

Predator-prey dynamics in Sydney Harbour: five millennia of naticid predation

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This thesis is written in the form of a journal article from *Palaio*, with a few exceptions to the author instructions: (1) figures and figure captions are embedded into the body as opposed to being contained in separate files, (2) line spacing is 1.5x, as requested by Macquarie University, and (3) the thesis is written in Australian English, rather than US English.

Declaration

All research described in this report is my own original work and has not been submitted for a higher degree to any other university or institution.



Kathleen Perry

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Abstract

Predation shapes communities by altering the relative abundances of species and the flow of energy through the food web. The structure of food webs and predator-prey interactions are vulnerable to anthropogenic disturbances, particularly in high-density urbanised environments such as estuaries. Drill holes in mollusc shells provide evidence of predation by gastropods on their prey. They can therefore be used to measure predation frequency and how predation frequency may have changed over time. This study quantifies the intensity of drilling predation in the three most common bivalve species (*Callista disrupta*, *Chioneryx cardioides*, and *Fulvia tenuicostata*) in Sydney Harbour over the last 5 thousand years in the context of European colonisation. Surficial death assemblage drilling frequencies are also compared to a global compilation of drilling frequency studies, which indicate that the drilling frequencies in Sydney Harbour are similar to other locations in terms of the overall magnitude of predation and the variation amongst taxa at a site. Drilling predation is an important control within the molluscan community of Sydney Harbour, with 30-70% of individuals drilled over the last 5ka. During the time period that includes the European colonisation and subsequent urbanisation *Fulvia* drilling frequency declines to approximately half the pre-colonial predation rate. However, *Callista* and *Chioneryx* record a consistent drilling frequency over the past ~2,000 years. This suggests that the European colonisation of Sydney had species specific impacts on gastropod-bivalve predator-prey interactions.

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INTRODUCTION

Humans have broad and disproportionate impacts on ecosystems. Urbanisation has resulted in habitat loss and the alteration of community structure and biotic interactions (Klein et al. 2011; Stuart-Smith et al. 2015; Mayer-Pinto et al. 2018). These changes result in disturbances to ecosystem functioning and stability (Hautier et al. 2015) and can ultimately lead to ecosystem collapse (Connell et al. 2017).

Coastal ecosystems are vulnerable due to their environmental complexity and high concentration of human populations (Crain et al. 2009). The access to both land and sea-based resources in coastal ecosystems has resulted in the near coast zone (<100 m elevation and <100 km from the sea) becoming densely populated and highly urbanised, containing 27% of the global population in 9% of the Earth's total land surface area (Kummu et al. 2016). The concentration of human activities in coastal environment has resulted in rapid transformations to the ecosystems (Cloern et al. 2016).

Sydney Harbour (NSW, Australia) is a tide-dominated estuary and drowned river valley, created ~10,000 years ago following sea level rise after the last glacial period (Hutchings et al. 2013; Johnston et al. 2015). Sydney Harbour contains a diversity of habitats, including mangroves, seagrass, subtidal rocky reefs, rocky intertidal shores, and soft sediment (Johnston et al. 2015). These habitats support a high diversity of marine life, particularly in comparison to nearby bays and estuaries (Hutchings et al. 2013). However, the biodiversity of Sydney Harbour is threatened by anthropogenic disturbances. Sydney, Australia's largest city with a population of 5 million (ABS 2016), is built around the harbour. The urbanisation of Sydney Harbour's catchment has resulted in habitat modification, chemical contamination, and introduced species, all of which are key threats to the ecosystem stability and biodiversity of marine life in the harbour (Mayer-Pinto et al. 2015).

The shoreline of Sydney Harbour has been heavily modified over that last 200 years. Throughout the 19th and early 20th century, Sydney industrialised and became an important centre for the distribution and manufacturing of goods (Banks et al. 2016). This resulted in the alteration of shorelines to accommodate factories and shipping, with the construction of pilings and sea walls. The modernisation and cultural development of Sydney in the latter half of the 20th century saw a decrease in industry, but an increase in seawalls (Banks et al. 2016). Currently, over 50% of the shoreline of Sydney Harbour has been replaced with artificial structures (Chapman and Bulleri 2003; Mayer-Pinto et al. 2015). Artificial structures often differ from the natural shoreline in their slope, orientation, and surface texture. Therefore, artificial structures have the potential to support different biotic assemblages than the original shoreline (Mayer-Pinto et al. 2015). Changes to the biotic structure of shoreline habitats can result in changes to ecosystem functioning by altering diversity, biomass, water filtration rates and primary productivity (Bulleri and Chapman 2010;

Gittman et al. 2016). Mayer-Pinto et al. (2018) found that in Sydney Harbour, seawalls and pilings support a greater abundance of scavengers and a smaller abundance of grazers than natural rocky shores. They also found that seawall habitats also contained more non-indigenous species than pilings and rocky shores. Similarly, Lindegarth (2001) found that the presence of boat-mooring pontoons had the potential to alter benthic assemblages. Sites with pontoons were found to have greater assemblage variability and richness variability than sites without pontoons, but also less variability in total abundance.

Chemical contaminants in the harbour include heavy metals such as lead, and non-metallic compounds such as dioxins, polycyclic aromatic hydrocarbons and pesticides (Mayer-Pinto et al. 2015). The industrialisation of Sydney throughout the 19th and early 20th century brought paint manufacturers, oil refineries, power stations and metal foundries to the area, from which industrial pollution was released directly into the harbour (Banks et al. 2016). Although effluent decreased during the latter half of the 20th century, stormwater continues to deposit oil, pesticides, metals and litter to the harbour from urbanised catchments (Banks et al. 2016). As a result, Sydney Harbour is one of the most contaminated estuaries in the world (Birch and Taylor 2002; Mayer-Pinto et al. 2015). Currently, ~30% of the surface sediments across the harbour have a 49% probability of causing adverse effects to marine biota (Birch and Taylor 2002). Contamination directly impacts organisms by causing disease and cellular stress, impairments in development and reproduction (Edge et al. 2012). Indirectly, organisms can be affected through the predation and herbivory of contaminated biota. Sediment contaminates can therefore cause changes to benthic and infaunal assemblages. In Sydney Harbour, bays polluted with heavy metals have been found to have decreased biodiversity and species evenness than unpolluted bays (Stark 1998).

In Sydney Harbour, introduced species can be found across most habitats (Mayer-Pinto et al. 2015). Non-indigenous species have been introduced to Sydney Harbour as a result of international shipping, with species unintentionally being carried through ballast water; aquaculture, with the deliberate introduction of non-natives to the area for food; and through the south-ward expansion of tropical species resulting from global warming (Banks et al. 2016). This has led to the establishment of species such as the Pacific oyster (*Crassostrea gigas*), Indo-Pacific sergeant (*Abudefduf vaigiensis*), and green alga, *Caulerpa taxifolia* (Mayer-Pinto et al. 2015). Populations of non-indigenous species are often supported by modified habitats. In Sydney Harbour, Mayer-Pinto et al. (2018) found that more non-indigenous species could be found on artificial structures than natural structures. Introduced species can bring with them new diseases, displace native biota, and change herbivory and predation pressures (Mayer-Pinto et al. 2015). This can lead to alterations to community structure (Vergés et al. 2014; Mayer-Pinto et al. 2015).

Conservation palaeoecology

Palaeoecological data can supplement ecological records by providing long-term data from locations and species not previously studied (Dietl and Flessa 2011; Kosnik and Kowalewski 2016). Long-term data allows for environmental change to be identified, measured and contextualised (Cloern et al. 2016; Ratajczak et al. 2018) and is therefore essential for understanding the impacts anthropogenic disturbances have had on ecosystems. However, ecological studies are limited to the last ~70 years, with the majority of ecological observation periods beginning in the 1950s (Cloern et al. 2016; Kosnik and Kowalewski 2016). This length of time is insufficient in providing baseline data prior to anthropogenic disturbances (Kosnik and Kowalewski 2016). Furthermore, long-term ecological data is lacking for many locations across the globe, including Sydney Harbour (Johnston et al. 2015). As a result, much of our ecological data only measures human-altered environments (Jackson et al. 2001). The fossil record can therefore be a powerful tool for conservation, enabling researchers to assess how environments, populations, and species interactions have responded to human disturbances.

Fossil data on predation frequency is limited (Harper 2016). In the fossil record, indirect evidence for predation includes the functional morphology of predator and prey species and the behaviours of nearest living relatives (Kowalewski 2002). Direct evidence includes exceptional preservation events (where predator and prey are preserved while interacting), stomach contents, coprolites, and trace fossils. Most of these indicators of predation only reveal qualitative data (i.e. who potentially ate what) and are insufficient to test hypotheses regarding increases or decreases in predation over time (Kowalewski 2002; Harper 2016). Trace fossils, particularly drill holes, offer the most potential for quantifying predation data (Kelley and Hansen 2003; Harper 2016). Drill holes, therefore, allow us to analyse changes in predation frequency over time and space, as well as predator selectivity and prey defences (Klompmaaker et al. 2019).

Drilling predation as a window on ecosystem function

Predation shapes communities by altering the relative abundances of species and the flow of energy through the food web (Paine 1966; Aberhan et al. 2006). Predators influence the population dynamics of prey species by altering prey abundance, density, and spatial, age and size distributions (Gravem and Morgan 2017). The extent to which predation controls community structure is dependent on the intensity and selectivity of predation. Selective predators can limit the proliferation of dominant species and promote biodiversity (Paine 1966). Where predators are not selective or are selective towards non-dominant species, they can enable dominant species to outcompete less abundant species (Escobar et al. 2018). However, prey abundance also controls predator density. Therefore, high predation intensity can reduce the density of both prey and predator species (Menge and Lubchenco 1981).

The drill holes produced by predatory gastropods on shelled prey are a useful tool for measuring predator selectivity over time, to gain a greater understanding of the selective pressures on prey populations. Through the study of drill holes, drilling gastropods (predominately families Naticidae and Muricidae) have been demonstrated to be non-random predators, with prey selection based on maximising net energy gain (Kitchell et al. 1981; Chattopadhyay and Baumiller 2009; Mondal et al. 2010). As a result, drilling gastropods are species and size selective (Kingsley-Smith et al. 2003; Chiba and Sato 2012; Chattopadhyay and Dutta 2013). This selectivity can affect prey availability. For example, a reduction in average prey size proportional to predator size can increase predation frequency (Amaral et al. 2012; Sanford et al. 2014).

Sydney Harbour

Sydney Harbour is an ideal location to study the changes in drilling predation over time as there is a relatively rapid transition from Aboriginal settlements to western industrialised society (230 years). Despite the limited studies on ecological changes in the harbour, there are good written records on what land transformation took place during the transition (e.g. Birch et al. 2015). Therefore, there are exact dates for colonisation, the first factories, etc. to distinguish pre- and post-urbanisation time periods. In addition, Dominguez et al. (2016) shows that the stratigraphy of the seafloor sediment in Sydney Harbour is well suited for palaeoecological studies.

This thesis is the first study of drilling predation through time in Sydney Harbour. There has been little prior research on benthic molluscan communities in Sydney Harbour, and none that have analysed community structure (Johnson et al. 2015). However, sediment contamination (Stark 1998) and habitat modification (Lindgarth 2001) have been found to have altered the species composition of benthic communities in the harbour. Alterations to assemblages can cause an imbalance in trophic cascades, which cause further changes to assemblage structure. It would, therefore, be reasonable to predict that, as a result of changes to benthic assemblages in Sydney Harbour, predator-prey interactions have also changed.

Project aims

There are two aims for this thesis: (1) to quantify modern and historical drilling frequency for three common bivalve species, and (2) to investigate how the intensity of drilling predation has changed over the last ~5,000 years in the context of European colonisation of Sydney.

METHODS

Study site and sampling

Shell assemblages were collected from five outer Sydney Harbour sites (Fig. 1). These sites are all located on the flood tide delta (Johnston et al. 2015). At Chinamans Beach, Delwood Beach, Hunters Bay and Little Manly, surficial assemblages were collected from the top 0.2 m of sediment using a diver-operated air-lift and 0.25 m² quadrats, with total sample area varying between 1–4 m² across sites (Table 1). These surficial samples contain shells accumulating over colonial times (Dominguez et al. 2016). At Watsons Bay, a 1.8 m sediment excavation was used to collect death assemblages accumulating over the past ~ 4000 years (Dominguez et al. 2016). A 0.25 m² temporary retaining wall prevented the collapse of the excavation as sediment layers were excavated at ~ 5 cm intervals using an 80 mm diameter water dredge. The shell assemblages were sieved through 1, 2, 4, 8, and 16 mm sieves. The samples used here are the same samples as dated by Dominguez et al. (2016).

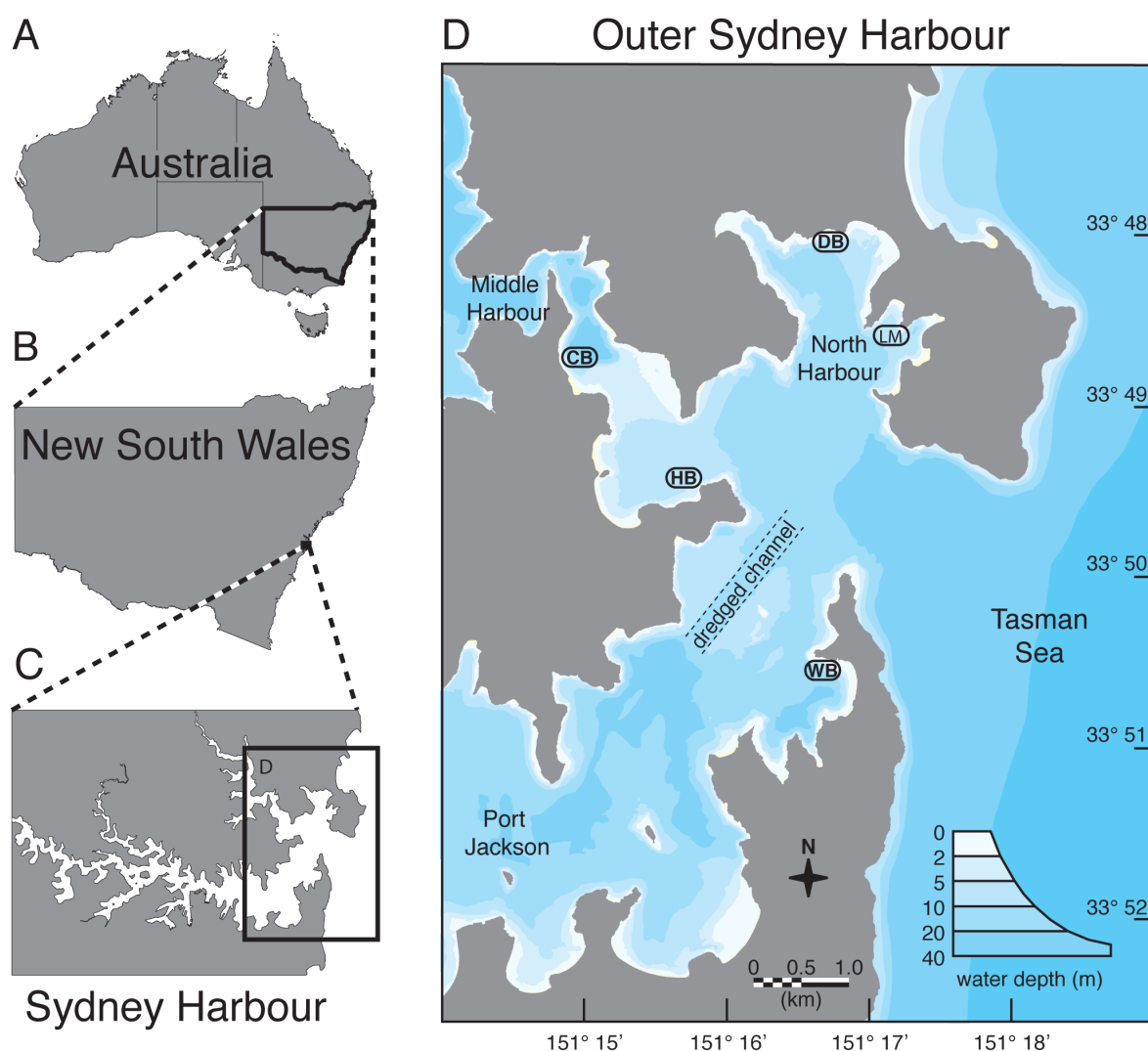


FIG 1.—A–C) Location of outer Sydney Harbour in Australia, D) Map of outer Sydney Harbour; modified from Dominguez et al. (2016, fig. 1). Site abbreviations are listed in Table 1.

TABLE 1.—Collection sites in Sydney Harbour. Location is indicated using WGS84 GPS coordinates. “Area” is the total area sampled per site. “Water depth” was taken from diver depth gauges and corrected to chart datum using Fort Denison tide measurements (R. Jacobs, Office of Environment and Heritage NSW, personal communication 2015). “Sediment depth” is the depth of the sediment layer sampled.

Site	Name	Location		Area (m ²)	Depth (m)	
					Water	Sediment
CB	Chinamans Beach	-33.81001	151.24805	2.00	8.3	0.00-0.20
DB	Delwood Beach	-33.80125	151.27892	1.00	9.3	0.00-0.20
HB	Hunters Bay	-33.82342	151.26195	4.00	7.5	0.00-0.20
LM	Little Manly	-33.80897	151.28543	1.00	7.9	0.00-0.20
WB	Watsons Bay	-33.84234	151.27757	0.25	10.4	
						0.30-0.35
						0.50-0.54
						0.66-0.72
						0.72-0.76*
						0.76-0.84*
						0.84-0.88
						0.98-1.03
						1.13-1.18
						1.28-1.33
						1.43-1.48
						1.58-1.63

Asterisk (*) = layers dated for this thesis. All other layers were dated by Dominguez et al. (2016).

Taxa

The shells of bivalves *Callista disrupta* (G. B. Sowerby II 1853), *Chioneryx cardioides* (Lamarck 1818), and *Fulvia tenuicostata* (Lamarck 1819) were selected for predation analysis due to their high abundance within the assemblages. In addition, there is no evidence for Aboriginal fisheries targeting with these taxa, or any other subtidal, soft-sediment molluscan communities, and therefore anthropogenic disturbances prior to European colonisation should be limited (Currie 2008; Derricourt 2011).

Chioneryx cardioides (Fig. 2A–B) live along the south-east coast of Australia, Tasmania, South Australia, and the south-west coast of Western Australia (Lamprell and Whitehead 1992; Atlas of Living Australia 2018b). *Chioneryx* shells are small, growing up to 17 mm, with pronounced ornamentation in the form of concentric and radial ribs (Lamprell and Whitehead 1992;

Beesley et al. 1998). Venerid bivalves, such as *Chioneryx*, are shallow to medium burrowers in sandy to muddy habitats (Beesley et al. 1998). The main predators of this family are drilling naticid and muricid gastropods, which they avoid by burrowing (Beesley et al. 1998).

Callista disrupta (Fig. 2C–D) live along the east coast of Australia, from Victoria to central Queensland (Lamprell and Whitehead 1992; Atlas of Living Australia 2018a). *Callista* shells grow up to 42 mm, are white and patterned with brown radial rays, and broad ridges created from concentric grooves (Lamprell and Whitehead 1992; Beesley et al. 1998). The elongated pallial sinus of *Callista* shells indicates they are deep burrowers (Beesley et al. 1998). Of the three taxa included in this study, *Callista* is the least common.

Fulvia tenuicostata (Fig. 2E–F) lives along the coast of south-east and southern Australia (Lamprell and Whitehead 1992; Atlas of Living Australia 2018c). Their shells are cream coloured with 50–60 radial ribs and can grow up to 55 mm (Lamprell and Whitehead 1992). The largest shell found within these samples was ~49 mm. Members of the family Cardiidae are shallow burrowers with short siphons that live in soft substrates (Beesley et al. 1998). They are capable of modest predator avoidance by flipping themselves sideways (Beesley et al. 1998). *Fulvia* is common throughout the depth of the excavation and was the most common species in the top sediment layers, however it is rarely found in the living assemblage (Dominguez et al. 2016).

The drill holes found in these three species were identified as the ichnospecies, *Oichnus paraboloides*. These drill holes are bevelled, with the outer drill hole diameter larger than the inner drill hole diameter, i.e. as the hole is drilled, the diameter gets smaller. *O. paraboloides* are typically produced by naticid gastropods (Dietl and Kelley 2006). *Conuber incei* (Philippi, 1853) was the only naticid species found in these samples, so they are considered the most likely predator.

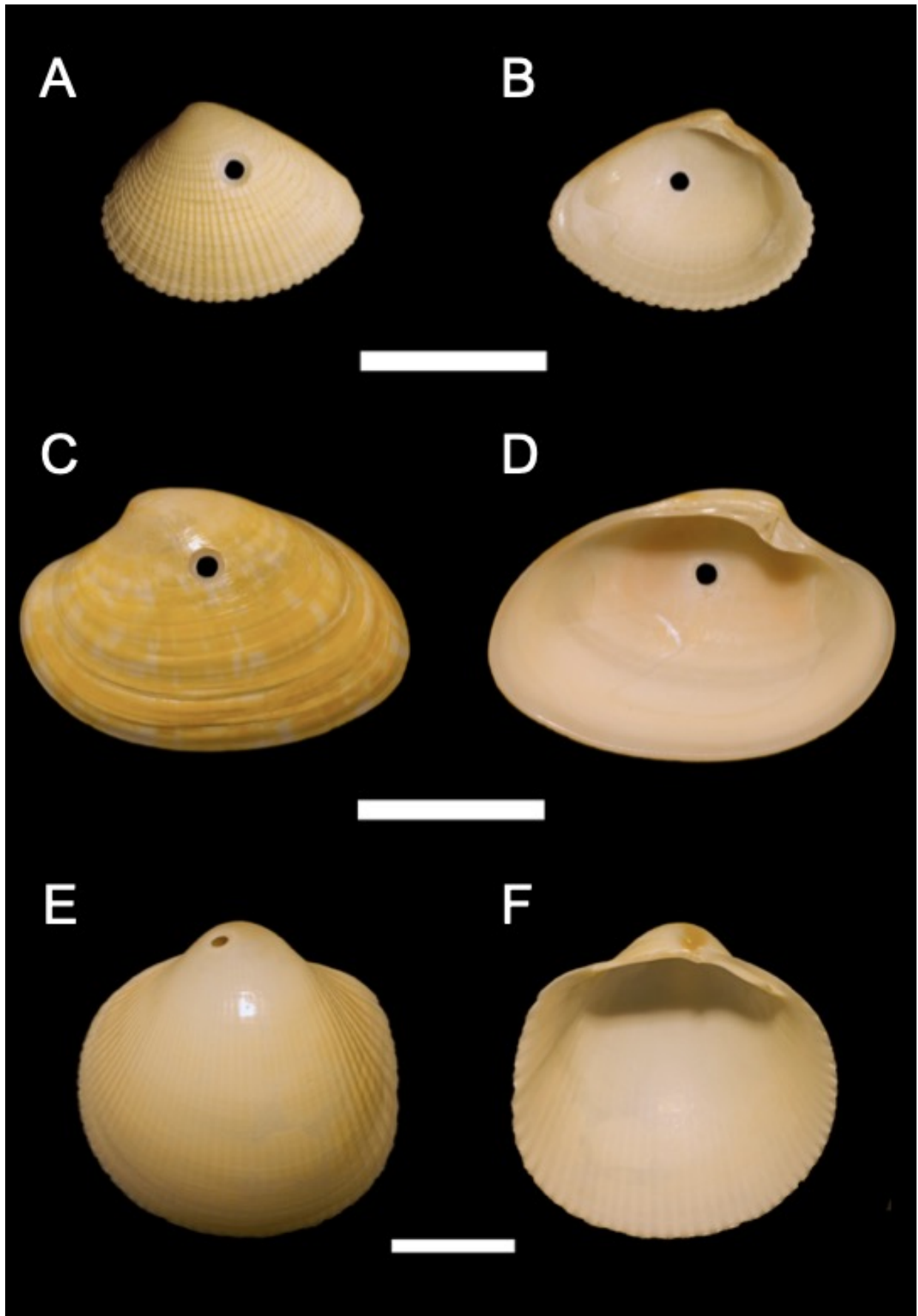


FIG 2.—Drilled specimens of the bivalve taxa used in this study. **A–B)** *Chioneryx cardioides* (CPL25346), **C–D)** *Callista disrupta* (CPL25347) and **E–F)** *Fulvia tenuicostata* (CPL25348). Scale bars = 1 cm.

Amino Acid Racemization

Dominguez et al. (2016) dated *Fulvia* shells from the surficial samples and nine layers of the sediment excavation (see Table 1) using radiocarbon calibrated amino-acid racemization, revealing an age range of ~150–4200 years and five distinct age assemblages. Undated layers between two layers with the same age distribution were assumed to be the age of the two adjacent layers. The surficial samples and the excavation layers between 0.30-0.54 m have a median age of ~150 years, the layer between 0.66-0.72 m has a median age of ~700 years, the layers between 0.84-1.18 m have a median age of ~2,300 years, the layer between 1.28-1.33 has a median age of ~3,300 years, and the layers between 1.43-1.63 m have a median age of ~4,200 years (Dominguez et al. 2016).

For this study, two additional undated sediment layers, 0.72-0.76 and 0.76-0.84 m, were selected for dating. These two layers were selected because between 0.72 m and 0.84 m there is over a 1,500 year age gap and they were the only two remaining undated layers that fell between the age assemblages at ~700 and ~2,300 years. To allow the new layers to be compared to the previously dated layers, the same dating methodology implemented by (Dominguez et al. 2016) was used for this study. Posterior fragments of 12 *Fulvia* right valves from each of the two undated layers and six right valves from 0.66-0.72 m that were previously dated by Dominguez et al. were prepared for amino acid racemization (AAR) analyses at Northern Arizona University, following protocol by (Wehmiller and Miller 2013). Cleaned shells fragments are demineralised with hydrochloric acid (20 ml of 7 M HCl per mg of CaCO₃) and then hydrolysed under N₂ gas at 110 °C for 6 hours, allowing the total hydrolysable amino acids to be recovered from the samples. The solution is then evaporated to dryness in a vacuum and rehydrated with 0.01 M hydrochloric acid. L-homo-arginine was used as a standard to calculate the relation between the concentration of amino acids and shell mass. The stereoisomers of eight amino acids (aspartic acid, glutamic acid, alanine, serine, valine, phenylalanine, leucine, and isoleucine) were separated using reversed-phase high-performance liquid chromatography (RP-HPLC), following methods described in Kaufman and Manley (1998).

To calculate the median assemblage age for the two newly dated layers and determine their relation to the previously dated layers, the same AAR calibration model methodology used by Dominguez et al. (2016) was implemented. The new D/L values from the layers at 0.66, 0.72 and 0.76 m were added to the dataset produced by Dominguez et al., which also included calendar ages for 22 radiocarbon dated shells (see Dominguez et al. 2016). A series of age models were constructed using the paired ¹⁴C dates and D/L ratios from seven amino acids (aspartic acid, glutamic acid, alanine, valine, phenylalanine, leucine, and isoleucine), three mathematical functions (time-dependent rate kinetics, constrained power-law kinetics, and simple power-law kinetics), two uncertainty distributions (gamma and lognormal), and two D/L ratios at the time of death (initial

value ($R_0 \equiv 0$, and an initial value fitted from the data ($0 > R_0 > \min(D/L)$)). Bayesian model averaging was then used to weigh the relative contributions of each age model, as characterized using the Bayesian Information Criterion (BIC), resulting in a final BIC-weighted average model.

The final model was constructed from four age models fit using Asp D/L values and a gamma uncertainty distribution (Table 2). 43.2 and 42.8% of the BIC weight were accounted for by the time-dependent rate kinetics (TDK) and simple power-law kinetics (SPK) functions, respectively, both with $R_0 \equiv 0$. The other 14% was accounted for by the TDK and SPK functions with R_0 fit from the data.

The output from the age model is a distribution of 10,000 age estimates for each shell that combined represent the total age-estimate variability of the layer. To determine which layers had overlapping age distributions, the total age-estimate variability for each layer was compared to the median age of the other layers. The similarity of each pair of layers was measured as the proportion of the total age-estimate variability of one layer that was less than the median of the second layer. Proportions between 0.25-0.75 were considered to sample the same time period, while proportions outside of 0.05-0.95 were considered to sample from distinct time periods. Layers with overlapping age distributions were grouped and analysis was repeated to determine the difference between groups of layers (assemblages).

TABLE 2.—Bayesian model averaging summary for the age models that contributed to the final model. All four are fit using Asp D/L values and a gamma uncertainty distribution.

“Function” refers to simple power-law kinetics (SPK) or time-dependent rate kinetics (TDK), “0” indicates the initial D/L concentration (R_0) was defined as 0, while “1” indicates R_0 was fit from the data. “K” = the number of model parameters. “BIC” = Bayesian information criterion, a measure of model fit. “ Δ BIC” = fit relative to the best model. “BIC weight” = the percentage of contribution of the model to the final averaged model.

Function	K	BIC	Δ BIC	BIC weight
TDK0	3	700.17	0.00	43.2%
SPK0	3	700.19	0.02	42.8%
TDK1	4	703.91	3.74	6.7%
SPK1	4	703.73	3.56	7.3%

Predation analysis

Predation analyses of *Chioneryx*, *Callista* and *Fulvia* and included only shells that were at least 90% complete to increase the certainty over whether a shell has been drilled or not, and shells that were larger than 8mm, to ensure consistency. The 8mm cut off was selected to prioritise adult

specimens over juveniles. Drill frequency can vary across size fractions (Chattopadhyay et al. 2016), so the results found here may not be reflective of results in smaller size fractions. Shells from each species were separated into left and right valves and sorted into one of four drilling categories: no drill hole, one complete drill hole, one incomplete drill hole, and multiple drill holes. Predatory drill holes were identified as holes with a regular shape, perpendicular to the shell surface and drilled from the exterior of the shell (Kelley and Hansen 2003; Fig. 2). Multiple drill holes were exceptionally rare (15 of ~17,800 total valves), so valves with at least one complete or incomplete drill hole were included in the complete or incomplete drilling category.

For each species, drilling frequency (DF) was calculated as the number of drilled specimens divided by the total number of specimens (Lower Taxon Frequency, Kowalewski 2002). As all the specimens in these samples were disarticulated, a correction was applied whereby the total specimen number was calculated as half the total number of valves (Kowalewski 2002). Incomplete drilling frequency (IDF) was calculated in the same way: the number of valves with incomplete drill holes, divided by half the number of valves overall. IDF differs from prey effectiveness (PE, the number of incomplete drill holes divided by the total number of drill attempts) in that it does not measure drilling success rate. Rather, IDF reports how common incomplete drill holes are in an assemblage. The 95% binomial confidence intervals for DF and IDF were calculated using the Pearson Klopfer method, as implemented in the R package 'binom' (Dorai-Raj 2014).

To compare the proportion of drilled and undrilled individuals across age assemblages, a series of chi-squared tests were used to compare each pair of assemblages. Within each species, the sequential Bonferroni correction (Rice 1989) was applied to account for the multiple comparisons. All *p*-values and *p*-critical values are reported in Table 6.

There are a number of assumptions that are made for these drilling predation analyses (Kowalewski 2002): (1) left and right valves are equally likely to be preserved, (2) the predator does not show valve selectivity, (3) predators leave a trace on one valve only, and (4) predatory traces do not reduce the likelihood of the valve being preserved. The first two of these assumptions can be directly tested within these samples. For each species, Fisher's exact tests were used to compare the number of drilled and undrilled shells between the left and right valves per age assemblage. The sequential Bonferroni correction (Rice 1989) was applied to account for the multiple comparisons within a species.

R version 3.4.1 was used for all statistical analyses and plotting. R code for predation analyses and predation data are provided in the Supplement files.

RESULTS

Age of dated layers

The new dates produced by this analysis were consistent with those reported by Dominguez et al. (2016), and the two newly dated layers at 0.72 and 0.76 m fit in with the stratigraphy of the rest of the excavation. The sediment layer at 0.72 had a median age of 931 and was not distinct from the layers between 0.66-0.72 m (Table 3). Therefore, it was combined with the layer at 0.66 m to form an assemblage between 0.66-0.76 m with a median age of 783 years (Table 4). The layer at 0.76 m was distinct from all other layers and formed an assemblage between 0.76-0.84 m with a median age of 1385 years (Table 3 & 4). When all layers with overlapping age distributions are grouped into assemblages, the assemblage age distributions do not overlap (Table 4), indicating that the groupings are a true reflection of the preserved age assemblages. Therefore, the surface sites and sediment excavation can be divided into six distinct age assemblages spanning 140 to ~4200 years old that can be used to track changes in drilling predation over time (Fig. 3).

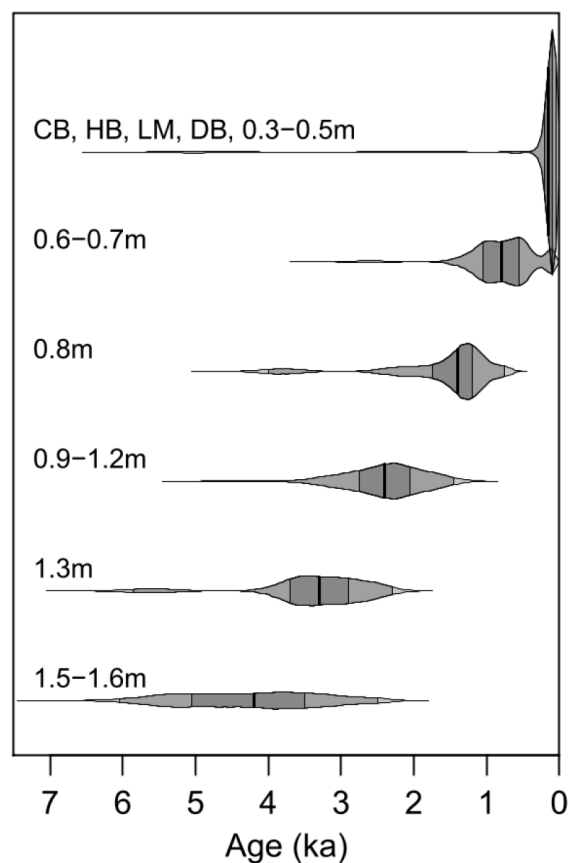


FIG 3.—Total age-estimate variability of *Fulvia* from each distinct age assemblage. The y-axis is grouped surface samples and excavation depths in meters. Spindles are histograms of the total age-estimate variability. Each spindle has the same area, and spindle height is proportional to the frequency of that age. The thick vertical line represents the median age estimate, the dark grey encompasses 50% of the age estimates, the medium grey encompasses 95% of the age estimates, and the lightest grey encompasses 100% of the age estimates.

TABLE 3.—Summary of layer age variability by excavation depth. Only the layers at 0.72 and 0.76 were dated for this project. The total age-estimate variability includes both time-averaging and age-estimation error (see Supplement files). The proportion of the total age-estimate variability that is less than the median describes the amount of overlap there is between the age of assemblages. Distributions outside of 5–95% are considered to sample distinct time periods whereas collections within 25–75% are considered to sample overlapping time periods.

Depth (m)	Total age-estimate variability (yr)						Proportion of the total age-estimate variability for each layer (rows, listed by depth) that is less than the median of another layer (columns)											
	0%	25%	50%	75%	100%	IQR	0.30	0.50	0.66	0.72	0.76	0.84	0.98	1.13	1.28	1.43	1.58	
0.30	7	100	140	198	6600	98	0.5	0.6	0.92	0.92	0.92	0.92	0.92	0.92	0.92	0.92	0.92	
0.50	12	111	159	700	5876	589	0.41	0.5	0.75	0.75	0.76	0.84	0.88	0.87	0.92	0.92	0.94	
0.66	22	481	717	1003	2267	522	0.05	0.07	0.5	0.68	0.97	1.00	1.00	1.00	1.00	1.00	1.00	
0.72	177	701	931	1196	3609	495	0.00	0.00	0.27	0.5	0.86	0.9	0.93	0.92	1.00	1.00	1.00	
0.76	476	1180	1385	1775	5182	595	0.00	0.00	0.01	0.07	0.5	0.84	0.9	0.89	0.92	0.98	1.00	
0.84	889	1805	2145	2487	4276	682	0.00	0.00	0.00	0.00	0.04	0.5	0.75	0.72	0.97	1.00	1.00	
0.98	1192	2223	2493	2813	4323	590	0.00	0.00	0.00	0.00	0.00	0.19	0.5	0.45	0.97	1.00	1.00	
1.13	937	2092	2440	2914	5506	822	0.00	0.00	0.00	0.00	0.01	0.29	0.54	0.5	0.87	0.96	0.98	
1.28	1732	2887	3300	3674	7170	787	0.00	0.00	0.00	0.00	0.00	0.01	0.07	0.06	0.5	0.9	0.91	
1.43	2148	3555	4100	4746	6739	1191	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.5	0.59	
1.58	1817	3467	4335	5356	7700	1889	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.03	0.21	0.43	0.5	

TABLE 4.—Summary of assemblage age variability by site and excavation depth. The total age-estimate variability includes both time-averaging and age-estimation error (see Supplement files). The proportion of the total age-estimate variability that is less than the median describes the amount of overlap there is between the age of assemblages. Distributions outside of 5–95% are considered to sample distinct time periods whereas collections within 25–75% are considered to sample overlapping time periods.

Assemblage	Total age-estimate variability (yr)						Proportion of the total age-estimate variability for each assemblage (rows) that is less than the median of another assemblage (columns)					
	0%	25%	50%	75%	100%	IQR	1	2	3	4	5	6
1 BC, HB, LM, DB, 0.30-0.54m	0	96	140	201	6535	105	0.50	0.91	0.92	0.95	0.96	0.96
2 0.66-0.76m	16	544	783	1050	3678	506	0.04	0.50	0.94	0.98	1.00	1.00
3 0.76-0.84m	432	1183	1385	1773	5072	590	0.00	0.03	0.50	0.88	0.92	0.99
4 0.84-1.18m	839	2043	2381	2766	5457	723	0.00	0.00	0.01	0.50	0.93	0.99
5 1.28-1.33m	1774	2887	3298	3678	7068	791	0.00	0.00	0.00	0.04	0.50	0.91
6 1.43-1.63m	1798	3519	4212	5055	7483	1536	0.00	0.00	0.00	0.01	0.18	0.50

Drilling predation

Differences between drilling in left and right valves.—All three bivalves are equivalve, and there is no significant difference in the proportion of drilled and undrilled shells between left and right valves in any species or distinct age assemblage (Table 5). *Callista* valves exhibit the greatest difference in drilling frequency between left and right valves. However, the 95% confidence intervals of all left-right pairs overlap (Fig. 4), and no p-value is smaller than the p-critical value when the sequential Bonferroni correction is applied (Table 5). With an average of 116 valves per analysis (compared to 737 for *Fulvia* and 630 for *Chioneryx*), there are insufficient *Callista* valves to determine with greater certainty if the differences in drilling frequencies of left and right valves are a result of a predator with valve selective behaviour. *Fulvia* and *Chioneryx* have similar drilling frequencies between left and right valves, and the 95% confidence intervals of all left-right pairs overlap (Fig. 4). No p-value is smaller than the p-critical value when the sequential Bonferroni correction is applied (Table 5). These samples are large enough to be confident that the predation is not valve selective.

The overlapping confidence intervals and supporting Fisher's exact tests suggest there is no left/right valve selectivity influencing the predation of *Callista*, *Fulvia* and *Chioneryx* in Sydney Harbour. This is consistent with a number of laboratory studies on drilling gastropod prey selection that have found that naticids display no valve preference (Kingsley-Smith et al. 2003; Visaggi et al. 2013). As a result, the rest of the drilling frequency analyses will combine the left and right valves.

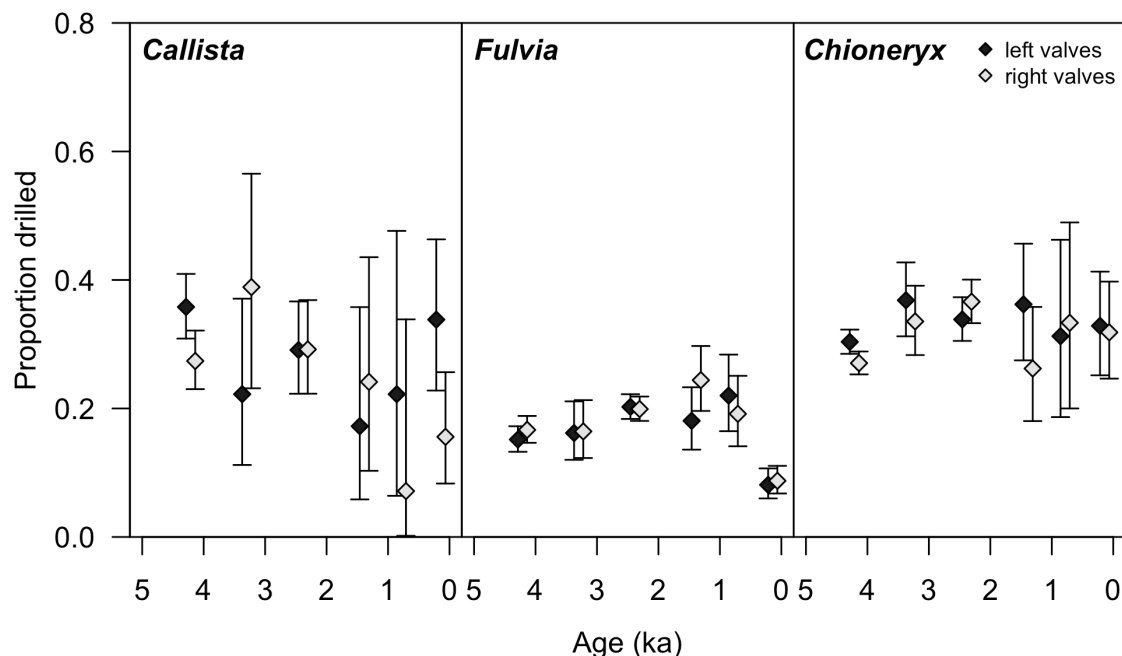


FIG 4.—Drilling frequency of left and right valves over time (ka, thousand years) for three species of bivalve found in Sydney Harbour. Points represent drilling frequency, calculated as the number of drilled valves divided by the number of valves present. Vertical bars represent 95% binomial confidence intervals.

Complete drilling.—Over the last ~5,000 years, the drilling frequency of *Callista* varied between ~0.30 and ~0.60 (Table 6; Fig. 5). All 95% confidence intervals are overlapping (Fig. 5) and no two age assemblages had a significantly different proportion of drilled and undrilled specimens (Table 7). While the 95% confidence intervals are primarily a function of sample size, these data include all of the *Callista* present in the samples. The relationship between drilling frequency and time is not significant ($F_{(1,4)} = 6.54$, $p = 0.06$). There is no significant change in *Callista* predation over time, despite the visually suggestive pattern in Figure 5.

The drilling frequency of *Fulvia* has varied between 17% and ~40% (Table 6), with no significant relationship between drilling frequency and time ($F_{(1,4)} = 0.13$, $p = 0.73$). The proportion of drilled and undrilled specimens in the assemblage at 4.2 ka is significantly different from the assemblage at 2.3 ka ($\chi^2_{(1)} = 22.09$, $p < 0.001$) and the assemblage at 1.3 ka ($\chi^2_{(1)} = 12.31$, $p < 0.001$), increasing from ~30% to ~40% (Fig. 5; Table 6). The proportion of drilled specimens in the most recent assemblage, 0.1 ka, is significantly less than all other assemblages (Table 7). While the drilling frequency of *Fulvia* assemblages older than ~200 years ranges between 32-43%, the assemblage at 0.1 ka has a drilling frequency of 17%. This indicates that *Fulvia* drilling predation in the post-colonial period is approximately half of what it was during the pre-colonial period.

The drilling frequency of *Chioneryx* varies between ~60% and ~70% (Table 6). The relationship between drilling frequency and time is not linear ($F_{(1,4)} = 0.13$, $p = 0.73$). The proportion of drilled specimens in the assemblage at 4.2 ka is significantly different from the assemblage at 3.2 ka ($\chi^2_{(1)} = 17.88$, $p < 0.001$) and the assemblage at 2.3 ka ($\chi^2_{(1)} = 43.04$, $p < 0.001$). The 95% confidence intervals for all other pairs overlap (Fig. 5) and do not have a significantly different proportion of drilled specimens (Table 7).

Multiple drill holes.—Only 15 of 17,790 total valves (0.08%) were found with multiple drill holes. If valves were drilled at random, the probability of having two holes in a valve is the probability of being drilled squared. In all three species, multiple drill holes are less common than would be expected by chance. One of 1,395 total *Callista* valves contained multiple drill holes (0.07% vs. 7% expected by chance), 4 of 8,839 total *Fulvia* valves (0.05% vs. 5% expected by chance), and 10 of 7,556 total *Chioneryx* valves (0.13% vs. 8% expected by chance). The actual instance of multiple drill holes is approximately 100 times less than expected if predators randomly drilled shells, indicating that the predator is effectively preferring living bivalve prey.

Incomplete drilling.—Incomplete drill holes were found to be rare throughout the sampled valves. Across all species and age assemblages, no species was found to have an incomplete drilling frequency above 2% (Table 6). No incomplete drill holes were found in seven of the 18 assemblages (60%), and no incomplete drill holes were found in any *Fulvia* assemblage.

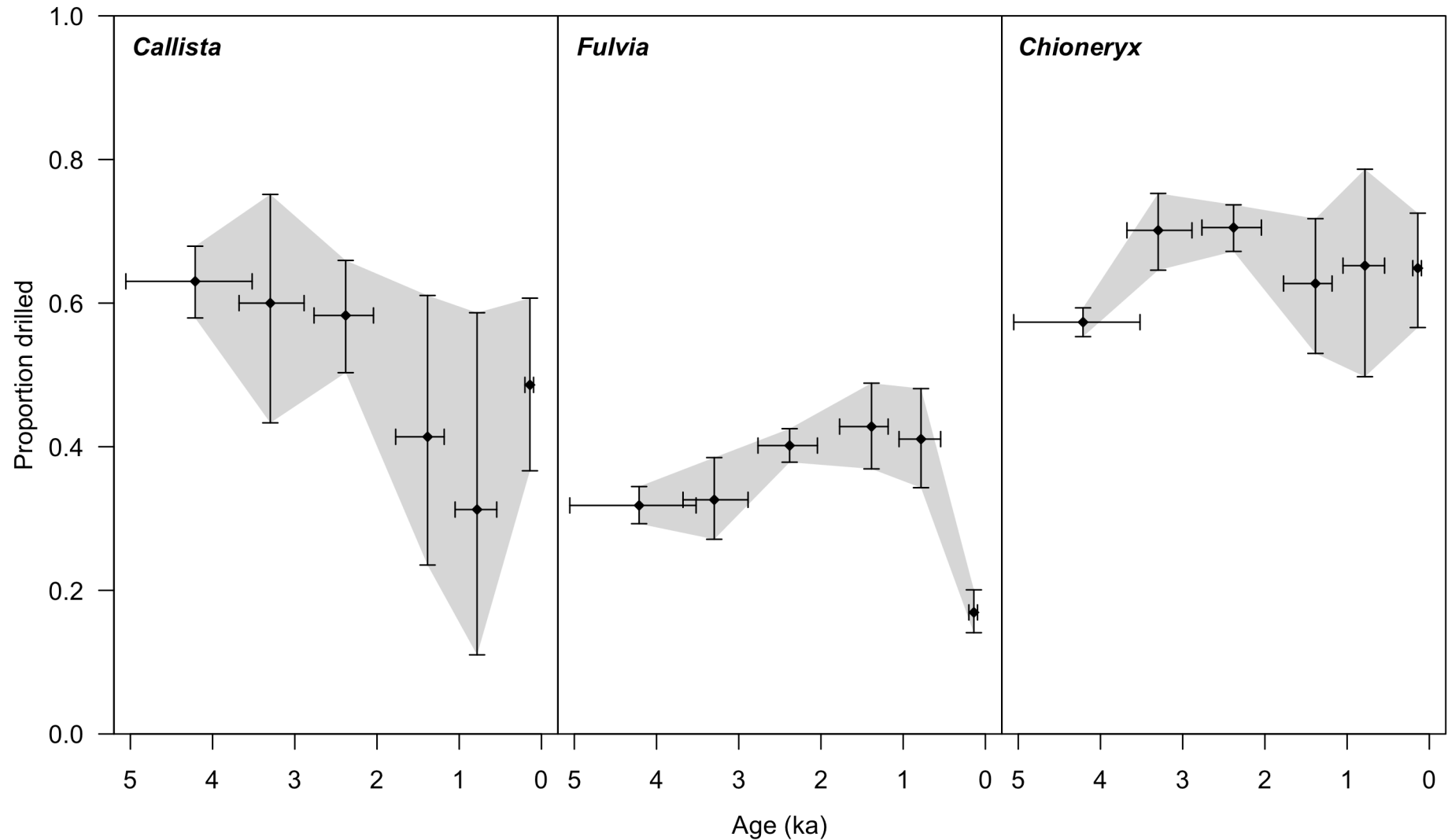


FIG 5.—Drilling frequency over time (ka, thousand years) for three species of bivalve found in Sydney Harbour. Points represent drilling frequency, calculated as the number of drilled valves divided by the number of individuals present (i.e., half the total number of valves). Vertical bars represent 95% binomial confidence intervals. Horizontal bars represent the interquartile range of age variability, with the point placed at the median.

TABLE 5.—Comparison of complete drill holes in left and right valves. “DF” = drilling frequency. “95%” = 95% confidence intervals for DF. “ p ” = p -value from Fisher’s exact test comparing the proportion of drilled to undrilled shells between left and right valves. “ $p(k - i)$ ” is the adjusted significance level following the sequential Bonferroni correction. An asterisk (*) indicates the p -value is smaller than the adjusted significance level.

Species	Median age (ka)	Left valves				Right valves				Fisher's exact			
		Total	Drilled	DF	95%		Total	Drilled	DF	95%		<i>p</i> -value	<i>p</i> (<i>k</i> − <i>i</i>)
<i>Callista disrupta</i>	0.140	68	23	0.34	0.23	0.46	77	12	0.16	0.08	0.26	0.012	0.008
	0.783	18	4	0.22	0.06	0.48	14	1	0.07	0.00	0.34	0.355	0.017
	1.385	29	5	0.17	0.06	0.36	29	7	0.24	0.10	0.44	0.747	0.025
	2.381	165	48	0.29	0.22	0.37	161	47	0.29	0.22	0.37	1.000	0.050
	3.298	45	10	0.22	0.11	0.37	36	14	0.39	0.23	0.57	0.142	0.013
	4.212	366	131	0.36	0.31	0.41	387	106	0.27	0.23	0.32	0.015	0.010
<i>Fulvia tenuicostata</i>	0.140	567	46	0.08	0.06	0.11	709	62	0.09	0.07	0.11	0.762	0.017
	0.783	200	44	0.22	0.16	0.28	214	41	0.19	0.14	0.25	0.543	0.013
	1.385	260	47	0.18	0.14	0.23	295	72	0.24	0.20	0.30	0.078	0.008
	2.381	1724	349	0.20	0.18	0.22	1753	349	0.20	0.18	0.22	0.832	0.025
	3.298	272	44	0.16	0.12	0.21	280	46	0.16	0.12	0.21	1.000	0.050
	4.212	1299	197	0.15	0.13	0.17	1266	211	0.17	0.15	0.19	0.305	0.010
<i>Chioneryx cardioides</i>	0.140	140	46	0.33	0.25	0.41	157	50	0.32	0.25	0.40	0.901	0.025
	0.783	48	15	0.31	0.19	0.46	45	15	0.33	0.20	0.49	1.000	0.050
	1.385	116	42	0.36	0.27	0.46	103	27	0.26	0.18	0.36	0.145	0.010
	2.381	771	261	0.34	0.31	0.37	803	294	0.37	0.33	0.40	0.268	0.013
	3.298	285	105	0.37	0.31	0.43	310	104	0.34	0.28	0.39	0.439	0.017
	4.212	2335	709	0.30	0.29	0.32	2443	661	0.27	0.25	0.29	0.013	0.008

TABLE 6.—Summary of drill hole data for each species and age assemblage. “Total specimens” = the total number of drilled and undrilled specimens, corrected for disarticulation. “D” = the number of drill holes. “DF” = drilling frequency. “IDF” = incomplete drilling frequency. “95%” = 95% binomial confidence intervals for DF.

Species	Median age (ka)	Total specimens	Complete			Incomplete			
			D	DF	95%	D	IDF	95%	
<i>Callista disrupta</i>	0.140	72	35	0.49	0.37 0.61	1	0.01	0.00 0.07	
	0.783	16	5	0.31	0.11 0.59	0	0.00	0.00 0.21	
	1.385	29	12	0.41	0.24 0.61	0	0.00	0.00 0.12	
	2.381	163	95	0.58	0.50 0.66	3	0.02	0.00 0.05	
	3.298	40	24	0.60	0.43 0.75	0	0.00	0.00 0.09	
	4.212	376	237	0.63	0.58 0.68	3	0.01	0.00 0.02	
<i>Fulvia tenuicostata</i>	0.140	638	108	0.17	0.14 0.20	3	0.00	0.00 0.01	
	0.783	207	85	0.41	0.34 0.48	0	0.00	0.00 0.02	
	1.385	278	119	0.43	0.37 0.49	1	0.00	0.00 0.02	
	2.381	1738	698	0.40	0.38 0.43	5	0.00	0.00 0.01	
	3.298	276	90	0.33	0.27 0.38	0	0.00	0.00 0.01	
	4.212	1282	408	0.32	0.29 0.34	4	0.00	0.00 0.01	
<i>Chioneryx cardioides</i>	0.140	148	96	0.65	0.57 0.73	1	0.01	0.00 0.04	
	0.783	46	30	0.65	0.50 0.79	0	0.00	0.00 0.08	
	1.385	110	69	0.63	0.53 0.72	0	0.00	0.00 0.03	
	2.381	787	555	0.71	0.67 0.74	12	0.02	0.01 0.03	
	3.298	298	209	0.70	0.65 0.75	4	0.01	0.00 0.03	
	4.212	2389	1370	0.57	0.55 0.59	24	0.01	0.01 0.01	

TABLE 7.—Table of results from chi-squared tests comparing the proportion of drilled to undrilled specimens between each pair of age assemblages within a species. Each row represents a test between a pair of assemblages, with the median age of the two assemblages listed in the “Comparison” column. “ $p(k-i)$ ” is the adjusted significance level following the sequential Bonferroni correction. An asterisk (*) indicates the p -value is smaller than the adjusted significance level.

Species	Comparison	χ^2	p -value	$p(k-i)$
<i>Callista disrupta</i>	0.140 - 0.783	1.591	0.207	0.007
	0.140 - 1.385	0.435	0.510	0.017
	0.140 - 2.381	1.890	0.169	0.006
	0.140 - 3.298	1.338	0.247	0.008
	0.140 - 4.212	5.269	0.022	0.004
	0.783 - 1.385	0.450	0.502	0.013
	0.783 - 2.381	4.318	0.038	0.004
	0.783 - 3.298	3.783	0.052	0.005
	0.783 - 4.212	6.562	0.010	0.003
	1.385 - 2.381	2.851	0.091	0.005
	1.385 - 3.298	2.336	0.126	0.006
	1.385 - 4.212	5.330	0.021	0.004
	2.381 - 3.298	0.039	0.843	0.050
	2.381 - 4.212	1.084	0.298	0.010
	3.298 - 4.212	0.142	0.706	0.025
<i>Fulvia tenuicostata</i>	0.140 - 0.783	51.658	<0.001	0.004*
	0.140 - 1.385	69.562	<0.001	0.004*
	0.140 - 2.381	112.383	<0.001	0.003*
	0.140 - 3.298	27.915	<0.001	0.005*
	0.140 - 4.212	48.107	<0.001	0.004*
	0.783 - 1.385	0.148	0.701	0.017
	0.783 - 2.381	0.063	0.803	0.050
	0.783 - 3.298	3.659	0.056	0.010
	0.783 - 4.212	6.867	0.009	0.006
	1.385 - 2.381	0.695	0.404	0.013
	1.385 - 3.298	6.130	0.013	0.007
	1.385 - 4.212	12.314	<0.001	0.006*
	2.381 - 3.298	5.704	0.017	0.008
	2.381 - 4.212	22.087	<0.001	0.005*
	3.298 - 4.212	0.064	0.800	0.025
<i>Chioneryx cardioides</i>	0.140 - 0.783	0.002	0.965	0.050
	0.140 - 1.385	0.125	0.724	0.013
	0.140 - 2.381	1.884	0.170	0.005
	0.140 - 3.298	1.270	0.260	0.006

0.140 - 4.212	3.230	0.072	0.004
0.783 - 1.385	0.087	0.768	0.017
0.783 - 2.381	0.585	0.444	0.008
0.783 - 3.298	0.454	0.500	0.010
0.783 - 4.212	1.144	0.285	0.007
1.385 - 2.381	2.769	0.096	0.004
1.385 - 3.298	2.030	0.154	0.005
1.385 - 4.212	1.247	0.264	0.006
2.381 - 3.298	0.016	0.901	0.025
2.381 - 4.212	43.040	<0.001	0.003*
3.298 - 4.212	17.881	<0.001	0.004*

DISCUSSION

While predation controls population characteristics of prey species and can be altered through human disturbances, evidence for how humans have affected predator-prey interactions is limited due to the lack of temporal data. This is the first study of drilling predation through time in Sydney Harbour. In this study, drilling frequency was calculated for the three most abundant bivalves in the soft-sediment of Sydney Harbour over the last ~5,000 years to examine the drilling predation in Sydney Harbour in the context of the pre-colonial variation in the ecosystem.

One of the three species, *Fulvia tenuicostata*, experienced a significant decrease in drilling frequency in the last ~500-200 years, the time period in which Sydney was colonised by Europeans. By ~140 years ago, the drilling frequency of *Fulvia* had fallen to 17%, a frequency approximately half of that seen in earlier assemblages (~30-40%). The other two species did not experience a similar decrease in drilling frequency. Instead, the post-colonial assemblages of *Callista disrupta* and *Chioneryx cardioides* had drilling frequencies similar to that over the previous ~1,400 years. As this is the first study to analyse drilling frequency in the context of western colonisation, there is no analogous study with which to compare these results.

The relative abundance of *Fulvia* in comparison to *Callista* and *Chioneryx* (Table 8, data collected from Table 6) did not change following the European colonisation of Sydney. Despite *Fulvia* drilling frequency halving between 0.78 and 0.14 ka, the relative abundance of *Fulvia* only decreases by 3%, and *Fulvia* remained the most common bivalve. It should, however, be noted that when sampling, Dominguez et al. (2016) found that *Fulvia* was rarer in surficial samples (top 20 cm) than in the top layers of the sediment excavation (30-54 cm). This suggests that additional data and analysis of *Fulvia* abundance relative to the amount of sediment sampled is warranted.

Over the last ~5,000 years, drilling predation was found to be a frequent cause of death for *Callista*, *Fulvia* and *Chioneryx*, with up to 63%, 43%, and 71% of individuals drilled, respectively. This high mortality due to predation may suggest that naticid predation is a controlling factor on the three bivalve populations. However, for predation to truly be a control, predation must also be selective. While size selectivity was not specifically tested in this study, *Chioneryx*, which had the highest overall drilling frequency, is the smallest of the three taxa studied.

Comparison to other studies

The surficial death assemblage drilling frequencies of *Callista*, *Fulvia* and *Chioneryx* were compared to the drilling frequencies of other modern samples published in the literature to contextualise the results found here. Drilling frequencies were used from studies of drilling predation in Recent bivalves that reported the total number of valves or specimens, and either the number of drilled specimens or drilling frequency. The search was limited to studies whose collection methods involved bulk sampling on site, i.e. no museum collections or laboratory studies.

To maintain consistency, drilling frequency and 95% confidence intervals were recalculated according to the methods used in this study. Analysis was only done on species with at least 100 specimens. The data used from previous studies and recalculated values are reported in Table 9.

TABLE 8.—The relative abundances of *Callista disrupta*, *Fulvia tenuicostata* and *Chioneryx cardioides*. Specimen numbers were taken from Table 6, and percentages were calculated as percent of the three species total.

Median age (ka)	Number of specimens				Percent drilled		
	<i>Callista</i>	<i>Fulvia</i>	<i>Chioneryx</i>	Total	<i>Callista</i>	<i>Fulvia</i>	<i>Chioneryx</i>
0.140	72	638	148	858	8	74	17
0.783	16	207	46	269	6	77	17
1.385	29	278	110	417	7	67	26
2.381	163	1738	787	2688	6	65	29
3.298	40	276	298	614	7	45	49
4.212	376	1282	2389	4047	9	32	59

TABLE 9.—Complete drill hole data from previously published Recent studies. “Lat” is the latitude of the sampling site, rounded to the nearest whole number. Where a tilde (~) is used, the exact latitude of the site was not reported and therefore estimated. “Sediment type” describes the dominant sediment type at the sampling location. “Water depth” refers to the water depth at the sampling location. Where water depth is 0, sampling was done subaerially. “Predator” describes the drilling gastropod/s that were either identified as the predator by the study, or, where the predator was not specifically identified, the drilling gastropod/s also sampled by the study. “Species name” is the species name reported by the study, unless the study grouped specimens by genera, in which case only the genus name is reported. All species are infaunal, unless denoted by an asterisk (*). “Reported” values are those reported by the study; “total” is the total number of specimens, “drills” is the total number of specimens with a complete drill hole. “Calculated” values are those recalculated for this study using the same methods as described above; “DF” is the drilling frequency, and “CI” denotes the lower and upper 95% confidence intervals.

Paper	Location	Lat	Sediment type	Depth (m)	Predator	Species name	Reported		Calculated		
							Total	Drills	DF	CI	
Dietl et al. 2004	Gulf of Mexico, USA	~26	Siliclastic		Muricids	<i>Chione elevata</i>	118	13	0.11	0.06	0.18
	<i>Bonita Beach</i>										
	<i>Captiva Island</i>	~26				<i>Chione elevata</i>	221	32	0.15	0.10	0.20
	<i>Marco Island</i>	~26				<i>Chione elevata</i>	224	17	0.08	0.05	0.18
	<i>Naples</i>	~26				<i>Chione elevata</i>	140	52	0.37	0.29	0.46
	<i>Sanibel Island</i>	~26				<i>Chione elevata</i>	459	33	0.07	0.05	0.10
	<i>Anna Maria Island</i>	~27				<i>Chione elevata</i>	169	50	0.30	0.23	0.37
	<i>Laurel Beach</i>	~27				<i>Chione elevata</i>	210	24	0.11	0.08	0.17
	<i>Ft. DeSoto</i>	~28				<i>Chione elevata</i>	565	69	0.12	0.10	0.15
	<i>Honeymoon Island</i>	~28				<i>Chione elevata</i>	355	76	0.21	0.17	0.26
	<i>St. Josephs Bay</i>	~29		<2		<i>Chione elevata</i>	105	24	0.23	0.15	0.32

Gordillo and Archuby 2014	San Jorge Gulf, Argentina	-45	Siliclastic	0	Muricids	<i>Venus antiqua</i>	554	124	0.22	0.19	0.26
Hausmann et al. 2018	Gulf of Aqaba, Jordan	29	Carbonate	13	Naticids, Muricids	<i>Redicirce sulcata</i>	164	32	0.20	0.14	0.26
						<i>Wallucina erythraea</i>	474	217	0.46	0.41	0.50
				5	Naticids, Muricids	<i>Acar plicata</i>	166	7	0.04	0.02	0.09
						<i>Hytissa</i> sp. juv.	178	50	0.28	0.22	0.35
						<i>Septifer forskali</i> *	620	36	0.06	0.04	0.08
Herbert 2018	Gulf of Mexico, USA <i>St. Josephs Bay</i>	29	Siliclastic	<2	Muricids	<i>Chione elevata</i>	2523	311	0.12	0.11	0.14
					Naticids	<i>Chione elevata</i>	2523	16	0.01	0.00	0.01
Huntley & Scarponi 2015	Grado, Italy	46	Siliclastic	0		<i>Chamalea gallina</i>	198	0	0.00	0.00	0.02
	Caorle, Italy	46				<i>Chamalea gallina</i>	585	9	0.02	0.01	0.03
	Lido di Jesolo, Italy	46				<i>Chamalea gallina</i>	538	0	0.00	0.00	0.01
	Chioggia, Italy	45				<i>Chamalea gallina</i>	344	0	0.00	0.00	0.01
	Casal Borsetti, Italy	45				<i>Chamalea gallina</i>	456	0	0.00	0.00	0.01
						<i>Varicorbula gibba</i>	1013	1	0.00	0.00	0.01
						<i>Lentidium mediterraneum</i>	1699	0	0.00	0.00	0.00
	Marina di Ravenna, Italy	44				<i>Chamalea gallina</i>	746	0	0.00	0.00	0.00
						<i>Donax semistriatus</i>	234	0	0.00	0.00	0.02
						<i>Lentidium mediterraneum</i>	1113	0	0.00	0.00	0.00
						<i>Varicorbula gibba</i>	131	0	0.00	0.00	0.03

	Cervia, Italy	44				<i>Scapharca inaequivalvis</i>	124	0	0.00	0.00	0.03
	Cattolica, Italy	44				<i>Chamalea gallina</i>	213	0	0.00	0.00	0.02
	San Biagio, Italy	44				<i>Chamalea gallina</i>	319	0	0.00	0.00	0.01
	Senigallia, Italy	44				<i>Chamalea gallina</i>	279	1	0.00	0.00	0.02
Jonkers 2000	Papanui Canyon, New Zealand	-46	Siliclastic	400+	Muricids	<i>Zygochlamys delicatula*</i>	222	34	0.15	0.11	0.21
Martinelli et al. 2015	One Tree Reef, Australia	-23	Carbonate	4-6	Naticids	<i>Abranda jeanae</i>	771	57	0.07	0.06	0.10
						<i>Ctena bella</i>	264	8	0.03	0.01	0.06
						<i>Fragum fragum</i>	246	14	0.06	0.03	0.10
						<i>Loxoglypta clathrata</i>	1010	107	0.11	0.09	0.13
						<i>Pinguitellina robusta</i>	4119	235	0.06	0.05	0.07
						<i>Scissulina dispar</i>	995	39	0.04	0.03	0.05
Sawyer and Zuschin 2010	Gulf of Trieste, Italy	46	Siliclastic		Naticids, Muricids	<i>Chamelea gallina</i>	711	193	0.27	0.24	0.31
						<i>Corbula gibba</i>	1878	563	0.30	0.28	0.32
						<i>Lentidium mediterraneum</i>	2019	45	0.02	0.02	0.03
						<i>Mysella bidentata</i>	2001	852	0.43	0.40	0.45
						<i>Parvicardium papillosum</i>	933	159	0.17	0.15	0.20
Visaggi and Kelley 2015 ^[1]	North Eastern Brazil	-9	Siliclastic	0	Naticids	<i>Anadara</i>	341	75	0.22	0.18	0.27
						<i>Anomalocardia</i>	530	80	0.15	0.12	0.18

					<i>Chione</i>	223	40	0.18	0.13	0.24
					<i>Codakia</i>	104	49	0.47	0.37	0.57
					<i>Divalinga</i>	430	202	0.47	0.42	0.52
					<i>Mulinia</i>	385	108	0.28	0.24	0.33
					<i>Strigilla</i>	181	74	0.41	0.34	0.48
					<i>Tivela</i>	1320	40	0.03	0.02	0.04
Eastern Brazil	-18	Siliclastic	0	Naticids	<i>Anadara</i>	1475	103	0.07	0.06	0.08
					<i>Chione</i>	385	23	0.06	0.04	0.09
					<i>Codakia</i>	719	209	0.29	0.26	0.33
					<i>Divalinga</i>	604	362	0.60	0.56	0.64
					<i>Mulinia</i>	1775	89	0.05	0.04	0.06
					<i>Strigilla</i>	211	63	0.30	0.24	0.37
					<i>Tivela</i>	3498	210	0.06	0.05	0.07
South Eastern Brazil	-32	Siliclastic	0	Naticids	<i>Anadara</i>	696	21	0.03	0.02	0.05
					<i>Anomalocardia</i>	371	4	0.01	0.00	0.03
					<i>Chione</i>	153	8	0.05	0.02	0.10
					<i>Codakia</i>	1452	305	0.21	0.19	0.23
					<i>Divalinga</i>	435	235	0.54	0.49	0.59
					<i>Mulinia</i>	148	16	0.11	0.06	0.17

						<i>Strigilla</i>	101	40	0.40	0.30	0.50
						<i>Tivela</i>	497	5	0.01	0.00	0.02
Zuschin and Ebner 2015 ^[1]	Gulf of Aqaba, Egypt	28	Siliclastic	<2	Naticids, Muricids	<i>Cardiolucina semperiana</i>	138	10	0.07	0.04	0.13
						<i>Chavania erythraea</i>	366	304	0.83	0.79	0.87
						<i>Divalinga arabica</i>	144	61	0.42	0.34	0.51
						<i>Glycymeris arabica</i>	236	21	0.09	0.06	0.13

[1] Visaggi and Kelley (2015) and Zuschin and Ebner (2015) reported the total number of specimens and DF, therefore the number of valves drilled was calculated based on their reported formula for DF and given values.

TABLE 10.—Incomplete drill hole data from previously published Recent studies. All species are infaunal, unless denoted by an asterisk (*). “Total” is the total number of specimens, “Drills” is the total number of specimens that were drilled, “IDF” is the incomplete drilling frequency, and “Confidence intervals” are the lower and upper 95% confidence intervals.

Paper	Location	Species	Total	Drills	IDF	Confidence intervals	
Gordillo & Archuby 2014	San Jorge Gulf, Argentina	<i>Venus antiqua</i>	554	59	0.11	0.08	0.14
Huntley & Scarponi 2015	Grado, Italy	<i>Chamalea gallina</i>	198	1	0.01	0.00	0.03
	Caorle, Italy	<i>Chamalea gallina</i>	585	0	0.00	0.00	0.01
	Lido di Jesolo, Italy	<i>Chamalea gallina</i>	538	1	0.00	0.00	0.01
	Chioggia, Italy	<i>Chamalea gallina</i>	344	0	0.00	0.00	0.01
	Casal Borsetti, Italy	<i>Chamalea gallina</i>	456	0	0.00	0.00	0.01
		<i>Varicorbula gibba</i>	1013	0	0.00	0.00	0.00
		<i>Lentidium mediterraneum</i>	1699	0	0.00	0.00	0.00
	Marina di Ravenna, Italy	<i>Chamalea gallina</i>	746	0	0.00	0.00	0.00
		<i>Donax semistriatus</i>	234	0	0.00	0.00	0.02
		<i>Lentidium mediterraneum</i>	1113	0	0.00	0.00	0.00
		<i>Varicorbula gibba</i>	131	0	0.00	0.00	0.03
	Cervia, Italy	<i>Scapharca inaequalvis</i>	124	0	0.00	0.00	0.03
	Cattolica, Italy	<i>Chamalea gallina</i>	213	0	0.00	0.00	0.02
	San Biagio, Italy	<i>Chamalea gallina</i>	319	0	0.00	0.00	0.01
	Senigallia, Italy	<i>Chamalea gallina</i>	279	0	0.00	0.00	0.01

Jonkers 2000	Papanui Canyon, New Zealand	<i>Zygochlamys delicatula</i> *	222	4	0.02	0.00	0.05
Sawer & Zuschin 2010	Gulf of Trieste, Italy	<i>Mysella bidentata</i>	2001	4	0.00	0.00	0.01
		<i>Parvicardium papillosum</i>	933	0	0.00	0.00	0.00
		<i>Chamelea gallina</i>	711	11	0.02	0.01	0.03
		<i>Corbula gibba</i>	1878	530	0.28	0.26	0.30
		<i>Lentidium mediterraneum</i>	2019	1	0.00	0.00	0.00

The drilling frequencies calculated within Sydney Harbour are comparable the global compilation of modern studies of drilling predation. Globally, the proportion of complete drill holes varies between 0.01 and 0.83 (Table 9) with a median of 0.15 (Fig. 6A). The drilling frequencies reported here, 0.49, 0.17 and 0.65 (for *Callista*, *Fulvia* and *Chioneryx*, respectively) fall within this global range, but are higher than the global median. The proportion of incomplete drill holes reported here is very similar to that reported from other studies, with 0.01, 0.00 and 0.01 reported here (for *Callista*, *Fulvia* and *Chioneryx*, respectively), and 0.00 – 0.28 globally with a median of 0.01 (Fig. 6B). It should, however, be noted that the number of studies reporting incomplete drilling frequency is relatively small. The dominant drilling predators in Sydney Harbour are naticid gastropods (*Conuber incei*), but the compiled data suggest that the overall drilling frequencies are not driven by predator identity (Fig. 7). This suggests that drilling predator-prey dynamics in Sydney Harbour are not atypical of other locations where drilling predation has been studied.

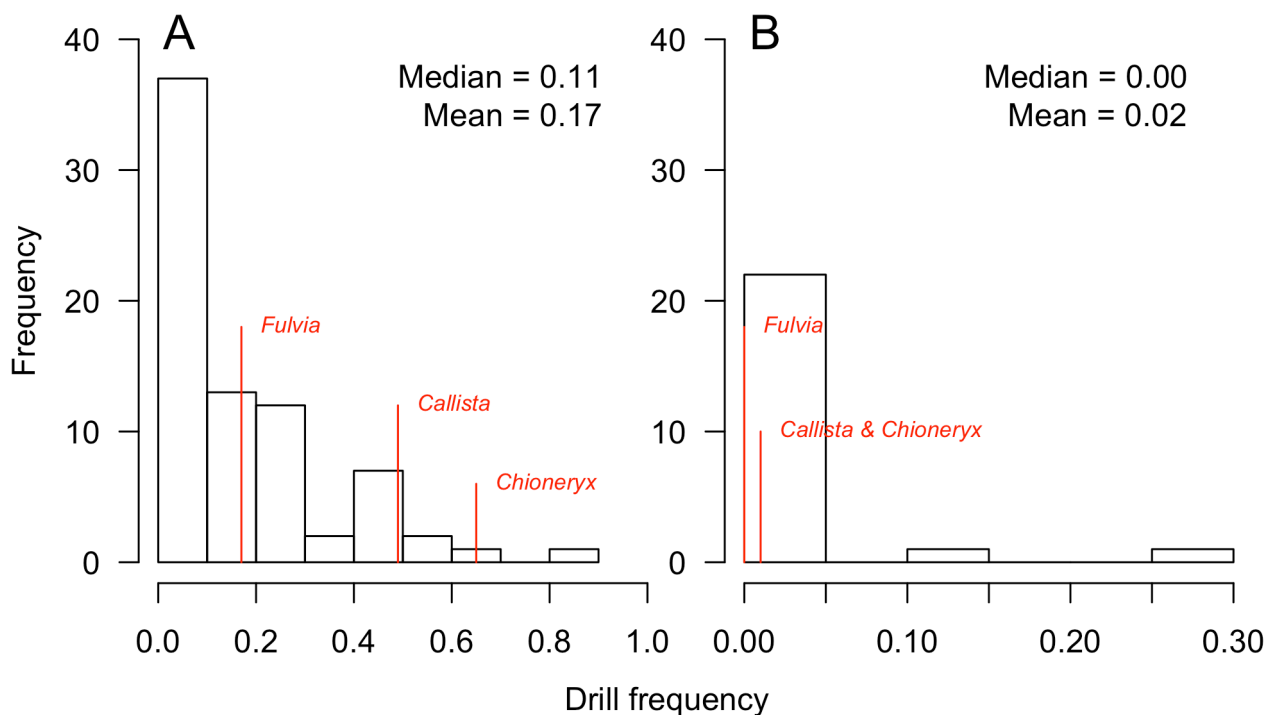


FIG 6.—Drilling frequency reported in previously published Recent studies. **A)** complete drill holes, **B)** incomplete drill holes.

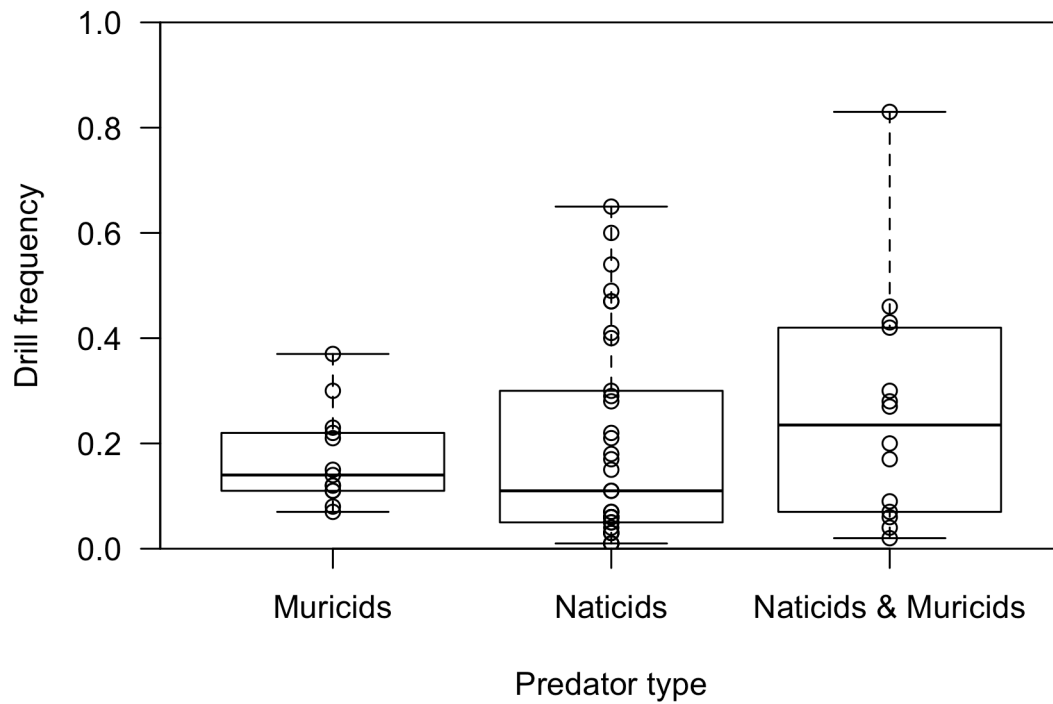


FIG 7.—Drilling frequency by predator type from previously published Recent studies (see Table 9). Points represent drilling frequency for a prey species, boxes represent the interquartile range (25-75%), and bolded line represents the median.

There is not a strong latitudinal gradient in the available data on modern drilling predation (Fig. 8). The drilling frequencies found in Sydney Harbour are similar to that reported from other locations both in terms of the overall magnitude of predation as well as the variation amongst taxa at a location. Globally, there is an uneven geographic distribution of drill frequency studies. While study locations in or adjacent to the Atlantic Ocean span both hemispheres, studies located in or adjacent to the Pacific are limited to the Southern Hemisphere and studies in or adjacent to the Indian Ocean are limited to the Northern Hemisphere. In addition, only two studies analysed drilling frequency from carbonate environments. There is not a strong water depth gradient in the available data on modern drilling predation (Fig. 9). The majority of studies collected samples from a water depth of less than 6 meters, meaning drilling is better understood at intertidal rather than subtidal depths.

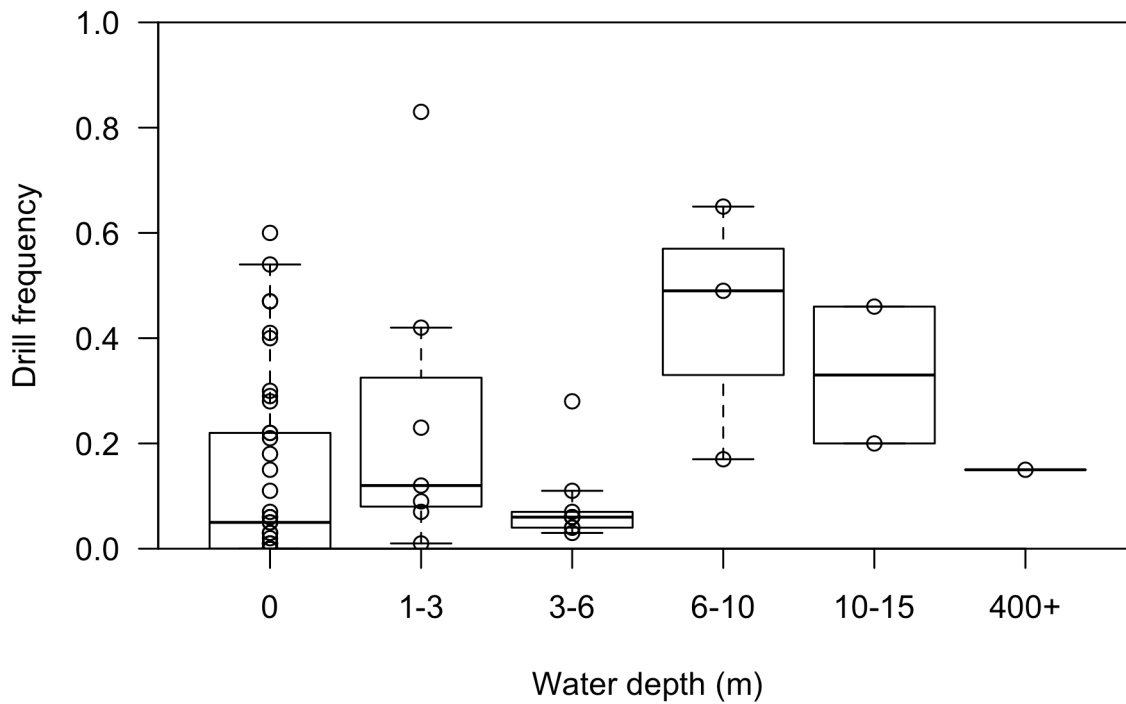


FIG 9.—Drilling frequency by collection water depth from previously published Recent studies (see Table 8). Points represent drilling frequency for a prey species, boxes represent the interquartile range (25-75%), and bolded line represents the median.

Future work

Drill holes provide important insights into the history of predator-prey dynamics. Most of this work has focused on Phanerozoic scale changes (e.g. Vermeij 1987; Kowalewski 1998; Kelley and Hansen 2003; Huntley and Kowalewski 2007; Klompmaker et al. 2017; Mondal et al. 2019), with comparatively little on Recent systems (see Table 9). In addition, the use of drill holes to infer changes in predatory-prey dynamics associated with anthropogenic effects is potentially powerful. While this study is a proof of concept, many more studies of drilling predation spanning anthropogenic changes are required before general patterns and conclusions can be drawn.

Conclusion

This work is a demonstration of the potential to use the Recent fossil record to identify potential human-induced changes to predator-prey interactions in molluscan communities. Here, drilling frequencies spanning 5 thousand years were quantified for three common bivalve species in Sydney Harbour. These drilling frequencies indicate that naticid predation was a leading cause of death for these species. The frequencies were not dissimilar to frequencies reported by other studies. For one species of bivalve, *Fulvia*, drilling intensity halved 700 to 100 years ago, corresponding with the European colonisation of Sydney. For the other two species, drilling frequencies did not significantly change. Predator-prey interactions have changed during this time period, and bivalve species were unevenly affected.

Data like these can be especially useful in estuaries such as Sydney Harbour where time series data are lacking. This work demonstrates the potential of the Recent fossil record to identify human-induced changes to predator-prey interactions in molluscan communities.

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SUPPLEMENT FILES

R code & drill data:

<http://marinescience.mq.edu.au/postgrad/perry/supplement1.zip>

Time averaging data:

<http://marinescience.mq.edu.au/postgrad/perry/supplement2.zip>