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RESEARCH ARTICLE

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Enamel growth rates of anterior teeth in males and females from modern and ancient British populations

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Abstract

Objective: This study explored biological sex differences in the regional daily growth rates of human anterior enamel from modern and ancient populations in Britain.

Methods: Maxillary permanent incisors (n = 80) and canines (n = 69) from Roman, Anglo-Saxon, Medieval, and Modern day populations were analyzed using histological methods. Daily secretion rates (DSRs) were collected for inner, mid, and outer regions of cuspal and lateral enamel. Modern day samples were of known sex, archeological individuals had sex determined using standard osteological methods. Variation in DSRs between the sexes, both between and within populations, was sought using parametric and nonparametric tests.

Results: When all samples were pooled, there was no significant difference between males and females. Similarly no significant differences in DSRs were identified between male and females within each population. When DSRs were compared between the populations, DSRs decreased from the more ancient to the more recent populations for males, and for females. More interpopulation differences were observed in males.

Discussion: This study presents evidence for the relative consistency of enamel DSRs between male and female groups within each British population. Interpopulation analyses found DSRs slowed significantly between Roman and modern day populations for both sexes, with male DSRs showing the greatest variation between populations.

KEYWORDS

canines, incisors, secretion rates, sex differences

1 | INTRODUCTION

Studies of enamel daily secretion rates (DSRs) of human teeth have tended to focus on permanent molars (e.g., Aris, Mahoney, O'Hara, & Deter, 2020; Beynon, Dean, & Reid, 1991b; Lacruz & Bromage, 2006; Mahoney, 2008) and deciduous dentition (e.g., Birch & Dean, 2009; Mahoney, 2012, 2015). Relatively less research has been undertaken on growth rates of the anterior dentition (incisors and canines) (e.g., FitzGerald, 1998; Reid, Beynon, & Ramirez Rozzi, 1998; Schwartz, Reid, & Dean, 2001). Of these studies only a few sought biological sex differences in the daily rate at which enamel forms (Schwartz et al., 2001). Schwartz et al. (2001) sought sex differences in permanent canine DSRs in a sample of humans and nonhuman hominoids. Their analysis of 16 mandibular human canines revealed no difference in DSRs when compared between the sexes (Schwartz et al., 2001), though whether there are sex differences in incisor enamel growth rates has not been examined.

The aim of this study is to explore sex differences in DSRs from anterior teeth in ancient and modern populations. First, DSRs from equivalent enamel regions of permanent incisors and canines will be compared between males and females using a pooled sample of all British populations. Second, DSRs will be compared between the sexes within each population. Third, DSRs will be compared between the populations, for males, and then for females.

1.1 | Amelogenesis and markings of incremental growth

Amelogenesis is the process of enamel formation which commences as the cells of the inner epithelium differentiate into ameloblasts (Nanci & Smith, 1992; Smith & Nanci, 2003). Differentiation of these cells initiates in those positioned at the tip of the dentine horn, with adjacent cells progressively differentiating following a path toward the dental cervix along enamel dentine junction (EDJ). Once an ameloblast has differentiated it immediately begins secreting enamel matrix (Berkovitz, Holland, & Moxham, 2002). Short-period cross striations are formed along the path followed by the differentiated cells (e.g., Berkovitz et al., 2002; Boyde, 1979, 1989; Dean & Scandrett, 1996; Desoutter et al., 2019; FitzGerald, 1998; Newman & Poole, 1974; Smith & Nanci, 2003) (Figure 1). Cross striations form daily as a result of the circadian rhythm of enamel matrix secretion (e.g., Antoine, 2000; Antoine, Hillson, & Dean, 2009; Boyde, 1963, 1990; Bromage, 1991; Dean, 1995; Lacruz & Bromage, 2006; Shellis, 1998), and possess a refractive index that differs to the majority of mature enamel, allowing them to be observed under transmitted light when sampled using histological methods (e.g., Berkovitz et al., 2002; Zheng et al., 2013). Due to the consistent and regular formation patterns of cross striation, they are used to calculate regional DSRs.

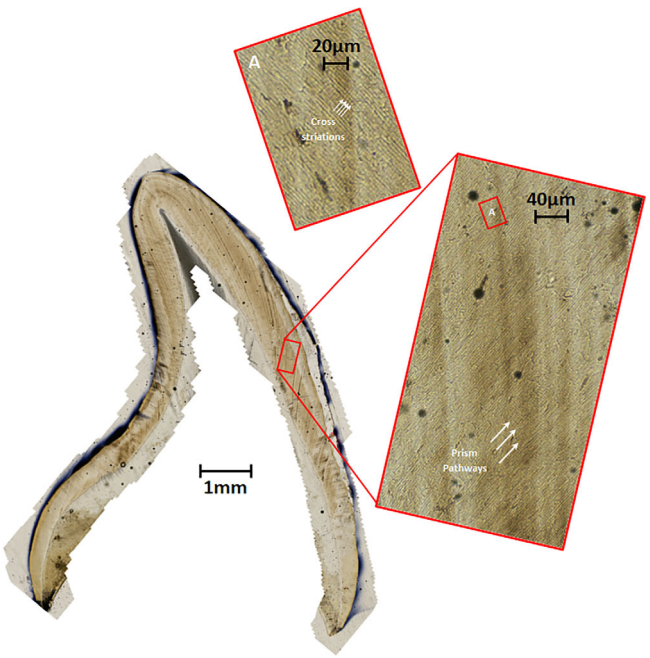

FIGURE 1 Cross-section of a Roman central incisor displaying the appearance of interior enamel formations and prism pathways under microscopic observation. The two superimpositions highlight the cross striations and the prism pathways they follow

1.2 | Intraspecific study of human enamel secretion rates

Intraspecific studies of human cross striations have identified daily formation patterns (e.g., Antoine et al., 2009; Beynon, Clayton, Ramirez Rozzi, & Reid, 1998; Beynon & Reid, 1987; Boyde, 1979; Kajiyama, 1965). Subsequent research has outlined the exact growth patterns followed by human enamel, and how secretion patterns vary throughout the enamel cap. Beynon (1992) identified that the volume of enamel secreted between adjacent cross striations in modern human anterior teeth increased with distance from the EDJ toward the outer enamel surface, a pattern consistent within all regions of the enamel cap. In addition, cross striation spacing also decreased from the cuspal, through lateral, to the cervical enamel region (Beynon, 1992). These findings have since been replicated across multiple studies of human molars (Beynon et al., 1991b; Lacruz & Bromage, 2006; Mahoney, 2008; Smith et al., 2006) and anterior dentition (Birch & Dean, 2009; FitzGerald, 1998; FitzGerald & Hillson, 2009; Reid et al., 1998a; Schwartz et al., 2001). As a result of varying cross striation spacing, DSRs are calculated for inner, mid, and outer regions of cuspal and lateral enamel (see methodology for detail; Figure 4).

The majority of human anterior tooth DSR analyses have focused on deciduous dentition. Research by FitzGerald and Hillson (2009) conducted histological analysis on 36 infants from first century AD Greece in order to study variations in appositional growth rates of enamel. Birch and Dean (2009) conducted a similar analysis with the aim of mapping the differences in DSRs across the varying regions of the enamel cap for mandibular deciduous tooth types including anterior teeth. They found that deciduous enamel DSRs varied similarly to permanent enamel, with DSRs increasing with proximity to both the cuspal and outer enamel areas. More recently Mahoney presented deciduous anterior tooth DSRs (Mahoney, 2012, 2015). Across Medieval British (Mahoney, 2012, 2015) and a few modern day Swedish samples (Mahoney, 2015), the mean DSRs presented were notably slower than those previously presented (Birch & Dean, 2009; FitzGerald & Hillson, 2009). While these papers only concern deciduous teeth, they do highlight the inter-population differences present within anterior tooth types concerning their daily growth rates for modern humans.

Schwartz et al. (2001) compared DSRs between human males and females as part of a study into the developmental mechanisms underlying canine dimorphism in extant hominoids. Their analysis of 16 mandibular human canines revealed the expected pattern of enamel secretion whereby rates were fastest in the cuspal region and with distance from the EDJ. Rates were consistent when compared between human males and females. It was also found that there was no significant difference between the DSRs of equivalent regions between the sexes (Schwartz et al., 2001). Incisor enamel DSRs were not an aim of their study, so little is known about this aspect of daily enamel growth in this tooth type. In particular, variation between male and female groups within a wider

selection of human populations, between the same populations, and for data gathered from incisor enamel, has yet to be researched.

2 | MATERIALS AND METHODS

2.1 | Dental sample

Maxillary permanent anterior teeth (n = 149) were selected from British populations that date to archeological and modern periods. The incisor sample (n = 80) consisted of maxillary first incisors: Roman (n = 10); Early Anglo Saxon (n = 22); Late Anglo-Saxon (n = 10); Medieval (n = 26); Modern day (n = 12). The maxillary canine sample (n = 69) consisted of Roman (n = 11), Early Anglo Saxon (n = 20), Late Anglo-Saxon (n = 10), Medieval (n = 16), and Modern day (n = 12). Right teeth were selected unless they were unavailable or the left was better preserved.

Figure 2 illustrates the location of the samples within Britain. The Roman population (70–400 AD) is represented by individuals excavated from cemeteries of Bath Gate and St. James' Place, in Cirencester, Gloucestershire (McWhirr, Viner, & Wells, 1982). The Early-Anglo Saxon samples (500–600 AD) come from individuals excavated from Ozengell Grange, Ramsgate, Kent (Millard, Jarman, & Hawkes, 1969) The Late Anglo-Saxon samples (800–1,200 AD) came from individuals excavated from Black Gate Cemetery, Newcastle-Upon-Tyne, Northumberland (Swales, 2012). The Medieval population is represented by individuals from St. Gregory's Priory, Canterbury, Kent (1,100–1,500 AD) (Hicks & Hicks, 2001) and Fishergate House, York, North Yorkshire (1,000–1,600 AD) (Holst, 2005).

The modern day samples are from the UCL/Kent Collection. These samples are dental extractions from 1964 and 1973 conducted in dental surgeries from northern England and Southern Scotland. These samples are held in the Skeletal Biology Research Centre, University of Kent. Ethical approval for the histological analysis of this dental sample was obtained from the UK National Health Service research ethics committee (REC reference: 16/SC/0166; project ID: 203541).

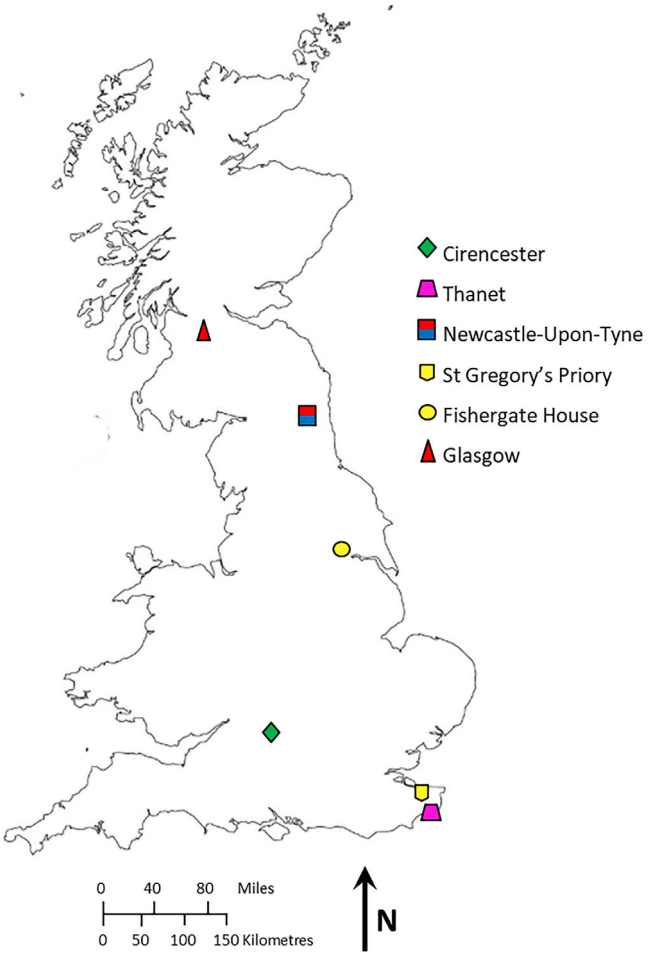

FIGURE 2 Map of the United-Kingdom detailing the geographic location where the archeological samples were excavated/modern day samples extracted. Object colors dictate the time period of origin of the populations collected from each location: Red, Modern day; Yellow, Medieval; Blue, Late Anglo-Saxon; Pink, Early Anglo-Saxon; Green, Roman

2.2 | Estimating sex

The modern day dental samples were all of known biological sex. The archeological samples were assigned sex using established osteological methods of the skull and pelvis, utilizing a 1–5 scale (1 = definitely female; 2 = likely female; 3 = indeterminate; 4 likely male; 5 = definitely male) (Ferembach, 1980; Krogman & Isçan, 1986; Loth & Henneberg, 1996; Patriquin, Steyn, & Loth, 2005; Phenice, 1969; Schwartz, 1995). Sex assessment using the skull involved assessing 25 features known to be sexually dimorphic (as defined by: Ferembach, 1980; Krogman & Isçan, 1986; Loth & Henneberg, 1996; Schwartz, 1995). Assessment of the pelvis involved analyzing a further 20 sexually dimorphic skeletal features (as defined by: Ferembach, 1980; Krogman & Isçan, 1986; Phenice, 1969; Schwartz, 1995) were also analyzed. In addition, where the pelvis was not fragmented metric analyses were also used to give a sex determination score (Patriquin et al., 2005). Once all viable features of the skull and pelvis had been assigned a 1–5 score, all scores for an individual were given an average which equated to the overall sex assessment. Individuals with a clear sex determination (i.e., not indeterminate) were then used for further analyses. Where possible all sex assessment methods were utilized, however, in some cases methods could not be used due to the preservation of skeletal remains. For this reason only individuals with at least well preserved cranial or pelvic features were utilized.

2.3 | Sample preparation

Before conducting destructive analysis, high resolution images and one-to-one scale resin casts were produced for each tooth (Aris, 2020).

Standard histological methods were used to produce thin sections for each tooth (e.g., Aris, 2020; Mahoney, 2008; Schwartz & Dean, 2005). First, each tooth was embedded in a four-to-one hardener and epoxy resin solution (Buehler®). By embedding the teeth, the risk of fracturing was minimized and allowed for easier alignment of each sample within a precision vice (Buehler®) during sectioning. Each embedded tooth was cut using a diamond-edged wafering saw blade (Buehler® IsoMet 1000 Precision Cutter), spun at a low speed along their longitudinal axis through their cusp apex. Once cut, each sample was mounted on a glass microscope slide before being lapped using fine grinding pads (Buehler®) until around 100–120 μm thick. Sections were polished using 0.3 μm aluminium oxide powder (Buehler®) to remove all evidence of lapping. Thin sections were then placed within an ultrasonic bath, for 2 min periods in order to remove any remaining debris. Finally, each dental sample was dehydrated using 90% and 100% concentrations of ethanol solution (Fisher scientific®) and cleared (using Histoclear®). To protect sections from contamination, each was mounted with a glass cover slip using a mounting medium (DPX®). Cover slipped samples were analyzed under polarized light using a BX53 upright microscope (Olympus®) and micro imaging software (cellSens; see below for detail).

2.4 | Daily secretion rates

Using standard methods, the DSRs for both the incisors and canines were calculated for the inner, mid, and outer areas of the lateral and cuspal enamel of each tooth (e.g., Beynon, Dean, & Reid, 1991a; Mahoney, 2008; Schwartz et al., 2001). Each area within the cuspal and lateral regions was determined by dividing the length of the enamel regions into three equidistant portions, following the longitudinal axis of local enamel prisms (Figure 3). Regions of cuspal enamel

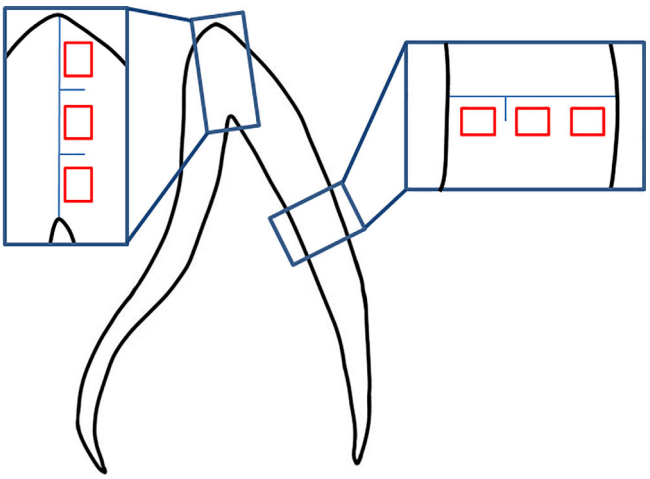

FIGURE 3 Cross-sectional diagram of an incisor displaying the breakdown of cuspal and lateral enamel into areas for DSR calculation. The *left* superimposition shows the cuspal enamel. The *right* superimposition shows lateral enamel. The red squares indicate the regions where DSR measurements were taken for the, moving upward, inner, mid, and outer areas

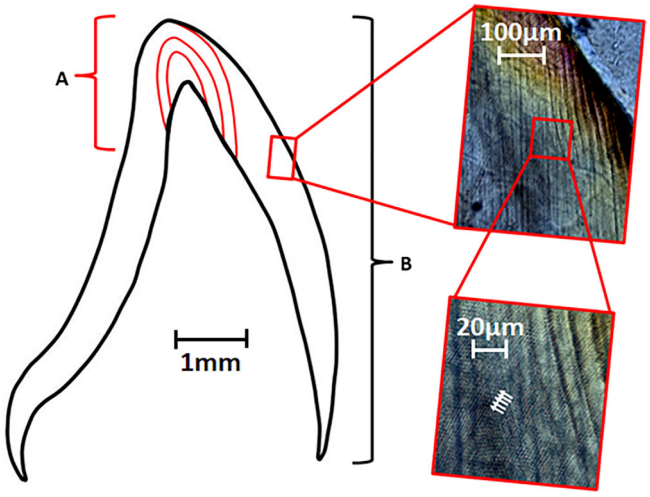

FIGURE 4 Cross-sectional diagram of a canine. (a) Appositional enamel and (b) Imbricational enamel. The *top* superimposition shows the mid-outer lateral region. The *bottom* superimposition shows cross striations, indicated by the small white arrows, of the outer lateral region. Both images were captured at ×20 magnification under polarized light

were determined within the appositional enamel starting near the dentine horn. The lateral enamel areas were determined within the section of imbricational enamel of equal distance from the dental cervix and dentine horn.

Within each isolated enamel region, a measurement was made of five consecutive cross striations along the length of an enamel prism. This measurement was subsequently divided by five, giving a mean daily rate of secretion (μm/day). This process was repeated until six mean DSRs were produced. These results were then similarly divided to give a grand mean and standard deviation. All cross striation measurements were taken between ×20 and ×40 magnification (Figure 4).

2.5 | Statistical analysis

Mann–Whitney *U* tests were run to identify any differences between the sexes in regional DSRs of incisor and canines. Where regional DSRs presented adequate sample sizes, and were consistent between tooth types in all populations, they were pooled into a single anterior tooth sample set for subsequent analyses. A series of Independent Samples *T*-tests were then conducted to test for differences in DSRs between the male and female groups across all populations. Further Mann–Whitney *U* tests were then conducted to search for differences between males and females within each of the five populations separately.

Kruskal–Wallis tests with Dunn-Bonferroni pairwise comparisons and Jonckheere-Terpstra tests (for the majority of DSRs), and a series of Mann–Whitney *U* tests (for cuspal DSRs), one each for the male and female samples, were conducted to compare DSRs between the populations. This was undertaken to identify significant in DSRs in males when compared between the time periods, and in females when compared between the same periods. In the few cases where $n < 5$

for a given sample (where *n* = number of teeth), mean values and standard deviations were compared between groups.

While nonparametric tests were required in most cases, parametric tests were conducted where sample sizes allowed in order to strengthen the statistical analyses where possible. All statistical analyses were performed using the SPSS 24.0.

3 | RESULTS

3.1 | Differences between tooth types

Results of the Mann–Whitney *U* tests (Table S1) revealed DSRs from equivalent enamel regions did not differ significantly when compared between incisors and canines within any of the British populations. As a result, the data for both tooth types were pooled to create DSRs from anterior teeth for each population. These DSRs from anterior teeth were used for all subsequent statistical analyses.t

3.2 | Differences in DSRs between biological sex groups

Table 1 reports the results of DSRs compared between biological male and females when all of the British populations were pooled. Independent Samples *T*-tests revealed no significant differences in DSRs when compared between males and females. Table 2 reports the same tests conducted separately for each population. There was no significant difference between the sexes when DSRs from equivalent regions were compared within each population.

3.3 | Differences in DSRs between biological sex groups and between populations

Tables 3 and 4 report mean inner, mid, and outer DSRs for cuspal and lateral regions (respectively) of the anterior tooth samples from the male individuals of each population. In addition the tables include the descriptive data and results of the Kruskal–Wallis and posthoc Dunn-Bonferroni pairwise comparisons.

Mean DSRs from the inner cuspal enamel region of male anterior teeth were significantly slower in the modern day sample compared to the Roman sample. The inner region mean DSRs of the male cuspal anterior tooth enamel slowed between the Roman and modern day samples by 0.40 μm/day. This slowing displayed a followed a significant trend through time ($p < .00$). The Roman mean DSRs were significantly faster than that of the Medieval and modern day populations ($p < .00$). The mean DSRs of the mid cuspal male anterior tooth enamel between the Roman and modern day samples slowed by a rate of 0.92 μm/day. The trend toward slowing for the enamel region was also significant ($p < .00$). In addition, the Roman mean DSRs were significantly faster than that of the modern day ($p < .00$) population. The mean outer cuspal male anterior tooth DSRs also alluded to a slowing in secretions rates over time between populations. The mean Roman DSRs were significantly faster than the modern day population ($p < .00$), with a mean difference of 1.08 μm/day.

The inner region mean DSRs of the lateral anterior tooth enamel slowed between the Roman and modern day samples by 0.70 μm/day, and displayed a significant slowing trend through time ($p < .00$). The Roman mean DSRs were significantly faster than that of the Medieval and modern day (both at $p < .00$) populations. The mean DSRs of the mid lateral anterior tooth enamel between the Roman and modern day samples slowed by a rate of 0.72 μm/day, and with a significant trend toward slowing ($p < .00$). The Roman and Early Anglo-Saxon mean DSRs were significantly faster than that of the modern day ($p < .00$ and $p = .01$, respectively) population. The mean Roman DSRs were also significantly faster than in the Medieval ($p = .03$) population. The mean DSRs of the outer lateral anterior tooth enamel between the Roman and modern day samples slowed by an increased rate of 0.82 μm/day. The region also displayed a significant trend toward slowing ($p < .00$). The Roman and Early Anglo-Saxon mean DSRs

TABLE 1 Results of the independent samples *T*-tests for variation in DSRs when the sexes were pooled for all populations

Feature	Sex	*N*	Mean	*SD*	Min	Max	Sig.
Inner lateral DSR	M	44	3.16	0.33	2.47	4.11	.19
	F	39	3.31	0.32	2.45	4.24	
Mid lateral DSR	M	44	3.65	0.33	2.99	4.42	.13
	F	41	3.80	0.31	2,86	4.29	
Outer lateral DSR	M	42	4.05	0.37	3.35	4.75	.11
	F	40	4.15	0.40	3.03	4.81	
Inner cuspal DSR	M	32	3.24	0.33	2.41	4.16	.69
	F	32	3.26	0.32	2.51	3.26	
Mid cuspal DSR	M	33	3.72	0.38	2.91	4.58	.22
	F	33	3.81	0.31	2.86	4.29	
Outer cuspal DSR	M	27	4.17	0.50	3.42	5.05	.25
	F	31	4.31	0.48	3.16	5.37	

TABLE 2 Results of the Mann–Whitney *U* tests for variation in DSRs compared between the sexes for the anterior tooth sample of each population

Population	Feature	Sex	*N*	Mean	*SD*	Min	Max	Sig.
Roman	Inner lateral DSR	M	8	3.62	0.22	3.35	4.11	.79
		F	8	3.58	0.36	3.12	4.24	
	Mid lateral DSR	M	8	4.04	0.18	3.67	4.28	.84
		F	9	4.04	0.18	3.68	4.29	
	Outer lateral DSR	M	8	4.48	0.17	4.28	4.75	.77
		F	9	4.41	0.25	3.88	4.81	
	Inner cuspal DSR	M	7	3.65	0.28	3.35	4.16	.33
		F	7	3.57	0.38	3.22	4.23	
	Mid cuspal DSR	M	8	4.17	0.21	3.94	4.58	.90
		F	7	4.13	0.23	3.67	4.35	
	Outer cuspal DSR	M	8	4.74	0.28	4.16	5.05	.52
		F	7	4.72	0.12	4.53	4.92	
Early Anglo-Saxons	Inner lateral DSR	M	9	3.18	0.15	3.05	3.43	.60
		F	13	3.39	0.13	3.11	3.62	
	Mid lateral DSR	M	9	3.76	0.29	3.36	4.42	.90
		F	13	3.96	0.19	3.48	4.17	
	Outer lateral DSR	M	8	4.33	0.22	3.94	4.74	.28
		F	12	4.40	0.19	3.96	4.69	
	Inner cuspal DSR	M	5	3.25	0.15	3.05	3.43	.35
		F	9	3.32	0.19	2.85	3.32	
	Mid cuspal DSR	M	5	3.75	0.25	3.47	3.99	.38
		F	9	3.92	0.19	3.38	4.29	
Medieval	Inner lateral DSR	M	7	2.96	0.19	2.72	3.22	.24
		F	5	3.18	0.16	2.97	3.43	
	Mid lateral DSR	M	7	3.53	0.14	3.35	3.74	.28
		F	6	3.64	0.18	3.42	3.91	
	Outer lateral DSR	M	7	3.84	0.18	3.61	4.11	.15
		F	6	4.04	0.28	3.60	4.49	
	Inner cuspal DSR	M	7	3.10	0.12	2.91	3.29	.56
		F	5	3.09	0.20	2.94	3.45	
	Mid cuspal DSR	M	7	3.71	0.08	3.62	3.85	.11
		F	6	3.81	0.26	3.34	4.09	
Modern day	Inner lateral DSR	M	14	2.92	0.23	2.47	3.22	.53
		F	10	2.99	0.28	2.45	3.32	
	Mid lateral DSR	M	14	3.32	0.19	2.99	3.65	.10
		F	10	3.46	0.31	2.86	3.80	
	Outer lateral DSR	M	13	3.66	0.17	3.35	3.84	.55
		F	10	3.66	0.33	3.03	4.06	
	Inner cuspal DSR	M	9	3.00	0.32	2.41	3.34	.86
		F	9	3.06	0.30	2.51	3.43	
	Mid cuspal DSR	M	9	3.25	0.21	2.91	3.59	.15
		F	9	3.41	0.33	2.81	3.86	
	Outer cuspal DSR	M	9	3.66	0.17	3.42	3.95	.25
		F	9	3.77	0.32	3.16	4.09	

TABLE 3 Results of the Mann–Whitney U and independent samples Kruskal–Wallis tests with posthoc pairwise Dunn-Bonferroni analysis, and Jonckheere-Terpstra testing for variation between the *male cuspal* DSRs (μm/day) across all populations

								Dunn-Bonferroni adjusted sig.			
Enamel region	**Population**	***N***	**Mean**	***SD***	**Min**	**Max**	**Kruskal–Wallis sig.**	**Early Anglo-Saxon**	**Medieval**	**Modern day**	**Jonckheere-Terpstra sig.**
Inner	Roman	7	3.65	0.28	3.35	4.16	**.01**	.45	**.00***	**.00***	**−.00***
	Early Anglo-Saxon	5	3.25	0.15	3.05	3.43					
									.51	.43	
	Medieval	7	3.10	0.12	2.91	3.29				1.00	
	Modern day	9	3.00	0.32	2.41	3.34					
Mid	Roman	8	4.17	0.21	3.94	4.58	**.00***	.52	.07	**.00***	**−.00***
	Early Anglo-Saxon	5	3.75	0.25	3.47	3.99			1.00	.11	
	Medieval	7	3.71	0.08	3.62	3.85				.32	
	Modern day	9	3.25	0.21	2.91	3.59					
							Mann–Whitney *U* sig.				
Outer	Roman	8	4.74	0.28	4.16	5.05	**.00***				
	Modern day	9	3.66	0.17	3.42	3.95					
	Early Anglo-Saxon	4	4.35	0.33	3.99	4.64					
	Medieval	4	3.88	0.09	3.77	4.01					

Note: Mann–Whitney *U* tests were used in the case of the outer enamel data as only two populations supported statistical analysis (as other samples were ≥*n* = 5). Where populations presented sample sizes too small for statistical analysis they are still presented here for future comparisons. The Dunn-Bonferroni significance values have been adjusted to account for Bonferroni corrections. Inclusion of—on Jonckheere-Terpstra results indicate a trend toward reduction. Significant results are marked in bold.

*$p < .00$.

TABLE 4 Results of the independent samples Kruskal-Wallis, posthoc pairwise Dunn-Bonferroni analysis, and Jonckheere-Terpstra testing for variation between the *male lateral* DSRs (μm/day) across all populations

								Dunn-Bonferroni adjusted sig.			
Enamel region	**Population**	***N***	**Mean**	***SD***	**Min**	**Max**	**Kruskal–Wallis sig.**	**Early Anglo-Saxon**	**Medieval**	**Modern day**	**Jonckheere-Terpstra sig.**
Inner	Roman	8	3.62	0.22	3.35	4.11	**.00***	.11	**.00***	**.00***	**−.00***
	Early Anglo-Saxon	9	3.18	0.15	3.05	3.43			1.00	.54	
	Medieval	7	2.96	0.19	2.72	3.22				1.00	
	Modern day	14	2.92	0.23	2.47	3.22					
Mid	Roman	8	4.04	0.18	3.67	4.28	**.00***	1.00	**.03**	**.00***	**−.00***
	Early Anglo-Saxon	9	3.76	0.29	3.36	4.42			1.00	**.01**	
	Medieval	7	3.53	0.14	3.35	3.74				1.00	
	Modern day	14	3.32	0.19	2.99	3.65					
Outer	Roman	8	4.48	0.17	4.28	4.75	**.00***	1.00	**.00***	**.00***	**−.00***
	Early Anglo-Saxon	8	4.33	0.22	3.94	4.74			.09	**.00***	
	Medieval	7	3.84	0.18	3.61	4.11				1.00	
	Modern day	13	3.66	0.17	3.35	3.84					

Note: The Dunn-Bonferroni significance values have been adjusted to account for Bonferroni corrections. Inclusion of—on Jonckheere-Terpstra results indicate a trend toward reduction. Significant results are marked in bold.

*$p < .00$.

TABLE 5 Results of the independent samples Kruskal–Wallis tests with posthoc pairwise Dunn-Bonferroni analysis, and Jonckheere-Terpstra testing for variation between the *female cuspal* DSRs (μm/day) across all populations

								Dunn-Bonferroni adjusted sig.			
Enamel region	**Population**	***N***	**Mean**	***SD***	**Min**	**Max**	**Kruskal–Wallis sig.**	**Early Anglo-Saxon**	**Medieval**	**Modern day**	**Jonckheere-Terpstra sig.**
Inner	Roman	7	3.57	0.38	3.22	4.23	**.04**	1.00	.19	**.05**	**–.00***
	Early Anglo-Saxon	9	3.32	0.19	2.85	3.32			1.00	.64	
	Medieval	5	3.09	0.20	2.94	3.45				1.00	
	Modern day	9	3.06	0.30	2.51	3.43					
Mid	Roman	7	4.13	0.23	3.67	4.35	**.00***	1.00	.89	**.00***	**–.00***
	Early Anglo-Saxon	9	3.92	0.19	3.38	4.29			1.00	.07	
	Medieval	6	3.81	0.26	3.34	4.09				.67	
	Modern day	9	3.41	0.33	2.81	3.86					
Outer	Roman	7	4.72	0.12	4.53	4.92	**.00***	1.00	.31	**.00***	**–.00***
	Early Anglo-Saxon	12	4.40	0.35	3.96	5.37			1.00	**.00***	
	Medieval	6	4.26	0.16	4.08	4.41				.65	
	Modern day	9	3.77	0.32	3.16	4.09					

Note: The Dunn-Bonferroni significance values have been adjusted to account for Bonferroni corrections. Inclusion of—on Jonckheere-Terpstra results indicate a trend toward reduction. Significant results are marked in bold.

*$p < .00$.

TABLE 6 Results of the independent samples Kruskal–Wallis, posthoc pairwise Dunn-Bonferroni analysis, and Jonckheere-Terpstra testing for variation between the *female lateral* DSRs (μm/day) across all populations

								Dunn-Bonferroni adjusted sig.			
Enamel region	**Population**	***N***	**Mean**	***SD***	**Min**	**Max**	**Kruskal–Wallis sig.**	**Early Anglo-Saxon**	**Medieval**	**Modern day**	**Jonckheere-Terpstra sig.**
Inner	Roman	8	3.58	0.36	3.12	4.24	**.00***	1.00	.17	**.00***	**−.00***
	Early Anglo-Saxon	13	3.39	0.13	3.11	3.62			.73	**.01**	
	Medieval	5	3.18	0.16	2.97	3.43				1.00	
	Modern day	10	2.99	0.28	2.45	3.32					
Mid	Roman	9	4.04	0.18	3.68	4.29	**.00***	1.00	**.02**	**.00***	**−.00***
	Early Anglo-Saxon	13	3.96	0.19	3.48	4.17			.07	**.00***	
	Medieval	6	3.64	0.18	3.42	3.91				1.00	
	Modern day	10	3.46	0.31	2.86	3.80					
Outer	Roman	9	4.41	0.25	3.88	4.81	**.00***	1.00	.47	**.00***	**−.00***
	Early Anglo-Saxon	12	4.40	0.19	3.96	4.69			0.42	**.00***	
	Medieval	6	4.04	0.28	3.60	4.49				1.00	
	Modern day	10	3.66	0.33	3.03	4.06					

Note: Mann–Whitney *U* tests were used where sample sizes only supported the analysis of two populations. The Dunn-Bonferroni significance values have been adjusted to account for Bonferroni corrections. Inclusion of—on Jonckheere-Terpstra results indicate a trend toward reduction. Significant results are marked in bold.

*$p < .00$.

were significantly faster than that of the modern day (both at $p < .00$) population. The mean Roman DSRs were also significantly faster than in the Medieval ($p < .00$) population.

Tables 5 and 6 report the mean inner, mid, and outer DSRs for the cuspal and lateral region (respectively) of the anterior tooth samples compromised of the female individuals of each population. In addition the tables include the descriptive data and results of the Kruskal–Wallis and posthoc Dunn-Bonferroni pairwise comparisons.

The inner region mean DSRs of the female cuspal anterior tooth enamel slowed by a rate of 0.51 μm/day between the Roman and modern day samples. Pairwise analyses found the mean Roman DSRs to be significantly faster than that of the modern day ($p = .05$), and the trend toward slowing through time was also significant ($p < -.00$). The mean DSRs of the mid cuspal female anterior tooth enamel between the Roman and modern day samples slowed by a rate of 0.72 μm/day and the trend toward slowing DSRs was significant ($p < .00$). In addition, the Roman mean DSRs were significantly faster than that of the modern day ($p < .00$) population, with a mean difference of 0.95 μm/day. The mean outer cuspal DSRs also slowed between populations, at a rate of 0.95 μm/day between the Roman and modern day populations. The trend toward slowing was again significant ($p < -.00$). Male modern day mean outer cuspal DSRs were also significantly slower than those of both the Roman and Early Anglo-Saxon populations (both at $p < .00$).

The inner region mean DSRs of the lateral anterior tooth enamel slowed between the Roman and modern day samples by 0.59 μm/day. Changes in DSRs between populations through time, again followed a significant slowing trend ($p < .00$). The Roman and Early Anglo-Saxon mean DSRs were significantly faster than that of the modern day ($p < .00$ and $p = .01$, respectively) population. The mean DSRs of the mid lateral anterior tooth enamel between the Roman and modern day samples slowed by a similar rate of 0.58 μm/day, and with a significant trend toward slowing ($p < .00$). The Roman and Early Anglo-Saxon mean DSRs were significantly faster than that of the modern day ($p < .00$ and $p = .01$, respectively) population. The mean Roman DSRs were also significant faster than in the Medieval ($p = .02$) population. The mean DSRs of the outer lateral anterior tooth enamel between the Roman and modern day samples slowed by an accelerated rate of 0.74 μm/day, and displayed a significant trend toward slowing ($p < .00$). The Roman and Early Anglo-Saxon mean DSRs were again significantly faster than that of the modern day (both at $p < .00$) population.

4 | DISCUSSION

This study compared DSRs of anterior teeth between biological male and females, from modern and archeological populations from Britain. These comparisons revealed no significant difference in DSRs when males were compared to females, either when British populations were combined into a single sample, or within each population. However, there was a significant trend toward a slowing of DSRs across the 2000 year period, from the Romano-British to the modern day populations, for males, and for females. There were a greater number of significant differences between the populations when males were compared, in comparison to the number of significant differences observed in females.

4.1 | DSRs compared between the sexes within each populations

There was no significant difference between the anterior teeth for males and females in this study. This analysis reveals that the daily enamel growth of permanent human anterior tooth enamel is consistent between the sexes, within these ancient and modern British populations. Our findings for permanent anterior tooth enamel DSRs are consistent with findings for DSRs from permanent canines from a single human population (Schwartz et al., 2001).

4.2 | DSRs compared between the sexes, from ancient to modern populations

While all regional DSRs from male and female groups slowed over time (Tables 4-6), the male samples displayed a higher volume of significant differences when compared between populations. Cuspal enamel analyses revealed four such variations, whereas the equivalent analyses of the female samples identified only two pairwise significant differences. Analyses of lateral enamel DSRs displayed a similar trend with eight significant differences between the enamel of male groups, with slightly fewer significant differences in the female groups.

4.3 | DSRs compared between populations

Pairwise analysis of both male and female samples revealed a number of significant inter-population differences in DSRs of cuspal and lateral anterior tooth enamel. All these differences display an additional significant trend toward a slowing trajectory in DSRs between populations from the Roman to modern day populations. Indeed, only in the single case of the female inner cuspal DSRs were the mean Roman values not significantly faster than the modern day ($p = .07$; Table 5). While the male sample displayed the most pairwise significant differences between populations, the trends toward slowing were consistent for all enamel regions across both male and female analyses (Tables 4–6).

4.4 | DSRs compared to posterior teeth

Past research utilizing the same British populations, has identified a significant trend toward slowing enamel DSRs from the Roman to modern period in permanent first molar teeth (Aris et al., 2020). This

trend is similar to those observed here in both male and female samples. These results show the trend toward the slowing of daily enamel growth in Britain over the last 2000 years, has been consistent in both anterior and posterior teeth. Where the differences in enamel growth rates between populations were similar in the anterior teeth and first molars of the British populations, this was not the case specifically in differences between the Roman and Early Anglo-Saxon populations. In their study, Aris et al. (2020) commented on the similarities in the growth rates of the two populations, most notably in the cuspal enamel where mean rates were near identical. Conversely, in almost all anterior tooth enamel regions presented here, both male and female DSRs can be observed to vary between the Roman and Early Anglo-Saxon population. Only in the mid and outer lateral enamel of the female sample can comparable similarities to that seen in the molar teeth of the sample populations (Aris et al., 2020) be observed, between the Roman and Early Anglo-Saxon populations. These differences in findings between anterior teeth and molar growth rates suggest that, within a consistent trend of slowing overtime, variation between tooth types has also occurred. This further suggests that no single tooth type should necessarily be considered representative of the dental arcade when investigating differences in enamel growth rates between human populations. Future analysis of premolar enamel would be valuable.

Comparison of DSRs for equivalent enamel regions and British populations between tooth types identifies further variation growth patterns. Comparing mean regional DSRs calculated from male and female anterior tooth samples (presented here) to mean DSRs for molar regions (see: Tables 2 and 3 in Aris et al., 2020) shows permanent first molar enamel, in the majority of 24 comparisons, to have been secreted at a faster rate than that of anterior teeth. In 11 of these cases molar regions grew faster, but only by a rate of ≤0.15 μm/day. In four of the seven cases where molar enamel secreted at a slower rate, the difference in DSRs between molar and anterior teeth was also only ≤0.15 μm/day. Interestingly these were almost always in outer region DSRs. In the remaining six cases of the initial 24 comparisons, more notable differences were seen between the regional DRSs of molar and anterior teeth. One difference was isolated to a single case of the Early Anglo-Saxon population in which inner cuspal molar enamel was secreted at a rate of 0.40 μm/day faster than that of the anterior teeth. In another single case, the mid lateral anterior tooth enamel of the modern day population grew at a faster rate by 0.23 μm/day. For the remaining four cases where notable differences between tooth types were observed, all were within comparisons of the medieval population. In the inner lateral and cuspal regions Medieval molar enamel secreted at a faster rate (by 0.29 and 0.26 μm/day, respectively), where conversely the outer lateral and cuspal regions Medieval anterior tooth enamel secreted faster (by 0.23 and 0.40 μm/day, respectively). While preliminary, the findings of comparing anterior tooth and molar enamel DSRs within British populations does allude to variable growth patterns between tooth types. Overall, permanent molar enamel appears to develop faster, particularly in the inner and mid regions. Conversely, anterior tooth types can develop faster in the outer regions, most notably the cuspal outer regions. The cause for this difference is as of yet unknown, but appears to be most active in the Medieval British population.

The discovery of variation in permanent enamel DSRs, both between tooth types within populations and within tooth types between populations, provides further evidence to the idea that permanent enamel DSRs are highly variable in humans, even over as short a period as 2000 years. Furthermore, the reasons underlying the slower DSRs from the more ancient to modern period have probably influenced the anterior and posterior teeth, as both of these tooth types show a similar trend.

5 | CONCLUSIONS

Results presented here display a consistency in DSRs when compared between biologically male and female groups, in both archeological and modern British populations. In contrast to these findings, DSRs have varied to a greater degree between British populations. DSRs, from cuspal and lateral enamel regions, were observed to have significantly slowed throughout the last 2000 years in Britain. This pattern is consistent to that previously observed for DSRs in molar enamel. Future research would benefit from integrating life history, genetic, and environmental factors in order to widen our understanding of how diversity in human enamel growth has, and may continue to, evolve.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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