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NONDAILY DEPOSITION OF STRIAE IN THE BAY SCALLOP *ARGOPECTEN IRRADIANS* (*CONCENTRICUS*) IN THE LABORATORY

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ABSTRACT Small (~15 mm) and large (~30 mm) calcein-marked bay scallops, *Argopecten irradians*, held for 2, 4, and 6 wk in the laboratory under natural illumination and conditions of high and low flow rates deposited significantly more striae on the surface of the left (dark) shell valve compared with the right (light) shell valve. Small scallops deposited an average of 0.55 stria per day, 0.42 stria per day, and 0.34 stria per day, respectively, during the 2-, 4-, and 6-wk experiments, whereas large scallops had a lower frequency of stria formation (0.20 stria per day, 0.18 stria per day, and 0.17 stria per day, respectively). Striae deposition and interstria distance were highly variable among small *A. irradians*. No relationship in interstria distance was obvious in *A. irradians* that deposited the same number of striae during 6 wk (0.45 striae per day) and held under conditions of high flow rate, indicating that stria formation is not synchronous with changes in the environment. Our results demonstrate unequivocally that in *A. irradians*, stria formation is nondaily and is related to shell growth rate. The largest and oldest scallops (~30 mm and 1.4 y old) formed striae at a rate of 0.17–0.2 stria per day whereas smaller and younger fast-growing *A. irradians* formed between 0.34 striae per day and 0.55 stria per day—clear evidence of nondaily and nonrhythmic deposition of striae in this pectinid species. Thus, striae cannot be used as a chronological marker with which environmental conditions can be compared.

KEY WORDS: scallop, *Argopecten irradians*, shell growth, striae deposition

INTRODUCTION

The bay scallop *Argopecten irradians* (*concentricus*) is a commercially important species with a short life span of ~1–2 y (Marshall 1963, MacFarlane 1999). Historically, *A. irradians* populations inhabited eelgrass *Zostera* spp. beds along the Atlantic coast of the United States; however, many of these populations have experienced declines after recent anthropogenic disturbances together with periods of poor reproduction and recruitment failure, which have led to the collapse of local scallop fisheries (see MacFarlane (1999) for examples). Changes in scallop populations have been attributed to fluctuations in seagrass *Zostera* spp. density because they act as important nursery areas for postlarval and juvenile bay scallops; the shoots provide a firm substratum for attachment and afford protection from predators during the early, vulnerable post-settlement stage (Marshall 1947, Eckman 1987). The fragile nature of seagrass habitats coupled with the commercial value of *A. irradians* has recently led to restoration efforts to reintroduce this scallop into local seagrass habitats along the eastern seaboard of the United States (MacFarlane 1999). To facilitate its successful reintroduction, it is beneficial to have an understanding of its growth patterns and life history.

Previous studies have considered the value of bivalve shells as archives of information because their shells contain historical records of different aspects of their life history, including disturbance events, seawater temperature fluctuations, predator disturbance, and elemental ratios in surrounding water masses (Richardson 2001). The shells contain incremental growth lines that represent various time frames, depending on the species. For example, long-lived species (>150 y) such as *Arctica islandica* and *Glycymeris glycymeris* deposit annually resolved growth lines in their shell (e.g., Butler et al. 2010, Brocas et al. 2013) whereas short-lived species such as *Cerastoderma edule* and *Mytilus edulis*

deposit incremental series with a tidal periodicity (Richardson 1989). Some bivalve families, notably the Pectinidae, have representatives that form external ridges, or striae, externally on their shell surface. It is thought that these striae are formed with a daily (Clark 1968, Clark 1975, Antoine 1978, Broom & Mason 1978, Wrenn 1972, Helm & Malouf 1983) or twice daily (Chauvaud et al. 1998, Chauvaud et al. 2005, Thébault et al. 2006) periodicity. Others have demonstrated, using controlled laboratory experiments, that striae deposition in juvenile *Pecten maximus* is related to the rate of shell growth, and daily deposition is only closely approached in the fastest growing shells (Gruffydd 1981, Owen et al. 2002).

The mechanisms controlling stria formation are unclear, although it has been suggested that daily fluctuations in illumination, seawater temperature, and food availability may control deposition (Clark 1968, Kirby-Smith 1970, Wrenn 1972, Broom & Mason 1978, Wallace & Reines 1985, Wilson 1987). What is clear from previous studies is that, although some scallops deposit striae close to a daily periodicity, stria formation in other individuals falls significantly short of a daily periodicity. A number of studies, such as those by Chauvaud et al. (1998, 2005) and Thébault et al. (2006), have used scallop striae in a chronological context, and analyzed geochemically each dated daily striae formed during the period of fastest shell growth in the spring and summer. What remains unclear from many of the previous studies is whether a daily periodicity of stria formation remains constant and reliable over an annual cycle even during periods of slow autumn and winter shell growth. We investigated whether striae form fortuitously with a daily periodicity during periods of fast shell formation, and also whether deposition is independent of shell growth rate and shell size. We tested these by studying stria formation in a fast-growing scallop species, *Argopecten irradians*, which displays clear surface striae and attains a maximum size of ~50 mm in less than 2 y, at a time when seawater temperatures were declining during the autumn season (September to December). We exposed experimentally marked individuals

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of known age from 2 size (age) cohorts for 6 wk to seasonally changing seawater temperatures and to 2 different flow rates and food availability to determine how flow rate and temperature controlled stria formation.

MATERIALS AND METHODS

The work was undertaken between September 2011 and December 2011 at the Virginia Institute of Marine Science Eastern Shore Laboratory as part of a program to restore *Argopecten irradians* into seagrass meadows along the coast of Virginia. The cohorts of *A. irradians* used in the field and laboratory experiments were spawned in the laboratory during April and May 2010 and during May 2011, and were reared in bags suspended in a tidal creek in Wachapreague Inlet, VA (37°35'9.25" N, 75°38'1.12" W).

To investigate the periodicity of formation of striae and the increment of shell deposited under the different environmental conditions, each scallop was marked individually using the fluorochrome dye calcein. Calcein has been shown to be a reliable marker in bivalve shells and to cause low mortality (Day et al. 1995, Kaehler & MacQuaid 1999, van Der Geest et al. 2001, Thébault et al. 2006, Linard et al. 2011). Unlike the studies of Kaehler and MacQuaid (1999), in which a concentrated solution (125 mg/L) of calcein was injected by syringe into the pallial cavity of brown mussels (*Perna perna*), the *Argopecten irradians* used in this experiment were fully immersed in a low concentration of calcein solution. Linard et al. (2011) demonstrated that immersion in calcein solution is more successful than injection, because it allowed all scallops in their study to be marked simultaneously. In an initial trial in our study, 3 groups of 3 small (~15 mm) and 3 large (~30 mm)

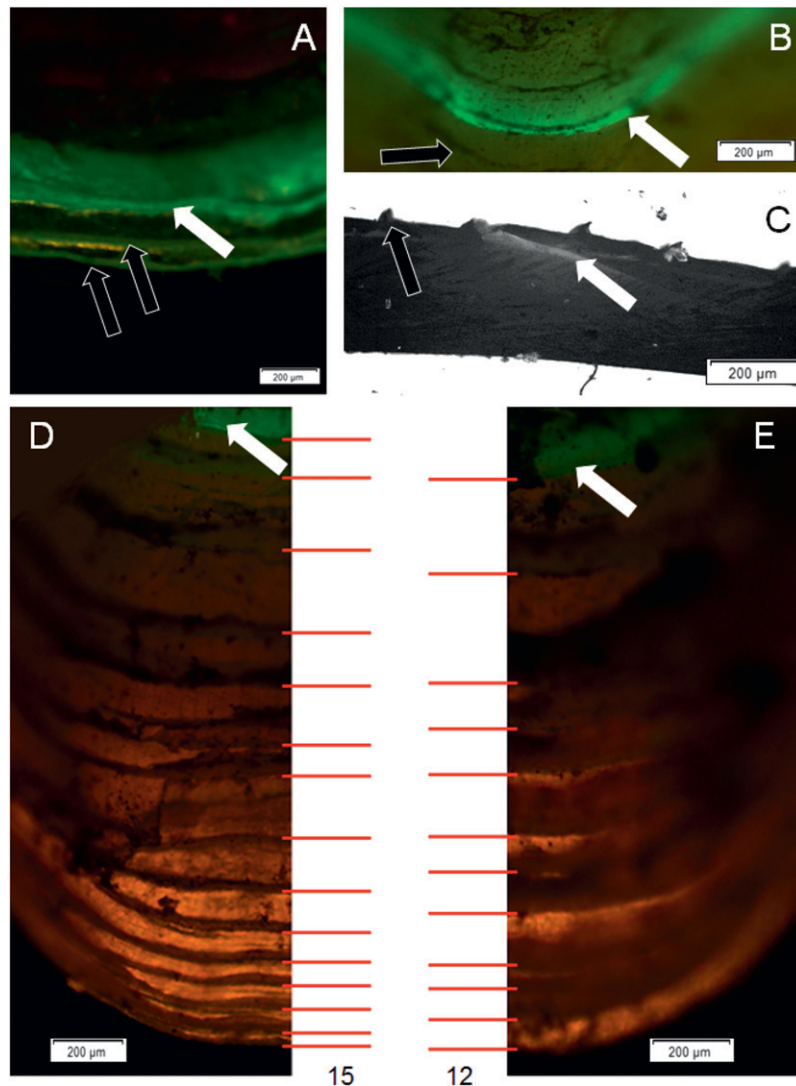


Figure 1. Calcein-marked shells of *Argopecten irradians* to demonstrate the incorporation of the fluorescent dye calcein into the mineralizing shell. (A) Fluorescent mark (white arrow) at the margin of the shell after exposure to calcein solution (3 days after exposure) and 2 striae (black arrows). (B) Calcein staining (white arrow), 2 wk after exposure, close to the shell margin with 1 postmarking stria shown (black arrow). (C) Photomicrograph in transmitted light of a polished thin section to illustrate the position of the calcein incorporation (white arrow) and normal postmarking stria deposition (black arrow). Shell growth is from right to left. (D, E) Shell surface of 2 scallops marked with calcein (white arrow) and grown for 4 wk under a high flow rate to show a difference in striae deposition (horizontal red lines): 15 striae (D) and 12 striae (E) during the same period of time.

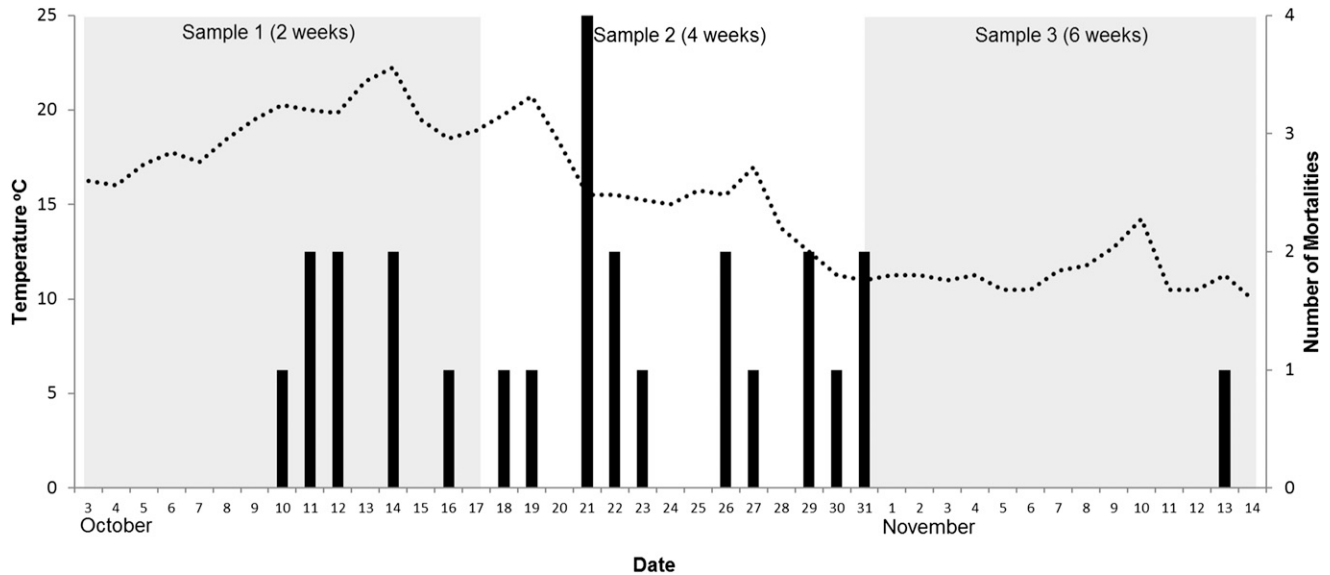


Figure 2. Average daily seawater temperature (spotted line) and daily mortality of scallops (bars) during the study period.

A. irradians were immersed in aquaria containing 2 aerated solutions of different-strength calcein for different periods of time. Bay scallops were either exposed to 3 L of 50 mg/L calcein for 24 h or 125 mg/L calcein for 7 h, or were held in a control aquarium containing seawater only. The scallops were fed 10 mL/L cultured microalgae every 8 h. After exposure to calcein, scallops were transferred to a flow-through seawater aquarium for 2 days to incorporate the calcein into the shell. Whole shells were examined for fluorescence under a microscope (Olympus CKX41 inverted microscope with X-Cite series 120-Q fluorescence light source using a B-range filter block), and all the calcein-marked shells subsequently displayed a thin, green fluorescent line close to the shell margin (Fig. 1A–C). There was no difference between the strength of the fluorescent line produced under the 2 different concentrations, so in all subsequent marking experiments, the lower concentration (50 mg/L for 24 h) was used to mark the shells.

One hundred eighty ~0.3-y-old *Argopecten irradians* obtained from 2 laboratory-induced spawns (young; May 12, 2012, and May 25, 2012) and 175 ~1.4-y-old scallops (old) taken from 4 induced spawns in April 2010 and May 2010 were stained simultaneously by immersion in 50 mg/L calcein for 24 h. The young and older scallops were each divided into 2 groups, placed in open top mesh trays to raise them off the bottom of the aquarium and to avoid smothering by accumulating sediment, and then transferred to 1 of 2 flow-through seawater tables. Scallops were exposed in the seawater tables to either a high (10 L/min) or low (5 L/min) flow rate with ambient seawater pumped from Wachapreague Channel. Flow (measured as volume flux in liters per minute) and seawater temperature were monitored 3 times a day (0900 HR, 1300 HR, and 1700 HR) and the tanks were cleaned by siphoning off the sediment every 3 days to minimize disturbance to the scallops. Scallop mortalities were recorded. After 2 wk, a third of the

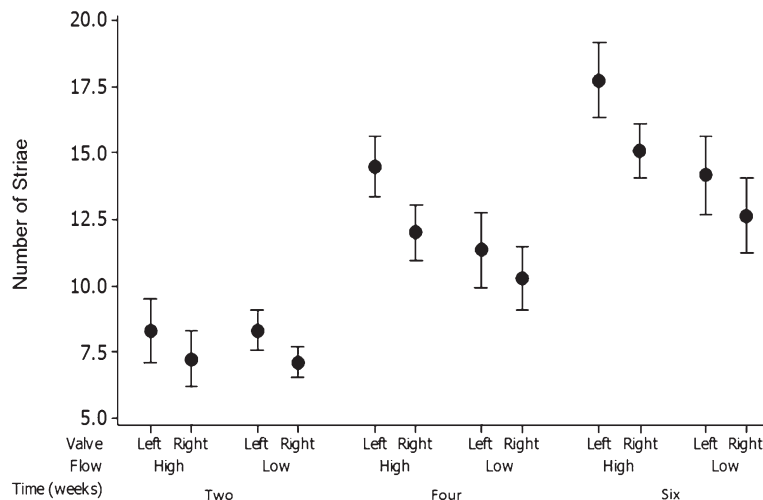


Figure 3. Interval plot. The mean number of striae ($\pm 95\%$ CI) deposited on the left and right shell valves of *Argopecten irradians* reared for 2, 4, and 6 wk under high and low flow rates in the laboratory.

TABLE 1.

Summary of striae deposition on the right (light) and left (dark) shell valves by 2 age groups (young, ~0.3 y old; old, ~1.4 y old) of *Argopecten irradians* held under high and low flow rates after 2, 4, and 6 wk. Average number of striae +/- standard deviation.

Condition	Scallop age	Valve	Average no. of striae ± SD	Average interstriae distance ± SD (µm)	Growth ± SD (%)
Sample 1 (14 days)					
High flow	Young	Light	7.23 ± 2.87	158.48 ± 55.48	3.18 ± 1.37
		Dark	8.3 ± 3.23	123.83 ± 35.59	2.95 ± 1.30
Low flow	Young	Light	7.1 ± 1.56	134.34 ± 50.61	2.85 ± 1.38
		Dark	8.3 ± 2.00	112.76 ± 37.65	2.79 ± 1.35
High flow	Old	Light	2.1 ± 1.25	62.07 ± 36.09	0.25 ± 0.30
		Dark	2 ± 1.17	70.26 ± 33.81	0.25 ± 0.21
Low flow	Old	Light	3.6 ± 1.13	69.03 ± 29.56	0.47 ± 0.28
		Dark	3.63 ± 1.57	55.39 ± 22.01	0.39 ± 0.24
Sample 2 (28 days)					
High flow	Young	Light	11.73 ± 2.83	166.65 ± 61.07	5.38 ± 2.24
		Dark	13.7 ± 3.74	135.68 ± 39.00	5.19 ± 2.19
Low flow	Young	Light	10.27 ± 3.18	122.86 ± 34.71	3.53 ± 1.68
		Dark	11.33 ± 3.74	105.3 ± 25.18	3.34 ± 1.61
High flow	Old	Light	3.05 ± 2.22	68.09 ± 40.30	0.45 ± 0.64
		Dark	3.75 ± 2.61	65.51 ± 33.66	0.53 ± 0.65
Low flow	Old	Light	6.39 ± 3.13	86.86 ± 22.86	1.08 ± 0.56
		Dark	7.17 ± 2.50	78.43 ± 18.48	1.11 ± 0.53
Sample 3 (42 day)					
High flow	Young	Light	14.79 ± 3.29	188.02 ± 59.19	7.63 ± 2.56
		Dark	17.38 ± 4.47	156.25 ± 40.76	7.41 ± 2.37
Low flow	Young	Light	11.88 ± 4.36	133.34 ± 35.88	4.51 ± 2.04
		Dark	13.30 ± 4.67	116.36 ± 28.53	4.47 ± 1.98
High flow	Old	Light	5.82 ± 3.49	87.87 ± 43.43	1.00 ± 0.75
		Dark	7.12 ± 4.43	74.23 ± 20.20	1.03 ± 0.79
Low flow	Old	Light	8.15 ± 3.05	70.77 ± 27.97	1.09 ± 0.55
		Dark	7.78 ± 3.60	74.16 ± 28.42	1.13 ± 0.74

scallops (30 young and 25 old) were removed from each flow treatment, dissected carefully to avoid damage to the delicate shell margins, the flesh was removed, and the shells were labeled and left to dry (sample 1). Another third of the scallops were culled after 4 wk (sample 2) and then after 6 wk (sample 3), and prepared in a similar way. The position of the calcein mark on both the left and right shell valves was identified under fluorescence, labeled with a pencil mark on the shell valve, and all subsequent shell growth was related to the mark (Fig. 1D, E). On both shell valves, the number of striae was counted and the total increment of growth was measured (using Olympus CellSens image analysis software) between the calcein mark and the shell margin along the midline of maximum growth between the hinge and shell margin (Fig. 1D, E). Occasionally, shell valves were embedded in resin to investigate the extent of the calcein mark and its possible impact on postmarking striae production (Fig. 1C). To achieve this, the left convex shell valve was embedded in Metaset resin for ~24 h before radially sectioning along a line through the hinge region to the shell margin using a precision Buheler Isomet 4000 diamond saw. The cut surfaces were ground on successive wet and dry paper (400 grit and 1,000 grit) lubricated with water, polished with 5-µm and then 1-µm diamond paste, and attached with Super-glue to a microscope slide. A thin section of the shell attached to the slide was then sliced off using the Buheler Isomet saw, and was ground and polished using the same process to achieve a section less than 1 mm in thickness. This thin section was then

analyzed under a low-power transmitted fluorescent microscope and photographed.

RESULTS

After calcein staining, 99.5% of young, small scallops showed a clear fluorescent calcein mark (Fig. 1-C) followed by deposition

TABLE 2.

Results of 3-way GLM differences in the number of striae, total growth, and the striae production time, among the flow conditions, left and right valves, and sampling time.

Response	df	F ratio	P value
Striae (n)			
Valve	1	24.08	<0.001
Flow rate	1	26.48	<0.001
Time (wk)	2	170.69	<0.001
Total growth			
Valve	1	0.53	0.466
Flow rate	1	81.96	<0.001
Time (wk)	2	102.14	<0.001
Striae production time			
Valve	1	20.8	<0.001
Flow rate	1	22.16	<0.001
Time (wk)	2	84.86	<0.001

of striae; only 1 scallop died during the 6-wk experiment. Eighty-six percent of the older (larger) scallops displayed a calcein mark with subsequent striae deposition, although many of these scallops either exhibited little or no shell growth or had damaged shell margins and the increment of shell growth could not be measured reliably. Analysis of striae deposition therefore focused on the small, younger scallops in which shell deposition had occurred after calcein marking. Twenty-five percent of the large scallops died in the flow-through tanks, often after a sudden change in seawater temperature (Fig. 2). During the 6-wk period, the average seawater temperature decreased 7.6°C, from $18.9 \pm 0.5^\circ\text{C}$ during the first 2 wk (high, 22.3°C ; low, 16°C) to $11.3 \pm 0.31^\circ\text{C}$ during the last 2 wk (high, 14.3°C ; low, 10.5°C ; Fig. 2).

The mean number of striae ($\pm 95\%$ CI) deposited on the left and right shell valves of *Argopecten irradians* reared for 2, 4, and 6 wk under high and low flow rates in the laboratory are shown in Figure 3 and are tabulated in Table 1. General linear model (GLM) analysis of square root-transformed (to ensure compliance with normality) striae data from small *A. irradians* demonstrated that significantly more striae were deposited on the left shell valve of *A. irradians* than the right during the 2-, 4-, and 6-wk experiments (Table 2, Fig. 3). Five scallops that showed atypical slow growth rates were not included in the analyses. The average number of striae deposited increased significantly with increasing time, and striae deposition was greater under a high flow rate than a low flow rate (GLM; Table 2). No significant difference in the growth of the right or left shell valve was observed, although shell growth was enhanced significantly under the high flow rate (GLM; Table 2).

If the deposition of striae is controlled diurnally through changes in illumination, changes in seawater temperature, or food supply, then there should be a clear relationship between the duration of the experiment, the number of striae deposited, and the interstria distance. Small scallops deposited an average of 0.55 stria per day, 0.42 stria per day, and 0.34 stria per day,

respectively, during the 2-, 4-, and 6-wk experiments whereas larger scallops had a lower frequency of stria formation (0.20 stria per day, 0.18 stria per day, and 0.17 stria per day, respectively). Striae deposition and interstria distance were highly variable among the small *Argopecten irradians* (Table 2). We compared the interstria distance on the shells from 5 individuals that had deposited the same number of striae during the 6-wk period (0.45 striae per day) under conditions of high flow rate (Fig. 4). There was a general decline in interstria distance in these 5 shells during the 6 wk, but with no obvious correspondence in the distance between specific striae in the 5 scallops, indicating that the factors that control interstria distance and subsequent stria formation do not respond synchronously to changes in the environment in the flow-through tanks. The production of striae is clearly a function of the increment of shell deposited. Figure 5 shows there are relationships between striae production in small and large *A. irradians* maintained under high and Low flow over 2, 4, and 6 wk. Scallops that grew slowly produced a small number of striae compared with fast-growing individuals that deposited a large number of striae; only a few *A. irradians* deposited 14 striae in 14 days, 20 in 28 days, and 25 in 42 days (Fig. 5); most individuals deposited striae with a periodicity below that of a daily periodicity.

DISCUSSION

In this study we investigated the evidence for a daily periodicity of formation of the external striae on the shell of *Argopecten irradians* and examined whether the striae could be used as a chronological marker of shell formation over a 6-wk period of the scallops' life span. To be used as a chronological marker, a periodic structure must have an environmentally controlled periodicity of formation. We have demonstrated unequivocally that stria formation on the shell of *A. irradians* is related to growth of the shell and is independent of an environmental periodicity, daily or otherwise.

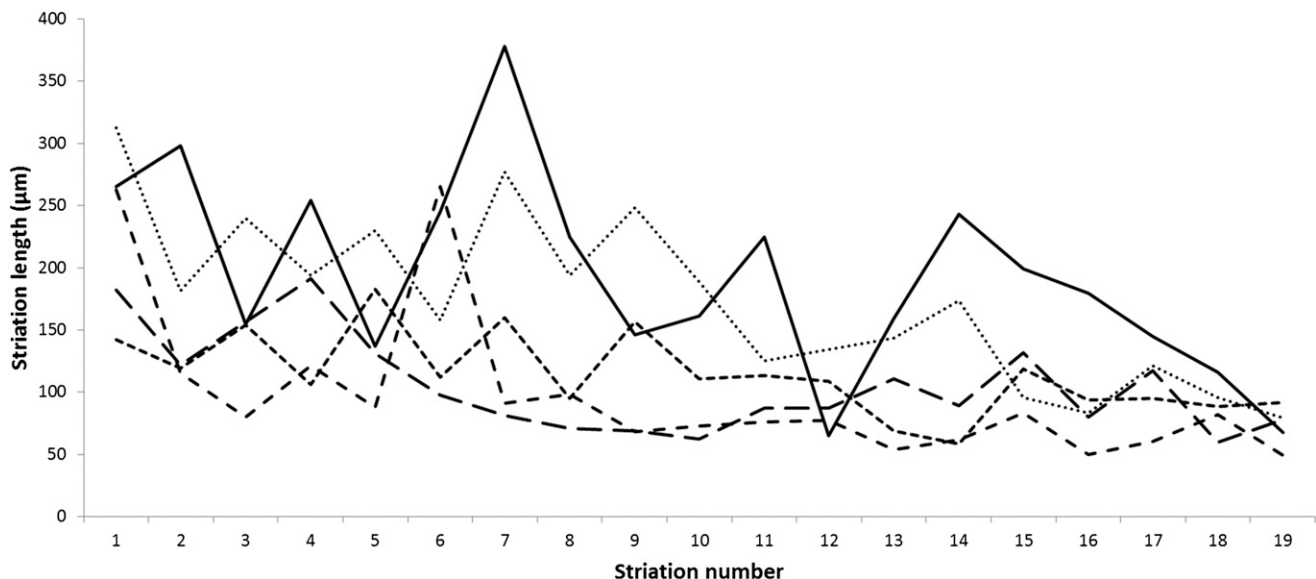


Figure 4. Variation in interstria distance in 5 *Argopecten irradians* reared for 6 wk in the laboratory under a high flow rate. Each shell deposited 19 striae.

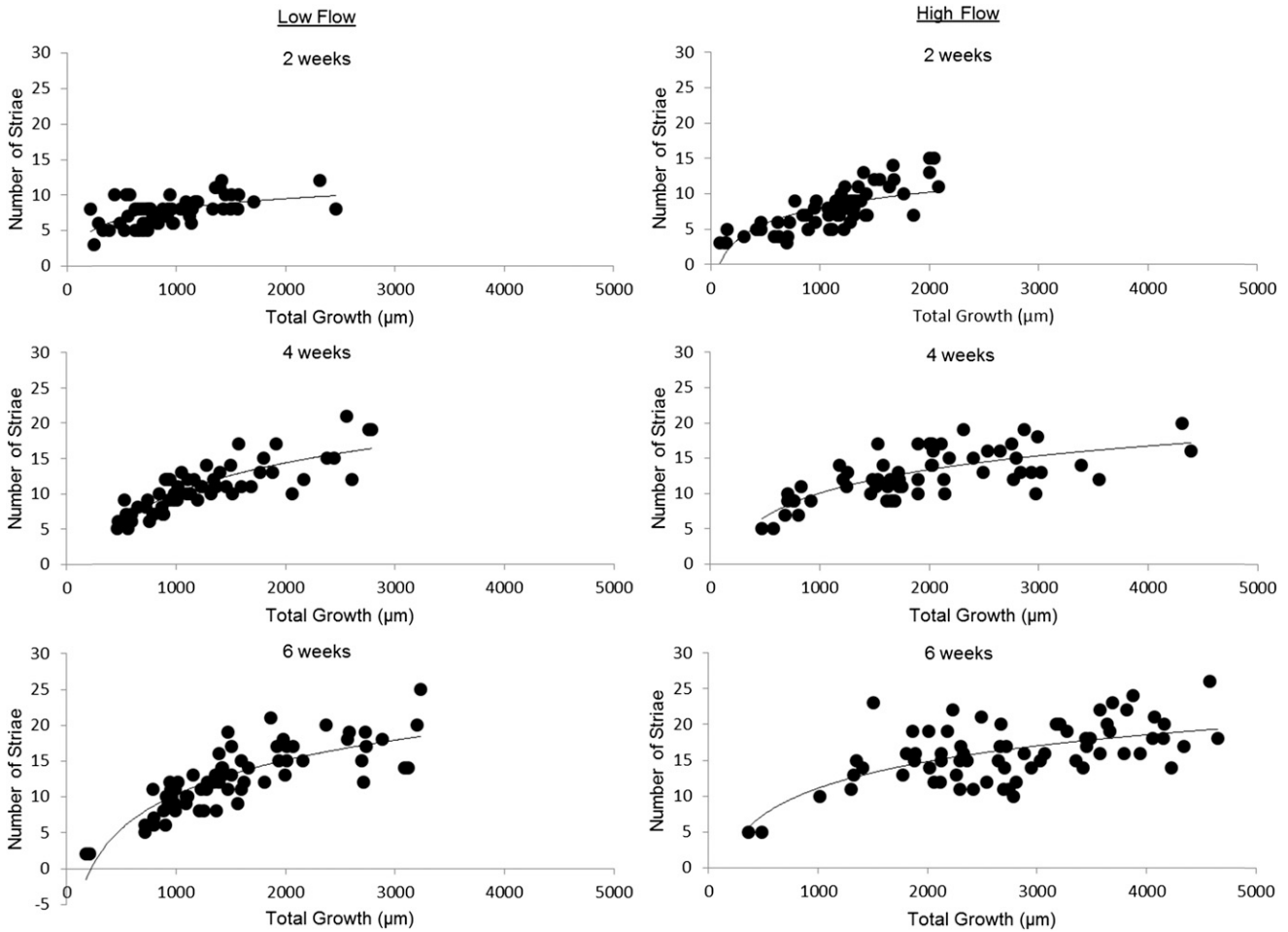


Figure 5. Scatterplots showing a plot of the number of striae formed against the total growth throughout the study. Plots only contain data from the young scallops; individual plots are shown for both high and low flow rates after 2, 4, and 6 wk. The trend lines shown are logarithmic.

Significantly more striae were deposited on the left valve compared with the right valve during the 2-, 4-, and 6-wk experiments, even though there was no significant difference in the growth of the right or left valves. This illustrates that the 2 shell valves are forming striae at different rates in an individual *A. irradians*. This scallop positioned itself in the aquaria with its right, light-cream color valve on the substratum; the left, darker color valve was orientated uppermost. It is unclear why the frequency of striae deposition was significantly different in the 2 shell valves, although the inclusion of natural coloration in the organic matter in the left, darker shell valve may have increased stria formation time in some way. The frequency of striae (ridge) production on the shell valves of juvenile *Pecten maximus* was shown to be nonuniform around the edge of the shell (Gruffydd 1981). Gruffydd (1981) showed that the maximum number of striae were deposited on the central ridge (maximum umbo-rim axis), but that striae numbers declined over a range of 5 ribs, either side of the central one, and that counting of striae became very difficult on either side of the ventral ridge. Striae formation was asymmetrical along the shell margin, with maximum ridge production to the left (posterior) of the midline (dorsal hinge toward the observer) (Gruffydd 1981).

It has been demonstrated that illumination regime (i.e., the number of hours of light and dark) has no effect on the number of striae produced by *Pecten maximus*, and that deposition rates are less than 1 stria per day (Gruffydd 1981). Several studies have reported that striae production only approaches a daily periodicity under the most optimal of conditions. For example, Joll (1988) reported from a tag-recapture experiment with the scallop *Amusium balloti* that the number of fine concentric rings on the external surface was always less than the number of days after marking. The experiments were conducted during the summer growing season for periods of between 107 days and 140 days, and scallops deployed for the longest periods showed the greatest discrepancy between the number of observed striae and the expected number of days. Earlier, Broom and Mason (1978) reported that, although *Chlamys* (= *Aequipecten*) *opercularis* produced 1 stria per day during May and June, on either side of these months, striae production decreased. Similar observations were reported by Helm and Malouf (1983). These observations suggest a strong link between shell growth rate and striae production rather than an environmental control of stria formation.

Our experiments were designed to investigate stria formation in 2 cohorts of *Argopecten irradians* of known age and

environmental history at a time of suboptimal growing conditions for shell growth in terms of food supply and seawater temperature. Our results demonstrate that, under these conditions, stria formation in *A. irradians* is nondaily and is related to shell growth rate. The largest and oldest scallops (40 mm and 1.4 y old) formed striae at a rate between 0.17 striae per day and 0.2 stria per day, whereas smaller and younger fast-growing *A. irradians* formed between 0.34 striae per day and 0.55 stria per day—clear evidence of nondaily and nonrhythmic deposition of striae in this pectinid species. Under conditions with an increased food supply (high flow), the scallops responded by increasing stria production, and significantly increasing interstria distance than scallops held in a low flow rate. These observations are indicative of stria formation under the control of shell growth and not the result of a rhythmic phenomenon. The analysis of the interstria distance in 5 juvenile *A. irradians* shells that had formed 19 striae under a high flow rate during the 6-wk experiment provides further evidence of a lack of environmental control of stria formation. The absence of synchrony in interstria growth indicates that no relationship exists in our experiments between the production of striae and seawater temperature, flow rate, and food supply. Therefore, shell surface striae in *A. irradians* cannot be used reliably as a chronological marker and cannot be related to environmental conditions, although such correlations have previously been recorded in a related pectinid species, *P. maximus* (Chauvaud et al. 1998, Chauvaud et al. 2005), based on a

presumed daily periodicity of stria formation. Ontogeny is known to affect interstria distance in *P. maximus* (Dare 1991, Owen et al. 2002). Dare (1991) noted a gradual change in stria abundance associated with the seasonal (winter) growth cessation. He demonstrated, using stable oxygen isotope analysis, that periods of greater stria abundance (number of striae per millimeter) correlated to the coolest winter seawater temperatures and, similarly, Owen et al. (2002) showed that growth of *P. maximus* in the Menai Strait, North Wales, was slowest between February and March, when the production of striae per millimeter was greatest. Evidence in this species and the pectinids as a group is firmly against the use of striae as chronological markers with which environmental conditions can be compared. Based on the findings of this investigation and previously published studies concerning stria production rates in pectinids, the evidence strongly suggests that the periodicity of stria formation varies among species, seasons, age, and environmental conditions. Therefore, any future study of this group of species should assume no reliable periodicity in the formation of striae, unless it is shown to be reliable over a full annual cycle.

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