PALAIOS
Emphasizing the impact of life on Earth's history

PALAIOS, 2010, v. 25, p. 742–753
Research Article
DOI: 10.2110/palo.2010.p10-015r

# FORENSICS ON THE HALF SHELL: A SCLEROCHRONOLOGICAL INVESTIGATION OF A MODERN BIOLOGICAL INVASION IN SAN FRANCISCO BAY, UNITED STATES

DAVID H. GOODWIN,[1]* ANDREW N. COHEN,[2] and PETER D. ROOPNARINE[3]

[1]*Denison University, Department of Geosciences, Granville, Ohio 43023, USA;* [2]*Center for Research on Aquatic Bioinvasions, 5994 McBryde Avenue, Richmond, California 94805, USA;* [3]*California Academy of Sciences, Department of Invertebrate Zoology and Geology, 55 Music Concourse Drive, San Francisco, California 94118, USA*

*e-mail: goodwind@denison.edu*

## ABSTRACT

**Stable oxygen- and carbon-isotope profiles from recent specimens of the exotic oyster *Crassostrea gigas* collected in southern San Francisco Bay were analyzed in conjunction with *in situ* records of environmental variability to determine the timing of the initial biological invasion and the number of annual cohorts present. Two distinct patterns of isotopic ($^{18}O/^{16}O$ and $^{13}C/^{12}C$) variation were identified. The first, found in specimens collected alive from two sites in 2006, is characterized by several unique features that correlate with predicted oxygen-isotope values calculated from temperature and salinity measurements and with records of phytoplankton blooms, indicating that these oysters were recruited at the end of 2001 or early in 2002. The isotope profiles from other specimens differ from these, and do not show evidence of significant environmental events that occurred in 2003, 2004, and 2006, despite the fact that some of these oysters were also collected alive in 2006. These oysters were likely recruited between 1998 and 2000, based on shell growth rates estimated with the von Bertalanffy growth function and on the record of phytoplankton blooms. Poor resolution due to slowed shell growth associated with senescence probably accounts for the absence of the 2003–2006 environmental events in these shell isotope records. These findings indicate that at least two cohorts of *C. gigas* settled in San Francisco Bay in recent years. That two successful recruitment events occurred over a relatively short time suggests that further recruitment may occur. Such studies as the one conducted here can potentially be used to identify favorable environmental conditions or circumstances associated with past biological invasions as well as those likely to come.**

## INTRODUCTION

The extraordinary ecological consequences and economic costs associated with exotic species emphasize the need to understand the dynamics of biological invasions (Pimental et al., 2005). Unfortunately, in many instances, the environmental conditions and or vectors associated with individual invasions are unknown (Carlton, 2003), in part because basic facts about the invasion are often constrained poorly: for example, when did the invasion happen?

In 2006, several hundred adults of the non-native Pacific oyster, *Crassostrea gigas*, were discovered attached to hard media (=substrates) in San Francisco Bay, California, United States. The species is native to Japan, but has been cultured extensively in many parts of the world, including the west coast of North America from Alaska, United States to Baja California, Mexico. While cultured *C. gigas* have spawned regularly in coastal waters throughout much of this range, significant larval recruitment is rare (Carlton, 1979; Coan et al., 2000). Here, we take advantage of a technique often associated with paleontological research—sclerochronology—to constrain the timing of a modern biological invasion in San Francisco Bay, the abruptness of which suggests at least one, perhaps several episodes of successful larval recruitment in preceding years.

Sclerochronology, originally defined as the skeletal equivalent of dendrochronology (Hudson et al., 1976), is the study of physical and chemical variation in the accretionary skeletons of organisms (e.g., Jones, 1983; Wefer and Berger, 1991; Jones and Quitmyer, 1996). In the marine realm, sclerochronological studies have focused on a wide variety of invertebrate groups, including: mollusks (e.g., Davenport, 1938; Pannella and MacClintock, 1968; Evans, 1972; Jones et al., 1978, 1989; Jones, 1980; Koike, 1980; Steuber, 1996; Goodwin et al., 2001; Elliot et al., 2003; Schöne and Giere, 2005), corals (e.g., Wells, 1963; Dodge and Vaisnys, 1975; Hudson et al., 1976; Pätzold, 1984; Cole and Fairbanks, 1990; Gagan et al., 1994; Cole, 2003), bryozoans (e.g., Pätzold et al., 1987; Smith and Key, 2004; O'Dea, 2005), brachiopods (e.g., Buening and Carlson, 1992; Barbin and Gaspard, 1995; Tomašových and Farkaš, 2005), and arthropods (barnacles) (e.g., Killingley and Newman, 1982; Achituv et al., 1997; Schöne et al., 2006). In addition, numerous sclerochronologic studies have been carried out on freshwater and estuarine organisms (e.g., Patterson, 1999; Vander Putten et al., 2000; Dettman et al., 2001; Surge et al., 2001; Gillikin et al., 2005, 2006). While this list is far from exhaustive, sclerochronologic techniques clearly can be applied to most organisms with accretionary skeletons.

Sclerochronologic approaches have been used to address a wide range of biologic, climatologic, geologic and evolutionary hypotheses (e.g., Wells, 1963; Jones and Allmon, 1995; Dettman et al., 2004; Ivany et al., 2003, 2004; Goodwin et al., 2004, 2008). Several recent studies have focused on improving sclerochronologic techniques, including skeleton preparation techniques (e.g., Schöne et al., 2005), geochemical sampling techniques (e.g., Dettman and Lohmann, 1995; Wurster et al., 1999), and geochemical sampling strategies (e.g., Goodwin et al., 2003; Høie et al., 2004). Regardless, however, of taxonomic group, research question, or preparation technique, all sclerochronologic studies are fundamentally concerned with the temporal context in which the skeletal record formed.

A sclerochronologic archive can facilitate resolution of the order of events in the life of an organism, but in many cases the dates of specific events in the archive cannot be determined (i.e., a floating chronology). If, however, individual features of sclerochronologic records can be associated with events known to have occurred at specific times, skeletal archives can be related to calendar time and the dates of events can be resolved or constrained for the remainder of the chronology (i.e., a fixed chronology; Goodwin et al., 2001). For example, by using a live-collected organism with a known date of collection, we can assign precise calendar dates to the end (date of death) and potentially to other events in its sclerochronologic record.

* Corresponding author.

 0883-1351/10/0025-0742/$3.00

Our strategy in investigating the invasion of *C. gigas* is to determine the timing of larval recruitment by documenting the stable oxygen- and carbon-isotope ($\delta^{18}O$ and $\delta^{13}C$) profiles from shells of *C. gigas*, and calibrate these with *in situ* records of environmental variability. Our objectives are to (1) develop a minimum estimate of the time elapsed since the introduction of *C. gigas*, and (2) determine whether multiple year-classes of *C. gigas* are present in San Francisco Bay, since their presence would indicate substantial potential for the population to become permanently established. These results in turn may help environmental managers and policy makers to assess the status of the invasion and the value of eradication or control efforts, and to establish which of several possible mechanisms and transport events are most likely to have introduced the oyster.

## MATERIALS AND METHODS

The study area is located in San Francisco Bay, an estuary on the north-central coast of California, United States (Fig. 1). Ocean water enters the bay at the Golden Gate. The Sacramento and San Joaquin rivers provide 90% of the bay's freshwater inflow by way of the inland Delta region where these two major river systems join, while the remainder comes from local streams and treated wastewater discharges (Conomos, 1979). Inflow from the Delta is highly seasonal, with most arriving in the winter and early spring with storms and snowmelt (Conomos et al., 1979).

In July 2006, live *C. gigas* were discovered in southern San Francisco Bay—herein referred to as the South Bay—near the eastern end of the Dumbarton Bridge on California State Route 84. By the end of that year, 262 live and 7 dead *C. gigas* were collected from San Francisco Bay, with a mean shell height of 118 mm (range 71–223 mm). Nearly all of these were collected on the east shore of the South Bay from Hayward Landing to just south of Dumbarton Bridge, and all were collected in the intertidal zone. Each dead *C. gigas* collected consisted of a pair of valves attached by the hinge ligament, with the left valve firmly cemented to a rock or concrete structure. These valves pairs were in good, uneroded condition, similar to the shells of the live-collected *C. gigas*. They held no trace of oyster tissue; some were filled with mud and infaunal organisms, and in others the inner surfaces of the valves were colonized by attached epifauna. Single, unattached and highly eroded *Crassostrea* valves were encountered occasionally; these were assumed to be relics of commercial farming or experimental plantings of *Crassostrea* species, which ended in San Francisco Bay in the 1930s and by 1981, respectively (Carlton, 1979; T. Moore, personal communication, 2006); these were not included in the collections.

Five live *C. gigas* collected near Dumbarton Bridge and two collected at Hayward Landing were sacrificed shortly after collection and the flesh removed. Tissues were preserved for genetic analysis, which later confirmed their identity as *C. gigas* (P. Gaffney, personal communication, 2007). The left valves of these specimens and of one dead-collected specimen from the Dumbarton Bridge site (total of eight specimens) were cleaned, and the resilifer in each left valve was lightly abraded with a wire brush to remove the aragonitic ligostracum (Carriker and Palmer, 1979). Samples weighing ~50 µg were hand-drilled from the foliated calcite layer by drilling down ~1 mm into the ligamental area using a 300 µm diameter drill bit. Each shell was sampled from the umbo to the ventral margin of the resilifer. The isotope profiles derived from these samples thus reflect environmental conditions experienced during the span of shell growth, from settlement to death. All carbonate isotopic analyses were performed on a Finnigan MAT 252 mass spectrometer equipped with a Kiel III automated sampling device at the Environmental Isotope Laboratory, Department of Geosciences, University of Arizona. Samples were reacted with >100% orthophosphoric acid at 70 °C. Repeated measurement of standard carbonates resulted in standard deviations of ±0.08‰ for both oxygen and carbon. Results are reported in $\delta$ notation (‰) by calibration to the NBS-19 reference standard ($\delta^{13}C = +1.95$‰ and $\delta^{18}O = -2.20$‰ VPDB). Carbon and oxygen correlations coefficients were calculated using the statistical package STATA.

We can predict the oxygen isotopic composition of biogenic carbonate from water characteristics, as the oxygen isotopic composition of biogenic carbonate ($\delta^{18}O_{carb}$) incorporated in a bivalve shell is a function of the temperature and the oxygen isotopic composition of the water ($\delta^{18}O_{water}$) in which it grew (e.g., Epstein et al., 1953; Grossman and Ku, 1986). Since high-resolution $\delta^{18}O_{water}$ records do not exist for the South Bay for the appropriate time period, we estimated $\delta^{18}O_{water}$ values using the linear relationship derived by Ingram et al. (1996) from $\delta^{18}O_{water}$ and salinity data at three locations in the San Francisco Bay estuary, with a modified intercept as calculated by Gillikin et al. (2005) from a re-analysis of the data (which agrees with our own re-analysis):

$$\delta^{18}O_{water} = 0.32 * \text{Salinity} - 10.95$$

We then calculated the predicted $\delta^{18}O_{carb}$ values using South Bay temperature data and the equilibrium fractionation equation for water and calcite (Friedman and O'Neil, 1977):

$$10^3 \ln\alpha_{c-w} = 2.78 * \left(10^6 * T^{-2}\right) - 2.89$$

where T is temperature in Kelvin and $\alpha_{c-w}$ is the fractionation between calcite and water. We did not use the newer Kim and O'Neil (1997) relationship because of potential disequilibrium fractionation in their experiment (see Chivas et al., 2002). This equation returns $\delta^{18}O_{carb}$ values relative to VSMOW, which we converted to the VPDB scale using the VSMOW to VPDB fractionation factor: $\alpha = 1.03091$ (Gonfiantini et al., 1995). We compared the predicted $\delta^{18}O_{carb}$ values with the values measured in the South Bay *C. gigas* shells to identify specific years and anchor the chronologies.

For these calculations we used average daily temperatures and salinities calculated from measurements taken by the U.S. Geological Survey near the east end of the Dumbarton Bridge, for the water years 2002–2006 (water year = October 1 through September 30). These measurements were collected ~1 m below the surface every 15 minutes at the end of a fishing pier adjacent to the Bridge, ~0.75 km from shore (37°30.4′N, 122°07′W; http://pubs.usgs.gov/wri/wri034005/). They provide a nearly continuous record for the period, with occasional interruptions, most notably in 2005.

We also obtained data on the main freshwater inflows to San Francisco Bay, derived from the Sacramento River and San Joaquin River basins and entering the bay through the Delta, to investigate the effect of seasonal inflows on the oysters' oxygen isotope profiles. Delta outflow data were retrieved from the California Department of Water Resources Interagency Ecological Program for the 2002–2006 water years (http://iep.water.ca.gov/dayflow/). We obtained data on chlorophyll *a* (Chl *a*) concentrations collected by the U.S. Geological Survey at two locations in the South Bay (Stations 30 and 33; Fig. 1; http://sfbay.wr.usgs.gov/access/wqdata) to compare with the oysters' carbon isotope values. During phytoplankton blooms, photosynthetic algae preferentially assimilate $^{12}C$, which results in the enrichment of $^{13}C$ in the dissolved inorganic carbon of seawater ($\delta^{13}C_{DIC}$) (see Hellings et al., 1999, 2001; Gillikin et al., 2006). Phytoplankton blooms may appear as positive spikes in a shell's carbon isotope profile because bivalve shell $\delta^{13}C$ in part reflects $\delta^{13}C_{DIC}$ (Mook and Vogel, 1969; Gillikin et al., 2006, 2007).

The von Bertalanffy growth function (von Bertalanffy, 1938), a common model for shell growth in oysters and other bivalves (e.g., Berthome, 1986; Harding and Mann, 2006; MacLean and Palomares, 2008), to estimate the age of specimens whose isotopic variation was equivocal. The von Bertalanffy function describes growth that declines asymptotically as the organism approaches a maximum size, such that the growth increment in any year is a fixed proportion of the growth

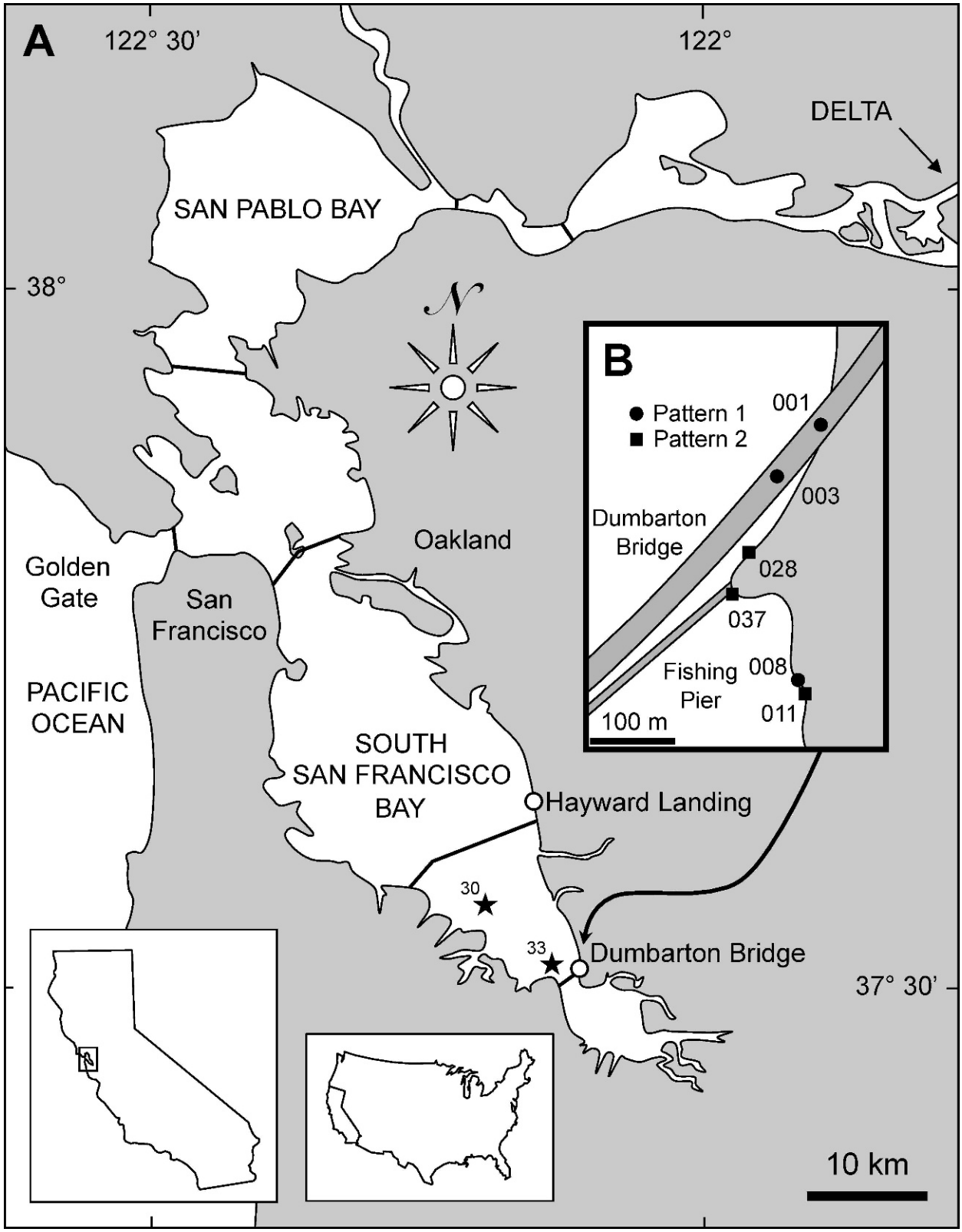


**FIGURE 1**—San Francisco Bay A) showing oyster shell collection sites = open circles; and chlorophyll sampling stations = stars. Heavy black lines mark the locations of bridges. B) Collection locations of *Crassostrea gigas* specimens from Dumbarton Bridge.

increment in the preceding year. That is:

$$\text{Increment}_n / \text{Increment}_{n-1} = R$$

where n–1 and n are subsequent years of life and the increment ratio R = $e^{-K}$, where K is the von Bertalanffy growth constant. We measured the sampling distance corresponding to each estimated calendar year to calculate the average R, and then used the average R to estimate the length of time represented by the sampling distance with equivocal isotopic variation.

## RESULTS

South Bay water temperatures and salinities during the 2002–2006 water years show strong seasonal variation, with the highest salinities recorded in late summer to early fall and low salinities in late winter (Figs. 2A and B). The lowest salinity of the period was in 2006, when there were two distinct salinity minima, and the second lowest annual salinity was in 2004. The low salinity records in the South Bay correlate with large Delta outflows (Fig. 2C), with two major outflow pulses in 2006 corresponding to the two salinity minima that year, and the highest and second highest annual outflows in 2006 and 2004, respectively, corresponding to the lowest and second lowest annual salinities.

The most obvious feature in the predicted $\delta^{18}O_{carb}$ values (Fig. 2D) is a prominent annual cyclicity, with the most enriched $\delta^{18}O_{carb}$ ratios occurring in the early winter over a two-and-a-half-week period between November 29 and December 17. These winter peaks are all approximately the same (range = 0.57‰). The minimum values occur in the spring or early summer over a 3-month period from March 20 to June 26, and show greater interannual variation (range = 4.44‰). The 2002, 2003, and 2005 minimum values fall within a ~1.5‰ range (−4.19‰ to −5.75‰). The 2004 minimum value is lower (−6.57‰), and the 2006 minimum is lower still (−8.64‰ on May 1, 2006), and was preceded by a distinct minimum earlier in the year (−5.99‰ on January 22, 2006). This reflects the patterns of variation in Delta outflow and South Bay salinity (Figs. 2B and C).

Stable oxygen- and carbon-isotope profiles from the eight specimens examined in this study are shown in Figures 3 and 4. Like the environmental factors and the model results, the profiles show strong seasonal variation. Though the shapes of the seasonal cycles in the $\delta^{18}O$ and $\delta^{13}C$ profiles often differ, with greater asymmetry—concave-down cycles rising gradually and falling steeply—in the $\delta^{18}O$ than in the $\delta^{13}C$ profiles, and the maxima and minima in the $\delta^{18}O$ and $\delta^{13}C$ profiles do not always coincide, the $\delta^{18}O$ and $\delta^{13}C$ profiles are positively correlated: Pearson product-moment correlation coefficients range between 0.32 and 0.69; 7 of the 8 shells have $p$ values less than 0.04, for specimen 011, $p = 0.08$. Another feature, seen in both the $\delta^{18}O$ and $\delta^{13}C$ profiles, is the progressive compression of the cycles; that is, in most cases each succeeding cycle comprises a smaller sample distance than the preceding one.

The specimens exhibit two distinct patterns of $\delta^{18}O$ and $\delta^{13}C$ variation. The first pattern is exemplified by specimen 003 (Fig. 3A), which shows four complete concave-down cycles in both the $\delta^{18}O$ and $\delta^{13}C$ profiles, with the possible end of an initial cycle near the umbo (left side of Fig. 3A), and the beginning of another, final cycle at the ventral margin of the resilifer (right side of Fig. 3A). Thus, five minima (filled arrows on the oxygen profile in Fig. 3A), define the end of an initial concave-down cycle, followed by four complete cycles and the beginning of a fifth. In the $\delta^{18}O$ profile, the most enriched (positive) values from each of the four complete cycles are approximately equal (range = 0.30‰), whereas the negative troughs are considerably more variable (range = 2.05‰). The values of the first, second, and fourth troughs are similar (~−3.00‰), whereas the third trough is lower, and the fifth is lowest. In the $\delta^{13}C$ profile, the most striking feature is the presence of a prominent ~1‰–2‰ spike near the end of the first cycle (open arrow in Fig. 3A). Together, these features characterize the first pattern of isotopic variation (Isotopic Pattern 1). Five shells (herein referred to as Group 1) all show this pattern—001, 003, and 008, collected live at the Dumbarton Bridge site, and 018 and 021, collected live at Hayward Landing (Fig. 3; Table 1)—except that the features at either end of the record (the end of an initial cycle and the start of a final cycle) are not seen in some of the profiles, possibly due to settlement times that differ by a few months or some erosion of the ends of the resilifers.

The features described in the $\delta^{18}O$ profiles of these five shells match the pattern in the predicted $\delta^{18}O_{carb}$ values, with a narrow range for the winter peaks, a broader range for the spring–summer troughs, similar values for the first, second and fourth troughs, a lower value in the third trough, and the lowest value in the fifth trough (Fig. 2D). This correspondence between the predicted and observed $\delta^{18}O$ profiles suggests that the observed profiles cover a period from the end of 2001 or early 2002 to 2006. In the predicted profile, peak annual $\delta^{18}O$ values occur between November 29 and December 17; in Figure 3, vertical lines were positioned just after each peak $\delta^{18}O$ value to mark the estimated beginning of a new calendar year. The carbon spike in the $\delta^{13}C$ profile near the end of the first concave-down cycle should thus correspond to shell growth that occurred in the spring of 2003 (Fig. 3). Figure 5 shows a time series of calculated Chl *a* concentrations from two sites in the South Bay, Station 30, which is closer to Hayward Landing, and Station 33, which is closer to the Dumbarton Bridge (see Fig. 1). The annual spring phytoplankton blooms, which are a well-known feature of the South Bay (see Cloern, 1996; Cloern et al., 2007 for detailed discussions), are clearly visible, and the pattern of annual variation is generally similar at the two stations, indicating that this pattern is a regional phenomenon applying to this portion of the South Bay. At both stations the largest bloom between early 2002 and the late summer of 2006—the approximate lifespan of the Group 1 oysters as determined from their $\delta^{18}O$ profiles (horizontal bars in Fig. 5)—occurred in the spring of 2003. As noted earlier, dissolved inorganic $^{13}C$ is enriched in seawater during phytoplankton blooms, so the carbon spikes in the isotope profiles of Group 1 probably reflect changes in $\delta^{13}C_{DIC}$ associated with the large 2003 phytoplankton bloom.

The second pattern of $\delta^{18}O$ and $\delta^{13}C$ variation (Isotopic Pattern 2) is exhibited by the profiles in Figure 4, from two live-collected specimens and a pair of empty valves, all collected near the Dumbarton Bridge in the same location as the oysters profiled in Figures 3A–C (see Fig. 1B). In Figure 4, the first portion of each $\delta^{18}O$ and $\delta^{13}C$ profile contains three concave-down cycles. The remainder of each profile is characterized by a lack of clear cyclicity, though it is possible to pick out patterns that may represent additional cycles. In the $\delta^{18}O$ profiles, there is a general trend toward more enriched values after the third cycle, while the $\delta^{13}C$ values vary over a 1.5‰–2.6‰ range without an upward or downward trend.

The profiles of these three specimens (herein referred to as Group 2) differ in several key features from those of Group 1: the annual troughs in the $\delta^{18}O$ profiles of Group 1 follow a regular pattern (1st, 2nd, and 4th troughs approximately equal, 3rd trough lower, 5th trough lowest) that matches the pattern in the predicted values for 2002–2006, but which is not exhibited by Group 2; in Group 1, $\delta^{18}O$ reaches its lowest value near the end of the record, while the Group 2 $\delta^{18}O$ values rise during the last third to half of the record; and the prominent carbon spike near the end of the first concave-down cycle in Group 1 is absent from Group 2. In addition, the maximum and minimum $\delta^{13}C$ values are consistently lower for oysters in Group 1 compared to Group 2: maximum values range from −3.73 to −3.41 in Group 1 and from −2.99 to −2.73 in Group 2, minimum values range from −8.37 to −7.21 in Group 1 and from −6.86 to −5.74 in Group 2. Finally, the proportional length of the profile that occurs after the end of the third concave-down cycle is much larger in Group 2 oysters (30–47% of the $\delta^{18}O$ profile and 27–43% of the $\delta^{13}C$ profile) than in Group 1 (9–17% of the $\delta^{18}O$ profile and 9–19% of the $\delta^{13}C$ profile).

Age estimates of individual specimens based on the von Bertalanffy growth function are shown in Table 2. For Group 1, the mean estimated time following the animals' 3rd calendar year of life is 1.2 years (range 0.8–1.5 years). The mean estimated age of these oysters, assuming that there has been no significant erosion of the resilifer, and not counting the 2–4 weeks of the typical planktonic larval stage, is 4.6 years (range 3.9–5.5 years). This agrees well with our estimates of ~1.6 years after the 3rd calendar year and 4–4.5 years for the entire profile, which are based on the correspondence of the observed profiles

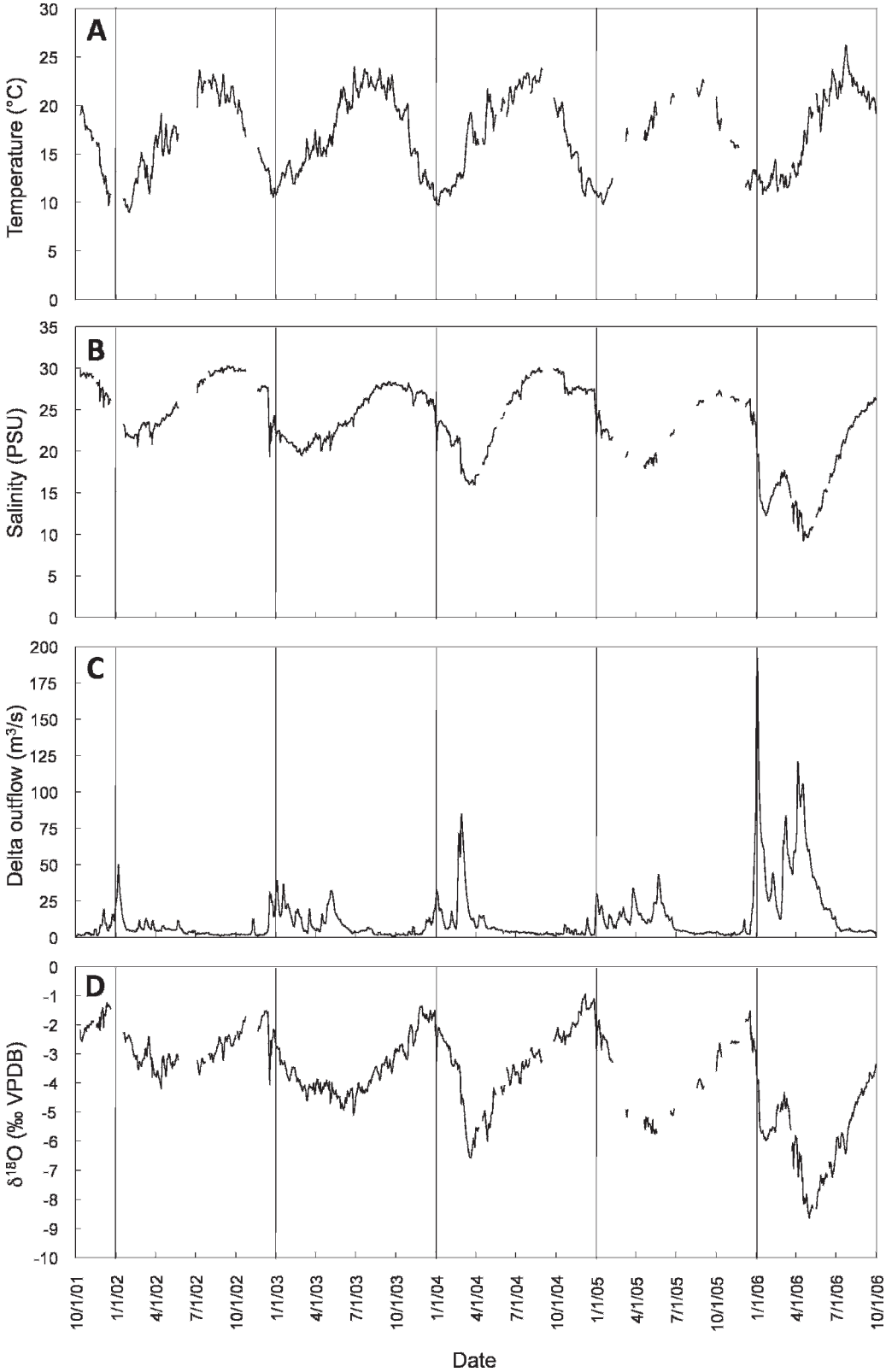


**FIGURE 2**—Average daily temperature A) and salinity B) calculated from U.S. Geological Survey measurements at the end of the fishing pier adjacent to the east end of the Dumbarton Bridge; Delta outflow C) estimated by the California Department of Water Resources Interagency Ecological Program; and predicted oxygen-isotope profiles for mollusk shell calcite in south San Francisco Bay D). Vertical lines mark the beginning of each calendar year.

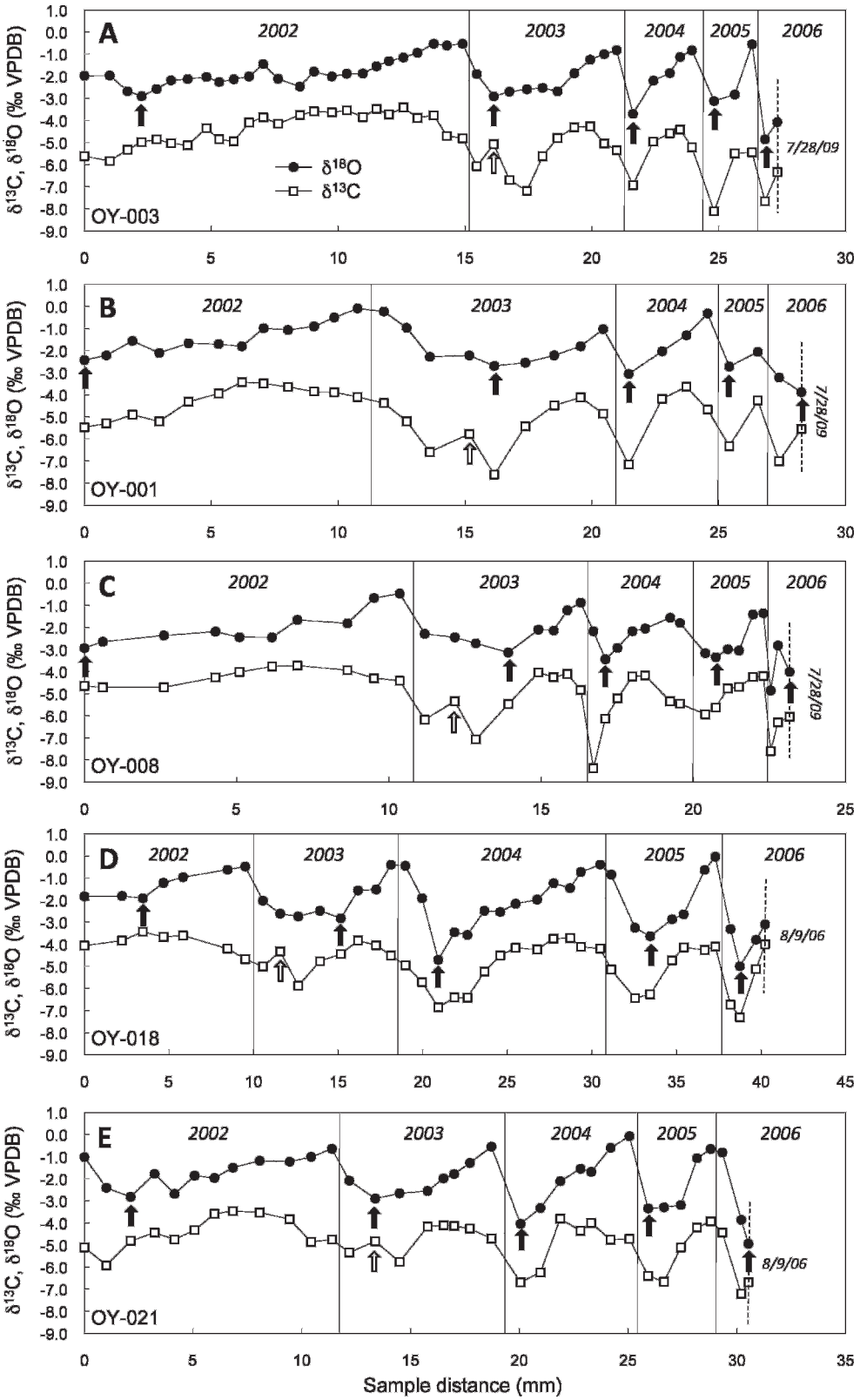


**FIGURE 3**—Oxygen- and carbon-isotope profiles of five live *Crassostrea gigas* collected at Dumbarton Bridge and Hayward Landing in 2006 (Isotopic Pattern 1). Vertical dashed lines and dates near the right side of the graphs mark the collection dates. Vertical solid lines represent the approximate beginning of each estimated calendar year at the top of the graph, based on correlations with predicted $\delta^{18}O$ values as described in the text. Filled arrows mark the end of each concave-down cycle and the open arrow marks the carbon spike.

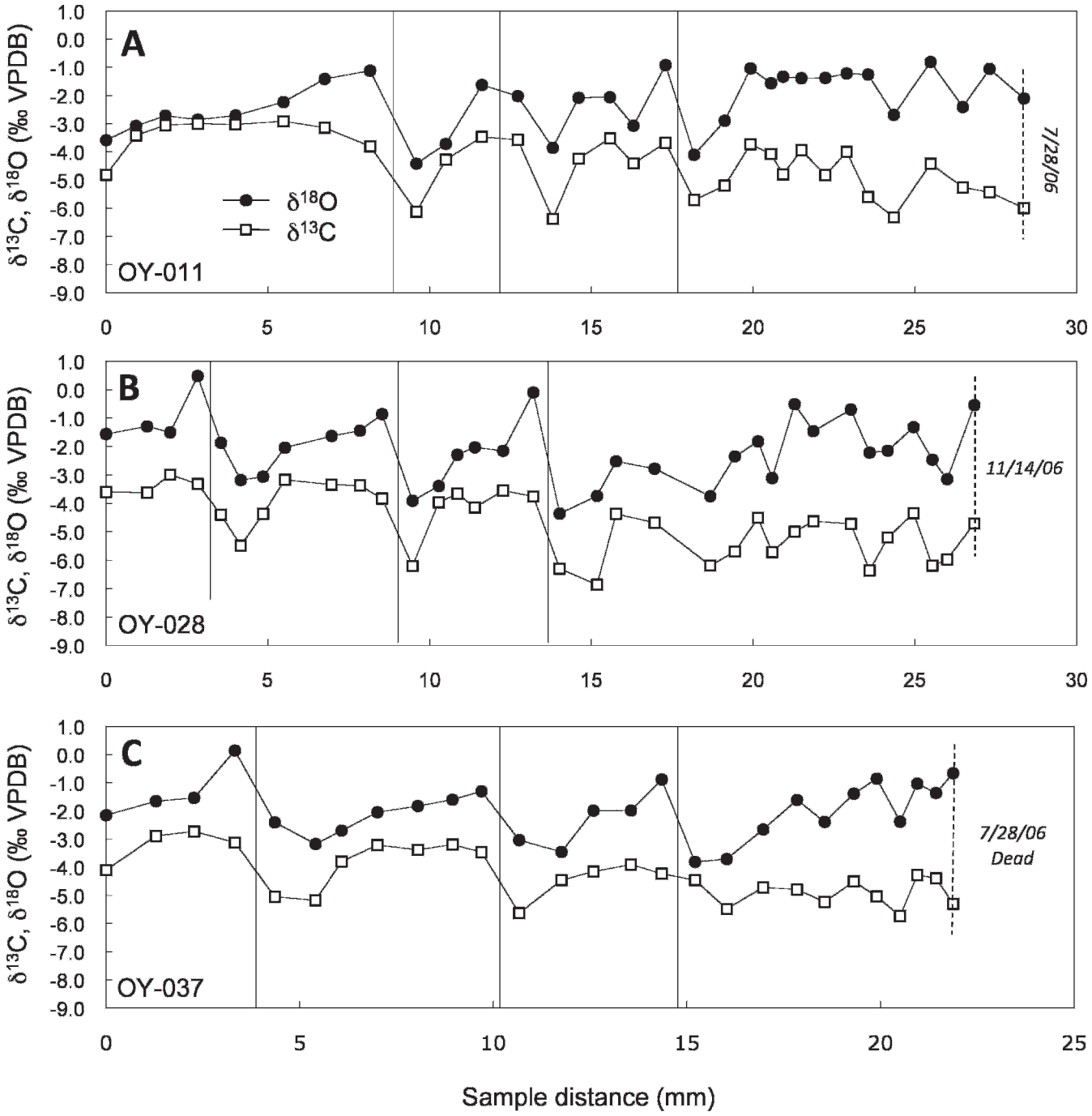


**FIGURE 4**—Oxygen- and carbon-isotope profiles of two live *Crassostrea gigas* and one shell collected dead at Dumbarton Bridge in 2006 (Isotopic Pattern 2). Vertical dashed lines and dates near the right side of the graphs mark the collection dates. Vertical solid lines represent the approximate beginning of an estimated calendar year as described in the text.

with environmental factors and the known time of collection. In contrast, the estimates for the two live-collected oysters in Group 2 (specimens 011 and 028) are 5.1 and 5.9 years after the 3rd calendar year and 8.6 and 8.3 years for the entire profile.

## DISCUSSION

The observed $\delta^{18}O$ profiles for the five Group 1 shells (Fig. 3) are similar to the predicted $\delta^{18}O_{carb}$ profile (Fig. 2D), which is based on South Bay salinity and temperature data for the 2002–2006 water years (Figs. 2A and B). Each of the $\delta^{13}C$ profiles for these shells contains a spike near the end of the first concave-down cycle (Fig. 3), which, based on the correspondence between the predicted and observed $\delta^{18}O$ profiles, would have occurred in the spring of 2003, coincident with the largest algal bloom of the period (Fig. 5). These correspondences provide compelling evidence that the Group 1 oysters settled at the end of 2001 or early in 2002, and were about 4–4.5 years old when they were collected in the summer of 2006.

There are three notable differences between the predicted and observed profiles from Group 1 oysters. First, in the predicted $\delta^{18}O$ profile, time is plotted on the x-axis (Fig. 2D), whereas sample distance is shown on the x-axis in the observed profiles (Fig. 3). In the observed profiles, the distance between successive minima—or maxima—decreases, indicating an ontogenetic decrease in growth rate (King,

**TABLE 1**—Data collected from *Crassostrea gigas* specimens analyzed.

| Specimen | Locality* | Collection date | Collection condition | Valve height (mm) | Valve length (mm) | Valve width (mm) | Isotopic pattern | $\delta^{18}O$ max. | $\delta^{18}O$ min. | $\delta^{13}C$ max. | $\delta^{13}C$ min. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 003 | DB | 7/28/06 | live | 110 | 71 | 39 | 1 | −0.53 | −4.86 | −3.41 | −8.12 |
| 001 | DB | 7/28/06 | live | 160 | 126 | 42 | 1 | −0.09 | −3.88 | −3.42 | −7.61 |
| 008 | DB | 7/28/06 | live | 134 | 108 | 46 | 1 | −0.47 | −4.85 | −3.73 | −8.37 |
| 018 | HL | 8/9/06 | live | 122 | 81 | 30 | 1 | −0.04 | −4.99 | −3.44 | −7.30 |
| 021 | HL | 8/9/06 | live | 223 | 120 | 48 | 1 | −0.07 | −4.94 | −3.46 | −7.21 |
| 011 | DB | 7/28/06 | live | 152 | 104 | 40 | 2 | −0.81 | −4.42 | −2.91 | −6.37 |
| 028 | DB | 11/14/06 | live | 122 | 79 | 46 | 2 | −0.48 | −4.36 | −2.99 | −6.86 |
| 037 | DB | 7/28/06 | dead | 119 | 88 | 47 | 2 | −0.14 | −3.81 | −2.73 | −5.74 |

* DB, Dumbarton Bridge; HL, Hayward Landing

1995; Appleyard and Dealteris, 2001; Goodwin et al., 2003). Thus, the later years in the observed profiles are compressed, and represented by fewer samples (see Goodwin et al., 2003).

Second, the predicted range of $\delta^{18}O$ variation is generally more negative than the observed ranges. The maximum predicted values for each year are between −2‰ and −1‰, whereas most of the observed maxima are between −1‰ and 0‰. Similarly, minimum predicted values (ranging between ~−8.5‰ and −4‰) are also more negative than the observed minima (ranging between −5‰ and −2‰). This is particularly evident in the years with large Delta outflows. The predicted minimum values for 2004 and 2006 are −6.57‰ and −8.64‰, respectively (Fig. 2D), whereas the lowest observed $\delta^{18}O$ values from these years were −4.71‰ and −4.99‰ (Fig. 3). This offset likely reflects the influence of several factors. First, the 95% confidence interval around the regression line for Ingram et al.'s (1996) salinity and $\delta^{18}O_{water}$ data indicates that between 20 and 35 PSU, $\delta^{18}O_{water}$ values can vary as much as 2‰ (see Gillikin et al., 2005). Second, the Ingram et al. (1996) equation is based on paired salinity–$\delta^{18}O_{water}$ measurements collected from three sites in the San Francisco Bay estuary: one in the northern part of the South Bay, another from San Pablo Bay, and a third in the Sacramento River. As the South Bay is influenced by a somewhat different combination of hydrologic factors than the sites in the northern portion of the estuary (Conomos, 1979; Conomos et al., 1979; Hager and Schemel, 1996), the salinity–$\delta^{18}O_{water}$ relationship in the South Bay is likely also somewhat different. Third, the Ingram et al. (1996) data were collected over 15 years ago and local hydrologic conditions may have changed, which in turn could alter the $\delta^{18}O$ of the freshwater end member of the mixing relationship. Finally, each sample was taken from a 300 µm diameter drill hole, with 300–500 µm of space between holes, so the samples could miss a sharp maximum or minimum, sampling from the slope on either side instead. In addition, each sample produces a weighted average across 300 µm of shell, which could represent a period of weeks or months (Goodwin et al., 2003). These sampling issues would tend to result in observed maxima and minima that are muted relative to the predicted maxima and minima.

The third difference between the predicted profiles and the observed profiles of Group 1 is that there are two distinct $\delta^{18}O_{carb}$ minima in the predicted profile in 2006 (Fig. 2D), resulting from two distinct pulses of Delta outflow (Fig. 2C), which produced two distinct salinity minima in the South Bay (Fig. 2B). There are no second minima in the final cycles of the observed profiles, however (Fig. 3). As noted, shell growth rates tend to decline as mollusks age, which decreases the resolution of isotope profiles based on time-averaged samples (Goodwin et al., 2003). Thus, our sampling resolution in shell representing the 4th or 5th year of an oyster's life may have been insufficient to distinguish the records of environmental events occurring 3 months apart.

In contrast to the shells in Group 1 (Fig. 3), the specimens in Group 2 show a quite different pattern of isotopic variation (Fig. 4). None of the diagnostic features characteristic of Isotopic Pattern 1 can be identified in these profiles—the distinctive order and position of $\delta^{18}O$ minima, and the carbon spike—indicating they were influenced by a different set of environmental conditions. If these two groups of oysters belong to the same cohort, they must have been exposed to two distinct water regimes, which differed in isotopic ratios and or temperatures. This could only occur if the two groups of oysters were spatially separated, such that they were bathed in water from different sources.

The two groups, however, were intermixed in the area near the east end of the Dumbarton Bridge (Fig. 1B). Group 1 oysters were found both north and south of Group 2 oysters, and specimens 008 (Group 1) and 011 (Group 2) were growing on top of the same abandoned culvert, at the same tidal elevation, separated by no more than about 10 m. The $\delta^{18}O$ profiles of Group 1 correspond closely to the profile predicted from the regional salinity and temperature patterns in the South Bay, with the salinity values largely reflecting the inflow of large volumes of freshwater from the Delta into the northern part of the bay. The other inputs of water that are closest to the Dumbarton Bridge collection site are Newark Slough, 3 km to the south around Dumbarton Point, and Coyote Slough, over 6 km to the north. It is inconceivable that oysters in Group 2 could have been predominantly exposed to these or other, more distant distinct water inputs, over a period of four or more years, while the Group 1 oysters, spatially intermixed with Group 2 oysters and growing in some cases less than 10 m away, were predominantly exposed to Delta inflows. The two groups, therefore, must represent two distinct cohorts.

How old, then, is the second group of oysters? In Figure 4, vertical lines have been placed just after the peak $\delta^{18}O$ values in each of the three clear concave-down cycles in the younger part of the profiles. As in Figure 3, each of these vertical lines should approximate the end of a calendar year. The part of the profiles to the right of the third vertical line in Figure 4, which lacks well-defined cyclicity, represents an unknown number of years of growth after the oysters' third calendar year of life. Subtracting the estimated life spans (Table 2) from the known dates of collection yields estimated settling dates in December 1997 for specimen 011 and July 1998 for specimen 028. Given the variance in R ($R = 0.80 \pm 0.11$ (SE) and $K = 0.22$) and the sensitivity of the calculations to average R, these settlement dates are uncertain; but it nonetheless seems clear that these two oysters at least represent a separate cohort from Group 1, older by some years. We do not exclude the possibility that 011 and 028 could represent two distinct older cohorts: since (unlike Group 1) we were unable to match any significant features in their isotope profiles, we cannot tell if they settled in the same year.

To check the estimated ages of these two oysters, we would ideally match features of their isotope profiles with known environmental perturbations. Since these oysters were collected alive in the latter half of 2006, they must have experienced the winter–spring low salinity events in 2004 and 2006 as well as the spring 2003 phytoplankton bloom. Since none of these events are apparent in the three well-defined concave-down cycles of the oysters' isotope profiles (left side of Figs. 4A and B), the events probably occurred later in the oysters' lives, during the period when the isotope profiles lack well-defined cyclicity. This lack of cyclicity is probably a function of slowed shell growth

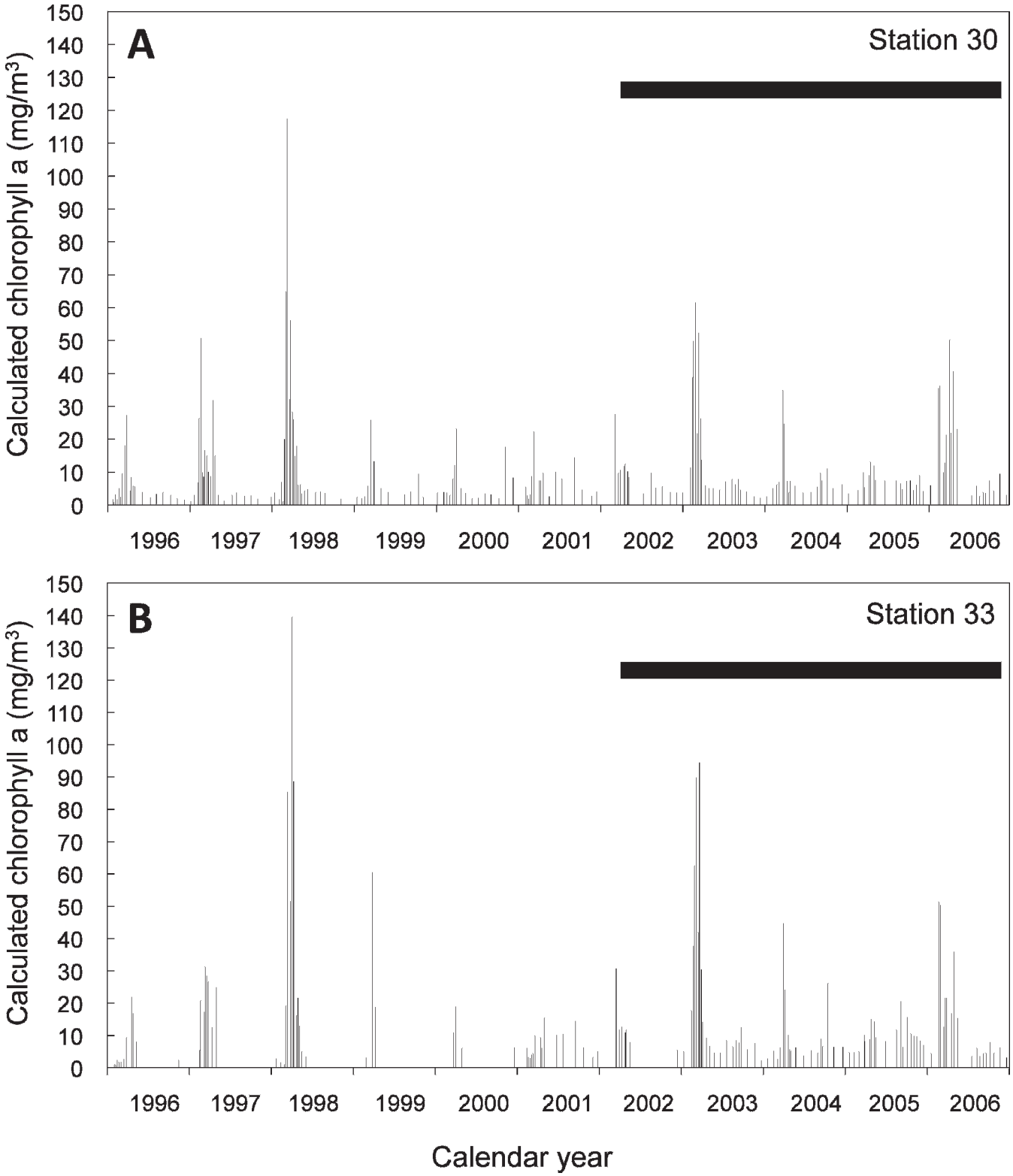


**FIGURE 5**—Time series of calculated chlorophyll a concentrations from two sampling stations in the South Bay (see Fig. 1 for locations). Horizontal bars represent approximate lifespan of specimens in Group 1.

associated with senescence (King, 1995; Appleyard and Dealteris, 2001; Goodwin et al., 2003), which results in poorer resolution of seasonal cycles due both to time averaging (Goodwin et al., 2003) and to the unsampled shell material between drill holes representing greater amounts of time and thus greater chances for the isotope profiles to miss distinctive features. Thus, we would expect the $\delta^{13}C$ spike and the $\delta^{18}O$ minima of 2004 and especially 2006, which are conspicuous in the Group 1 profiles, to be inconspicuous or missing from the profiles of oysters that are several years older.

Despite our inability to establish the exact age of the second group of oysters, we may be able to constrain the timing of their recruitment. The Chl *a* record from the South Bay indicates that, in addition to the

**TABLE 2**—Estimated time represented by portions of the isotope profiles, based on the Von Bertalanffy growth function.

| Specimen | Isotopic pattern | Ontogenetic age after 3rd calendar year (years) | Complete ontogenetic age (years) |
|---|---|---|---|
| 001 | 1 | 0.8 | 3.9 |
| 003 | 1 | 1.1 | 5.5 |
| 008 | 1 | 1.5 | 5.3 |
| 018 | 1 | 1.4 | 4.1 |
| 021 | 1 | 1.1 | 4.3 |
| 011 | 2 | 5.1 | 8.6 |
| 028 | 2 | 5.9 | 8.3 |
| 037 | 2 | 2.2 | 4.7 |

large 2003 phytoplankton bloom, a substantially larger bloom occurred in the spring of 1998 (Fig. 5). If we are correct in our supposition that the 2003 carbon spike in the Group 1 profiles reflects a bloom-associated enrichment of $^{13}C$ in dissolved inorganic carbon, then we would expect to see an at least equally prominent carbon spike in the isotope profiles of any oysters that were living in the South Bay in the spring of 1998. The absence of any apparent carbon spike in the three clear cycles at the start of the Group 2 isotope profiles suggests that these oysters settled after the spring 1998 bloom and at least three years before the spring 2003 bloom, that is, between spring 1998 and spring 2000, which is roughly consistent with the estimates based on shell growth rates. Alternatively, these specimens could have recruited prior to 1995—that is, at least three years before the 1998 bloom—though this is inconsistent with the shell growth rate estimates.

Specimen 037, the third specimen in Group 2, was estimated by the von Bertalanffy growth function to have a somewhat longer period of shell growth after the end of the 3rd calendar year compared to the Group 1 oysters, but an estimated overall lifespan about equal to theirs (Table 2; Fig. 4C). This specimen was collected as a pair of empty valves, devoid of soft tissue, in July 2006 at the same time the first Group 1 oysters were collected. These factors, the absence of any of the distinctive Group 1 features in its isotope profiles, their overall similarity to the other Group 2 profiles, and the absence of a carbon spike in any of its first three concave-down cycles, suggest that it is older than the Group 1 oysters, probably settled between spring 1998 and spring 2000, and possibly settled at the same time as the other Group 2 specimens.

Taken together, the data presented here shed light on the complex history of recruitment of *C. gigas* in San Francisco Bay. The $\delta^{13}C$ and $\delta^{18}O$ profiles from specimens in Group 1 indicate that a successful recruitment event occurred in late 2001 or early 2002 in at least two localities, at Dumbarton Bridge and Hayward Landing. The specimens in Group 2 clearly represent one or more older cohorts, although the timing of their settlement is uncertain. The most likely scenario is that they arrived in the bay sometime after the 1998 phytoplankton bloom and before the first part of 2000.

This analysis produced two results of interest to resource managers. First, the presence of at least two cohorts indicates that the unusually large (for the region) settlement observed in San Francisco Bay was not a one-time occurrence, resulting from a low probability coincidence of favorable factors, but rather is an event that happened at least twice in recent years, and thus may reasonably be expected to occur again. For managers this means that the risk of the population becoming permanently established is significant, and that efforts to eradicate *C. gigas* from the bay may be of value. Second, the invasion occurred at least as early as the settlement of the oldest oysters analyzed in this study, or sometime in or before early 2000. This conclusion may help researchers determine the mechanism(s) responsible for the invasion, which is a necessary step toward preventing similar invasions in the future. Furthermore, because we accurately established the timing of recruitment of the specimens in Group 1, the potential exists to link specific environmental conditions with a successful biological invasion. Therefore, special attention should be paid to the environmental conditions that existed in the South Bay early in 2002.

## CONCLUSIONS

Stable oxygen- and carbon-isotope profiles from recent specimens of the non-native Pacific oyster *Crassostrea gigas* collected in San Francisco Bay were compared with *in situ* records of inter-annual environmental variation. The following conclusions were reached based on these comparisons:

1. Two distinct patterns of isotopic variation were identified in the shells analyzed in this study. The first, Isotopic Pattern 1, found in specimens from two localities (Dumbarton Bridge and Hayward Landing), is characterized by strong cyclicity, low $\delta^{18}O$ values at the start of the 3rd and 5th concave-down cycles, and a prominent ~1‰–2‰ carbon spike near the end of the 1st cycle. The second, Isotopic Pattern 2, found in specimens from a single locality (Dumbarton Bridge) has three clear cycles at the beginning of both the $\delta^{18}O$ and $\delta^{13}C$ profiles, followed by an interval lacking clear cyclic variation but with a general trend toward more enriched $\delta^{18}O$ values, a greater length of shell growth after the 3rd cycle than in the Group 1 oysters, and higher $\delta^{13}C$ values than in the Group 1 oysters.
2. A predicted $\delta^{18}O_{carb}$ profile based on temperature and salinity data from the South Bay for water years 2002–2006 displays pronounced annual cyclicity and has a distinctive rank order of annual $\delta^{18}O$ minima, which reflects the influence of Delta outflow.
3. Isotopic Pattern 1 closely correlates with the predicted $\delta^{18}O_{carb}$ profile. Furthermore, the carbon spike correlates with an unusually large phytoplankton bloom that occurred in spring 2003. These indicate that the observed isotope variations in the Group 1 shells reflect regional environmental changes in South Bay during water years 2002–2006, with recruitment at the end of 2001 or early in 2002.
4. The isotope profiles from the other specimens examined here (Group 2) do not correlate with environmental variations during water years 2002–2006 despite the fact that some were collected alive in 2006. The inability to correlate these records likely reflects poor sample resolution in the latter part of the isotope profiles of Group 2 associated with slow growth of older individuals. These observations, the record of phytoplankton blooms in the South Bay, and estimates of the age at death based on shell growth rates modeled with the von Bertalanffy growth function, suggest that Group 2 probably settled between 1998 and 2000.
5. These findings indicate that at least two annual cohorts of *C. gigas* have settled in San Francisco Bay in recent years. That two successful recruitment events occurred over a relatively short time, suggests that further recruitment of this species is likely.
6. This study highlights the utility of sclerochronology for understanding biological invasions. The ability to correlate skeletal archives with records of environmental variation can help researchers and resource managers to establish the timing and status of a particular invasion. Furthermore, and perhaps more significantly, analyses like the one conducted here can potentially be used to identify favorable environmental conditions or circumstances associated with past biological invasions as well as those likely to come.

## ACKNOWLEDGMENTS

We acknowledge the contributions of Andy Chang at the University of California, Davis, who discovered the first *C. gigas* shells in the bay in 2004, Rena Obernolte who found the first live oysters, and Patrick Gaffney at the University of Delaware who identified the oysters through molecular genetics. Thanks also to David P. Gillikin for insightful discussions of carbon isotopes. The California State Coastal

Conservancy, the San Francisco Bay Regional Monitoring Program for Trace Substances, the National Fish and Wildlife Foundation, the San Francisco Bay Joint Venture, and Denison University provided the funding for this study. We are grateful to Dana Geary and three anonymous reviewers whose detailed comments and recommendations greatly improved the original manuscript.

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ACCEPTED AUGUST 17, 2010