Coastal upwelling in Norway recorded in Great Scallop shells

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Abstract
The shells of bivalve mollusks have been shown to contain a wealth of information about the environment in which the organisms lived as well as about their life histories. Shells of the Great Scallop Pecten maximus were collected in 1987 and 1988 at 15–25 m depth close to the Austevoll islands (Norway). A sharp slowdown in growth was detected in 1986 for all age classes, resulting in a growth-rate decrease of nearly 45% over 10 d. Measurements of stable isotopes (δ18O and δ13C) in four specimens suggested that this slowdown was concurrent with a drop in water temperature. In situ measurements of environmental parameters (temperature, salinity, wind) and data from a numerical coastal model system (NorKyst-800) confirmed that a temperature drop of 3°C occurred in July 1986 due to a sudden change in wind direction and speed along the western coast of Norway. These northerly winds parallel to the coast induced an upwelling of deep cold water along the coast. Thus, the present study demonstrated a clear relationship between regional climatic phenomena acting on an oceanographic process and the growth of a benthic invertebrate. Bivalve shells should be used to describe and characterize local upwelling events, for example, in terms of duration and intensity, in current environments and in paleoenvironments.

Reconstructing the history of the oceans is dependent on our ability to reliably extract information on physical, chemical and biological processes from the sediment or biogenic archives (Hickson et al. 2000; Knies et al. 2003; Johnson et al. 2009). Exploring Holocene climate fluctuations is a major prerequisite for understanding natural climate variability and its impact on human history, as well as for developing reliable prognostic climate models (Lamb 1995). Physical processes regulating the vertical structure of the ocean partly determine marine productivity. In particular, coastal upwelling systems are of fundamental importance in the study of the physics, chemistry and fertility of the ocean and in global fisheries (Ryther 1969; Chavez and Toggweiler 1995). In many coastal waters, primary production rates benefit from the upwelling of nutrient-rich, deep water (Smith et al. 1983; Mann and Lazier 2006).

Upwelling circulation operates on a wide range of time scales including short (hours), intermediate (days) and long (seasonal and interannual) scales. While extensive knowledge is available on the behavior of upwelling areas over the course of glacial/interglacial cycles (Knies et al. 2003; Chavez and Messié 2009), there is not much known about the response of these cycles to the comparably small climate variations during the Holocene. There is evidence that the short-term fluctuations in global climate observed for the last glacial period continue throughout the Holocene, although they are less pronounced (Clarke and Lebe-dev 1999). Upwelling regions are probably particularly sensitive to such millennial-scale climate changes and may also display centennial-to-decadal fluctuations related to the well-known modes of modern interannual climate variability.

The ocean’s role in climatic change via heat transport and the control of carbon dioxide is increasingly being recognized (IPCC 2013). This awareness and the urgency for understanding the mechanisms of climatic change have led to the initiation of large, integrated efforts in physical and chemical oceanography. In this context, several analytical tools have been developed in recent years, such as satellite imaging, remote sensing, and modeling. These tools, which have been primarily applied to major upwelling events, allow the characterization of their temporal frequency. Many questions remain, however, regarding the functioning of these events and their impacts on benthic organisms (Chavez and Messié 2009; Lachkar and Gruber 2011; Lachkar and Gruber 2012).

Bivalve shells grow by accretion of calcium carbonate crystals in the form of calcite or aragonite or both, depending on the species (Marin and Luquet 2004). Periodic growth
to the Norwegian coastline, upwelling events may rapidly develop during summer. These events have been described for the northern Norwegian fjords (Cushman-Roisin et al. 1994; Knies et al. 2003; Skarðhamar and Svendsen 2005), but little information relative on the western fjords is available (Sætre et al. 1988).

This study aims to examine the slowdown in growth visible on the valves of *P. maximus* harvested in Norway associated with upwelling occurring in 1986. We demonstrate through the joint analysis of growth pattern and isotopic composition of these bivalves that they may serve as proxies for upwelling events, and they can be used to characterize the frequency and duration of such events.

**Materials and methods**

**Sampling**

Live *P. maximus* specimens were collected by scuba divers at 15-25 m depth in Austevoll (60°09′N, 5°15′E, Norway; Fig. 1) on a monthly basis from May 1987 to December 1988 (Strand and Nylund 1991). Seventy shells from this sampling were used for the current investigation. These shells were aged three to six years and had shell heights of 65-105 mm.

**Acquisition of environmental data**

Temperature and salinity vertical profiles were obtained from the coastal monitoring station of the Institute of Marine Research at Utsira, Norway (59°19′N, 04°59′E; Fig. 1); observations were made at depths of 0-300 m approximately every 10 d since 1942. For 1985–1987, a total of 92 conductivity–temperature-depth profiles were considered. In addition, water temperatures were simulated with a numerical coastal model system, NorKyst-800 (Albretsen et al. 2011) which provides suitable reproduction of physical variables (sea level, temperature, salinity, and currents) with a spatial horizontal resolution of 800 m along the Norwegian coast from the Swedish border to Russia. Three time series of temperature for mid-June to August in 1985, 1986, and 1987 were extracted for depths of 10 m, 20 m, 50 m, and 100 m at a position in the Korsfjord with a maximum depth of 690 m and corresponding to the scallop sampling site on the northern shores of Austevoll (Fig. 1).

Wind data representing the outer coastal area were obtained from the Norwegian Meteorological Institute (http://met.no) and were measured at Slåtterøy lighthouse on the coast south of Austevoll and at Utsira even further south (Fig. 1). Two wind indices were calculated based on three records (07:00, 13:00, and 19:00): a positive index from daily cumulative north wind speed (in m s⁻¹) and a negative index from the daily cumulative south wind speed (in m s⁻¹).

**Estimating growth parameters**

Daily growth rate was determined individually on the external surface of the left valve according to Chauvaud...
et al. (1998). From the earliest detectable striae to the outer edge of the shell (Fig. 2), the distances between two successive daily growth striae were measured on images acquired with a high-resolution video camera (Sony DFW-X700) and analyzed with Visilog 5.4® (Noesis).

Since P. maximus growth stops in winter (Chauvaud et al. 1998, 2005; Lorrain et al. 2000;), individual growth trajectories were averaged within each age class for the specific year. By convention the age class is the number of January 1 days experienced by the specimen. Growth before the first winter, corresponding to age class 0, will not be described. A synchronization procedure was used, based on the minimization of the sum of the differences between individual series in pairwise comparisons. The mean daily growth rates for each age class were then ordered following the position of striae along the growth axis, from the umbo to the outer ventral edge. The succession of growth striae describing a “time” axis (days of growth) thus provided a continuous representation of successive growth years (truncation of winter episodes without growth).

Isotope sample collection

Once growth measurements were performed, four shells were sampled to analyze oxygen and carbon isotopes composition. Three samples of age class III were collected in May, September, and November 1987 (i.e., individuals born in 1984); these samples were named A1, A2, and A3, respectively. A fourth sample of age class VI, named A4, was collected in September 1988 and was born in 1982. After cleaning the samples with Milli-Q water, the outer calcite layer of the left valve was ground using a Dremel drill with a 0.3-mm grinding tip. Small grooves were sampled parallel to growth striae at ~1–3-day intervals (Fig. 2) along the axis of maximum growth, from closer to the umbo to the ventral edge of the shell. Each groove was cut to a depth < 150 μm to ensure that sample powder was not collected from different layers of calcite deposition.

Aliquots of P. maximus calcite (N = 99, 87, 157, and 53, for scallops A1 to A4, respectively), weighing on average 77 ± 19 μg (mean ± SE), were acidified in 100% phosphoric acid at 70°C for 470 s and analyzed with an automated Finnigan MAT Kiel III carbonate device coupled to a Finnigan MAT 252 isotope ratio mass spectrometer at Stanford University. Results are reported in per mil (‰) deviations relative to Vienna Pee Dee Belemnite carbonate standard. Regular analysis of standards NBS-19 (National Institute of Standards and Technology, NIST SRM 8544) and SLS-1 (Stanford Isotope Lab Standard) during this study yielded standard deviations of 0.06‰ and 0.06‰ for δ18O, respectively, and of 0.03‰ and 0.03‰ for δ13C, respectively. All isotope data are expressed with the conventional delta (δ) notation in ‰.

Dating isotopes signals

For the four specimens, each isotopic sample was related to growth trajectory, since the number of striae grooved and left between two samples was known, permitting dating in days of growth. The isotopic paleotemperature method has been utilized in previous studies and was validated for P. maximus by Chauvaud et al. (2005) from scallops collected in the Bay of Brest (France) as:

$$T({}^\circ\text{C}) = 14.84 - 3.75 \times (\delta^{18}\text{O}_{\text{shell}} - \delta^{18}\text{O}_{\text{water}})$$  \hspace{1cm} (1)

where T is the water temperature (°C) and δ18Oshell is the oxygen isotope value of the shell relative to the Vienna Pee Dee Belemnite standard. δ18Owater is the oxygen isotope value of the water relative to Vienna standard mean ocean water standard, estimated as a function of the salinity by the relation determined by Mikalsen and Sejrup (2000) at Sognefjorden basin 65 km north of Austevoll:

Fig. 2. Surface of the left valve of P. maximus. (A) Winter marks (W1–W5) deposited during the restarting of growth in the spring allow unambiguous age determination. (B) In this species, daily growth striae can be observed without any treatment aside from surface cleaning (at right) (see Chauvaud et al. 1998, 2005 for details); striae were drilled for stable isotope determination (at left). Individual drilled samples are marked with solid circles.
Based on this established association between $\delta^{18}O_{\text{shell}}$ and water temperature, the oxygen isotopic signal of each shell was compared and synchronized with in situ temperature, assigning a calendar date to each isotope sample (Chauvaud et al. 2005).

As no data were available for Austevoll, salinity was estimated from the water temperature estimated by the numerical model and based on the $\delta^{18}O_{\text{shell}}$ (Eqs. 1, 2) and compared with salinity measurements at Utsira (Fig. 3B).

$\delta^{18}O_{\text{water}} = 0.31 \times \text{salinity} - 10.492$  

(2)

Results

Environmental data

Water temperatures measured in the first 20 m of depth at Utsira were 2–4°C in February and 14–16°C in August (Fig. 3A). At 50 m and 100 m, the maximum temperature was generally 12–13°C and was reached later in October, with the exception of July 1985’s temperature of 14°C at 50 m. Salinity varied over a large range, from 27 PSU at the surface due to input of freshwater to 35 PSU at 100 m depth (Fig. 3B).

At the beginning of July 1986, the water temperature dropped by 5.3°C and 2.8°C at 10 m and 20 m depth, respectively, while salinity increased from 30 to 33.3 PSU and from 32.1 to 34.3 PSU, respectively (Fig. 3). Below 50 m depth, water masses remained stable. The temperature drop measured in July 1986 corresponded to a single event with an amplitude greater than the cool down events recorded between 1985 and 1987 at Utsira (i.e., with amplitude of 1°C (± 1°C) in seven days at 10 m and 20 m depth). Simultaneously, winds measured at Slatterøy were mainly from the south except for 10 July 1986–14 July 1986, a period characterized by strong northerly winds (Fig. 4).

The results obtained from the numerical model for 1986 described a similar tendency and showed that the temperature drop observed for 13–16 July was valid for a fairly large region in the Korsfjord area corresponding to the northern shore of Austevoll (Fig. 5). The change in wind direction induced a horizontal current field at the surface and at 10 m depth, with a strong offshore component in the Korsfjord area and outside the mouth of this fjord (Fig. 5). This change resulted in a net seaward movement of the warm surface water, which was replaced by colder and deeper water inside the fjord and along the coast. Then, on 16 and 17 July 1986, the winds shifted to a southerly direction, pushing warm coastal water onshore and into the Korsfjord area.

Growth parameters

The growth trajectories of four age classes (III–VI, Fig. 6) demonstrated that the maximum daily growth rate and the length of the growth season increased during the first four years (>200 μm d$^{-1}$ and 120 d, respectively), followed by a regular decrease. A slowdown in growth occurred in 1986, resulting in a decrease in growth rate of nearly 45% over 10 d (from 229.4 ± 26.3 μm d$^{-1}$ to 127 ± 24.2 μm d$^{-1}$), before returning to values close to 200 μm d$^{-1}$ (Fig. 6). Isotopic signals

As the oxygen isotopic signal was significantly correlated with in situ temperature (Spearman correlation on the four shells > −0.65, all p < 0.001), it was synchronized with the measured temperature, allowing us to date the growth curves. During their first four years (after the first winter), the shells grew over a period stretching from early mid-June to mid-October or early November (Fig. 7).
For the shells examined, the slowdown in growth observed in 1986 was concurrent with a sudden increase in $\delta^{18}O$ signal of: 1.3 ± 0.2‰ for the three scallops of age class III for 12-17 July (± 1 d) and of 0.7‰ for the scallop of age class VI for 12-20 July (Fig. 7, left).

The salinity estimated at Austevoll from the temperature given by the numerical model and $\delta^{18}O_{\text{shell}}$ values indicated an increase of 3.4 ± 1.2 PSU for three shells of age class III (from 30.4 to 33.8 PSU) and an increase of 2 PSU for the shell of age class VI (from 31.6 to 33.6 PSU). These variations

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**Fig. 5.** Simulations from the numerical model NorKyst-800 of temperature at 10 m depth (color code ranges from 9°C to 14°C) from 11 to 19 July 1986, for the Korsfjord area. Austevoll North, where the scallop shells were collected, is marked with black circle on all panels and identified by an arrow on the July 11 panel.
were close to the salinities measured at Utsira at 20 m depth (Fig. 3B).

During 1986, the carbon isotopic signal of the four shells did not exhibit a particular increase or decrease during growth slowdown (Fig. 7, right).

**Discussion**

The validated numerical coastal model system NorKyst-800 indicated that an upwelling event occurred along the western coast of Norway in July 1986, affecting the area of Austevoll from which we sampled scallop shells. Preceded by a period of winds generally from the south, an episode of strong northwesterly winds persisted through 10–14 July, producing an offshore flux of surface water and an upwelling of colder and saline deeper water as a replacement. The subsequent drop in water temperature of \( \sim 3-5^\circ C \) and the increase in salinity of 2–3 PSU for the upper 20 m represent an event that is not uncommon along the Norwegian west coast. Indeed, the number of northerly wind recordings greater than 15 m s\(^{-1}\) between 1950 and 2013 has been increasing since the 1980s with more than 20 episodes per year (each lasting two to seven days).

Regions characterized by strong upwelling systems are the most productive in the world, for example the northwest coast of South Africa (Brown 1992), north central Chile (Ruttlant and Montecino 2002) and north-western Spain (Álvarez-Salgado et al. 2005), with annual production rates of 700 g C m\(^{-2}\) yr\(^{-1}\) (Mann and Lazier 2006). Little information is available to determine the effects of the upwelling in the Korsfjord area on primary production. Lund (1990) observed a peak of chlorophyll \( a \) (Chl \( a \)) concentration from \( <1 \) to 3 \( \mu \)g L\(^{-1}\) during July 1986 that could be attributed to the stimulation of diatom growth, perhaps due to the upwelling. However, the upwelling event was short (\( <7 \) d) and was directly followed by southerly winds that pushed warm coastal water onshore, replacing or diluting the upwelled water. The western Norwegian fjords are typically nutrient-limited during summer. The typical annual rates of primary production are on average 110–140 g C m\(^{-2}\) yr\(^{-1}\), of which 60% takes place after the spring bloom during March and April (Eilertsen and Taasen 1984; Erga and Heimdal 1984; Erga 1989b). Aure et al (2007) reported that an artificial upwelling in a western Norwegian fjord approximately tripled the mean Chl \( a \) concentration and related primary production rate during the summer. From the start of the artificial upwelling, approximately one week was needed before the phytoplankton concentration increased (Aure et al. 2007). However, the fjord environment in the Korsfjord area is very different in terms of size and the influence of coastal waters, and hence in its physical dynamics. The silicate content of the deeper water stimulated enhanced level of phytoplankton biomass dominated by diatoms (nontoxic species) inside the area influenced by artificial or natural upwelling in fjords (Aksnes et al. 1985; Paasche and Erga 1988; Erga 1989a).

The impact of upwelling on phytoplankton and zooplankton was the subject of numerous studies, but few studies analyzed the effects of such local environmental changes on macrobenthos over a scale of days.

Here, our joint analysis of growth patterns and stable isotopes showed that the upwelling of July 1986 had a clear impact on shell growth (slowdown of nearly 45%) in scallops. Such slowdown of growth has already been described by previous studies of *P. maximus* in the Bay of Brest associated with the presence of high concentrations of Chl \( a \), suggesting that phytoplankton blooms were the main driver.
(Chauvaud et al. 1998; Lorrain et al. 2000). This explanation cannot be considered in the present study as low Chl a concentration was measured during the upwelling. Although the temperature has already been assumed as influencing the growth of shells (Buestel et al. 1987; Wilson 1987; Chauvaud et al. 1998), the present study is the first demonstration of the effect of abrupt changes in temperature, occurring during the upwelling event in 1986 (3°C at 20 m depth), on shell growth of P. maximus.

Descriptions of fluctuations in upwelling have previously been made based on O and C isotopic analysis from modern marine mollusks like Mytilus californianus (Killingley and Berger 1979; Glassow et al. 1994; Kennett et al. 1997), Meso-desma donacium (Sadler et al. 2012) or strombid snails (Wefer and Killingley 1980). The oxygen isotope ratio is known to be particularly sensitive to changes in water temperature and salinity and is preserved in calcareous fossils such as mollusk shells (Wefer and Berger 1991). For P. maximus, this relationship was previously demonstrated in the Bay of Brest (Chauvaud et al. 2005). In our study, we used the oxygen isotopic ratio to date the growth curve of scallops by their relationship with temperature variations and to estimate the timing and magnitude of temperature changes. Although the timing of the drop in temperature, estimated at 5°C over seven days, is consistent with environmental conditions, the amplitude was slightly overestimated. This difference is due primarily to the change in salinity in the presence of more-saline upwelled water, which impacted the estimation of δ18Owater used in the isotopic paleotemperature equation (Eq. 2). The accuracy in estimating the temperature by this

Fig. 7. Comparison of daily growth increments (grey continuous line), δ18Oshell (dark line in left panel) and δ13Cshell (dark line in right panel) for samples A1 (A–B), A2 (C–D), A3 (E–F), A4 (G–H). Arrows indicate the upwelling of July 1986.
paleotemperature equation was previously estimated at 0.53°C in the Bay of Brest (Chauvaud et al. 2005).

The carbon isotopic ratio was also used as a proxy of upwelling although the origin of its variability is still under debate (McConnaughey and Gillikin 2008, for review). However, it appears that the carbon employed during shell calcification depends on the metabolism of the shell, for example through respiration and feeding (Lorrain 2002; Lorrain et al. 2004; McConnaughey and Gillikin 2008), and on variations in dissolved inorganic carbon and food availability (Chauvaud et al. 2005). As previously hypothesized for the Bay of Brest (Lorrain et al. 2002; Chauvaud et al. 2005), in the present study the δ13C in Norwegian shells decreased over the entire lifetime of the organisms due to an increasing contribution of metabolic carbon to the shell during ontogeny (Chauvaud et al. 2011). During an upwelling event, the upwelled waters are depleted of 13C due to sedimentation and remineralization of organic matter (including plants rich in 12C) in the sediment-water interface. The CO2 produced was enriched in 12C and is preferred by the carbon anhydrase and incorporated into the calcite shell, impacting the shell’s carbon isotope signals (McConnaughey et al. 1997). Following these events, an enrichment of the δ13CDOC signal can be attributed to preferential uptake of 12C within the photic zone by phytoplankton during bloom events (Hellings et al. 2000), increasing δ13Cshell and reflecting changes in marine productivity during upwelling events (Killingley and Berger 1979; Jones and Allmon 1995; Sadler et al. 2012). Unlike these previous studies, the analyzed shells from Aустеволль did not exhibit significant variations in δ13C during the upwelling (Fig. 7). Perhaps the phytoplankton bloom induced by the upwelling was insufficient to impact δ13C in these shells. A Chl a concentration of 3 μg L⁻¹ remains modest compared to what has been observed in the Bay of Brest (Chauvaud et al. 1998; Lorrain et al. 2000; Chauvaud et al. 2005). However, the main reason for the discrepancies between our investigation and previous research may be the brevity and intensity of the event analyzed here. Indeed, previous studies (Killingley and Berger 1979; Kennett et al. 1997; Sadler et al. 2012) analyzed mollusc shells collected in the most active and seasonal upwellings in California, Iberia/Canary and Humbold ecosystems (Chavez and Messié 2009). Moreover, the incorporation time of carbon isotope signal in shells has been estimated of three to four days in Crassostrea gigas (Goodwin et al. 2013) and more than one week for Rudites philippinarum (Poulain et al. 2010) and for P. maximus (Marchais et al., unpubl).

In the present study, regional climatic phenomena acting on an oceanographic process clearly impacted a benthic invertebrate at 15–25 m depth. P. maximus could thus be used as an eulerian sensor to record both the frequency and the duration of upwelling. Analyzing the isotopic signals in scallop shells should allow us to describe the dynamics of both modern and past continental-shelf upwelling systems during the Holocene. Unlike the study of long-lived species such as Arctica islandica used to describe the dynamics of environmental conditions over one or more centuries (Schöne et al. 2005; Wanamaker et al. 2008), measurements from P. maximus are limited to less than 10 years per individual. However, the daily analysis provides a finer resolution, necessary to detect these local upwelling events. Thus, the study of P. maximus shells from archaeological sites or museum collections should provide narrow but high resolution time windows of paleoenvironment. Although the salinity data would not available to dissociate an upwelling event from a simple cool down episode, we have shown in this study that these events stand out by their intensities. Whereas the duration of upwelling events can be describe by the joint study of growth patterns and isotopic composition of scallop’s shells, their magnitude cannot. Finally, an analysis of the trace element composition and especially metals should be performed on these paleo-shells to identify water masses change occurring during an upwelling.

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