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Published online Jul Boender ,1,2 Erik A. See Appl Environ Microbiol. This article has been cited by other articles in PMC. Abstract Growth at near-zero specific growth rates is a largely unexplored area of yeast physiology. To investigate the physiology of *Saccharomyces cerevisiae* under these conditions, the effluent removal pipe of anaerobic, glucose-limited chemostat culture dilution rate, 0. This setup enabled prolonged cultivation with complete cell retention. After 22 days of cultivation, specific growth rates had decreased below 0. Over this period, viability of the retentostat cultures decreased to ca. The viable biomass concentration in the retentostats could be accurately predicted by a maintenance coefficient of 0. This indicated that, in contrast to the situation in several prokaryotes, maintenance energy requirements in *S.* After 22 days of retentostat cultivation, glucose metabolism was predominantly geared toward alcoholic fermentation to meet maintenance energy requirements. The strict correlation between glycerol production and biomass formation observed at higher specific growth rates was not maintained at the near-zero growth rates reached in the retentostat cultures. In addition to glycerol, the organic acids acetate, d-lactate, and succinate were produced at low rates during prolonged retentostat cultivation. This study identifies robustness and by-product formation as key issues in attempts to uncouple growth and product formation in *S.* Laboratory studies on microorganisms are often performed in batch cultures. During the initial phase of batch cultivation, all nutrients are usually present in excess. In chemostat cultures fed with a medium containing a single growth-limiting nutrient, the dilution rate determines the specific growth rate. Chemostat cultivation therefore offers the possibility to study microbial physiology at carefully controlled, submaximal specific growth rates and to investigate the effect of specific growth rate on cellular physiology Chemostat cultivation of the yeast *Saccharomyces cerevisiae* has demonstrated strong effects of specific growth rate on biomass composition 26 , 51 , product formation 5 , 37 , and cell size Moreover, during energy-limited growth at low specific growth rates, a relatively large fraction of the energy substrate has to be dissimilated for maintenance-related processes such as maintenance of chemi-osmotic gradients and turnover of cellular components Not surprisingly, recent genome-wide studies have shown strong effects of specific growth rate on levels of mRNAs and proteins 9 , 14 , In chemostat studies on *S.* While this range is relevant for many industrial applications, there are several incentives to study growth of this yeast at even lower specific growth rates. Furthermore, in industrial applications, *S.* This problem is further augmented when the excess yeast biomass cannot be valorized because it is genetically modified or has been used for the production of compounds that are not compatible with use as, for example, cattle feed. A third incentive for exploring the physiology of *S.* At near-zero growth rates, the age of individual yeast cells becomes much higher than can be achieved in conventional batch or chemostat cultures. Studies on extremely slow growth of *S.* Retentostat cultivation, first proposed by Herbert 18 , is a modification of chemostat cultivation that has been specifically designed to study microbial physiology at near-zero specific growth rates. In a retentostat, sometimes referred to as recycling fermentor or recyclost, the growth-limiting energy substrate is fed at a constant rate, and biomass is retained in the fermentor by an internal filter probe connected to the effluent line or by an external filter module. Prolonged retentostat cultivation should, in theory, result in a situation where the specific growth rate becomes zero and where the specific rate of substrate consumption equals the maintenance energy requirement. This situation is fundamentally different from starvation, which involves deterioration of physiological processes, and from resting states typified by spores, which have little or no metabolic activity. Retentostat cultivation has been applied to several bacterial systems including *Escherichia coli* 11 , *Paracoccus denitrificans*, and *Bacillus licheniformis* 49 and the autotrophs *Nitrosomonas europaea* and *Nitrobacter winogradskyi* 46 , These studies demonstrated that the physiology of these prokaryotes at extremely low specific growth rates could not be accurately predicted by a simple extrapolation of results obtained at higher

specific growth rates. In particular, near-zero specific growth rates coincided with increased levels of ppGpp 2, which induces the stringent response, a regulatory program that diverts cellular resources from growth to amino acid biosynthesis 10. Furthermore, it was concluded that extremely slow growth led to a reduction of the maintenance energy requirement of prokaryotes. A recent quantitative analysis on cell retention cultures of *S. cerevisiae*. The goal of the present study was to quantitatively analyze the physiology of *S. cerevisiae*. To this end, an internal filter probe was introduced in the effluent line of standard laboratory chemostat fermentors and used in long-term cultivation runs with complete cell retention. Anaerobic conditions were chosen to facilitate quantification of catabolic fluxes and growth energetics. The prototrophic laboratory strain *S. cerevisiae*. The strain was grown to stationary phase in YPD yeast-peptone-dextrose medium 42 at pH 6. To minimize variation in medium composition and, more especially, in the glucose concentration during long-term cultivation, liter batches of medium were prepared, filter sterilized, and used for the chemostat and retentostat runs. At the same time, 1. Triplicate anaerobic chemostat cultivations were performed at a dilution rate of 0. The working volume was kept at 1. To maintain anaerobic conditions, both the fermentor and the medium vessel were sparged with N₂ 5. The autoclavable AppliSense sample filter assembly Applikon, Schiedam, The Netherlands consists of a hydrophobic tubular polypropylene filter with a pore size of 0. The filter was then thoroughly rinsed with a buffer solution 8. After reaching steady state, the fermentors were switched from chemostat to retentostat mode by withdrawing the effluent through the AppliSense sample filter assembly instead of using the standard effluent tube. Retentostat cultures were operated at a dilution rate of 0. As withdrawal of samples could disturb biomass accumulation inside the retentostat, sample volume and sampling frequency were minimized. Substrate, metabolites, and biomass determination. Culture dry weight was measured according to Postma et al. Detection was by means of a dual-wavelength absorbance detector Waters and a refractive index detector Waters Succinate, acetate, d-lactate, and residual glucose were also measured enzymatically Boehringer Roche Diagnostics GmdH, Mannheim, Germany. Samples for analysis of residual glucose were rapidly quenched with cold steel beads Trehalose and glycogen measurements were performed as described by Parrou and Francois Glucose released by glycogen and trehalose conversion was determined using the UV method based on Roche kit number Almere, The Netherlands. Trehalose and glycogen amounts were determined in triplicate measurements for each sample. Assessment of culture viability. Tenfold dilution series 5 to 7 dilutions were made in 0. Metabolically active cells were identified and counted based on the formation of red cylindrical intravacuolar structures revealed by fluorescence microscopy Imager-D1; Carl-Zeiss, Oberkochen, Germany equipped with Filter Set 09 fluorescein isothiocyanate long-pass filter; band-pass filter with excitation at to nm; nm beam splitter [dichroic mirror]; long-pass filter with emission at nm; Carl-Zeiss. At least cells were counted. To assess cell lysis, the concentration of proteins released in culture supernatants was assayed by a Quick Start Bradford Protein Assay Bio-Rad Laboratories, Hercules, CA using bovine serum albumin fatty acid free; Sigma as a standard. Prediction of retentostat growth kinetics. Growth kinetics in retentostat cultures were predicted with two mass balance equations, one for biomass equation 1, which assumes complete cell retention and constant volume and one for substrate equation 2. Calculation of fluxes from concentrations in retentostat cultures. The volumetric fluxes r_i of products i were calculated with the mass balance equation: Curve fits were inspected visually by plotting the residuals. To account for evaporation, the volumetric production of ethanol was calculated from the production of carbon dioxide after subtraction of CO₂ produced for the formed acetate 1 mol per mole of acetate and biomass 5. The viability of the cultures was measured, and specific fluxes were corrected by assuming that only the viable biomass was metabolically active equation 6: Only the viable biomass can replicate, and by assuming that no lysis i . The maintenance energy requirement has a profound impact on growth at low specific growth rates. To estimate the maintenance energy requirement of *S. cerevisiae* PKD in anaerobic, glucose-limited cultures, a set of reference chemostat cultures was run at different specific growth rates 0. In these chemostat cultures, a linear relationship was found between the specific growth rate and the specific rate of glucose consumption Fig. This relationship is consistent with a growth rate-independent maintenance energy requirement The maintenance energy coefficient m_s calculated from these experiments was 0. This value is in good agreement with an early publication on microaerobic growth of a

respiratory-deficient S. The maximum biomass yield corrected for maintenance Y_{SXmax} calculated from the data shown in Fig.

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In European Brewery Convention Monograph 28, EBC Symposium on Yeast Physiology, A New Era of Opportunity. p. Google Scholar Dickinson, J.R. and Schweizer, M. () The Metabolism and Molecular Physiology of Saccharomyces cerevisiae.

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Chapter 3 : Quantitative Physiology of *Saccharomyces cerevisiae* at Near-Zero Specific Growth Rates

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Chapter 6 : Nicole Sanchez : USDA ARS

Growth thus involves the de novo synthesis of new yeast cells, i.e. the synthesis of yeast cell constituent macromolecules. The mechanisms by which these syntheses occur are found in the biochemical reactions of the metabolism of the yeast cells.