mollusk *Phacosoma japonicum* in Japan. Mar. Biol. 142, 473–485.

Silva N., Konow D., 1975, Contribucion al conocimiento de las masas de agua en el Pacifico Sudoriental. Expedicion KRILL. Crucero 3-4 Julio-Agosto 1974. Rev. Comm. Perm. Pac. Sur 3, 63–75.

Sobarzo M., Figueroa D., 2001, The physical structure of a cold filament in a Chilean upwelling zone (Peninsula de Mejillones, Chile, 23˚S). Deep-Sea Res. Part I 48, 2699–2726.

Stotz W., 2000, When aquaculture restores and replaces an overfished stock: is the conservation of the species assured? The case of the scallop *Argopecten purpuratus* in northern Chile. Aquac. Int. 8, 237–247.

Stotz W., González S.A., 1997, Abundance, growth, and production of the sea scallop *Argopecten purpuratus* (Lamarck, 1819): bases for sustainable exploitation of natural scallop beds in north-central Chile. Fish. Res. 32, 173–183.

Thébault J., Chauvaud L., Clavier J., Fichez R., Morize E., 2006, Evidence of a 2-day periodicity of striae formation in the tropical scallop *Comptopallium radula* using calcein marking. Mar. Biol. 149, 257–267.

Thouzeau G., 1991a, Experimental collection of post-larvae of *Pecten maximus* (L.) and other benthic macrofaunal species, in the Bay of Saint-Brieuc. II - Reproduction patterns and post-larval growth of 5 mollusc species. J. Exp. Mar. Biol. Ecol. 148, 181–200.

Thouzeau G., 1991b, Déterminisme du pré-recrutement de *Pecten maximus* (L.) en baie de Saint-Brieuc: processus régulateurs de l'abondance, de la survie et de la croissance des post-larves et juvéniles. Aquat. Living Resour. 4, 77–99.

Thouzeau G., Robert G., Smith S.J., 1991, Spatial variability in distribution and growth of juvenile and adult sea scallops, *Placopecten magellanicus* (G.), on eastern Georges Bank (Northwest Atlantic). Mar. Ecol. Prog. Ser. 74, 205–218.

Urban H.-J., 1994, Upper temperature tolerance of ten bivalve species off Peru and Chile related to El Niño. Mar. Ecol. Prog. Ser. 107, 139–145.

Vélez A., Freites L., Himmelman J.H., Senior W., Marín N., 1995, Growth of the tropical scallop, *Euvola (Pecten) ziczac*, in bottom and suspended culture in the Golfo de Cariaco, Venezuela. Aquaculture 136, 257–276.

Wallace J.C., Reisnes T.G., 1985, The significance of various environmental parameters for growth of the iceland scallop, *Chlamys islandica* (Pectinidae), in hanging culture. Aquaculture 44, 229–242.

Wilson J.H., 1987, Environmental parameters controlling growth of *Ostrea edulis* L. and *Pecten maximus* L. in suspended culture. Aquaculture 64, 119–131.

Wolff M., 1987, Population dynamics of the peruvian scallop *Argopecten purpuratus* during the El Niño phenomenon of 1983. Can. J. Fish. Aquat. Sci. 44, 1684–1691.

Wolff M., Garrido J., 1991, Comparative study on growth and survival of two colour morphs of the chilean scallop *Argopecten purpuratus* (Lamarck, 1819) in suspended culture. J. Shellfish Res. 10, 47–53.

Wolff M., Mendo J., 2000, Management of the peruvian bay scallop (*Argopecten purpuratus*) metapopulation with regard to environmental change. Aquat. Conserv. Mar. Freshw. Ecosyst. 10, 117–126.

Wrenn S.L., 1972, Daily increment formation and synchronization in the shell of the bay scallop. Am. Zool. 12, 32.