Testing ecological and environmental changes during the last 6000 years: a multiproxy approach based on the bivalve *Tawera gayi* from southern South America

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This paper evaluates if the bivalve Tawera gayi *from southern South America represents an opportunity to test ecological variability and environmental changes during the last 6000 years in southern South America. For this purpose, we analyse both modern and fossil (mid-to-late Holocene)* T. gayi *shells from Tierra del Fuego using different techniques, including taphonomy, stable isotopes, cathodoluminiscence (CL) and linear morphometrics. Taphonomic analysis shows that differences between modern and fossil shells appear best related to local variations of physical factors such as current speed, wave action and freshwater input along the non-uniform Beagle Channel coast. However, slight changes of hydraulic energy regimes throughout the Holocene cannot be ruled out. The analysis of stable isotopes on* T. gayi *shells indicates a mixing of oceanic waters with freshwater from precipitation, river runoff and glacier meltwater during the mid-to-late Holocene. The high depletion of $\delta^{18}O$ at ~4400 years before present would be associated with a period of warmer temperatures, the so-called Hypsithermal. Under CL modern and fossil* T. gayi *shells show a well defined pattern related to the growth dynamics of the shell, which can lead to a better understanding of its biology, adding details to further palaeoenvironmental analysis. Finally, conventional metrics shows that fossil* T. gayi *shells are smaller and shorter than modern shells. These differences could be related to Holocene environmental changes, but here are best explained on the basis of a predator–prey relationship. This study shows that* T. gayi *may be a good candidate for looking at evidences of environmental changes in southern South America, and multi-proxy data are necessary to better understand the driving mechanisms of ecological variability and changes over short geological time intervals of few thousands of years.*

Keywords: *Tawera gayi*, Bivalvia, South America, taphonomy, stable isotopes, shell microstructure, shell shape, drill-holes

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INTRODUCTION

During the last years, the interest in using biogenic hard parts as ecological and environmental variables, and archives of past climate, has been reflected by a rapidly increasing number of publications and research groups focused on different types of conchological studies: i.e. groups devoted to the fields of sclerochronology (Dunca *et al.*, 2005; Schöne *et al.*, 2005; among many others), archaeomalacology (Claassen, 1998; Bar-Yosef Mayer, 2006) and actualistic taphonomy (Kowalewski & LaBarbera, 2004; and references therein).

This study evaluates if the marine bivalve *Tawera gayi* (Hupé in Gay, 1854) from Tierra del Fuego represents an opportunity to test ecological variability and environmental changes during the last 6000 years (mid-to-late Holocene) in southern South America. The choice of a target species (and not pooled species) was based on the possibility of eliminating differences in preservation among taxa, associated with shell properties, life habits and habitat. *Tawera gayi* was selected for this study because of two reasons: firstly, it has a thick and solid shell, and secondly, it is a common species in modern and mid-to-late Holocene assemblages (Gordillo, 1999; Lomovasky *et al.*, 2005).

Although with much smaller amplitude than the huge climatic oscillations which occurred during the Late Pleistocene, Holocene global and regional climatic variability can be reconstructed on the basis of multi-proxy data. In Tierra del Fuego, palaeoecological and stable isotope records from peat cores and marine terraces taken from different sites along the Beagle Channel have yielded valuable palaeoclimatic proxies (Heusser, 1998; Obelic *et al.*, 1998; Gordillo *et al.*, 2005; Borromei & Quattrocchio, 2007; Strelin *et al.*, 2008; Candel

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et al., 2009) which can be combined to illustrate an image of Holocene climate change in this region. Furthermore, considering the biases affecting fossil records, a wide range of tools is necessary to better understand the driving mechanisms of climate and environmental change during the Holocene. For this purpose, we analysed both fossil (mid-to-late Holocene) and modern *T. gayi* shells from this region using different techniques, including taphonomy, stable isotopes, cathodoluminiscence and linear morphometrics.

A taphonomic analysis allows death assemblages to be interpreted by observing the shell remains in the context of physical and biological processes; and a strong signal of the living community can be captured in the initial death assemblage stage of accumulating a fossil record (Kidwell & Bosence, 1991; Kidwell, 2002).

By using geochemistry, a more complete understanding of past climate and environmental conditions can be obtained from stable isotopes in conjunction with many other techniques (e.g. cathodoluminiscence and X-ray) as proxy evidence. On the one hand, skeletal carbonate oxygen ($\delta^{18}O$) and carbon ($\delta^{13}C$) isotopic compositions of shells are frequently used as a proxy of environmental factors such as temperature and productivity (Wang & Peng, 1990; Brand & McCarthy, 2005; Goman *et al.*, 2008; among many others). On the other hand, X-ray examination of shells gives information related to mineralogical composition, and cathodoluminiscence (CL) applied to recent benthic biogenic carbonates such as mollusc shells shows growth patterns (Barbin, 1992; Barbin & Gaspard, 1995). X-ray and CL analysis respectively can therefore be useful when comparing mineralogy and growth rates of fossil and modern organisms belonging to the same species.

In relation to shell morphology, changes in space and time need not be interpreted solely as a species-level phenomenon, but can and should be considered in a community or palaeo-community context, in which phenotypic variation between localities may represent a source of ecological information suitable for the evaluation of environmental changes. In a previous study, Gordillo *et al.* (2010) analysed the significance of the overall shell shape of *T. gayi* from different regions within the Magellan Region, concluding that morphological variability of this species is the product of both heredity and environmental conditions. Besides contour analysis, linear morphometrics applied to bivalves remains a potent tool for describing patterns of shell variation within species (e.g. Gordillo, 1995; Roy *et al.*, 2001; Laudien *et al.*, 2003).

In this paper we attempt to answer the following questions: (i) does the taphonomic analysis of *T. gayi* shells give information on physical changes between sites and/or through time?; (ii) can *T. gayi* shells be used as geochemical archives of palaeoenvironmental conditions during the last 6000 years?; and (iii) is morphometric analysis a palaeoenvironmental tool for discriminating between fossil and modern *T. gayi* shells from the Beagle Channel?

General characteristics of the studied area

The Strait of Magellan (53°36′S 68°–74°W; Figure 1) separates Patagonia from Tierra del Fuego. It was repeatedly occupied by outlet glaciers from an expanded southern Andean ice cap during successive Pleistocene glaciations (Porter *et al.*, 1992; Killian *et al.*, 2007). Today, the Strait of Magellan is dominated by an indented rocky shoreline and characterized by semi-diurnal and heterogeneous tides with mean amplitudes ranging from 1.2 m on the west coast to 9 m in the Atlantic inlet of the east coast (Andrade, 1991). In southern Tierra del Fuego, the Beagle Channel (54°53′S 67°–68°W; Figure 1) links the Atlantic and Pacific Oceans, thus separating Isla Grande de Tierra del Fuego from the southern islands of the Fuegian Archipelago. It is 180 km in length and was also covered during the Last Glacial Maximum (Rabassa *et al.*, 2000). Today, the Beagle Channel is dominated by an indented rocky shoreline, with pocket gravel beaches. Tides are semi-diurnal with average amplitudes of around one metre (e.g. 1.1 m at Ushuaia; Servicio de Hidrografía Naval, 1981).

Climatic fluctuations and sea level changes during the Holocene

In Tierra del Fuego, a variety of evidence indicates climatic fluctuations during the Holocene. One of the most significant palaeoclimatic events which took place during the Early to Middle Holocene was marine transgression (from ∼8000 to 4500 years BP), with a progressive decrease until the present level (Porter *et al.*, 1984; McCulloch *et al.*, 2005). The Holocene marine transgression is documented as marine terraces of different altitudes distributed along the coasts of the Strait of Magellan and the Beagle Channel (Gordillo *et al.*, 1992, 1993; Brambati *et al.*, 1998). The altitude of these terraces, ranging between 1 and 10 m above sea level (a.s.l.) is the result of a combination of tectonic, eustatic and isostatic factors (Porter *et al.*, 1984; Rabassa *et al.*, 1986, 2000; De Muro *et al.*, 2000; Brambati *et al.*, 1998).

In the marine realm, Obelic *et al.* (1998) recognized that sea temperature of the Beagle Channel in ∼6000 ^{14}C years BP was 1.5°C lower than the present one. After 5000 ^{14}C years BP, the seawater temperature in this channel shows a warming trend, with a maximum around 4500 ^{14}C years BP, and slightly warmer temperatures than at present (Obelic *et al.*, 1998). For this region, evidence based on diversification of mollusc taxa also supports the theory that the climate optimum took place ∼4500–4000 years BP (Gordillo *et al.*, 2005). After that, seawater temperature in this channel decreased again to a minimum around 3500 ^{14}C years BP, which would have been about 1°C below the present mean value, with another seawater temperature increase in the Beagle Channel shortly before 3000 ^{14}C years BP (Obelic *et al.*, 1998). Finally, during the Late Holocene, new cooling periods were recorded between 2000 and 900 ^{14}C years BP, and more recently between 400 and 100 ^{14}C years BP, in correlation with the Little Ice Age (Obelic *et al.*, 1998; Strelin *et al.*, 2008). The last 100 years interval was characterized by a clear temperature increase, with a last neoglacial event around 60 years BP (Strelin *et al.*, 2008). A water temperature reconstruction covering the last 6000 years, based on data obtained by Obelic *et al.* (1998), is shown in Figure 2.

MATERIALS AND METHODS

Both fossil and modern mollusc assemblages containing *T. gayi* shells were collected from several localities along the northern coast of the Beagle Channel and from two sites on the Strait of Magellan (Figure 1). Fossil *T. gayi* shells were
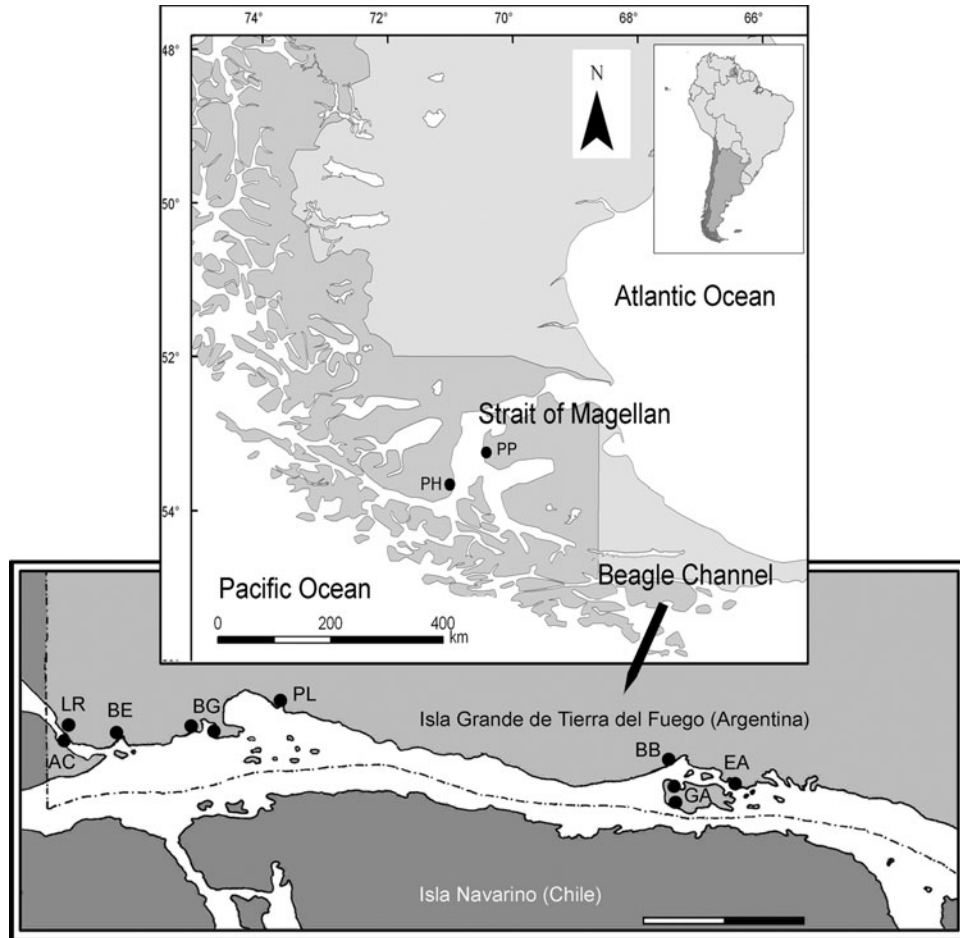
Fig. 1. Location map of Tierra del Fuego and a Beagle Channel sector showing localities considered in this paper. Abbreviations in Table 1.

taken from bulk sediment samples of ~500 cm³ coming from selected Holocene raised marine terraces, while modern shells were collected from the active beach and sampled using a 0.5 × 0.5 m quadrat (Table 1).

Taphonomic analysis was based on 981 individual *T. gayi* shells (201 modern and 780 fossil shells). The taphonomic features studied include the ratio of opposite valves, fragmentation, wear, encrustation, drilling and size-sorting.

The ratio of opposite valves refers to the number of left and right valves of *T. gayi* in each assemblage. This feature was analysed in seven fossil sites (Archipiélago Cormoranes × 3, Bahía Golondrina × 2, Punta Palo and Isla Gable) and in four modern sites (Bahía Golondrina × 4). The left/right ratio is useful for evaluating transport from the original community. An exact binomial test was used to assess if the proportion of left and right at each site differed from random distributions.

Fragmentation, wear, encrustation and drilling were evaluated on a three-grade scale from best preservation to poorest: good, fair and poor, following Kowalewski *et al.* (1995). The degree of taphonomic features for individual shells was studied in each sample, and was then averaged over the entire sample. These features and grades are displayed in Figure 3 and a brief description of the qualitative categories can be found in Table 2. Each taphonomic variable was analysed individually using ternary taphograms (Kowalewski *et al.*, 1995). These diagrams constitute a simple graphic technique that permits a rapid comparison of the taphonomic characteristics among samples (De Francesco & Hassan, 2008).

Fragmentation is associated with the breakage of shells and serves as a proxy of environmental energy. The degree of shell fragmentation tends to be highest in environments with high water turbulence and coarse substrates, such as beaches and tidal channels, as a consequence of impact with other shells, rocks and waves (Parsons & Brett, 1991), although it can also be influenced by ecological interactions, like shell-breaking predation or bioturbation (Zuschin *et al.*, 2003), and postmortem compaction (Klompmaker, 2009). *Tawera gayi* shells were classified as unbroken (Figure 3A), broken (up to ~30% missing; Figure 3B) or fragmented (more than ~30% missing; Figure 3C) shell.

Wear is related to abrasive agents, which produce the loss of surface ornamentation and shell details (Parsons & Brett, 1991). The three taphonomic grades of shells were: shell not abraded (Figure 3D); shell abraded (Figure 3E); and shell with internal layer exposed (Figure 3F).

Encrustation refers to organisms (e.g. epibionts) that use shells as substrate. *Tawera gayi* shells were classified as shells without encrustation (Figure 3G), shells with encrustation on the external surface only (Figure 3H), and shells with encrustation on the internal surface (Figure 3I).

Drilling predation is the result of a search for food by predator organisms (in this case drilling gastropods). These
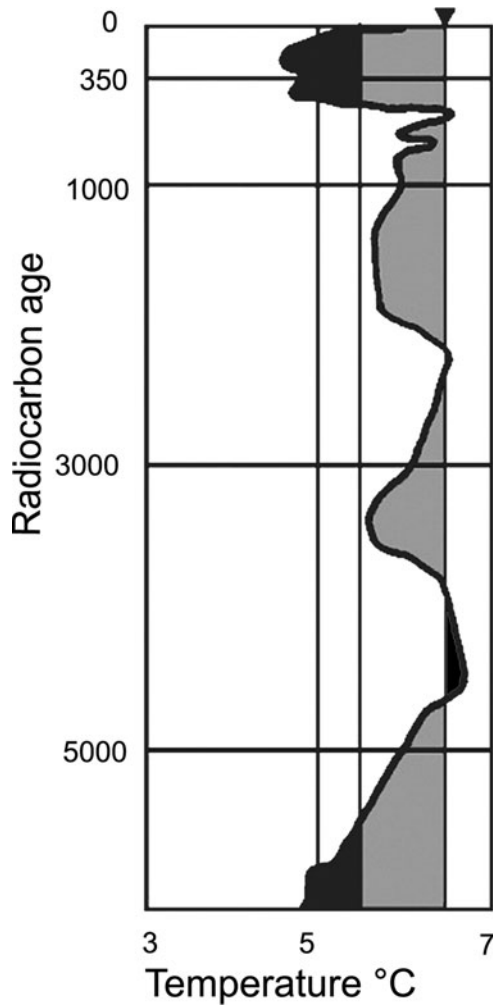
Fig. 2. Climatic fluctuations during the Middle–Late Holocene in the Beagle Channel. Data obtained by Obelic *et al.* (1998) and graphic reconstruction taken from Strelin *et al.* (2008).

borings are easily distinguished from others produced by clionid sponges or algae and fungal borings. The identification of drill-holes is based on previous works in this region (Gordillo, 1994, 1998). *Tawera gayi* shells were classified as unbored (undrilled) shells (Figure 3J), shells with one drill-hole or bored shells (Figure 3K), and shells with an incomplete drill-hole (Figure 3L). To test changes of drilling frequencies through time we compared values of drilling predation in modern assemblages from Bahía Golondrina, with fossil assemblages from Archipiélago Cormoranes corresponding to the mid-Holocene Hypsithermal interval (~4500–4000 years BP). To make this analysis comparable, the subsample AC-20 containing a large number of juvenile specimens was excluded. In each assemblage, the number of drilled valves was divided by the total number of valves (unbroken + less than 30% fragmentation). We included fragmented valves (less than 30%) because they also exhibit drill-holes. A *t*-test was used to assess if there were differences between the drilling frequencies of fossil and modern shells.

In relation to size sorting, although size is not a taphonomic attribute, size–frequency can indicate some taphonomic processes such as selection by hydrodynamic or aeolian processes. Sorting involves a systematic segregation

of shells, and size-sorted associations imply selective winnowing and transport of shells by currents in high energy settings (Speyer & Brett, 1988).

Carbon and oxygen isotopic analyses on modern and fossil *T. gayi* shells from the Beagle Channel were made at Instituto de Geocronología y Geología Isotópica (INGEIS, CONICET—Universidad de Buenos Aires). Ratios of isotopes are measured as relative deviations from a laboratory standard value. The standards (δ) employed here are PDB (Belemnite shell) for the analysis of carbonates and Standard Mean Ocean Water (SMOW) for the analysis of water. The isotope ratios are presented in pro mille (‰). High values of these parameters indicate the enrichment of oxygen or carbon in heavy isotopes, while the low values mark the depletion in heavy isotopes relative to the standards. The new values were compared with previous isotopic data by Panarello (1987) on *T. gayi* shells from the Beagle Channel. More details of $\delta^{18}O$ and $\delta^{13}C$ in carbonates of marine organisms can be found in Lowe & Walker (1997).

Concerning CL, one modern *T. gayi* shell from Bahía Golondrina and two other fossil *T. gayi* shells from Archipiélago Cormoranes (dated at 4425 years BP) and from Isla Gable (dated at 4790 years BP) were observed under CL. For this purpose, these shells were first air-dried and embedded in epoxy resin, and then sectioned along a plane perpendicular to the shell surface. A high sensitivity CL-microscope (hot cathode), which allows the observation of low-intensity luminescence was used for this study (instrument described in Ramseyer *et al.*, 1989).

Furthermore, to distinguish aragonite from calcite, the mineralogical composition of one modern (from Bahía Golondrina) and seven fossil *T. gayi* shells (from Lago Roca, Archipiélago Cormoranes, Bahía Golondrina, Ushuaia, Bahía Brown, Isla Gable and Estancia Harberton) were also observed by X-ray diffraction. This analysis was performed at the INGEIS, using the technique described in Do Campo (1991).

Finally, for conventional morphometric analysis, two linear distances, shell length and shell height, were measured with a caliper in 304 unbroken *T. gayi* shells (194 modern and 110 fossil shells). Only fossil shells from Archipiélago Cormoranes previously dated in ~4500–4000 years were used for this analysis. The height/length ratio was used as a proxy for shape. Differences in size and height/length ratio between modern and fossil shells were evaluated with a non-parametric test.

RESULTS AND DISCUSSION

Taphonomic analysis

The ratio of opposite valves (Figure 4) and size–frequency distribution (Figure 5) of *T. gayi* shells in different modern and fossil mollusc assemblages indicate, respectively, the degree of lateral transport and size-sorting.

Fossil and modern assemblages showed no divergences from random in the proportion of right to left valves (i.e. fossil assemblages displayed values between 37% and 52% and modern assemblages between 42% and 56%). The high rate of disarticulated *T. gayi* shells seems to be associated with the high to moderate energetic conditions prevailing in

Table 1. Localities and chronological control performed by different authors. See geographical location in Figure 1.

Locality	Site m (above sea level)	Latitude/longitude	^{14}C Radiocarbon age
Bahía Golondrina (BG)	Península Ushuaia; 5m	54°51′S 68°18′W	Not dated, fossil shells
Bahía Ensenada (BE)	Ensenada; 2.20 m	54°51′S 68°30′W	2120 +/−45 ^{14}C years (5)
Bahía Golondrina (BG)	Península Ushuaia; 10m	54°51′S 68°18′W	5460 +/−110 ^{14}C years (3)
Bahía Brown (BB)	Terrace III; 2.6 m	54°53′S 67°31′W	985 +/−135 ^{14}C years (5)
Estancia Harberton (EA)	Terrace III; 2.3 m	54°53′S 67°24′W	2770 +/−50 ^{14}C years (5)
Lago Roca (LR)	Lago Roca 2; 6.4 m	54°48′S 68°36′W	5920 +/−90 ^{14}C years (2)
Archipiélago Cormoranes (AC)	Alakush; 5 m	54°50′S 68°34′W	4440 +/−120 ^{14}C years (1)
Playa Larga (PL)	High terrace; 8 m	54°49′S 68°14′W	5615 +/−120 ^{14}C years (5)
Playa Larga (PL)	Low terrace; 1.6 m	54°49′S 68°14′W	405 +/−55 ^{14}C years (5)
Isla Gable (GA)	North-west terrace; 5 m	54°53″S 67°31′W	4790 +/−100 ^{14}C years (4)
Bahía Golondrina (BG)	Tolkeyen; 2 m	54°50′S 68°21′W	Not dated, fossil shells
Lago Roca (LR)	Lago Roca 1; 4 m	54°48′S 68°36′W	Not dated, fossil shells
Archipiélago Cormoranes (AC)	Río Ovando; 3 m	54°51′S 68°35′W	4425 +/−55 ^{14}C years (2)
Archipiélago Cormoranes (AC)	Río Ovando (in situ); 3 m	54°50′S 68°34′W	4160 +/−45 ^{14}C years (7)
Archipiélago Cormoranes (AC)	Río Ovando 4; 3 m	54°50′S 68°34′W	Not dated, fossil shells
Bahía Golondrina (BG)	Península Ushuaia; 2.5 m	54°51′S 68°18′W	Not dated, fossil shells
Isla Gable (GA)	South-west terrace 2; 3.3 m	54°54′S 67°31′W	Not dated, fossil shells
Archipiélago Cormoranes (AC)	Entre Ríos 2; 3 m	54°50′S 68°34′W	Not dated, fossil shells
Archipiélago Cormoranes (AC)	Laguna Verde; 3 m	54°50′S 68°34′W	Not dated, fossil shells
Bahía Golondrina (BG)	Península Ushuaia; 2.5 m	54°51′S 68°18′W	Not dated, fossil shells
Puerto del Hambre (PH)	Terrace III; 1.5 m	53°36′S 70°55′W	4000–5000 ^{14}C years (6)
Punta Palo (PP)	Terrace III; 3.0 m	53°17′S 70°27′W	4000–5000 ^{14}C years (6)
Punta Palo (PP)	Terrace IV; 1.0 m	53°17′S 70°27′W	1000–2000 ^{14}C years (6)
Bahía Golondrina (BG)	Q 1	54°49′S 68°19′W	Not dated, modern shells
Bahía Golondrina (BG)	Q 2	54°49′S 68°19′W	Not dated, modern shells
Bahía Golondrina (BG)	Q 3	54°49′S 68°19′W	Not dated, modern shells
Bahía Golondrina (BG)	Q 4	54°49′S 68°19′W	Not dated, modern shells

Source of data: (1) Figuerero & Mengoni, 1986; (2) Rabassa *et al.*, 1986; (3) Gordillo, 1990; (4) Gordillo, 1991; (5) Gordillo *et al.*, 1992; (6) Brambatti *et al.*, 1998; (7) Coronato *et al.*, 1999. Q, quadrat

the Beagle Channel. However, the similar number of right and left valves indicates that they were transported together preventing a differential lateral transport or left/right sorting (Frey & Henderson, 1987) characterized by uneven distribution of right and left valves.

In comparison, size–frequency histograms of modern shells (Figure 5A) show greater size-sorting than fossil ones (Figure 5B). These differences can be explained on the basis of different origin of the assemblages involved; i.e. modern shells from Bahía Golondrina belong to allochthonous assemblages, while fossil shells from Archipiélago Cormoranes belong to mixed autochthonous and parautochthonous assemblages (Kidwell & Bosence, 1991). Therefore, size–frequency data are best related to post-mortem processes. However, slight variations in size-sorting between fossil and modern *T. gayi* shells could be associated with changes of hydraulic energy regimes throughout the Holocene. These variations were also observed in other taxa (Gordillo *et al.*, 2009).

Results of fragmentation, wear, encrustation and drilling are presented in Figure 6. The taphograms show the proportion of good, fair and poor shells at each site for each taphonomic feature. The entire sample can be characterized by the proportion of shells in each of these categories. This scheme allows each site to be represented by a single dot. The location of the samples within each ternary taphogram reflects the variation in the taphonomic features within a site, and among different sites (Kowalewski *et al.*, 1995).

Fragmentation (Figure 6A) was good in modern *T. gayi* shells (there are only a few fragmented shells), and varied from good to fair and poor in *T. gayi* fossil shells. The low fragmentation of modern shells collected in Bahía Golondrina is probably because these shells were transported short distances by waves and tides and accumulated in great abundance on the active beach. Some thick shells remain articulated. As Bahía Golondrina is influenced by western winds, the low fragmentation also indicates that thick *T. gayi* shells were able to pass through strong currents generated by storms or tides without either damage or breakage. Moreover, different degrees of fragmentation of fossil shells may reflect different hydrodynamic conditions along the northern coast of the Beagle Channel.

Wear (Figure 6B) was good–fair in modern *T. gayi* shells and varied greatly, from good to fair–poor, in fossil *T. gayi* shells. Typical features produced by shell dissolution, including the exposure of inner shell layers, were rare. However, abraded shells with loss of external ornamentation were common. The great variation between sites shows that this feature is strongly affected by local environmental factors.

Encrustation (Figure 6C) was good–poor in modern and fossil *T. gayi* shells. However, modern shells had more encrusters than fossil ones. These differences most probably reflect the fact that modern shells were exposed longer than the fossil ones, allowing postmortem encrustation. But, the lack of encrusters in fossil shells can also represent a bad preservation. *Spirorbis*, a tubed polychaete worm, is the most common species that colonizes *T. gayi* shells (13% of the valves), followed by boring sponges (probably *Cliona* (1% of the valves)), and finally coralline algae, barnacles and bryozoans (less than 0.2% of the valves).
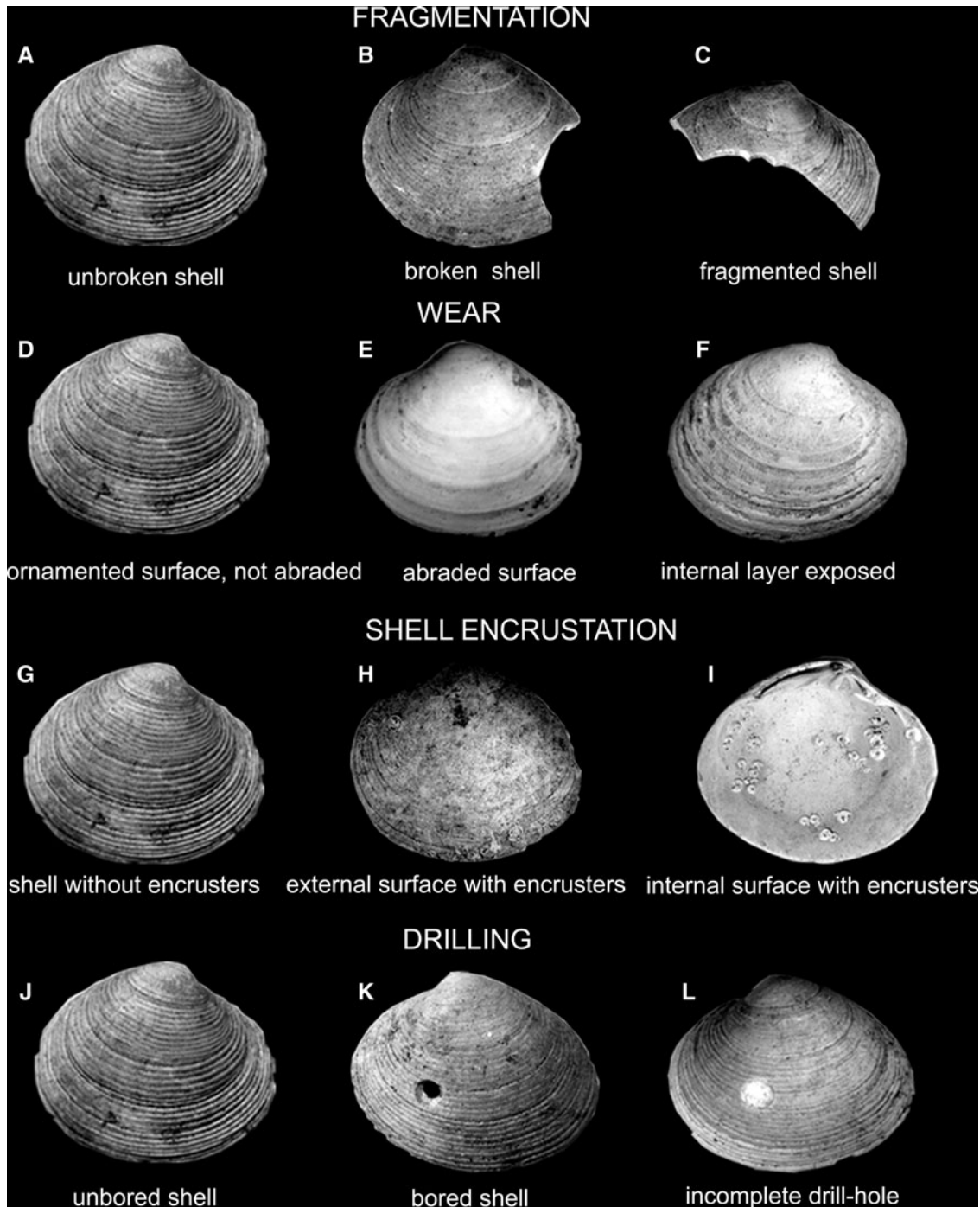
Fig. 3. Figure of *Tawera gayi* shells displaying the three taphonomic grades for fragmentation, wear, encrustation and drilling.

Table 2. Taphonomic attributes analysed for *Tawera gayi* shells (fragmentation, wear, encrustation and drilling) and their correspondence with qualitative categories (good, fair, poor).

	Fragmentation	Wear	Encrustation	Drilling
Good	Unbroken	Not abraded	Without encrusters	Undrilled
Fair	Broken ($<$30%)	Abraded	With external encrusters only	1 drill-hole
Poor	Fragmented ($>$30%)	Inner layer exposed	With internal encrusters	Incomplete

Drilling produced by boring gastropods (Figure 6D) was good in modern *T. gayi* shells and good–fair in fossil ones. Taking into account their biological implications, this feature was analysed (see below) in great detail.

Taphonomic analysis of these features shows that the preservation of *T. gayi* shells varies greatly from site to site, and differences between fossil and modern shells seem to be related to local variations of physical factors associated with hydrodynamic energy and freshwater input, with the consequent differences in postmortem transportation and differential destruction.
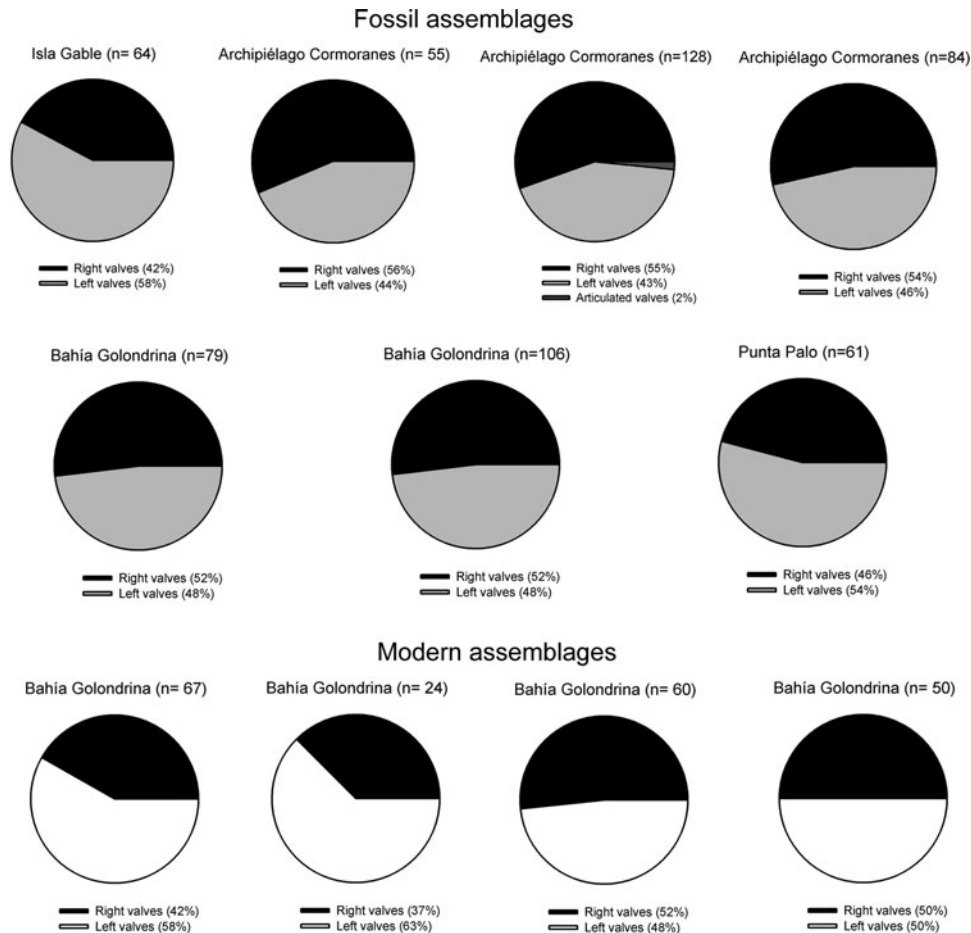
Fossil assemblages

Isla Gable (n= 64)
- Right valves (42%)
- Left valves (58%)

Archipiélago Cormoranes (n= 55)
- Right valves (56%)
- Left valves (44%)

Archipiélago Cormoranes (n=128)
- Right valves (55%)
- Left valves (43%)
- Articulated valves (2%)

Archipiélago Cormoranes (n=84)
- Right valves (54%)
- Left valves (46%)

Bahía Golondrina (n=79)
- Right valves (52%)
- Left valves (48%)

Bahía Golondrina (n=106)
- Right valves (52%)
- Left valves (48%)

Punta Palo (n=61)
- Right valves (46%)
- Left valves (54%)

Modern assemblages

Bahía Golondrina (n= 67)
- Right valves (42%)
- Left valves (58%)

Bahía Golondrina (n= 24)
- Right valves (37%)
- Left valves (63%)

Bahía Golondrina (n= 60)
- Right valves (52%)
- Left valves (48%)

Bahía Golondrina (n= 50)
- Right valves (50%)
- Left valves (50%)

Fig. 4. Ratio of opposite valves. Right and left valves do not differ significantly in proportion.

Drilling gastropod predation

Based on its morphology (see Gordillo 1994, 1998), drilling holes were attributed to the muricid gastropods *Trophon geversianus* (Pallas) and *Xymenopsis muriciformis* (King), two common species in benthic communities of this region. As in the ternary diagram (Figure 6D), Table 3 and Figure 7 also show a great variation in frequencies of muricid predation on modern and fossil *T. gayi* shells. However, frequencies of drilling predation on modern shells were statistically lower than those on fossil shells (*t*-test; $P = 0.02$). Differences between modern and fossil *T. gayi* shells could be caused by sampling different habitats, by taphonomic effects, or by random sampling variability, but changes in drilling frequency through time must also be considered. However, variation within fossil shell assemblages is attributed to a great proportion of small *T. gayi* shells (undrilled juvenile specimens) in one subsample (AC-20) of the Archipiélago Cormoranes site, which was eliminated for this analysis.

Burrowing behaviour of *T. gayi*, living semi-infaunally or partially buried, may increase predation risk by epifaunal muricid gastropods. This ecological explanation can be applied to fossil shells from Archipiélago Cormoranes collected in life position. A second phenomenon associated with storms explains better the presence of modern bored *T. gayi* shells along the exposed beach of Bahía Golondrina. The mode of life of *T. gayi*, just beneath the surface of the sediments, makes this species particularly vulnerable to storms or events with both strong winds and bottom currents. Under these conditions, *T. gayi* specimens would be exhumed from their life position, then transported alive and deposited outside the sediment, in relatively shallow waters with bottoms less suitable as habitat. There, unable to burrow down, *T. gayi* would probably be easily preyed upon by muricid predators. The mortality of clams (mass mortality) after storms, which facilitates their attack by invertebrates and fish, has been previously described in other shallow marine ecosystems (e.g. Thórarindsóttir *et al.*, 2009). This phenomenon must be taken into account when comparing drilling frequencies of fossil and modern shells, since it would artificially shorten the differences in drilling frequency between the two sets of data.

Stable isotopes of *T. gayi* shells from the Beagle Channel

Table 4 shows the results of carbon and oxygen isotopic analysis on *T. gayi* shells from the Beagle Channel. These values are in good accordance with the stable isotopic data previously obtained by Panarello (1987).

The isotopic composition of carbonate shells depends on the organism's environment and metabolism (McConnaughey, 1989). Then, shell $\delta^{18}O$ depends on temperature and $\delta^{18}O$ of the water at the time of precipitation (Epstein *et al.*, 1951). The $\delta^{13}C$ value of marine shells is controlled by the $\delta^{13}C$ value of dissolved inorganic carbon found in the organism's internal water pool at the site of calcification (McConnaughey *et al.*,
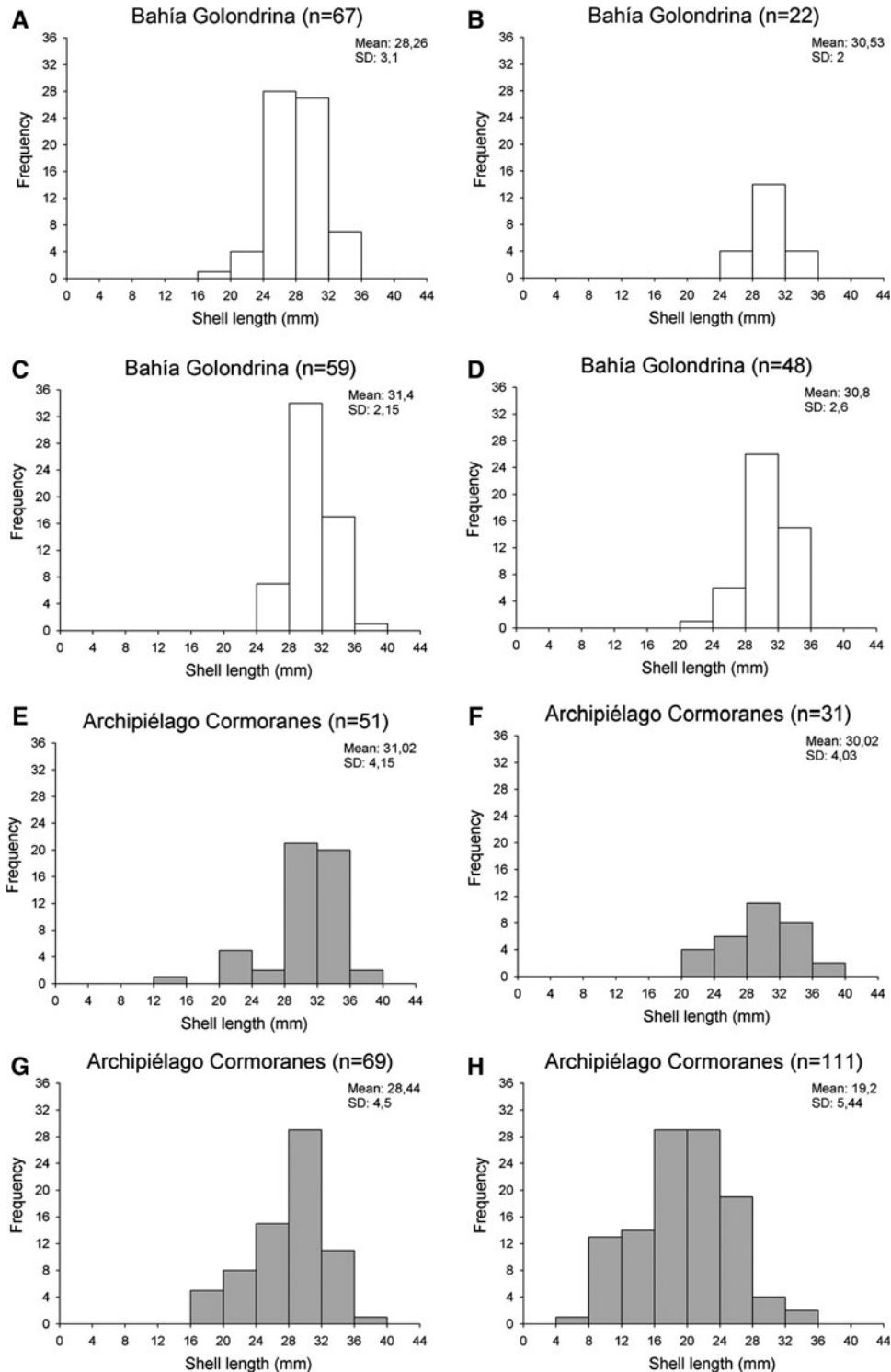
Fig. 5. Shell size–frequency distribution for modern and fossil *Tawera gayi* shells from different sites. (A) Modern shells from Bahía Golondrina locality; (B) fossil shells from Archipiélago Cormoranes locality (for location of sites see Figure 1).

1997). Therefore, one aspect that makes our interpretations difficult when estimating palaeotemperatures for the Beagle Channel is the lack of information on salinity and isotopic composition of the surface seawater, a discrepancy also noted by Obelic *et al.* (1998).

Figure 8 shows oxygen isotopic data versus carbon isotopic data (Figure 8A), and versus their respective relative radiocarbon ages (Figure 8B; AK, Alakush).

These diagrams show that carbon and oxygen isotopic analysis on *T. gayi* shells gave values within a same range, with the exception of the Alakush site, which showed lower values (i.e. high depletion in heavy isotopes relative to the standard).

Carbon values are within the −2 and +2 interval, which is associated with marine environments (Keith *et al.*, 1964). In comparison, waters coming from rivers are relatively deficient
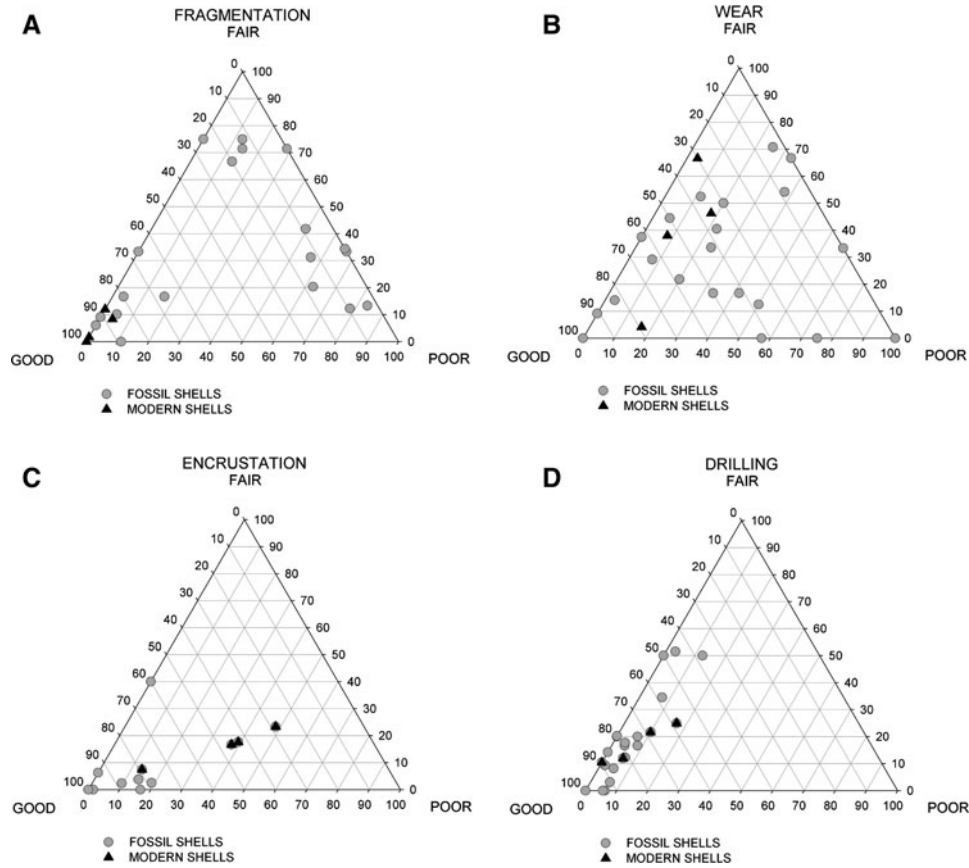
Fig. 6. Ternary taphograms showing variation among sampling sites for different taphonomic attributes of *Tawera gayi* shells. (A) Fragmentation; (B) wear; (C) encrustation; (D) drilling. Modern shell assemblages are represented by black triangles and fossil ones by grey circles.

in ^{18}O and ^{13}C and isotopically more variable: $\delta^{18}O < -2‰$; $\delta^{13}C < 0‰$ (Epstein & Mayeda, 1953, Keith et al., 1964).

Similarly, the oxygen isotopic analysis of *T. gayi* shells (with the exception of shells from Alakush site) gave values within a similar range.

These isotopic data are difficult to explain (particularly carbon) due to the fact that shells from the shallow marine environments along the Beagle Channel coast were exposed to freshwater, which derived from glacial ice melting that discharged into rivers that lead into the sea. In this regard, as shell carbonate is controlled by temperature and by the isotopic composition of ambient water, stable isotopic composition of mollusc shells from freshwater environments shows wider and more depleted values than those from marine environments. This is due to the relative deficiency in $\delta^{18}O$ and $\delta^{13}C$ and the isotopically more variable nature of freshwater (see Wang et al., 1991). Besides, in the Magellan Region, the mixture of seawater and freshwater from melting Andean snow also produces cooler waters

Table 3. Number of individuals with less than 30% of the valve fragmented, number of drilled individuals and drilling frequency (%) for the different sites analysed.

Locality	N individuals (unbroken + <30% fragment)	N drilled	Drilling frequency
Archipiélago Cormoranes 14	55	19	34.55
Archipiélago Cormoranes 15	33	17	51.52
Archipiélago Cormoranes 19	81	17	20.99
Archipiélago Cormoranes 20	124	12	9.68
Archipiélago Cormoranes-I	61	26	42.62 (*)
Bahía Golondrina 25	67	7	10.45
Bahía Golondrina 26	23	6	26.09
Bahía Golondrina 27	60	13	21.67
Bahía Golondrina 28	50	6	12.00
Bahía Golondrina-II	543	118	21.73 (*)

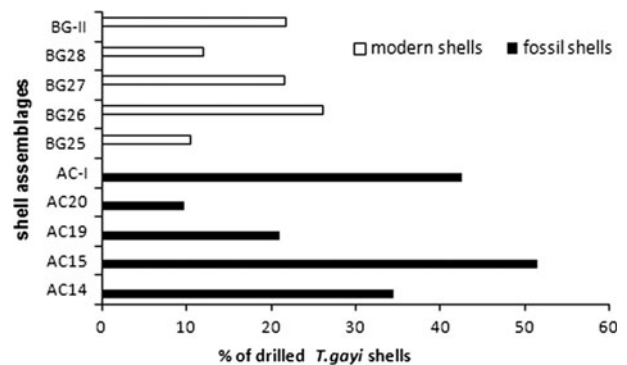*, source of data: Gordillo (1994).

Fig. 7. Comparison of drilling frequencies of *Tawera gayi* shells for modern (BG) and fossil (AC) shell assemblages. BG, Bahía Golondrina; AC, Archipiélago Cormoranes. Numbers identify subsamples. Localities with roman numbers (AC-I, BG-II) indicate data obtained by Gordillo (1994).

Table 4. Isotopic analysis on modern and fossil *Tawera gayi* shells from the Beagle Channel. See localities in Figure 1.

Site	C[14] age	δ[13] carbon (pro mille)	δ[18] oxygen (pro mille)	Source
Alakush	4400	0.7	−1.9	This study
Alakush	4400	0.6	−1.4	This study
Ushuaia	5160	1.2	−0.3	This study
Ushuaia	5160	0.9	0.2	This study
Estancia Harberton	2770	1.2	0.1	This study
Estancia Harberton	2770	1.2	−0.2	This study
Bahía Golondrina	Modern	0.1	0.1	This study
Beagle Channel	Modern	0.8	−0.15	Panarello (1987)
7D (shell midden)	5630	0.8	0.3	Panarello (1987)

(Massimo, 1991; in Palma & Aravena, 2001). However, the great isotopic differences between Alakush (~4400 years BP) and the other sites could be associated with warmer temperatures during the Hypsithermal (Obelic *et al.*, 1998; Strelin *et al.*, 2008), and a high volume of freshwater entering the Beagle Channel, partly due to an increase in rain (Candel *et al.*, 2009), and partly from melting snow at this period. During this period, large volumes of water enriched in ¹⁶O came back into the seas, resulting in lower ratios.

Further studies including more isotopic data, combined with individual growth using sclerochronology, and calibrated against temperatures, are needed to evidence the impact of climatic changes on shell growth and structure, and to discriminate between environmental changes and ecological reasons. To have a more precise understanding of the isotopic data, further analysis will include Mg/Ca ratio as an alternative proxy of palaeotemperatures (Purton-Hildebrand *et al.*, 2001; Richardson *et al.*, 2004) to verify climate assumptions.

Cathodoluminiscence and X-ray examination: modern versus fossil *T. gayi* shells

The X-ray diffraction showed that modern and fossil *T. gayi* shells are composed of aragonite (100%). The fact that fossil *T. gayi* shells do not have a mixed composition of aragonitic and calcitic is due to the absence of post-depositional recrystallizations (i.e. from aragonite to calcite) in fossil shells.

Under CL-microscopy, modern and fossil *T. gayi* shells show a well defined pattern, with parallel spaced CL lines (Figure 9A–E). This zonation reflects the cycles of skeletal growth and a luminescence intensity typical of aragonitic shells, and may be related to the alternating amount of manganese present in the aragonite (Barbin, 1992).

Rapid growth rate during the earlier life stages of *T. gayi* (Figure 9A), and CL lines that terminate in an external growth line (Figure 9B), as well as the regular repetition of CL with outlines approaching the shape of internal structures, indicate that these lines are related to the growth dynamics of the shell (see discussion in Tomašovych & Farkaš, 2005).

The aragonitic *T. gayi* shells give a weak blue-green luminescence (probably due to a slower growth rate) alternating with dark areas associated with periods with a different growth rate (or a cessation of growth). In addition, a different luminescence (light, bright yellow luminescence) affecting outer and inner shell surfaces is interpreted as a bioeroded surface caused by external factors (i.e. bacteria and microboring organisms), but not produced by the mollusc biomineralization process (Figure 9C).

Although the data presented on shell structure of *T. gayi* under CL is not enough to explain the true reasons behind the differences or changes between shells, it does indicate that CL lines correspond to zones recording changes in growth rate. Thus, the analysis of CL lines in this species can provide another important tool for the evaluation of *T. gayi* growth rates, in addition to external growth rates, isotopes and trace elements, since CL lines in bivalves are correlated with periods of slow growth, such as winter, spawning seasons or environmental disturbance (Barbin, 1992; Barbin & Gaspar, 1995). A systematic examination of CL line pattern in *T. gayi* can be useful for adding to our knowledge of changes during the Holocene.

Shell morphology and possible causes of variation

Linear morphometric analysis applied to fossil and modern *T. gayi* shells shows that whereas the modern shells are more rounded, the fossil ones are slightly elongated. Fossil shells
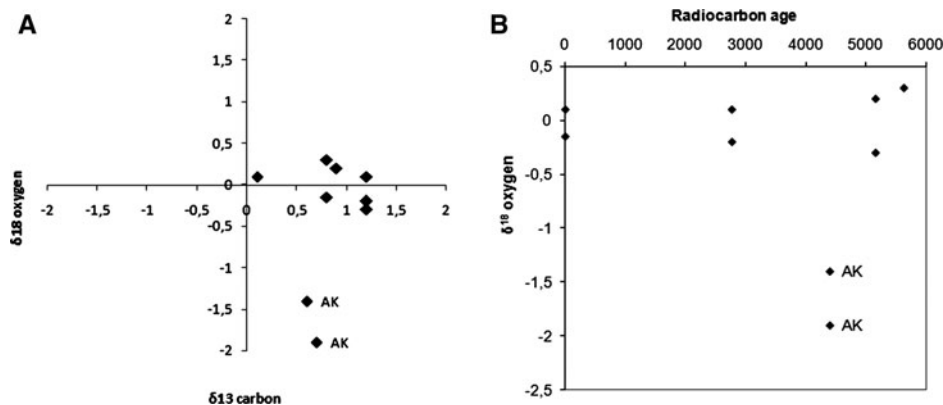
Fig. 8. Stable isotopes of *Tawera gayi* (see references in Table 2). (A) Relationship between oxygen and carbon isotopic composition in *T. gayi* shells; (B) scatter plot of oxygen isotopic values on *T. gayi* shells and their radiocarbon age.
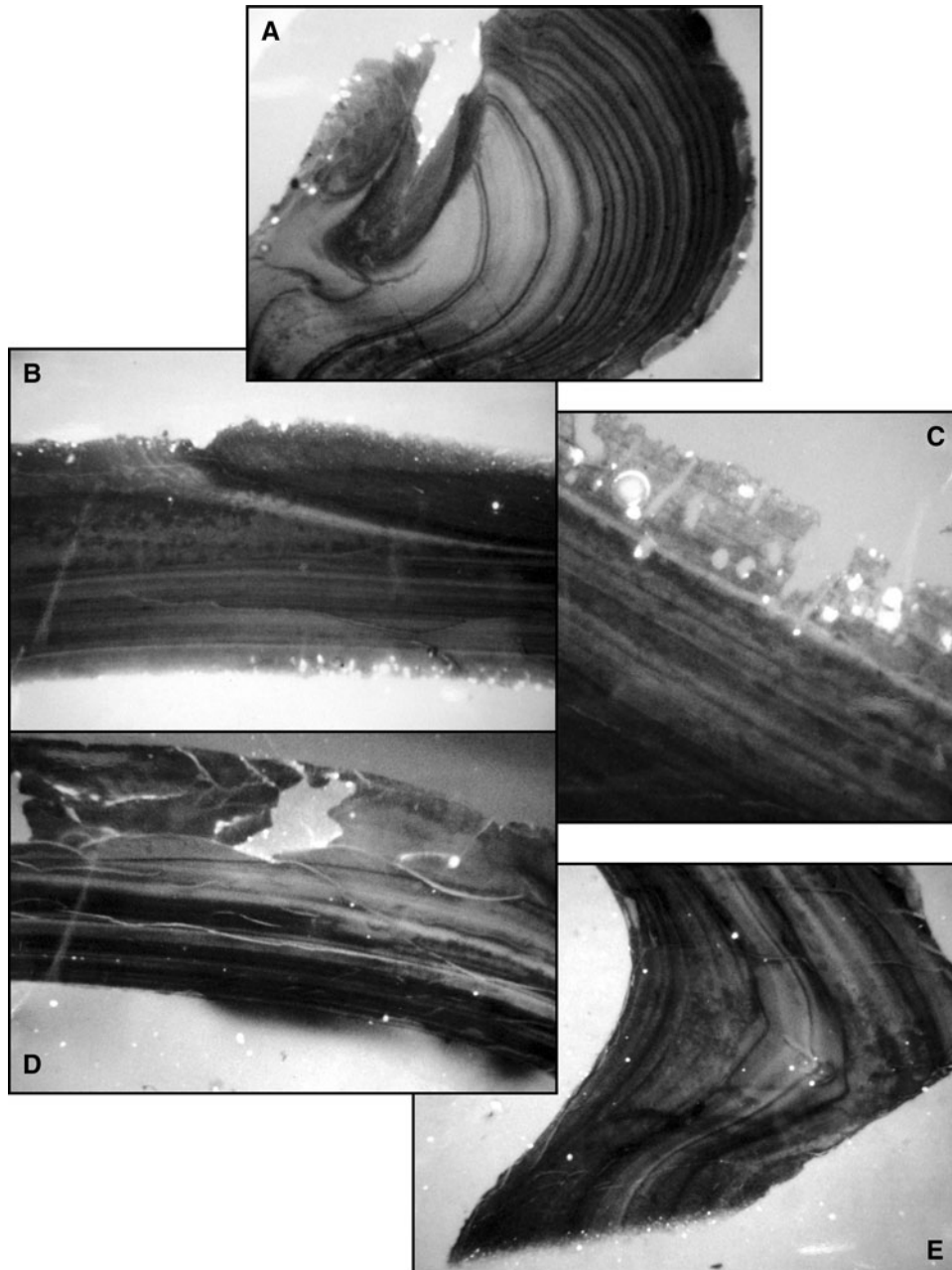
Fig. 9. View under cathodoluminiscence (CL) of sections of modern (A) and fossil (B–E) *Tawera gayi* shells showing a well defined pattern of CL lines, almost concentric. Luminescent bands (here light bands) border the winter (dark) growth rings. (A) Modern specimen, Bahía Golondrina; (B &C) fossil specimen, Archipiélago Cormoranes (4425 years BP); C is the high magnification of a sector of B (10X); (D & E) fossil specimen, Isla Gable (4790 years BP). Scale: 2.5X.

are significantly smaller (Figure 10A) and shorter for their length (Figure 10B) than modern shells (Mann–Whitney rank-sum test; $P < 0.001$ in both cases).

To discuss the possible causes of variation in shell morphology different factors were taken into account, as mentioned below.

Previous studies on bivalves (Kirby, 2000; Vermeij, 1990) and turritelid gastropods (Allmon, 1992; Teusch *et al.*, 2002) offer strong evidence that size and shape differences in shells may be explained by different temperature and productivity conditions. In southern South America, recent studies on venerids from Patagonia also show that shell variation is related to phenotypic plasticity as the result of different environmental conditions (Márquez *et al.*, 2009; Gordillo

et al., 2010). In addition, other works indicate that morphological variations in molluscs may also result from biotic interactions as predator–prey relationships (Hagadorn & Boyajian, 1997; Teusch *et al.*, 2002). Therefore, to explain the changes in size and shape between modern and fossil *T. gayi* shells from the Beagle Channel, environmental and ecological factors including temperature, productivity and biotic interactions have been taken into account.

Because *T. gayi* is a suspension feeder and directly dependent on primary productivity for growth, it is assumed here that increased primary productivity has a positive effect on shell growth. As modern *T. gayi* shells exhibit larger size than fossil shells it is reasonable to infer that the increase in nutrient concentrations may have played a role in affecting
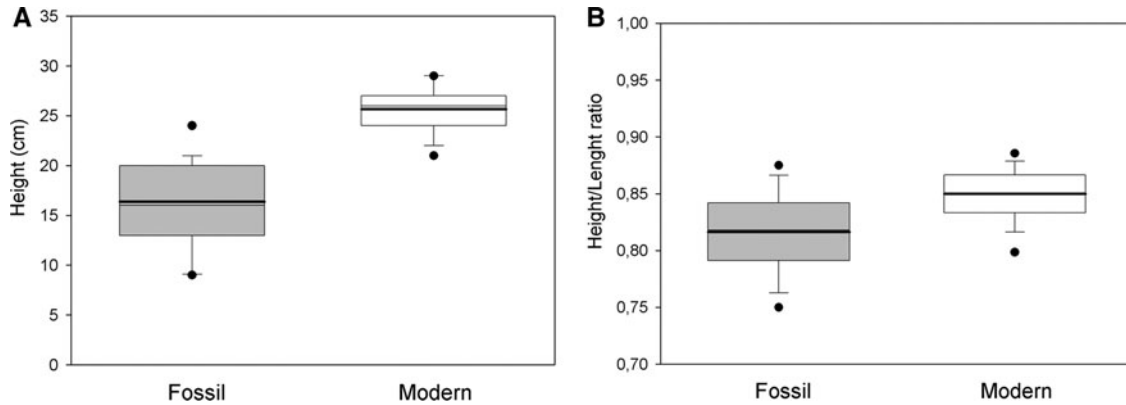
Fig. 10. Boxplots showing the differences in size (left) and shape (right) between fossil and modern *Tawera gayi* shells. The dots represent 5 and 95 percentiles, upper part of the box 50 percentiles, low part 75 percentiles, line represents median, and whiskers represent 10 and 90 percentiles, respectively. Modern shells reached larger sizes and are more quadrangular than fossil *T. gayi* shells.

shell size. However, a higher productivity does not explain the different shape between both ages with modern shells more rounded than fossil ones.

Under this situation, another reason is postulated here as the possible cause of modern shells reaching a more rounded shape than the fossil ones: a greater chance of avoiding drilling predation. This interpretation is supported by the fundamental relationship between shape and function in clams (Stanley, 1975), and the development of antipredatory adaptation. Morphometric data obtained in this work, together with differences in drilling frequency through time also sustain this explanation, as detailed below.

Stanley (1975) observed that the prosogyrous condition and the rotational mechanism of burrowing are fundamental adaptations of burrowing clams, showing that each rocking motion of a typical clam involves purely rotational movement, with no translational component. Thus, one can predict that the prosogyrous shape and flattened lunule should cause a backward rotation, shifting the axis of rotation towards the anterior region. The relationship between the length axis and the height axis (height/length ratio), therefore, has a significant effect on the burrowing of clams, and more rounded modern *T. gayi* shells may burrow faster than the more elongated fossil *T. gayi* shells.

Taking into account data on shell-boring gastropods on *T. gayi*, it is also plausible that *T. gayi* from the Beagle Channel developed an antipredatory strategy. For this region, a slight decrease in predation by drilling gastropods is noticed (see also Gordillo (1994) and Gordillo (1998)). This decrease in predation risk probably correlates with changes in the shape of *T. gayi*. In other words, changes in *T. gayi* shape are perhaps an evidence of effective resistance adaptation against drilling by gastropods (antipredatory adaptation). As fossil shells are more elongated, the burrowing mechanism is less effective than in modern shells. Modern shells are more rounded than fossil shells, thus offer less resistance to the substrate and consequently burrow faster in order to avoid predation by muricid gastropods such as *T. geversianus* or *X. muriciformis*. These statements become even more relevant when considered together with the short South American biogeographical history of *Tawera*, which apparently arrived from New Zealand during the Quaternary (Gordillo, 2006), and the need to improve strategies for avoiding predators in its new environment in South

America. More work on this topic is needed to reinforce these assumptions.

FINAL REMARKS

Taphonomic analysis has been used as a tool for interpreting the environmental characteristics associated with the studied bivalve indicating that shell variations of *T. gayi* between different sites are best associated with physical factors that prevail in each site than to changes during the Holocene, although slight changes in energy during the Holocene would also have occurred.

The carbon isotopic analysis of *T. gayi* shells indicates the existence of a mixing of waters from pure marine waters to marine waters with signs of freshwater influence. The high depletion of $\delta^{18}O$ at ~4400 years BP would be associated with warmer temperatures during the Hypsithermal, and a maximum freshwater input to the Beagle Channel, probably due to an increase in rain during this period. In addition, under CL modern and fossil *T. gayi* shells show a well defined pattern, with parallel spaced CL lines related to the growth dynamics of the shell. Holocene *T. gayi* shells can, hence, be utilized as environmental and climate proxy archives and a systematic examination of the internal growth pattern in combination with isotopes and traces can lead to a better understanding of their biology and can add detail to palaeoenvironmental analysis.

When considering *T. gayi* shell shape, linear morphometrics showed that fossil *T. gayi* shells are smaller and more elongated than the modern shells. As morphological variation of *T. gayi* shells is the product of both heredity and environment, morphological changes should be considered in a community or palaeocommunity context, in which phenotypic variation between localities may represent a source of ecological information suitable for the evaluation of environmental changes. In *T. gayi* from the Beagle Channel morphological differences in shells are best explained on the basis of biotic interactions rather than Holocene environmental changes. However, further studies that include a wider range of geological time will be essential to reinforce these interpretations. In this regard, the theory of co-evolution and the escalation hypothesis (Vermeij, 1987, 1994; Thompson, 2009) suggest that microevolutionary variation is influenced by local conditions and biotic

interactions, and *T. gayi* represents an opportunity to test this assertion.

This integrated approach indicates that *T. gayi* is a good candidate for looking at evidences of environmental changes in southern South America, and multi-proxy data are necessary to better understand the driving mechanisms of ecological variability and changes over short geological time intervals of hundreds to thousands of years.

ACKNOWLEDGEMENTS

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