Factors limiting oyster growth in Willapa Bay (Washington, USA) evaluated with in situ feeding experiments

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A B S T R A C T

Natural and anthropogenic environmental changes in estuaries affect the growth and health of organisms living there, often along spatiotemporal gradients. Throughout the world's estuaries, aquaculture and wild oyster populations support food and cultural systems, so quantifying factors affecting growth may inspire interventions to prevent future losses of oyster productivity. In Willapa Bay (Washington, USA), an estuary that produces 10–20% of US oysters, oysters are primarily harvested for market from the lower estuary, putatively due to food limitation up-estuary. We present studies in which in situ experimental systems were designed to manipulate food availability in the upper, and in one case contrasting to the lower, estuary. Contrary to expectations, food addition did not improve survival, shell growth rate or tissue mass of post-metamorphosis juvenile Pacific oysters, Crassostrea gigas. Instead, the experiment did not recapitulate the impaired growth up-estuary that typifies on-bottom oyster outplants, and irrespective of food addition, growth rates in the upper estuary were equivalent to rapid summer growth (> 10 mm month−1) in other regions of the bay. Multiple lines of evidence suggest that elevating oysters above the substrate in the experimental systems removed food limitation caused by reduced clearance rates, thus allowing oysters to grow rapidly, even when other environmental conditions such as carbonate chemistry were poor. This observation is consistent with experience of shellfish growers and a valuable observation for managers of wild and aquaculture shellfish in estuaries.

1. Introduction

Biological performance often differs for conspecifics living along environmental gradients (Hollarsmith et al., 2019; Kimbro et al., 2009). Disentangling factors limiting production from observational data is challenging because many environmental conditions covary along estuarine gradients. For benthic suspension-feeders, their abiotic environment such as temperature, salinity, water energy, turbidity, and sediment grain size, as well as biotic factors such as food quality, food quantity, and predator assemblages, influence growth and typically differ between upper and lower estuaries (Banas et al., 2007; Pusack et al., 2018; Ruesink et al., 2015). This suggests that pressures facing wild and aquaculture populations of benthic suspension-feeders vary in space and time. Willapa Bay, Washington, contributes a substantial portion (10–20%) of total United States oyster production. The primary aquaculture oyster, Crassostrea gigas, exhibits differential growth along the estuarine gradient (Lowe et al., 2018; Ruesink et al., 2003). This differential was first recognized in the scientific literature almost eight decades ago by the identification of a “fattening line” dividing the bay into an upper (southern) region where oysters recruit naturally from the lower (northern) region of rapid oyster growth and successful conditioning (Chapman and Esveldt, 1943). This pattern has endured interannual and long-term environmental variability in the bay and has been observed in studies spanning the eight decades since the first description of the fattening line. From an oceanographic perspective, the fattening line coincides with a steep shift in summer water residence time: one month in the upper estuary, compared to one week in the lower estuary (Banas et al., 2007). The regions also differ in temperature and food availability. Relative to the lower estuary, the upper estuary can be up to 5 °C warmer in summer, and chlorophyll concentrations typically decline up-estuary from >5 μg L−1 to <3 μg L−1 (Ruesink et al. 2003, 2018). Observationally, oyster growth maps onto these environmental conditions. Ruesink et al. (2003) showed that oyster spat (C. gigas) grew ~8 mm month−1 in the upper estuary and ~12 mm month−1 in the lower estuary in summer. Lowe et al. (2018) found a similar spatial pattern for juvenile oysters: 7.6 vs. 11.2 mm month−1 at upper and lower estuary sites, respectively.

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Oyster growers contend with variable estuarine conditions by adapting culture methods (Thomas et al., 2019). One culture method adopted for oyster grow-out is elevation off-bottom on lines or in mesh cages, even in shallow areas where on-bottom culture is feasible. This intensive approach requires substantial labor, materials, and attention, but can serve to protect oysters from on-bottom predators, jostle oysters to achieve a desired shape for half-shell product, and ameliorate some benthic impacts of culture. In some cases, off-bottom growth rates exceed those on-bottom, especially after accounting for tidal elevation (Ruesink et al., 2003). Stable isotope analyses indicate that on-vs. off-bottom oysters may have access to different food sources or different energetics (Ruesink et al., 2003), and environmental factors such as water flow or resuspension could also differ vertically in the water column. Predicting responses to future environmental change and adapting aquaculture methods requires a better understanding of these factors.

Experimental manipulations of potential limiting factors in the field provide a key approach to reveal mechanisms governing spatial patterns of estuarine secondary productivity. Growth rates of oysters have been well-explained by three environmental parameters included in dynamic energy budgets: temperature, food availability, and seston, the last interfering at high concentrations due to reduced filtering rate or clogged gills (Ren and Ross, 2001). Recently, ocean acidification has emerged as a concern for oyster aquaculture (Barton et al., 2012) and is expected to exact an energetic toll during calcification, which would reduce shell growth. Field experiments have attempted to ameliorate harmful effects of carbonate chemistry on oysters by co-locating them with seagrass, which scrubs CO2 during daytime photosynthesis (although any net effect on pH may be small; Kowek et al., 2018). In a recent study of oysters in Willapa Bay, positive effects of associating with seagrass were weak and generally restricted to lower estuary habitats (Lowe et al., 2018), where low-pH conditions typically occur up-estuary associated with river inputs (Ruesink et al., 2015). Patterns of fatty acid concentrations provided greater support for food limitation than carbonate chemistry stress (Lowe et al., 2018), a mechanism consistent with other studies of shellfish growing in seagrass (Allen and Williams, 2003; Bologna and Heck, 1999; Reusch, 1998). Direct manipulation of food availability in the field is challenging, especially considering the multitude of factors that can reduce ingestion rate by suspension feeders: phytoplankton concentration, species composition, interference from inorganic seston, or sedimentation. Although individual ingestion and assimilation rates may vary with these factors, bivalve growth generally responds positively to increased food availability. An experimental phytoplankton addition successfully alleviated expected effects of food limitation for mussels living in seagrass (Allen and Williams, 2003). Furthermore, experimental manipulations of oyster density in aquaculture settings have highlighted the importance of food availability to achieving maximum growth rates (Rheault and Rice, 1996). Manipulative experiments in the field can contribute to our understanding of how food availability influences aquaculture production, and potentially inform improved methods to maintain growth under variable environmental conditions.

We tested the efficacy of erasing the estuary-scale growth differential by manipulating the energetics of transplanted oysters in two experiments. We hypothesized that growth rates would increase in the upper estuary when oysters were provided with supplemental phytoplankton. In our first experiment, we simultaneously augmented phytoplankton resources on both sides of the fattening line. In our second experiment, in the upper estuary only, we added phytoplankton and ameliorated chemical conditions for calcification in a crossed design. Experimental systems were set up on floating platforms with structures that concentrated food (or seawater buffer) near the oysters to allow manipulation of food availability or carbonate chemistry while allowing natural environmental variation.

2. Materials and methods

2.1. Food addition above and below the “fattening line”

Hatchery-produced larvae of Pacific oysters (C. gigas) were settled onto the rough side of 11 × 11 cm ceramic tiles, and settlers were grown to an initial size of about 1 mm shell height in a common location in the field. Oyster count per tile was approximately 20. These tiles were out-planted to two sites that consistently differ in environmental conditions related to oyster growth (Ruesink et al., 2015): upper estuary (46.480°N, 124.024°W) and lower estuary (46.591°N, 124.018°W) in surface water off the side of a floating platform anchored in a 6-m deep channel (Figure 1). We used this floating-platform approach in order to augment phytoplankton availability in one of our experimental treatments. On top of the platform, 5-gallon buckets held concentrated cultured phytoplankton (Chaetoceras and Isochrysis) replenished every 1–2 days. A tube ran from the bottom of each bucket and was compressed to control the rate of water release from the bucket. The other end of the tube was attached to a hole in the center of a tile facing the oysters. Accordingly, the oysters were growing in the space between two tiles, 0.5 cm apart, where phytoplankton-rich water was regularly delivered. This Food-addition treatment was compared to a Control treatment with the same feeding apparatus, but draining buckets containing seawater without added phytoplankton. We also included two other plain-seawater treatments with fewer procedural interventions: a No-tube treatment with no tube attached to the facing tile, and a No-face treatment where the oysters had no facing tile. Each treatment at each site was replicated (N = 5). The experiment was initiated on 24 August 2003 and completed on 23 September 2003, during which time water temperatures generally declined from summer peaks, displaying a typical pattern of warmer temperatures up-estuary (Figure 2).

Oysters were initially 1–2 mm in size and identifiable as dark spots on the tiles. Initial photographs were compared with final photographs, and any oysters that did not appear in the final photograph contributed to the count of dead oysters; live oysters in the final photographs were counted and measured. Shell heights were averaged per tile prior to statistical analysis. Based on analysis of variance (ANOVA), we tested for shell differences between experimental treatments and control treatments. The 95% confidence interval for the mean shell height on the fattening line was calculated using the Tukey test in order to reveal whether significant differences existed between treatments. If significant differences were found, mean shell height was compared with the mean shell height of the Control treatment using the Tukey test. We conducted 8 replicates on the fattening line in both the upper and lower estuaries. Finally, we conducted ANOVA and performed a Tukey test to compare the growth rates of transplanted oysters in both the upper and lower estuaries with and without phytoplankton addition.
height response to site, treatment, and their interaction. The analysis of survival as a function of site, treatment, and their interaction was performed with a generalized linear model (glm: binomial data structure accounting for the number of live and dead oysters per tile). Following any significant treatment effects, we made three planned contrasts: Food-addition vs. Control, Control vs. No-tube, and No-tube vs. No-face, each testing for a single aspect of our field food-augmentation system. We did not collect water samples to document phytoplankton concentrations near each treatment type because the experimental set up was identical in upper (reduced food availability) and lower (increased food availability) regions of the bay.

2.2. Food addition in the upper estuary

For this experiment, a site was chosen within Willapa Bay characterized by low pH (Ruesink et al., 2015) and poor oyster growth relative to other locations in the bay (Lowe et al., 2018; Ruesink et al., 2003). The experiment was conducted in mid-summer over 27 days in July–August 2016. Both 2003 and 2016 were warmer than average over this period by 0.6 °C (2003) and 0.4 °C (2016), but there have not been climate change-related increases in temperature over the period of 2003–2016 in Willapa Bay. An experimental tidal-powered Floating Upwelling System (FLUPSY) was designed, built and anchored in the upper estuary (46.432°N, 123.921°W) in ~4m depth. The FLUPSY contained 20–36 L mesocosms on an 8’ x 8’ raft (Figure 3). Each mesocosm had an aperture cut into the side that was plumbed to the central channel just below the surface of the water. The raft was anchored to orient into the current on the ebbing and flooding tide. Flow was concentrated in the central channel, creating low pressure zone that generated directional flow through the mesocosms from an aperture cut in the bottom of the mesocosm to the central channel. Conditions inside the mesocosms generally tracked external ambient conditions, but water residence time within the mesocosms was long enough to manipulate food concentrations by adding phytoplankton (Reed Mariculture, Inc. Shellfish Diet, 1800) and carbonate chemistry by adding 100% sodium bicarbonate. The bicarbonate was dissolved until near saturation into freshwater, then added to the seawater in 3-gallon buckets that served as reservoirs for treatment additions. The food and buffer were added by drip system from the reservoirs mounted on the raft and plumbed to the cage holding the oysters in the mesocosm (Figure 3). Buckets were filled with seawater and additional phytoplankton, buffer or both ~2 times per day.

During the second half of the study, a YSI 6600 sonde was deployed on the raft to measure ambient environmental conditions. The average temperature during this time was 20.6 ± 0.8 °C SD, average salinity was 25.2 ± 1.8, average pH(NBS) was 7.72 ± 0.1, and average dissolved oxygen saturation was 90.2 ± 6.3%. Using an alkalinity vs. salinity relationship derived from bottle samples collected in Willapa Bay (Alk = 53.5*Sal +550.16, N = 327) and observed pH, the calculated aragonite saturation state was <1 for 33.5% of this period. The average chlorophyll concentration (measured at 3 time points during the experiment) of ambient conditions in the No Buffer – No Food treatment was 5.4 ± 1.3 µg L⁻¹.

Taylor Shellfish provided the post-settlement juvenile Pacific oysters (C. gigas) for the experiment. Initial shell length was on average 25.3 mm with no differences between treatments. Six oysters were placed in a plastic-mesh cage and randomly assigned to each of five treatments: 1) mesocosm control in which the cages were suspended from the side of the raft, 2) No food and No Buffer (ambient), 3) No Food with Buffer added, 4) Food and No Buffer, and 5) Food and Buffer. Each treatment was replicated five times. The average growth rate per mesocosm was used in statistical analyses based on change in shell height from start to end or final tissue mass; effects of buffer, food, and their interaction were tested with ANOVA.

3. Results

3.1. Food addition above and below the “fattening line”

Although oysters typically perform better below the fattening line in Willapa Bay, our experimental results across two sites showed the opposite spatial pattern: oysters grew more slowly in the lower than upper estuary (Figure 4). Site effect was significant in an analysis of variance (F1,22 = 15.6, P < 0.001), as was treatment (F2,32 = 9.7, P < 0.001). Food addition did not result in any improvement in oyster growth at either site (F1,16 = 0.52, P = 0.48), and the only manipulation that was apparently consequential was that removing the tile facing the oysters slowed shell growth (F1,16 = 26.3, P < 0.01). The treatment without a facing tile allowed substantially more light access, and the oysters in this treatment were surrounded by a dense lawn of filamentous algae at the end of the experiment. The interaction of site x treatment was not significant (F3,32 = 1.4, P = 0.26).

Survival of oysters was better at the lower-relative to upper-estuary site, and improved only with a facing tile, not other treatments (Figure 4B). The interaction of site x treatment was not significant (Deviance = 5.45, Pχ², 3 = 0.14), but the site effect improved model fit (Deviance = 45.4, Pχ², 1 < 0.001). The treatment effect also improved model fit (Deviance = 56.14, Pχ², 1 < 0.001), and in pairwise comparisons between successive treatments, no-face had lower survival than no-tube treatment (Z1,18 = 5.6, P < 0.001), but no-tube was similar to control treatment (Z1,18 = 0.7, P = 0.46), and control to food added treatment (Z1,18 = 1.6, P = 0.11).

3.2. Food addition in the upper estuary

Oysters grew rapidly in the floating upwelling system, on average increasing shell length by 10.5 mm month⁻¹ (Figure 5A). Growth was significantly reduced by buffer addition to increase pH (F1,16 = 12.3, P = 0.003). The effects of Food addition and the interaction between Food and Buffer were not significant (F1,16 = 0.77, P = 0.39 and F1,16 = 1.52, 0.23, respectively). Shell growth rates were generally faster in mesocosms relative to cages hung off the raft, but improved growth was only significantly different in the No Buffer - Food and No Buffer - No Food treatments (P < 0.05 in both cases). Survival was high in the 2016 experiment, one oyster died in each of the Buffer – No Food, No Buffer – Food, No Buffer – No Food, and Control treatments.

Tissue mass was reduced by buffer addition (Figure 5B; F1,16 = 4.5, P = 0.049). The effect of Food and the interaction between Food and Buffer treatments were not significant (F1,16 = 0.2, P = 0.65 and F1,16 = 0.02, 0.90, respectively). Despite less shell growth, oysters hung off the raft...
had significantly higher tissue mass than oysters in mesocosms ($t_{14,20} = 4.97, \ P < 0.001$), by an average of 0.03 g.

4. Discussion

One of the primary benefits of bivalve aquaculture is that natural food availability is generally sufficient to produce market-sized oysters, yet conditions exist that limit maximal production. Indeed, many studies have suggested food availability to be a limiting factor in oyster productivity in the upper portion of Willapa Bay (Banas et al., 2007; Lowe et al., 2018; Ruesink et al., 2003; Wheat and Ruesink, 2013). These results are based on modeling studies of oceanographic properties, comparative studies of growth rates, and stable isotope and fatty acid trophic biomarkers. The upper region of Willapa Bay above the fattening line has generally higher settlement but low commercial oyster productivity, whereas most oysters are harvested for market from the lower estuary region due to favorable growth and condition there. Our two experimental manipulations of food availability to Pacific oysters, however, showed no benefit of food addition in the upper estuary, contrary to expectations. While survival of spat was lower in the upper estuary, neither experiment observed the expected pattern of reduced growth in the upper estuary compared to the lower estuary. Observations of reduced bivalve growth associated with reduced food availability come from a range of habitats (Judge et al., 1993), yet only one published study has experimentally augmented food availability, and ameliorated food limitation, to bivalves in the field (Allen and Williams, 2003). If food addition did not improve growth in these experiments, what led to the overall improved growth relative to previous observations?

Oysters in all treatments of our floating experimental systems grew rapidly, eliminating the expected geographical effect. In fact, the upper vs. lower estuary differential in growth was reversed in the experiment in 2003 (Figure 4). Shell growth rates in the experiment in 2016 of ~10 mm month$^{-1}$ were rapid for the upper estuary: Oysters from the same source population outplanted on-bottom to a mid-bay site during the same timeframe grew ~9.1 mm month$^{-1}$ (Lowe, unpublished data) and growth rates from the lower estuary in other studies were >10 mm month$^{-1}$ (Lowe et al., 2018; Ruesink et al., 2003). Tissue mass at the end of the experiment was greater than concurrent outplants at the mid-bay site (~0.12 g vs. 0.05 g; Lowe, unpublished data), and within the mid-range of tissue growth from previous experiments in Willapa Bay (0.05–0.21 g mo$^{-1}$; Lowe et al., 2018).

The estuarine gradient in summer in Willapa Bay involves a suite of environmental conditions: up-estuary temperatures are warmer (Figure 2), pH lower, chlorophyll concentrations lower, and sediment muddier (Ruesink et al., 2003, 2015). Experimental tests of limiting factors up-estuary help disentangle causality, since from first principles, each of these four factors could influence oyster growth or survival. The mechanism needs to accommodate both the stunting of oyster growth observed on-bottom in the upper estuary (Lowe et al., 2018; Ruesink et al., 2003), and the removal of that apparent constraint in our experimental systems. We specifically manipulated resources and water chemistry and did not observe improvements in oyster performance. We unfortunately did not collect water samples in 2003 that would allow us to test the effectiveness of our food delivery interventions, however, measurements in 2016 and experimental results provide clues to underlying processes. Oysters did not grow faster with food addition, which suggests sufficient resources were available for oysters in surface water,

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Figure 3. A) View of the FLUPSY raft with food and buffer reservoirs (Blue lid buckets), B) close-up of oyster mesocosms (green-rimmed Tupperware), and C) view down central channel of FLUPSY constructed for upper-estuary experiment in 2016.
which differs from on-bottom and across tidal flats (Wheat et al., 2019). The pH gradient in Willapa Bay is persistent in summer (Ruesink et al., 2015), and late summer, when the experiments were performed, has the lowest pH in the annual cycle due to warm temperature and enhanced respiration (Lowe et al., 2019). Overall, we found no evidence for a negative effect of water chemistry on juvenile oyster growth, despite regular exposure to low pH and aragonite saturation <1 during the 2016 experiment. Shell and tissue growth was actually slowed by buffer addition, cautioning against this method for shellfish growers to ameliorate poor carbonate chemistry conditions in situ. While carbonate chemistry may have contributed to decreased survival up-estuary in 2003, Pacific oysters appear tolerant of low pH in the field as juveniles, providing additional evidence that water carbonate chemistry is not a major constraint on oyster performance in Willapa Bay (Ruesink et al., 2018).

Water temperatures provide a potential mechanism for the geographic pattern of oyster growth in our 2003 experiment, but they are not likely to result in different patterns for benthic and surface oysters because the estuary is shallow and well-mixed. In Willapa Bay in summer, water temperatures reach but do not exceed optimal conditions for Pacific oysters. Maximum clearance rates occur at 18–20 °C (Ren and Ross 2001) or 15–20 °C (Gray and Langdon, 2018). Consequently, as water temperatures are more likely to become this warm in the upper than lower estuary, temperatures averaging 1 °C warmer up-estuary during the experiment in 2003 (Figure 2) could contribute to the improved growth observed there, but only if food resources were not limiting (Figure 4).

A likely driver of rapid growth in our experiments comes from growing oysters in the surface water of channels rather than on the bottom, a choice we made in order to allow continuous manipulation of the water reaching them. By elevating the oysters off the substrate, we may inadvertently have freed these oysters from interference by seston and sedimentation. Pacific oysters generally require Chl concentrations of >3 μg L⁻¹ to be food-replete (Hawkins et al., 2013; Snyder et al., 2017). In Willapa Bay, the ocean serves as a major source of phytoplankton (Roegner et al., 2002), and concentrations decrease into the upper estuary. Chlorophyll concentrations <3 μg L⁻¹ have been documented near our 2003 experiment (Ruesink et al., 2018), but measurements of Chl >5 μg L⁻¹ up-estuary in the 2016 experiment were sufficient for rapid growth. Phaeopigments were relatively high in water collected from mesocosms with buffer addition, which is consistent with lower growth rates in these treatments if high detritus was present from food addition/buffer interaction. If total suspended solid concentrations get too high, ingestion rates can decrease regardless of phytoplankton concentration (Gray and Langdon, 2018) and have a large influence on oyster condition (Saraiva et al., 2020).

Food ingestion is reduced by water column seston in two ways: by reduced pumping or clearance as non-food particles become denser (>50 mg L⁻¹), and by clogging of the gills at high seston concentrations (200 mg L⁻¹, Ren and Ross, 2001). In 2003, the only reduction of shell growth and survival came from removing the face-plate, which was counterintuitive because this should increase flow over oysters. Dense filamentous algal growth was observed on these tiles and could block flow and interfere with filtration rate similar to effects of macrophytes (Bologna and Heck, 1999; Reusch, 1996). In the 2016 mesocosms, sedimentation was extremely rapid, requiring that mud be removed from the bottom of the mesocosms nearly every day. Settlement of inorganic particulates could have improved access to phytoplankton for oysters in the

Figure 4. Performance of Pacific oysters (Crassostrea gigas) after one month experiencing different treatments in the upper and lower regions of Willapa Bay, Washington (Aug 24 to Sep 23, 2003). A) Final shell height; B) fraction surviving. Error bars show SE of N = 5 tiles, where heights of ~20 oysters per tile were first averaged. Initial size was 1 mm. Significance of treatment effect indicated by letters.

Figure 5. Shell growth per month (A) and final tissue mass (B) of Pacific oysters (Crassostrea gigas) in Willapa Bay, Washington (Jul 31 to Aug 27, 2016) in the upper estuary feeding experiment. Control treatment in gray denotes oysters grown in cages outside of mesocosms. All other treatments were grown in mesocosms within the floating upwelling system. Initial shell length was 25 mm. Significance of treatment effect indicated by letters.
mesocosm, leading to increased shell growth. However, greater tissue mass in control oysters suggests adequate food for all oysters suspended on the FLUPSY. Tidal mass in control oysters suggests adequate food for all oysters suspended in the lower estuary, particularly in macrotidal estuaries like Willapa Bay. Local oyster growers were unsurprised by the results, quipping that spat near the FLUPSY site easily grow to the size where they can be moved to a fattening area, but must be elevated above the bottom or else they won’t survive (J. Herrold, pers. comm.). Resuspension of fine particles at the sediment-water interface would interfere with food acquisition and growth of oysters grown on or near the bottom.

5. Conclusion

Our results from these food-addition experiments suggest that observed growth limitation in the upper portion of Willapa Bay may be less of a result of food availability and more due to benthic processes like sediment resuspension. This has important implications for oyster production in this and other similar bays: food limitation may not be especially important for the productivity of oysters grown off-bottom. Also, Pacific oysters seem to be able to handle sedimentation better than native Olympia oysters (Ostrea lurida; Gray and Langdon, 2018; Lowe et al., 2018), which means that Olympia oyster growth off-bottom might be especially improved via this culture method. Growers have options to manipulate the growing environment with infrastructure and off-bottom culture techniques. Wild oyster populations, in conservation or restoration contexts, do not. Therefore, attention should be put on selecting areas with good access to food (including sedimentation as a factor) and limiting anthropogenic increases to sedimentation in upper estuaries.

Declarations

Author contribution statement

A. Lowe and J. Ruesink: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Wrote the paper.

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Data availability statement

Data will be made available on request.

Declaration of interests statement

The authors declare no conflict of interest.

Additional information

No additional information is available for this paper.

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