Direct observation of individual cell behavior within a biofilm
by Andrew Ramsey Rice

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Civil Engineering
Montana State University
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Abstract:
The ability of microorganisms to form biofilms has been well characterized. Bacterial cells can transition from a planktonic state to a sessile state, replicate and subsequently populate a surface. Organisms which are the first to colonize a “clean” surface are referred to as “primary” biofilm cells. The progeny of the first generation of sessile cells are known as “secondary” biofilm cells. This study examined the growth of both primary and secondary biofilm cells.

The organism of interest in this study was Pseudomonas aeruginosa PA01. A parent strain, deficient of the ability to synthesize green fluorescent proteins (GFP) and a construct strain which constitutively produced GFP were used. This organism was grown in planktonic and biofilm environments. A parallel plate flow cell reactor was used with a glass substratum for the biofilm experiments. A population of only GFP+ cells was studied for planktonic and primary biofilm experiments, whereas a mix of GFP+ and GFP- cells were used to examine the growth of secondary biofilm cells.

It was found that primary cells apparently undergo a change in phenotype from planktonic to biofilm form and also experience a lag in their growth. This is referred to as a surface associate lag time. Planktonic and secondary biofilm cells both grew at a faster rate than the primary biofilm cells.

The growth of secondary biofilm cells is characterized by replication, emigration, and movement. Each of these behaviors was directly observed for individual cells. A dilute mix of GFP+ cells in a predominantly GFP- biofilm allowed was used. It was discovered that cells which are destined to emigrate are more active in terms of movement than their remaining counterparts. Also, cells emigrate at a median time 1/3 of that of the median time to replication. Finally, at least 1/3 of all cells emigrate which is consistent with the “spreading” mode of biofilm growth of Pseudomonas aeruginosa.
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by

Andrew Ramsey Rice

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Civil Engineering

MONTANA STATE UNIVERSITY-BOZEMAN
Bozeman, Montana
May, 1999
APPROVAL

of a thesis submitted by

Andrew Ramsey Rice

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ABSTRACT

The ability of microorganisms to form biofilms has been well characterized. Bacterial cells can transition from a planktonic state to a sessile state, replicate and subsequently populate a surface. Organisms which are the first to colonize a “clean” surface are referred to as “primary” biofilm cells. The progeny of the first generation of sessile cells are known as “secondary” biofilm cells. This study examined the growth of both primary and secondary biofilm cells.

The organism of interest in this study was *Pseudomonas aeruginosa* PA01. A parent strain, deficient of the ability to synthesize green fluorescent proteins (GFP) and a construct strain which constitutively produced GFP were used. This organism was grown in planktonic and biofilm environments. A parallel plate flow cell reactor was used with a glass substratum for the biofilm experiments. A population of only GFP+ cells was studied for planktonic and primary biofilm experiments, whereas a mix of GFP+ and GFP- cells were used to examine the growth of secondary biofilm cells.

It was found that primary cells apparently undergo a change in phenotype from planktonic to biofilm form and also experience a lag in their growth. This is referred to as a surface associate lag time. Planktonic and secondary biofilm cells both grew at a faster rate than the primary biofilm cells.

The growth of secondary biofilm cells is characterized by replication, emigration, and movement. Each of these behaviors was directly observed for individual cells. A dilute mix of GFP+ cells in a predominantly GFP- biofilm allowed was used. It was discovered that cells which are destined to emigrate are more active in terms of movement than their remaining counterparts. Also, cells emigrate at a median time 1/3 of that of the median time to replication. Finally, at least 1/3 of all cells emigrate which is consistent with the “spreading” mode of biofilm growth of *Pseudomonas aeruginosa*. 
It is important to understand how microbial biofilms form because of the complexity, prevalence, and impact of these communities. During the initial events of biofilm formation, the cells which originally colonize a particular surface become the parent organisms of the ensuing biofilm. The behavior exhibited by these cells appears to vary according to species (Lawrence and Caldwell, 1987a). Parent cells can form dense microcolonies and then disperse in a matter of minutes (O'Toole and Kolter, 1998a). Upon replication, daughter cells can pack tightly near the parent cell location, spread out upon the surface, be cast back into the bulk fluid, form long chains of cells, or roll along the substratum (Lawrence and Caldwell, 1987a; Korber et al., 1989; Power and Marshall, 1988; Shapiro and Hsu, 1989; Dalton et al., 1994).

Purpose

The general purpose of this research project was to examine the importance of initial events; or, to determine if the initial colonization pattern of cells had any
bearing upon the biofilm that resulted. This research involved studying the processes which occur after initial events to understand how a biofilm develops from a population of parent cells.

The practice of extrapolating the behavior of individual cells to that of a general population has been suggested by (Gualtieri et al., 1985) in the study of the motion of microorganisms. The consequence of this approach yielded two related areas of results: a quantitative description of individual cell behavior within an emerging biofilm matrix and a more qualitative account of an effect of the phenotypic transition of planktonic cells to sessile cells. When taken together, it is evident that the process of biofilm development is quite dynamic. Cells may have different growth rates depending upon their point of origin. They also are constantly repositioning themselves within the biofilm matrix; some move relatively short distances while others completely relocate over distances of hundreds of microns.

Much of the work responsible for the present scope of knowledge of biofilms was gained through direct observation approaches rather than efforts that were "hypothesis driven" (Costerton, 1999). It has been postulated that further gains in this field will stem from "very basic, extremely cross-disciplinary and sometimes esoteric research" (Palmer and White, 1997). The results of this study follow in this theme and are a product of direct, in situ observation of biofilm development utilizing flow cell and Confocal Scanning Laser Microscopy technology.
Microscopy and Image Analysis

The microscope is a key instrument for the investigation of bacterial behavior. Various means of employing the microscope in conjunction with the study of sessile organisms have been reviewed (Madigan et al., 1997). Transparent and/or opaque substrata coupled with automatic image analysis is one of the most prevalent combinations currently used in this field of research. The use of various fluorochromes in biofilm research is also becoming a method of choice due to the ability of specific organisms and various physiological parameters to be visualized with differing degrees of sample disturbance (McFeters et al., 1995). This research and others (Kuehn et al., 1999; Davies et al., 1998) are exploiting a new and indispensable technology which utilizes the insertion of genes into target bacteria which code for the production of a green fluorescent protein (GFP). Cells which possess the ability to produce this GFP are in essence, self-labeling. The protein provides a valuable way to observe individual bacteria in a biofilm with minimal to no sample preparation or disturbance.

Computer technology, image analysis techniques and video capture capability have enabled many researchers to conduct experiments that utilize time lapse microscopy to illuminate sequential events in biofilm processes (Mueller, 1996; Power and Marshall, 1988; Shapiro and Hsu, 1989; Lawrence and Caldwell,
This technique has enabled various modes of "recolonization" to be visualized (Lawrence and Caldwell, 1987a), the discrimination between and quantification of cell growth and attachment in the rate of surface accumulation (Mueller et al., 1992) and the rates of locomotion of bacteria on surfaces (Power and Marshall, 1988).

Confocal scanning laser microscopy (CSLM) has become the premier tool for studying biofilms in three dimensions. The major advantage of this microscope system is the ability to eliminate out of focus haze and produce very thin optical slices. When coupled with automated stages that can step in increments of sub-microns, very accurate three-dimensional images of biofilms can be created (Lawrence et al., 1991). CSLM has been used to determine fractal dimensions of biofilms (Hermanowicz et al., 1996). Three-dimensional imaging of morphological changes in biofilms has been used to illustrate the findings of Dalton et al. (1994). Moller et al. (1996) used fluorescent probes and CSLM to map the location of certain cells within a biofilm matrix. Further applications of CSLM and fluorescent probes have been reviewed by Costerton et al. (1995b).

Parallel Plate Flow Cell

The parallel plate flow cell has also become an important piece of equipment for the study of biofilms. The type that is used most commonly was first described by Sjollema et al. (1989) and modifications of which have been utilized by researchers at the Center for Biofilm Engineering (Camper et al., 1994; Hamilton et
The primary advantage of such a reactor system is that it allows the researcher to obtain images from biofilms with minimal physical disturbance. Real time studies of biofilm formation can also be carried out in flow cell reactors and time lapse images can be obtained. Many studies which have examined the initial attachment, detachment, and growth of bacterial cells on glass surfaces along with measurements of rates and types of movements have been conducted with a parallel plate flow cell reactor in conjunction with time-lapse microscopy (Korber et al., 1994; Lawrence et al., 1987b; Lawrence and Caldwell, 1987a; Lawrence et al., 1989; Caldwell and Lawrence, 1986; Korber et al., 1989; Lawrence et al., 1991). The research presented in the following chapters was carried out using similar methods.

Organization

The following terms will be used in this report and need to be clarified in advance:

1. **Primary biofilm cells**: Those cells which are the first to colonize a surface. In essence they are the first generation biofilm cells and have transitioned from a planktonic environment to a sessile state.
2. **Secondary biofilm cells**: Any generation of cells which arise from primary biofilm cells. These cells do not undergo a change in phenotype for they originate in a sessile state.

3. **Emigrate**: The action of a cell moving from its previous location. Cells which emigrate do not necessarily detach and partition into the bulk fluid. On the contrary, they usually remain intimately associated with the biofilm, but travel to a new location in what is termed a recolonization event (Lawrence *et al.*, 1987b).

This report is organized in two main sections; each describing a portion of the total research project. Both parts are a contribution to the understanding of biofilm development. Chapter 2 presents the more qualitative exposition of the effects of a change in phenotype upon primary biofilm cells and Chapter 3 is a quantitative description of the behavior of secondary biofilm cells. Two strains of the same organism, *Pseudomonas aeruginosa* PA01, were used in these experiments and are described below in more detail. The experiments that dealt with planktonic and primary biofilm cells used only the GFP+ strain, whereas the secondary biofilm experiments utilized a mix of GFP+ and GFP- strains; with 1% of the cells being GFP+. The content of each of these sections will be condensed and submitted as manuscripts to be published at a later date.
CHAPTER 2

APPARENT SURFACE ASSOCIATED LAG TIME OF PRIMARY BIOFILM CELLS

Background

Biofilms are complex communities of microorganisms pervasive in the natural environment. The current conceptual model of a biofilm portrays an ingeniously complicated multi-species entity where ecological microniches are created and occupied by specific organisms (Costerton et al., 1995b; Costerton, 1995). Bacteria are known to attach to both abiotic materials and other organisms in all manner of aqueous environments. Following attachment of the primary colonizing bacteria, growth of the sessile population and induction of new organisms into the community occurs. The resulting biofilm is an intricate assortment of micro- and macroorganisms (Fletcher, 1996) which can be responsible for many types of human infections, the corrosion of metals, the reduced efficiency of industrial heat dissipation equipment, and the degradation of waste materials (Costerton et al., 1995b).

Because of these pertinent biofilm effects, researchers are interested in knowing how these communities form. The term used to describe the first stages
of biofilm development is “initial events” and has been thoroughly studied but is not well understood. Surface topography can affect the manner in which bacterial cells colonize a substratum (Camper et al., 1994; Scheuerman et al., 1998). Cells which first colonize a particular surface become the parent organisms of the ensuing biofilm. The behavior exhibited by these cells is thought to vary according to species (Lawrence and Caldwell, 1987a). Parent cells can form dense microcolonies and then disperse in a matter of minutes (O'Toole and Kolter, 1998a). Upon replication, daughter cells can pack tightly near the parent cell location, spread out upon the surface, be cast back into the bulk fluid, form long chains of cells, or roll along the substratum (Lawrence and Caldwell, 1987a; Korber et al., 1989; Power and Marshall, 1988; Shapiro and Hsu, 1989; Dalton et al., 1994).

Prior Research

Initial Events Description. One of the most useful results from research regarding initial events in biofilm formation is a conceptual model of biofilm accumulation. The framework for this model was first established by Escher in 1986. When a “clean” substratum first comes in contact with an aqueous environment, a layer of organic molecules is almost instantaneously formed on the surface. This layer is known as a conditioning film and may have a substantial
influence on the subsequent biofilm as many surface bound nutrients can be present in this film (Chamberlain, 1992; Marshall, 1996).

Bacterial cells are then transported from the bulk solution to the substratum. This can also be a rapid process with measurable attachment within as little as 30 seconds (Vanhaecke et al., 1990). Several factors, including flow regime, motility and relative concentration of cells in the bulk fluid influence the rate at which cells are transported to the solid-liquid interface. Once organisms have come into contact with a substratum, there is a two-stage adsorption process: reversible adsorption followed by irreversible adsorption. Reversible adsorption is a weak bonding of the cell to the surface which is facilitated by one or a combination of the following: van der Waals forces, electrostatic and steric interactions, and polymer bridging. The time span of reversible adsorption is on the order of minutes. During this time cells may desorb from the surface and partition back into the bulk solution (Escher and Charaklis, 1990). Desorption of cells may also be a fairly rapid process. In an experiment that measured attachment and detachment during the first 120 minutes of biofilm formation, 60-80% of detaching cells had a surface residence time of less than 10 minutes (Wiencek and Fletcher, 1999).

Irreversible adsorption is a more permanent association of a cell with the substratum and is accomplished by the production of extracellular polymers. Net accumulation of a biofilm involves growth of the population of irreversibly attached cells, and the detachment of surface bound organisms either via erosion, sloughing or abrasion (Charaklis, 1990). Detachment events have usually been
thought of as mechanical failures of the biofilm matrix due to an applied shear force, but recent research has shown that these events may be initiated by enzymatic changes brought about by certain segments of the biofilm population as a response to environmental conditions (Davies et al., 1998).

The processes involved in the initial events of biofilm formation, described above, have been succinctly summarized by (Mueller et al., 1992):

1. Conditioning of the substratum by organic molecules
2. Transport of cells from the bulk water to the solid liquid interface
3. Adsorption of cells on the substratum
4. Transformation of irreversibly adsorbed cells to reversibly adsorbed cells
5. Desorption of reversibly adsorbed cells from the substratum into the bulk water
6. Growth of irreversibly adsorbed cells
7. Erosion of cells from adsorbed colonies into the bulk water.

**Attachment.** As described previously, the creation of a conditioning layer on a "clean" substratum has been thoroughly investigated and reported (Marshall, 1996). The initial attachment of cells to a substratum is influenced by the nature of the surface to which organisms are adhering. On a topographically homogeneous, stainless steel substratum, *Pseudomonas aeruginosa* displays a completely random spatial pattern of attachment. However, for a slightly rougher substratum, this organism exhibits a degree of aggregation, thereby proving that the topography of the substratum does have an influence on the initial attachment of this organism (Camper et al., 1994).
Further examination of the influence of topography on bacterial adhesion was performed by monitoring the attachment patterns of bacteria to a smooth silicon substratum in a flow cell reactor. The surface was marked by defined grooves creating a well-characterized structural heterogeneity. Results again showed that substratum topography has a bearing upon the bacterial attachment pattern. Cells were shown to preferentially attach to regions of the surface just downstream of the grooves whereas control experiments run with bacterial sized beads did not show the same pattern (Scheuerman et al., 1998).

Mueller (1996) has reported on a combination of processes in initial events of biofilm formation. Attachment, detachment and growth were observed using time-lapse microscopy and a parallel plate flow cell. Substrata of stainless steel, copper and silicon were exposed to a flowing bulk solution of Pseudomonas aeruginosa and nutrient media until a certain surface density was reached to monitor attachment and detachment rates. Subsequently, flow of sterile, cell free, nutrient media was initiated and growth and erosion of the attached cells was monitored. Silicon was the smoothest of the three materials and had the lowest rate of adsorption. Copper was the roughest material and showed the highest rate of irreversible attachment. However, no growth of attached cells on this surface was evident which is a result of the toxic effects of copper. Growth rates on silicon and stainless steel were found to be 0.28 hr⁻¹ and 0.33 hr⁻¹ respectively. This research showed that the net accumulation of cells on a surface was a result of attachment,
detachment and growth with growth being insignificant in the very early stages of biofilm development (Mueller, 1996)

Direct observation of attachment has been accomplished (Lawrence et al., 1987b). In this report, the characteristic behavior of *Pseudomonas fluorescens* was described. The planktonic cells approach the surface and attach. Rotational behavior was seen for up to half an hour on the surface with rotation gradually slowing and ceasing resulting in a longitudinal irreversible attachment. Rotational behavior was also seen with detaching or emigrating cells prior to moving to a nearby location where the sequence of rotation and attachment was repeated. Following longitudinal attachment, cell division occurred resulting in two daughter cells with a clear space of 0.2 to 0.3 μm. The standard colonization and growth pattern for *P. fluorescens* is adsorption to a surface in single cells, development of 8-16 cell microcolonies, and emigration of the daughter cells to form 8-16 cell microcolonies elsewhere.

**Observed differences between planktonic and biofilm cells.** There is a wide range of research topics which address various aspects of attachment and subsequent growth of sessile cells. It is known that planktonic organisms are much more susceptible to antimicrobial agents than those in a biofilm (Brown and Gilbert, 1993). Organisms which partition from near starvation conditions in the bulk fluid can flourish on a surface. This behavior is explained by the greater
amount of surface associated nutrients available to sessile cells (Habash et al., 1997; Kjelleberg et al., 1982). These studies illustrate advantages for cells to adhere to surfaces rather than remain in the bulk environment.

One of the first efforts to address differences, or lack thereof, between sessile and planktonic cells was reported by Bakke in 1984. In this work, it was shown that *Pseudomonas aeruginosa* does not behave differently in planktonic cultures than biofilm cultures where diffusional resistance is neglectable. This conclusion allowed the kinetic and stoichiometric parameters for *P. aeruginosa* derived from planktonic cultures to describe steady-state biofilm processes (Bakke et al., 1994).

A contradictory finding by (Moller et al., 1995) showed that the relationship between substrate concentration and growth rate for planktonic cells was not observed for sessile cells. A detailed review of surface and planktonic growth has examined several other contradictory findings where growth of a sessile population deviated from that of a planktonic population. The conclusion was that the lack of consistency is due to a variety of experimental conditions and analytical methods. More correlateable research is needed in this area (van Loosdrecht et al., 1990).

Another difference between biofilm and planktonic environments is seen in the composition of a dual species biofilm. Under identical planktonic conditions, *Klebsiella pneumoniae* has a specific growth rate double that of *Pseudomonas aeruginosa* and therefore controls the population distribution in that environment. However, when the two organisms are present in a biofilm, *K. pneumoniae* can not
displace *P. aeruginosa* due to the manner in which each behaves in a sessile environment (Stewart *et al.*, 1997).

**Phenotypic differences between planktonic and biofilm cells.** It is now a widely accepted premise that bacteria undergo phenotypic changes when a transition from a planktonic state to a sessile state occurs. In essence, the switch from a planktonic type organism to a sessile one is mediated by a large number of regulated genes which are either expressed or down regulated depending upon the environment. Adhesion to a surface appears to rapidly initiate the phenotypic expression of a range of genes not used by planktonic organisms (Costerton *et al.*, 1995b; Costerton, 1995; Korber *et al.*, 1995; Costerton and Lappin-Scott, 1995a).

Evidence of this type of behavior was first presented by Dagostino *et al.* in 1991: Two types of marine bacteria were shown to express unknown genes upon attachment to surfaces via the use of a *lacZ* reporter system. The same organisms did not express these genes while in a planktonic environment (Dagostino *et al.*, 1991). In many cases, genes which are involved in EPS production are up regulated after an attachment event (Fletcher, 1996). Supporting research has shown that new protein synthesis is required for *Pseudomonas fluorescens* to form biofilms on abiotic surfaces. The production of these unknown proteins is part of a speculated common genetic pathway used to form biofilms on a range of abiotic surfaces (O'Toole and Kolter, 1998b).
Specific research in this area has identified a portion of the regulated genes that are being expressed. An example is the \textit{algC} gene which is a key component in the alginate production pathway in \textit{Pseudomonas aeruginosa}. Within the span of minutes after a planktonic cell adheres to a surface, this gene is expressed and eventually results in the abundance of alginate which is a primary constituent of the EPS produced by biofilms of this organism (Davies \textit{et al.}, 1993).

The fact that biofilm cells are markedly different than planktonic cells is not trivial as this may help explain the increased resistance to antibiotics (Costerton \textit{et al.}, 1995b) and other morphological changes (Dalton \textit{et al.}, 1994).

\textbf{Purpose}

To initiate the development of a biofilm, bacterial cells in suspension are transported to a solid/liquid interface and adhere. Once these cells are in a sessile environment, they replicate and cover the surface to form a biofilm. The process of becoming a sessile organism may involve a sweeping number of genetic changes which causes the sessile cell to become phenotypically distinct from its planktonic counterpart (Costerton \textit{et al.}, 1995b). In the experiments described here, \textit{Pseudomonas aeruginosa} PA01 cells underwent this transition and there appeared to be a temporary halt in their growth and division cycle. This lag time may be a result of viable cells directing metabolic energy into other products, such as extracellular materials, rather than into replication (Fletcher, 1996).
The planktonic cells used for the experiments were cultivated in a chemostat reactor and then transferred to a parallel plate flow cell reactor for observation with CSLM. Also, inocula were placed in a batch reactor as a control. Under the conditions of these experiments, the results show that growth of primary biofilm cells is negligible during the first 12 hours following attachment, while no difference in growth is seen in planktonic cells which never became sessile. The growth of secondary biofilm cells was slower than planktonic cells but significantly faster than primary biofilm cells. Nutrient conditions for all three types of cells were held constant.

This finding is a result of direct, in situ observation of biofilm cells in a parallel plate flow cell visualized by confocal laser scanning microscopy. The purpose was to qualitatively compare the growth characteristics of cells in planktonic, primary biofilm and secondary biofilm environments.
Materials and Methods

Overview

The growth of bacteria in sessile and planktonic states was examined in this research project. The original bacterial cells which colonize a clean surface are referred to as "primary" biofilm cells and the subsequent progeny cells are termed "secondary". Both primary and secondary biofilm cells were observed using a parallel plate flow cell reactor and planktonic cells were studied in a standard batch culture. Batch culture experiments were conducted for periods of 6 and 12 hours while flow cell experiments lasted 8.5 and 12 hours.

Organism

The organism used in this study was *Pseudomonas aeruginosa* PA01. *Pseudomonas aeruginosa* is a motile, aerobic, Gram negative rod. This particular strain contained a plasmid that conveyed a resistance to 150 mg/l of carbenicillin and encoded the production of a green fluorescent protein (GFP). The GFP was constitutively expressed, thus enabling each cell to be "self labeling". The excitation wavelength of the GFP was 488-nm and an emission maxima was at 512-nm. This organism was obtained from Dr. Mike Franklin, at Montana State University.
Stock Culture

Stock cultures of the organism were prepared by streaking for isolated colonies on R2A agar (Difco) which contained 150 mg/l of carbenicillin (Sigma). Isolated colonies were then transferred to fresh R2A/carbenicillin agar and incubated until a confluent lawn was present. The culture was harvested, placed in a 2% peptone - 20% glycerol solution and stored in 2.0-ml vials at −70°C. For each experiment, approximately 1.0 ml of frozen stock culture was used as an initial inoculum.

Equipment Preparation

The equipment used in this study included media and waste containers, assorted tubing, a chemostat reactor, a parallel plate flow cell reactor, an inoculation vessel, a bubble trap, and a batch reactor. These components are illustrated in Figures 2.1 through 2.4 and described in following paragraphs.

The nutrient media for each experiment was prepared and sterilized separately from the remainder of the items as explained in the following section. The various vessels and tubing were cleaned by washing with soap and water and sterilized by autoclaving dry for 20 minutes at 121°C and 20 psi. The tubing upstream from each of the reactors was replaced for each experiment.
Media

The same nutrient media was used in the chemostat, flow cell, and batch reactor. The constituents are listed below in Table 2.1:

Table 2.1. Media Composition

<table>
<thead>
<tr>
<th>Constituent</th>
<th>Amount (grams per liter)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$K_2HPO_4$</td>
<td>0.70</td>
</tr>
<tr>
<td>$KH_2HPO_4$</td>
<td>0.30</td>
</tr>
<tr>
<td>$(NH_4)_2SO_4$</td>
<td>0.10</td>
</tr>
<tr>
<td>$MgSO_4 \cdot 7H_2O$</td>
<td>0.01</td>
</tr>
<tr>
<td>Glucose</td>
<td>0.40</td>
</tr>
</tbody>
</table>

The potassium salts and ammonium sulfate (Fisher) were added to glass carboys, an appropriate amount of reverse osmosis water was added and the containers were sealed and autoclaved for 15 minutes per liter. The solution was cooled to room temperature before the remaining constituents were added. Proper amounts of glucose (Fisher) and magnesium sulfate (Aldrich) were dissolved in approximately 25 ml of reverse osmosis water and added to solution via syringe and a 0.2-micron syringe filter.

Chemostat Operation

A chemostat was used to grow inocula for both the flow cell and batch culture experiments. The reactor was operated at room temperature with a volume of 500
ml and a 5-hour residence time. The culture in the reactor was well mixed by a magnetic stir bar and plate and aerated by the laboratory pressurized air system through bacterial air vents (Gelmen Sciences). A schematic diagram of the system is shown in Figure 2.1. After sterilizing all reactor components the system was assembled. The chemostat was filled with sterile nutrient media, inoculated with 1.0 ml of frozen stock culture and operated in batch mode for 24 hours. The pump was then turned on to supply media to the reactor and the effluent was pumped to a waste container. The bacteria were grown in a chemostat environment for 48 hours (approximately 10 residence times).

Figure 2.1. Schematic of one chemostat reactor system.
Batch Culture

A batch reactor was utilized with the media described above. 1.0 L of media was sterilized in a 2.0 L Erlenmeyer flask. An inoculum was withdrawn from a 48-hour chemostat culture and placed in the vessel. The batch culture was incubated at room temperature and well mixed using a magnetic stir bar and plate. Population measurements were made at the beginning, middle and end of a 12-hour period.

Figure 2.2. Parallel plate flow cell reactor.
Flow Cell Cleaning

Cells growing in an attached or sessile state were observed on the “wet side” of the coverglass in a parallel plate flow cell reactor (Figure 2.2). Cleaning of the flow cell prior to each experiment was carried out as follows:

The polycarbonate base was submersed in 95% ethanol for 30 minutes and then subjected to UV light for 30 minutes. Each experiment utilized a new glass coverslip that was washed twice with antibacterial soap and rinsed twice with 95% ethanol. The coverslip was then autoclaved for 20 minutes and dried at 115°C for 24 hours. Other assorted materials (tubing, coverplate, gasket, screw and nuts) were autoclaved for 20 minutes. After all parts of flow cell were sterilized or cleaned, the flow cell was assembled inside a biological hood.

Flow Cell Operation-Primary Cell Experiments

The entire flow cell reactor system (Figure 2.3) was set up on a laboratory cart to facilitate transportation to and from the microscope lab where the experiments were completed.

Prior to inoculation, the flow cell and all upstream tubing were filled with sterile media to purge air from the system. Approximately 15 ml of inoculum were withdrawn from a 48 hour chemostat culture and placed into the inoculation vessel, upstream of the flow cell. The inoculum was rapidly mixed using a magnetic stir bar and plate. A portion of the stirred inoculum was pumped through the flow cell
for approximately 1 minute. After cells had been introduced into the flow cell reactor, the inoculum flow was terminated and flow of sterile, cell free media commenced. The flow rate was set at 2.0 ml/minute which is laminar flow (Re~5.5) with flow channel dimensions being 12 mm x 1.5 mm in cross section and 37 mm in length.

![Flow cell reactor system](image)

**Figure 2.3. Schematic of flow cell reactor system**

In order to prevent bubbles from collecting in the flow cell, the media container was elevated so that the upper surface of the media was approximately 0.5 meter higher than the flow cell with the media effluent port at the bottom of the container. The effluent line from the flow cell was at an elevation approximately level with the reactor. By aligning the system in this manner, the elevation of the media reservoir...
served to slightly pressurize the reactor, preventing the formation of bubbles in the flow cell. A bubble trap (Figure 2.4) was also used downstream of the media reservoir to remove any large bubbles that may have entered the line during the initial start up or media container exchange. The pump is located downstream from the flow cell to minimize the amount of upstream tubing subject to initial cell inoculation. In this arrangement, the pump serves to hold flow back at the proper rate; without the pump in place, the media container would drain completely by gravity in a matter of minutes.

Figure 2.4. Bubble trap.
After inoculation of the flow cell reactor, the adhered cells were subjected to uninterrupted, cell free nutrient flow for 10 minutes. Subsequently, a random field of view was chosen to be observed. The flow cell reactor was left in place on the microscope stage and not moved for the duration of the experiment. The cells in this field of view were then observed using a confocal laser scanning microscope every 15 minutes for a period of 12 hours to determine population growth. At each interval, the desired field of view was first checked for focus by eye with transmitted white light. Subsequently, the image was captured using the laser light source. This method greatly reduced the amount of time the sample was subjected to bleaching and heating from exposure to the laser beam. Nutrient flow was halted temporarily for each image to prevent pulsing of the coverglass.

**Flow Cell Operation – Secondary Cell Experiments**

The flow cell was prepared and inoculated in the much the same fashion as detailed above and is described in the corresponding section in Chapter 3 of this report. Secondary biofilm cell experiments utilized a dilute mix of GFP+ cells in predominantly GFP- environment. This allowed for the certain identification of cells and their progeny. After inoculation, the flow cell reactor remained in operation, but not observed for a period of 24 hours. During this period of continuous sterile media flow, the biofilm grew to a depth of several cells (3-10 μm). The cell growth observed in this type of experiment was strictly growth of the secondary population.
Image Capture and Analysis

Various TIF format images from both batch culture (cells captured on filter) and flow cell experiments were produced using a Leica TCS-NT Confocal Microscope System. The fluorescence emitted from the GFP produced by the bacteria was used to locate individual cells. The excitation of the protein was achieved with the 488-nm laser light source. The fluorescent emission, maxima at 512 nm, was registered after passing through a BF filter block (500 to 550 nm, cutoff).

The TIF image files were imported into an image analysis software package, Image-Pro Plus, Version 3.00.00 (Media Cybernetics). The software was calibrated based on the actual dimensions (100 μm x 100 μm for images captured using 100X, 1.4 N.A., oil immersion objective) of each image. The auto-count feature was set to identify all objects (cells) within a specified area range, usually 0.5 to 2.5 μm². The software automatically assigned each cell an object number, and x and y coordinates, in μm, with the origin being the upper left corner of the image. Occasionally, several cells were overlapping and had to be manually tagged. In this event, the software still took record of the x,y coordinates of the object, however it was the researcher's task to identify and tag the locations of each of the overlapping cells.
Planktonic Cells

To determine population growth, direct cell counts were performed at the beginning and end of 6 and 12-hour periods using only GFP+ cultures. This was accomplished by removing 10 ml of the culture, vortexing to break up cell clusters, and filtering onto the surface of a 25 mm diameter, 0.2 micron pore size polycarbonate filter (Osmonics).

The filters were then placed on microscope slides and the fluorescent cells were examined using the same microscope, light source and filter settings described previously. From each filter, 12 to 15 separate fields of view were counted to determine the approximate number of cells per filter from which the number of cells per ml in the batch culture were extrapolated.

The average beginning and end cell concentrations and corresponding standard errors of the mean were calculated for each sample. Population increase was determined by dividing the change in cell concentration by the beginning concentration.

Biofilm Cells

Each of the cells in the initial field of view, or image, was identified and assigned an object number using image analysis software, as described previously. The original colonizing cells, their fate, and progeny were tracked over
the course of the experiment using the images and the object numbers. The following quantities were counted in each experiment:

- $N_0$: Initial number of cells on the surface
- $N_{0E}$: Number of original cells which emigrate
- $N_{OD}$: Number of original cells which divide
- $N_{0R}$: Number of original cells which remain but not divide/emigrate
- $n_P$: Number of progeny cells arising from dividing cells
- $n_{PE}$: Number of progeny cells which emigrate

From this data, various counts and percentages were determined as follows:

<table>
<thead>
<tr>
<th>Value</th>
<th>Formula</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total number of cells, $n_T$</td>
<td>$N_0 + n_P$</td>
</tr>
<tr>
<td>Base number of cells, $N_B$</td>
<td>$N_0 - N_{0E}$</td>
</tr>
<tr>
<td>% of original cells that emigrate</td>
<td>$\left{ \frac{N_{0E}}{N_0} \right}%$</td>
</tr>
<tr>
<td>% of original cells that divide</td>
<td>$\left{ \frac{N_{OD}}{N_0} \right}%$</td>
</tr>
<tr>
<td>% of original cells that do not divide or detach</td>
<td>$\left{ \frac{(N_0 - [N_{0E} + N_{0D}])}{N_0} \right}%$</td>
</tr>
<tr>
<td>% Surface accumulation increase</td>
<td>$\left{ \frac{n_P}{N_0} \right}%$</td>
</tr>
<tr>
<td>% Population increase</td>
<td>$\left{ \frac{n_P}{N_B} \right}%$</td>
</tr>
<tr>
<td>% Population detach</td>
<td>$\left{ \frac{(n_{PE} + N_{0E})}{n_T} \right}%$</td>
</tr>
</tbody>
</table>
Results

Summary

Three types of experiments were performed which dealt with the growth of planktonic, primary biofilm and secondary biofilm cells. In each case, the purpose was to quantify the growth of each population to determine any differences between primary biofilm cells, their progeny, and their planktonic counterparts.

As was described previously, planktonic cell counts were obtained from GFP+ batch cultures of various ages. The growth of two 6-hour cultures and four 12-hour cultures were measured and percent population increase was calculated.

Four flow cell reactor experiments were conducted for primary and secondary biofilm cells. Primary cell experiments were run with only GFP+ cells and secondary cell experiments used a mix of GFP+ and GFP- cells. The length of these experiments varied from 8 to 12.5 hours. Each time, a specific field of view was observed for the duration of the experiment and individual biofilm cells were tracked. Cells growing in the attached state were quite active. Many cells moved around during the experiment, the total distance moved being in the tens of microns. Also, a number of the cells detached or emigrated to leave the field of view. Without tracking individual cells on a 15-minute interval, it is difficult to follow those cells and make any accurate judgment concerning their growth. Due to this
behavior, it was necessary to maintain the same field of view. The result is detailed information on a limited number of cells.

**Planktonic Population Increase**

The cell concentrations of the batch cultures were measured at the beginning and end of each experiment. The average increase after 12 hours was 981%. The results are listed below in Table 2.3. The percent population increase was determined by:

\[
\text{% Increase} = \frac{\text{Change in concentration}}{\text{Initial concentration}} \times 100
\]

**Table 2.3. Planktonic Growth Results**

<table>
<thead>
<tr>
<th>Culture ID</th>
<th>Time (hr)</th>
<th>Initial Concentration (cells/ml)</th>
<th>SEM</th>
<th>Final Concentration (cells/ml)</th>
<th>SEM</th>
<th>% Population Increase</th>
<th>Average % Population Increase</th>
</tr>
</thead>
<tbody>
<tr>
<td>mar30-1</td>
<td>12</td>
<td>1.40E+04</td>
<td>1.08E+03</td>
<td>1.08E+05</td>
<td>4.78E+03</td>
<td>671.43</td>
<td></td>
</tr>
<tr>
<td>mar30-2</td>
<td>12</td>
<td>no count</td>
<td>N/A</td>
<td>1.44E+05</td>
<td>6.32E+03</td>
<td>N/A</td>
<td></td>
</tr>
<tr>
<td>mar30-3</td>
<td>12</td>
<td>1.31E+04</td>
<td>5.79E+02</td>
<td>1.72E+05</td>
<td>7.23E+03</td>
<td>1212.98</td>
<td></td>
</tr>
<tr>
<td>average</td>
<td></td>
<td>1.36E+04</td>
<td>8.30E+02</td>
<td>1.41E+05</td>
<td>6.11E+03</td>
<td></td>
<td></td>
</tr>
<tr>
<td>jan29-1</td>
<td>12.17</td>
<td>1.91E+05</td>
<td>7.95E+03</td>
<td>3.13E+06</td>
<td>1.10E+05</td>
<td>1538.74</td>
<td></td>
</tr>
<tr>
<td>jan29-2</td>
<td>12.17</td>
<td>2.25E+05</td>
<td>7.07E+03</td>
<td>no count</td>
<td>N/A</td>
<td>N/A</td>
<td></td>
</tr>
<tr>
<td>jan29-3</td>
<td>12.17</td>
<td>2.30E+05</td>
<td>4.95E+03</td>
<td>1.38E+06</td>
<td>4.47E+04</td>
<td>500.00</td>
<td></td>
</tr>
<tr>
<td>average</td>
<td></td>
<td>2.15E+05</td>
<td>6.66E+03</td>
<td>2.22E+06</td>
<td>7.74E+04</td>
<td></td>
<td></td>
</tr>
<tr>
<td>jan21</td>
<td>5.95</td>
<td>5.88E+04</td>
<td>1.84E+04</td>
<td>2.08E+05</td>
<td>8.63E+03</td>
<td>253.74</td>
<td>-12 hr 981 %</td>
</tr>
<tr>
<td>jan18</td>
<td>5.45</td>
<td>9.94E+04</td>
<td>8.60E+03</td>
<td>2.32E+05</td>
<td>1.24E+04</td>
<td>133.40</td>
<td>-6 hr 194 %</td>
</tr>
</tbody>
</table>

* SEM – Standard error of the mean
Primary and Secondary Biofilm Populations

A direct measurement of population growth was not possible due to the movement and emigration of biofilm cells. Because of this complication, an initial field of view was chosen and the cells identified. These original cells were then observed for the duration of the experiment and their fate was recorded. The description of the data and the calculations have been listed previously; the results are presented below in summary in Table 2.4 and in detail in Table 2.5.

The two key calculations made to illustrate the growth of biofilm cells are percent population change and percent surface coverage change. Invariably, there were cells present in the original field of view which emigrated before the end of the experiment. It is unknown whether these emigrating cells divided during the remainder of the observation period. The measurement of population increase is determined for only cells whose fate is known. Surface accumulation increase is a measure of the change in total numbers of cells attached in a field of view and is affected by cell division and emigration. There was no reattachment of cells in any field of view during these experiments of GFP+ cells. This is not surprising however, due to the very small percentage of GFP+ (therefore, visible) cells within the reactor.

The four experiments evaluating the behavior of primary biofilm cells were each carried out in separate reactors. The four sets of data resulting from the secondary biofilm experiments were taken from two reactors. The data from
experiment “nov21’ had the cells arranged in such a way that three areas of interest (AOI) were used, and thus three sets of data were created.

### Table 2.4. Summary Biofilm Cell Growth Results

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Time (hr)</th>
<th>% Surface Accumulation Increase</th>
<th>% Population Increase</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primary Biofilm Cells</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>jan21</td>
<td>12.57</td>
<td>26.1</td>
<td>28.6</td>
</tr>
<tr>
<td>feb02</td>
<td>12</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>mar29</td>
<td>12.42</td>
<td>26.5</td>
<td>31</td>
</tr>
<tr>
<td>average</td>
<td>12.33</td>
<td>17.53</td>
<td>19.87</td>
</tr>
<tr>
<td>Secondary Biofilm Cells</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>oct21</td>
<td>11</td>
<td>58.3</td>
<td>107.7</td>
</tr>
<tr>
<td>nov21-aoi#1</td>
<td>10</td>
<td>250.0</td>
<td>250.0</td>
</tr>
<tr>
<td>nov21-aoi#2</td>
<td>10</td>
<td>141.7</td>
<td>170.0</td>
</tr>
<tr>
<td>nov21-aoi#3</td>
<td>10</td>
<td>100.0</td>
<td>200.0</td>
</tr>
<tr>
<td>average</td>
<td>10.25</td>
<td>137.5</td>
<td>181.9</td>
</tr>
</tbody>
</table>

The planktonic population observed in the current project exhibits an average of nearly a 1000% increase over a 12-hour period and roughly a 200% increase in nearly 6 hours. The planktonic cells that were used to inoculate the batch reactors originated in a chemostat culture with a residence time of 5 hours, which corresponds to a doubling time of 3.5 hours (Madigan et al., 1997). If the cells were to continue to replicate at that rate, these population increases are exactly what would be expected. From this information, it is evident that the cells which were transferred from the planktonic state in the chemostat to the planktonic state of a batch culture incurred no significant lag time and continued to replicate without any hindrance at a specific growth rate of 0.2 hr⁻¹.
This was not the case with cells that made the transition from a planktonic state to a sessile state. In these experiments, the primary cells that originally colonize the surface are the first, or parent, generation of biofilm cells. The primary cells, as a group, only achieved an 18% increase in surface coverage, and a 20% actual population increase over 12 hours. Also, only 7% of the primary cells divided during the first 12 hours after initial colonization. Due to such a great proportion of cells exhibiting no growth, it was not possible to determine a representative mean time to division needed to estimate growth rate.

Once a primary cell replicates, the two daughter cells are known as secondary biofilm cells. These cells are different in one significant way from their parent cells. These bacteria did not undergo a change in environment; they originated in an attached state and did not partition onto the surface from the bulk, or planktonic phase. This group of cells did not grow as fast as their planktonic counterparts, but did grow at a greater rate than the primary cells. In approximately a 10-hour period, there was a 138% increase in surface accumulation and a 182% population increase. The mean specific growth rate was 0.1 hr⁻¹.

Comparing the patterns shown by primary and secondary biofilm cells, it is evident that the secondary cells are replicating at a significantly faster rate. In general, the secondary biofilm cells are more active than the primary cells; 76% of primary cells neither divided nor emigrated compared with only 6% of secondary cells. Also, only 7% of primary cells replicated during the 12-hour observation period compared to 65% of secondary cells.
Table 2.5. Detailed Biofilm Growth Results

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Time (hr)</th>
<th>begin # cells (N)</th>
<th># of orig. emigrate cells (N*)</th>
<th># of orig. cells divide (Nw)</th>
<th># of orig. cells not div/emgt (N«)</th>
<th># of cells from division (Nv*)</th>
<th># of daughter emigrate cells (IV*)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Primary BIOFILM CULTURE EXPERIMENTS</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>jan15</td>
<td>8.37</td>
<td>13</td>
<td>3</td>
<td>9</td>
<td>1</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>jan21</td>
<td>12.57</td>
<td>46</td>
<td>4</td>
<td>7</td>
<td>35</td>
<td>12</td>
<td>7</td>
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<td>feb02</td>
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<td>19</td>
<td>0</td>
<td>76</td>
<td>0</td>
<td>0</td>
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<tr>
<td>mar29</td>
<td>12.42</td>
<td>34</td>
<td>5</td>
<td>2</td>
<td>27</td>
<td>9</td>
<td>5</td>
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<tr>
<td>Total</td>
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<td>188</td>
<td>31</td>
<td>10</td>
<td>147</td>
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<td></td>
<td></td>
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<tr>
<td>Secondary BIOFILM CULTURE EXPERIMENTS</td>
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<td></td>
<td></td>
<td></td>
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<td>nov21-soi#1</td>
<td>10</td>
<td>4</td>
<td>0</td>
<td>3</td>
<td>1</td>
<td>10</td>
<td>3</td>
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<tr>
<td>nov21-soi#2</td>
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<td>10</td>
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<td>8</td>
<td>4</td>
<td>4</td>
<td>0</td>
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<td>Total</td>
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<td>48</td>
<td>17</td>
<td>30</td>
<td>1</td>
<td>49</td>
<td>31</td>
</tr>
<tr>
<td>Avg. %</td>
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</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Time (hr)</th>
<th>begin # cells (N)</th>
<th># of orig. emigrate cells (N*)</th>
<th># of orig. cells divide (Nw)</th>
<th># of orig. cells not div/emgt (N«)</th>
<th># of cells from division (Nv*)</th>
<th># of daughter emigrate cells (IV*)</th>
</tr>
</thead>
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<tr>
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<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Primary BIOFILM CULTURE EXPERIMENTS</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>jan15</td>
<td>8.37</td>
<td>14</td>
<td>10</td>
<td>23</td>
<td>8</td>
<td>69</td>
<td>7.7</td>
</tr>
<tr>
<td>jan21</td>
<td>12.57</td>
<td>58</td>
<td>42</td>
<td>9</td>
<td>15</td>
<td>76</td>
<td>26.1</td>
</tr>
<tr>
<td>feb02</td>
<td>12</td>
<td>95</td>
<td>76</td>
<td>20</td>
<td>0</td>
<td>80</td>
<td>0.0</td>
</tr>
<tr>
<td>mar29</td>
<td>12.42</td>
<td>43</td>
<td>29</td>
<td>15</td>
<td>6</td>
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<td>5</td>
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<td>11.7</td>
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<tr>
<td>Avg. %</td>
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<th># of orig. cells divide (Nw)</th>
<th># of orig. cells not div/emgt (N«)</th>
<th># of cells from division (Nv*)</th>
<th># of daughter emigrate cells (IV*)</th>
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Discussion

The purpose of this research was to contrast the growth of bacteria in three different settings: Planktonic, primary biofilm and secondary biofilm. Due to the length of the lag time exhibited by primary biofilm cells, it was not possible to determine a specific growth rate for that population. However, it was possible to estimate the specific growth rate of the planktonic and secondary biofilm population. The reason for comparing growth in these environments is to show that cells which transition from a planktonic state to a biofilm state endure a lag time or a period of no replication. The primary biofilm cells do not replicate at the same frequency as do their planktonic counterparts or their progeny.

In the past, the strict definition of the term planktonic has referred to cells which are suspended in solution and not attached to a surface or neighboring cells. A sessile organism has been defined as an organism that is attached to a surface and not suspended in a liquid culture. In recent years, the distinction between the two terms has come to imply not only environmental differences, but phenotypic differences as well (Costerton et al., 1995b; Costerton, 1995; Korber et al., 1995; Costerton and Lappin-Scott, 1995a; Fletcher, 1996). As an underlying tenet of this current research, it is believed that a change in phenotype does not occur instantaneously. Accordingly, a detached biofilm cell which is suddenly resuspended in the bulk fluid is an organism in a planktonic environment, but is expressing a biofilm phenotype. Research currently in progress is investigating
the time frame over which such changes in phenotype occur (Pulcini, 1999). For
the scope of this discussion, the terms planktonic and secondary biofilm refer
explicitly to phenotype, while the term primary biofilm describes a cell in transition.

Bakke et al. (1994) proposed that growth rates of *Pseudomonas aeruginosa*
biofilm cells and planktonic cells are the same provided the microenvironment of
the cells is the same. Therefore, the kinetic parameters determined for a
planktonic culture could be used to predict biofilm behavior while the biofilm is not
experiencing any diffusion limitation (Mueller, 1990). The biofilms studied in this
research are only a few microns thick and do not have any diffusion limitations;
however, there are differing growth rates depending on the source of the cell. This
result shows that the conclusions drawn by Bakke et al. do not apply for very early
stage biofilms.

Differences in the growth of planktonic and biofilm cells have been described
previously (Moller et al., 1995; Kjelleberg et al., 1982; Habash et al., 1997; Moller
et al., 1996; Dalton et al., 1994; van Loosdrecht et al., 1990; Xu et al., 1998;
Korber et al., 1994; Bakke et al., 1994). The results of these studies vary,
indicating that planktonic cells grow faster, slower and the same as biofilm cells.
The purpose of this current research, again, is not to refute or support any of these
findings. Rather, the aim is to show that cells that undergo a change in phenotype
from planktonic to biofilm, without a change in nutrient conditions, also endure a
lag time in their rate of replication.
The population increase of primary cells is virtually nonexistent in contrast to the growth experienced in the first 12 hours of a planktonic culture. From these results, it is apparent that the cells which transition from a planktonic phenotype to a biofilm phenotype endure a lag phase in their growth before significant biofilm accumulation can occur.

Quantifying the growth of a population of biofilm cells has been accomplished by others (Korber et al., 1994; Lawrence et al., 1987b; Lawrence and Caldwell, 1987a; Lawrence et al., 1989; Caldwell and Lawrence, 1986; Korber et al., 1989). In each case, the specific growth rate for various species of adhered cells was determined in a parallel plate flow cell via time lapse microscopy. Their results suggest that the organisms in each case did not exhibit any lag type behavior but rather were replicating from the moment of attachment. This would appear to contradict the findings of this research. However, their inocula consisted of biofilm phenotype cells rather than cells with a purely planktonic phenotype. Therefore, no lag time would be expected due to no change in phenotype occurring.

Mueller also has studied the behavior of sessile cells on various surfaces (Mueller et al., 1992; Mueller, 1996; Mueller, 1990). The flow cell reactor system used in these studies is operated in a similar manner to the one described herein and the organism is the same species but a different strain: *Pseudomonas aeruginosa* ERC. Mueller does not specifically discuss the aspect of a lag time but the data presented indicate the occurrence of such an event. The inocula for these experiments were drawn from chemostat culture where the cells would truly
be expressing a planktonic phenotype. Therefore, any adherence and subsequent growth on a surface would necessitate a change to a biofilm phenotype.

These results show that when *Pseudomonas aeruginosa* PA01 cells undergo transition from a planktonic environment to a sessile one, there is a lag time in growth associated with this change. This conclusion fits well with the idea that these cells have changed phenotypically as well. If the number of genes being up or down regulated is as large as has been postulated (Costerton et al., 1995b) then this would constitute a major change. Also, if several of these genes are involved in the production of extracellular materials (Davies et al., 1993), then it would seem that a portion of metabolic energy is now being required for this task at the expense of creating new cells. Overall, the results of this research fit very well with the current conceptual model of biofilm formation.
CHAPTER 3

MOVEMENT, REPLICATION, AND EMIGRATION OF SECONDARY BIOFILM CELLS

Background

Biofilms are communities of microorganisms that can be found in virtually every type of aqueous environment. A biofilm is an ingeniously organized multi-species entity where ecological microniches are occupied by specific organisms (Costerton et al., 1995b; Costerton, 1995). Bacteria can attach to both abiotic and biotic materials as is evidenced by many types of human infections, the corrosion of metals, the reduced efficiency of industrial heat dissipation equipment, and the degradation of waste materials (Costerton et al., 1995b).

Once bacteria have colonized a surface, growth of the attached population and induction of new organisms into the community occurs. The resulting biofilm is an intricate assortment of micro- and macroorganisms (Fletcher, 1996). Because of the amazing complexity, prevalence, and impact of microbial biofilms, it is important to understand how these communities form. The first stages of biofilm development, "initial events", have been studied in detail but are poorly understood. It is known that topography affects the manner in which bacterial cells
colonize a surface (Camper et al., 1994; Scheuerman et al., 1998). Cells which originally colonize a particular surface are the primary biofilm cells, or parent organisms of the ensuing biofilm. It has been reported that a certain species of primary cells forms dense microcolonies and then disperses in a matter of minutes (O'Toole and Kolter, 1998a). After replication of biofilm cells, daughter cells can spread out upon the surface, pack tightly near the parent cell location, be shed into the bulk fluid, roll along the substratum, or form long chains of cells (Lawrence and Caldwell, 1987a; Korber et al., 1989; Power and Marshall, 1988; Shapiro and Hsu, 1989; Dalton et al., 1994). It has been postulated that the various types of behavior exhibited by these cells is species dependent (Lawrence and Caldwell, 1987a).

Prior Research

Initial Events Description. One of the most valuable results from initial events research is a conceptual model of biofilm development. The processes involved in the initial events of biofilm formation have been summarized by (Mueller et al., 1992):

1. Conditioning of the substratum by organic molecules
2. Transport of cells from the bulk water to the solid liquid interface
3. Adsorption of cells on the substratum
4. Transformation of irreversibly adsorbed cells to reversibly adsorbed cells
5. Desorption of reversibly adsorbed cells from the substratum into the bulk water
6. Growth of irreversibly adsorbed cells
7. Erosion of cells from adsorbed colonies into the bulk water.
Attachment. The first step in biofilm formation is the creation of a conditioning layer on a “clean” substratum and has been thoroughly investigated and reported (Marshall, 1996). The second step, the initial attachment of cells to a substratum, is influenced by the nature of the surface to which organisms are adhering. Given a topographically homogeneous substratum of stainless steel, *Pseudomonas aeruginosa* displays a completely random spatial pattern of attachment. However, for a slightly rougher substratum, this organism exhibits a degree of aggregation, thereby indicating that the topography of the substratum does have an influence on initial attachment (Camper *et al.*, 1994; Hamilton *et al.*, 1995).

A further examination of the influence of topography on bacterial adhesion has been carried out (Scheuerman *et al.*, 1998). This was accomplished by observing the attachment patterns of bacteria to a smooth silicon coupon marked by distinct grooves creating a well-characterized structural heterogeneity. Results again proved that substratum topography has an impact upon the bacterial attachment pattern. Cells preferentially attached to regions of the substratum surrounding the grooves whereas control experiments with bacterial sized beads did not show any specificity in terms of adsorption location.

Growth. Growth of sessile cells occurs after attachment. Three types of measurements of growth rates of sessile bacteria have been presented which involve the time required for cell fission, the specific increase in cell number, and the specific increase of cell area (Caldwell and Lawrence, 1986; Lawrence *et al.*, 1986; Scheuerman *et al.*, 1998).
1989). These parameters were measured using image analysis techniques. It was shown that using the specific increase in cell area or size may give misleading results due to cells becoming smaller with each generation due to environmental conditions.

Direct observation of sessile cell growth has been reported (Lawrence et al., 1987b). In these studies, a characteristic growth pattern of *Pseudomonas fluorescens* was determined. Planktonic cells approach the surface and attach followed by rotational motion for up to half an hour with rotation gradually ceasing, resulting in a longitudinal irreversible attachment. Rotational behavior was also seen with detaching or emigrating cells which move to a nearby location and repeat the behavior of rotation and attachment. Subsequent to longitudinal attachment, cell division occurred resulting in two daughter cells 0.2 to 0.3 μm apart. After 3 to 4 generations, other movement was seen such as vibration, directional movement and eventually emigration. The standard colonization pattern reported was that *P. fluorescens* first colonizes a surface in single cells, 8 to 16 cell microcolonies arise from cell division, followed by emigration of the daughter cells to form 8 to 16 cell microcolonies elsewhere.

Further research into the development of *P. fluorescens* biofilms focused on the “recolonization” behavior of both motile and non-motile emigrating cells. It was reported that the average recolonization distance for motile cells was 47 μm which was 3 times greater than for non-motile cells. This characteristic behavior allows for the redistribution of cells across a substratum to virtually all vacant
spaces and is a key phase in the development of a confluent biofilm (Korber et al., 1989)

Another report of direct observation of growth and behavior of biofilm cells described 4 types of cell movement: packing, spreading, shedding and rolling (Lawrence and Caldwell, 1987a). This work involved the use of natural stream populations cultivated in flow cell reactors. The packing behavior arose from progeny cells remaining very close to the parent cell location which resulted in the formation of discreet, tightly packed microcolonies. Spreading of daughter cells by distances of 5–20 μm created diffuse microcolonies. Shedding behavior involved a parent cell being attached to the substratum while each daughter cell oriented away from the substratum and detached upon the completion of division. Rolling cells maintained contact with the surface but were not stationary nor did they form microcolonies. Exponential growth was observed in the microcolonies of the packing and spreading cells, but not for rolling or shedding cells. The authors state that these colonization maneuvers may be species characteristics and can only be discerned by continuous observation.

A related report addressed growth of marine bacteria on a surface bound substrate (Power and Marshall, 1988). The pseudomonad studied underwent growth and division while attached to the surface. Attached cells were observed to increase in size and then divide, with the two daughter cells moving away from each other. The cells tended to move great distances, up to 50 times their own length before completing another division cycle. The migration rate was relatively
slow with a mean of 0.15 \mu m/min. Detachment of cells from the substratum was also observed and suspected to be related to the unavailability of sorbed nutrients.

**Modeling**

Modeling of biofilm growth is a fundamental area of research. Cellular automata (CA) is a well-defined method (Wuensche, 1999) and has been described in the context of biofilms by (Picioreanu et al., 1998a; Picioreanu et al., 1998b; Wimpenny and Colasanti, 1997b; Wimpenny and Colasanti, 1997a). CA is a discrete dynamic array composed of “cells”. Each cell or compartment in the model is capable of being updated simultaneously according to rules set for the particular model. In the case of modeling biofilms, these compartments may contain bacterial cells, bulk fluid, EPS or another material. The rules governing a biofilm CA are designed to simulate cell growth, detachment, and other biofilm processes based on varying conditions within the biofilm as dictated by user specified rules.

One aspect unique aspect of biofilm CA models is that the rules governing substrate concentrations are based on differential equations where the predicted concentration gradient drives the instantaneous changes. However, cell growth and movement and detachment is still modeled in discrete steps (Picioreanu et al., 1998a; Picioreanu et al., 1998b). An interesting application of this type of modeling has been presented (Wimpenny and Colasanti, 1997b; Wimpenny and Colasanti, 1997a). In these models, the relative substrate concentration has
significant effects on the morphology of the predicted biofilm. When very high substrate concentrations are used, a dense, uniform biofilm is predicted. On the contrary, when a low substrate concentration in the bulk is modeled, a sparse dendritic structure results.

CA models are important in biofilm research because, when sufficiently developed, they can be used to complement laboratory findings. In some cases, the model can be used to formulate research hypotheses (Wimpenny and Colasanti, 1997b). The findings described herein can be used to further define cell behavior rules within a biofilm and contribute to the refinement of modeling input parameters.

Purpose

This research examined the following behaviors exhibited by individual cells growing in a biofilm environment on a glass substratum: growth, movement and emigration. Others have conducted similar research, however their work involved sessile cells on a sparsely colonized surface (Arturo, 1998; Power and Marshall, 1988; Lawrence et al., 1987b; Lawrence and Caldwell, 1987a). This research examines cells within a 3-10 μm thick biofilm composed of Pseudomonas aeruginosa PA01. The planktonic inocula used for the experiments were cultivated in a chemostat reactor and then transferred to a parallel plate flow cell reactor for observation with confocal scanning laser microscopy.
Materials and Methods

Overview

The early stages of biofilm development were studied by observing individual cells growing within a monospecies biofilm matrix inside a flow cell reactor. Flow cell inocula were grown in chemostats with glucose as the carbon source. The same nutrient media was utilized in both chemostat and flow cell reactors.

The purpose of this research was to quantify rates of replication, motion, and detachment of individual cells. This was accomplished by tracking the position of specific cells and their progeny over the course of each of three experiments and determining the time to replication, or detachment, and the distance moved for each cell. Images of bacterial cells within a biofilm were acquired using a confocal scanning microscope. Data from the images was extracted using image analysis software.

Organism

A parent strain and a construct of Pseudomonas aeruginosa PA01 were used in this study. Pseudomonas aeruginosa is a motile, aerobic, Gram negative rod. The parent strain contained a plasmid conveying a resistance to 150 mg/l of carbenicillin. The construct strain contained the same plasmid, but production of a green fluorescent protein (GFP) was also encoded. The GFP was constitutively
expressed, thus enabling each parent and daughter cell to be “self labeling”. The excitation wavelength of the GFP was 488 nm and the emission maxima was at 512 nm. These organisms were obtained from Dr. Mike Franklin, at Montana State University.

Cultures of the parent strain of the organism (PA01-GFP-) were kept separate from the GFP construct strain (PA01-GFP+) until the inoculation of the parallel plate flow cell reactor. A much greater ratio of parent cells to GFP construct cells was used in the flow cell reactor. The resulting biofilm was dilute mix of labeled, or visible, cells which made it possible to identify and track individual cells and their progeny within a biofilm matrix. The ratio was approximately 100:1 GFP- to GFP+.

Stock Culture

Stock cultures of both the parent strain and construct (PA01-GFP- and PA01-GFP+) were prepared by streaking for isolated colonies on R2A agar (Difco) which contained 150 mg/l of carbenicillin (Sigma). Isolated colonies were then transferred to fresh R2A/carbenicillin agar and incubated until a confluent lawn was present. The culture was harvested, placed in a 2% peptone–20% glycerol solution and stored in 2.0-ml vials at −70 C. For each experiment, approximately 1.0 ml of frozen stock culture was used as an initial inoculum for each organism.
**Equipment**

The equipment used in this study included media and waste containers, assorted tubing, two chemostat reactors, a parallel plate flow cell reactor, an inoculation vessel, and a bubble trap. These components are illustrated in Figures 1-4 and described in following paragraphs.

The nutrient media for each experiment was prepared and sterilized separately from the remainder of the items as explained in the following section. The various vessels and tubing were cleaned by washing with soap and water and sterilized by autoclaving dry for 20 minutes at 121 C and 20 psi. The tubing upstream from each of the reactors was replaced for each experiment.

**Media**

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<th>Constituent</th>
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<tr>
<td>KH₂HPO₄</td>
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</tr>
<tr>
<td>(NH₄)₂SO₄</td>
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<tr>
<td>MgSO₄ * 7H₂O</td>
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<td>Glucose</td>
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</table>

The same nutrient media was used in the chemostat, flow cell, and batch reactor. The constituents are listed above in Table 3.1. The potassium salts and
ammonium sulfate (Fisher) were added to glass carboys, an appropriate amount of reverse osmosis water was added and the containers were sealed and autoclaved for 15 minutes per liter. The solution was cooled to room temperature before the remaining constituents were added. Proper amounts of glucose (Fisher) and magnesium sulfate (Aldrich) were dissolved in approximately 25 ml of reverse osmosis water and added to solution via syringe and a 0.2-micron syringe filter.

Chemostat Operation

Two chemostat reactors were used to grow inocula for the experiments. The chemostats were each operated at room temperature with a volume of 500 ml and a 5 hour residence time. The cultures in the reactors were well mixed by a magnetic stir bar and plate and aerated by the laboratory pressurized air system and bacterial air vents (Gelman Sciences). A schematic diagram of the system is shown in Figure 3.1. After sterilizing all reactor components the system was assembled. Each reactor was filled with sterile nutrient media, inoculated with 1.0 ml of the appropriate frozen stock culture (PA01-GFP- or PA01-GFP+) and operated in batch mode for 24 hours. The pumps were then turned on to supply sterile media to the reactors and the effluent was pumped to a waste container. The bacteria were grown in a chemostat environment for 48 hours, or about 10 residence times.
Figure 3.1. Schematic of two chemostat reactor system.

Flow Cell Cleaning

Cells growing in an attached or sessile state were observed on the "wet side" of the coverglass in a parallel plate flow cell reactor (Figure 3.2). Cleaning of the flow cell prior to each experiment was carried out as follows. The polycarbonate base was submersed in 95% ethanol for 30 minutes and then subjected to UV light for 30 minutes. Each experiment utilized a new glass coverslip that was washed twice with antibacterial soap and rinsed twice with 95% ethanol. The coverslip was then autoclaved for 20 minutes and dried at 115°C for 24 hours. Other assorted materials (tubing, coverplate, gasket, screw and nuts) were autoclaved for 20
minutes. After all parts of flow cell were sterilized or cleaned, the flow cell was assembled inside a biological hood.

Figure 3.2. Parallel plate flow cell reactor.

**Flow Cell Operation**

The entire flow cell reactor system (see Figure 3.3) was set up on a laboratory cart to facilitate transportation to and from the microscope lab where the experiments were completed.
Prior to inoculation, the flow cell and all upstream tubing were filled with sterile media to purge air from the system. Using a sterile syringe, 20 ml of parent strain inoculum (PA01-GFP-) was withdrawn from a 48-hour chemostat culture and placed into the inoculation vessel along with 0.5 ml of PA01-GFP+ inoculum. The inoculum was rapidly mixed using a magnetic stir bar and plate to break up cell clumps.

The entire volume of the stirred inoculum was pumped through the flow cell in a series of three pulses. Approximately one third of the inoculum (7.0 ml) was drawn through the flow cell and flow was stopped for 5 minutes. The second and final 7.0 ml were pumped in a similar manner, with 5-minute stagnation periods before

Figure 3.3. Schematic of flow cell reactor system.
resuming flow. This method of introducing cells into the reactor was used to ensure that high initial cell densities on the coverglass were reached.

After the entire volume of inoculum had passed through the reactor and the final 5 minute no-flow period expired, flow of sterile, cell free media commenced. The flow rate was set at 2.0 ml/minute which is laminar flow (Re~5.5) with a flow channel of 12 mm x 1.5 mm in cross section and 37 mm in length.

Figure 3.4. Bubble trap.

In order to prevent bubbles from entering the flow cell, the media container was elevated so that the upper surface of the media was approximately 0.5 meter higher than the flow cell with the media effluent port at the bottom of the container.
The effluent line from the flow cell was at an elevation approximately level with the reactor. By aligning the system in this manner, the elevation of the media reservoir served to slightly pressurize the reactor, preventing the formation of bubbles in the flow cell. A bubble trap (Figure 3.4) was also used downstream of the media reservoir to remove any large bubbles that may have entered the line during the initial start up or media container exchange. The pump is located downstream from the flow cell to minimize the amount of upstream tubing subject to initial cell inoculation. In this arrangement, the pump serves to hold flow back at the proper rate; without the pump in place, the media container would drain completely by gravity in a matter of minutes.

Data Acquisition

After inoculation of the flow cell reactor, the adhered cells were subjected to uninterrupted, cell free nutrient flow for a period of 24 hours. This amount of time was sufficient to allow a biofilm of 3 to 10 microns in depth to form. At the end of this incubation period, a particular field of view was chosen for observation. The flow cell reactor was left in place on the microscope stage and not moved for the duration of the experiment. The cells in this field of view were then observed every 15 minutes for a period.

At each interval, the desired field of view was first checked for focus by eye with transmitted white light. Subsequently, the image was captured using the laser
light source. This method greatly reduced the amount of time the sample was subjected to bleaching and heating from exposure to the laser beam. Nutrient flow was halted temporarily for each image to prevent pulsing of the coverglass.

Each of the cells in the initial field of view, or image, was identified and assigned an object number using image analysis software, as is described in the following section. The original cells and their progeny were tracked over the course of the experiment using the sets of images and the object numbers. The time to division or detachment, the distance moved for each cell, and the growth of the population was determined from the sequence of images.

**Image Capture**

TIF format images of PA01-GFP+ cells growing in a biofilm were produced using a Leica TCS-NT Confocal Microscope System. The fluorescence emitted from the GFP identified the location individual cells. Excitation of the protein was achieved with the 488-nm laser light source. The fluorescent emission, maxima at 512 nm, was registered after passing through a BF filter block which only allowed the passage of light between 500 and 550 nm. PA01-GFP- organisms were also present in the reactor, but were not visible due to the absence of GFP.
Images were acquired at ~0.5 micron elevation intervals starting at, and proceeding away from, the "wet" surface of the coverglass (Figure 3.5). These "optical slices" were compiled to produce a three dimensional picture of cells within the biofilm matrix using software provided by Leica. A composite image, or "top down view", of images from each elevation at one time point was also stored in TIF format (Figure 3.6.)
Figure 3.6. Example 2D and 3D images. Left image is a rotated, three dimensional compilation and right image is a composite, top down, view of the same three dimensional image composed of 18 separate 2D optical slices. Dimensions of box in left image: 100 x 100 x 18.5 μm. Dimensions of right image: 100 x 100 μm.

**Image Analysis**

Extracting the data, or the x,y,z coordinates of each cell in the images was undertaken in two steps. The first step required that individual cells be uniquely identified and the two dimensional x,y coordinates of each cell be determined. The second step produced the third, or z coordinate of each cell.

To determine x,y coordinates of each cell, the composite image files (shown at right in Figure 6) were imported into an image analysis software package, Image-Pro Plus, Version 3.00.00 (Media Cybernetics). The software was calibrated based on the actual dimensions (100 μm x 100 μm for images captured
using 100X, 1.4 N.A., oil immersion objective) of each image. The auto-count feature was set to identify all objects (cells) within a specified area range, usually 0.5 to 2.5 μm². The software automatically assigned each cell an object number, and x and y coordinates, in μm, with the origin being the upper left corner of the image. Occasionally, several cells were overlapping and had to be manually tagged. In this event, the software still took record of the x, y coordinates of the object, however it was the researcher’s task to identify and tag the locations of each of the overlapping cells.

To determine the z coordinate of each cell, all the images in a particular stack were examined. An elevation of zero was assigned to the image nearest the location of the substratum. Each cell was in focus in a minimum of 2 adjacent images and it was therefore necessary to determine which image best reflected the location of the centroid of each cell. The absolute elevation of each cell was based on the image number in the stack and the distance between images.
Data Analysis and Results

Cell Movement

The final result of the image analysis process described previously was a list of cells for each particular image containing their assigned object number and x, y and z coordinates. An example of this is shown in Table 3.2; the microscope stage vertical step size and coordinate dimensions are in microns. The next step was to assign each cell a unique identification (i.e. A, B, C...) and then determine which cell/object number (i.e. 1, 2, 3...) from each image corresponded to that ID. The result was a chart similar to that of Table 3.3.

Table 3.2. Object Numbers and Coordinates

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Once the data were arranged in such fashion, each table was imported from Microsoft Excel 97 into Microsoft Access 97. Due to the microscope stage moving laterally by small amounts during the course of each experiment, mathematical corrections had to be made based upon the magnitude and direction of the image shifts. These correction distances were determined visually and a list, one correction for each image, was created and applied to all cell coordinates. The data was then sorted first by cell ID and second by time to produce a format such
as Table 3.4 which included the corresponding image number and time of observation.

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From the arrangement of data as presented above, the Euclidean distance each cell moved between each observation periods was determined. Cells which emigrated during the experiment were grouped separately from those that did not. The magnitude of all the distances moved were then sorted from least to greatest, and a cumulative distribution was plotted for emigrating and remaining cells based on the log 10 of the distance. The statistical analyses were completed by Dr. Martin Hamilton and the distributions are shown in Figures 3.7 and 3.8. The remaining cell movement distribution was fit by a student's t distribution while the distribution of emigrating cell movements was approximated best with a normal distribution. A list of descriptive statistics for each is included in Table 3.5 and a plot of both is presented in Figure 3.9 for comparison.

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<th>Variable</th>
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<th>Median</th>
<th>St. Dev</th>
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<td>-1.6091</td>
<td>.4595</td>
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</table>
Figure 3.7. Distribution of movements of remaining cells (dashed line represents \( t(5) \) distribution; solid line represents actual data)

Figure 3.8. Distribution of movements of emigrating cells (dashed line represents normal distribution; solid line represents actual data)
It is instructive to present these results in an additional format. When examining the differences between the two distributions, it is informative to consider the following descriptors of each distribution. These are based on movement distances for 15-minute intervals:

1. The median of each distribution:
   - 0.26 microns for remaining cells
   - 0.38 microns for emigrating cells

2. 0.51 microns is the 80th percentile of the remaining distribution. 0.51 microns is the 61st percentile of the emigrating distribution. 0.92 microns is the 80th percentile of the emigrating distribution.

3. 0.76 microns is the 90th percentile of the remaining distribution. 0.76 microns is the 75th percentile of the emigrating distribution. 1.46 microns is the 90th percentile of the emigrating distribution.

![Distribution of Cell Movements](image)

Figure 3.9. Fitted Cumulative Distributions of Cell Movements – Solid line for remaining cells (based on \( t(5) \) distribution for log 10 (distance)); Dashed line for emigrating cells (based on a normal distribution for log 10 (distance)).
Growth and Emigration

A similar method as described above was used to determine growth and emigration results. The analysis was somewhat simpler in that only the times to either division or detachment were tracked. Again, the times were sorted according to magnitude and arranged in a cumulative distribution. However, a large portion of the data is considered censored (either beginning before the period of observation or continuing past). Therefore, a non-parametric distribution analysis using the Kaplan-Meier method was performed with Minitab 12.1 statistical software. This type of data analysis is common in the pharmaceutical industry where the survival of patients is the variable. In these analyses, the window of observation can not encompass all participants so a non-parametric, right-censored distribution (Kaplan-Meier) analysis is used. In these results, the median of the distribution is the most informative parameter. The median time for cells to divide was 6.6 hours and the median time for cells to emigrate was 2.0 hours. Graphs of each distribution are shown below in Figures 3.10 and 3.11.
Distribution of Emigration Times

Figure 3.10. Cumulative distribution of emigration times. Dashed line represents 95% confidence interval.

Distribution of Division Times

Figure 3.11. Cumulative distribution of division times. Dashed line represents 95% confidence interval.
A third parameter measured in these experiments is the probability of a cell to emigrate. A tree diagram depicting lineage and fate of all observed cells is included as Appendix A. There were two ways to analyze this data. The first is to examine only division events and obtain the percentage of divisions that resulted in at least one cell emigrating. This method produced a 26% rate of emigration. However, this is in all likelihood a low estimate because all cells that were observed during the last time period were considered to have no chance of emigrating. Based on the behavior exhibited by others, many of these cells surely emigrated at some point after the experiment ended.

The other way of obtaining rate of emigration is to compare the number of cells emigrating with the total number of cells observed. This takes into account all the initially observed cells that detached before division occurred. This method yielded a 44% chance of emigration.

**Discussion**

The purpose of this research was to describe the behavior of individual cells within a biofilm matrix. The parameters chosen to accomplish this were: time to division, time to emigrate, movement distributions of emigrating and dividing cells, and probability of emigration following a division event. The quantification of these activities can be used in determining input parameters for modeling of biofilm behavior.
The median observed time to division for secondary biofilm cells was 396.5 minutes or 6.6 hours. This corresponds to a specific growth rate of 0.105 hr\(^{-1}\) (Madigan et al., 1997). In a similar, unpublished work, Arturo determined the median time to division of the same organism in a biofilm state to be 260 min or 4.33 hours, corresponding to a specific growth rate of 0.16 hr\(^{-1}\) (Arturo, 1998). This seems contradictory since the very same experimental set up was used for each experiment; however, the previous research examined the growth of primary cells as they emerged from their lag stage. Therefore, these growth rates were not measured from the same stage of biofilm development, and this might explain the difference. Also, Arturo sought out more active cells to observe and this might lead to a higher growth rate being measured. The median time to detachment measured by the current research was 121 minutes or 2.0 hours. The previous work measured this to be 90 min or 1.5 hours (Arturo, 1998). Again, the same possible explanations for this difference can be offered.

The cumulative distributions compiled for both the emigrating and remaining cells show that these cells, although enmeshed in a 3-8 micron thick biofilm matrix are still quite active in terms of movement. The distributions show that the cells which emigrate are significantly more dynamic than the cells which do not. It is suspected that the difference is even more striking than what these results indicate. As explained earlier, all cells which remained in view through the end of the observation period were analyzed as “remain” and not “emigrant” cells. Undoubtedly, some of these cells emigrated at some point after the experiment
ended based on the behavior evidenced by their predecessors. However, their movement was grouped with the remain cells for lack of an alternative.

A normal distribution fit the emigration data quite well. A t(5) distribution fit the “remain” data better than a normal distribution. This is a very interesting result. When two different normally distributed sets of data are compiled into one, the resulting distribution is likely to be a t distribution (Hamilton, 1999). Therefore, it is supposed that the “remain” distribution is actually a mix of two normally distributed data sets. This theory fits well with the idea that some of the cells are indeed emigrant cells, but sure evidence of this was unattainable due to the period of observation coming to an end. From these results, it is concluded that cells destined to emigrate display significantly more motion than those destined to remain in place.

Arturo also examined the movement of biofilm cells. His findings indicate a median distance moved in 15 minutes is 1.15 microns and the 90\textsuperscript{th} percentile is 3.82 microns (Arturo, 1998). For “remain” cells observed in the current research, the median movement for 15 minutes is 0.26 microns and the 90\textsuperscript{th} percentile is 0.76 microns. For cells which will emigrate, the median is 0.38 microns and the 90\textsuperscript{th} percentile is 1.46 microns. These results perfectly illustrate what has been observed during the course of performing the experiments: Once primary cells begin to replicate, they spread out upon the surface. Since there are not many other cells (i.e. biofilm is less than a monolayer at this point) to hinder their movement, the primary cells exhibit a significant amount of locomotion. As the
biofilm surpasses the monolayer stage, the cells are still quite active, but are not as free to move around. These distances moved over 15 minute intervals, show that cells in a several micron thick biofilm do not move as much as those on a sparsely covered substratum.

Similar movement of cells has been observed and quantified by others (Power and Marshall, 1988). *Pseudomonas* JD8 was studied in biofilms that were less than a monolayer in thickness. Cells moved distances of up to 150 microns before completion of a division cycle. The average movement distance for a 15-minute period measured was 2.25 microns. The nutrient and substrata conditions were different than in the work described in this manuscript, however, it is evident that the movement being is described and quantified is very similar (Power and Marshall, 1988).

In a study examining the replication patterns of various biofilm organisms from a natural stream population, the same behavior is seen (Lawrence and Caldwell, 1987a). The term given for this type of movement is “spreading”. This spreading behavior is displayed by *Pseudomonas aeruginosa* PA01 both when enmeshed in a biofilm matrix and on a sparsely colonized surface. During the time frame of the experiments described herein, there was no significant microcolony development with respect to daughter cells being located in close proximity to parent cell location. The spreading behavior persists into a maturing biofilm, although hindered by the biofilm matrix. This behavior also contributes to a rather flat, uniform biofilm structure during the early stages of accumulation.
Two methods for quantifying the tendency of a cell to emigrate have been described in this report and lead to estimates of 26% and 44%; neither method is satisfactory. The higher rate is more representative of the activity witnessed in these experiments. A more detailed analysis and a larger data set is needed to further refine this parameter. However, these results do suggest that emigration with \textit{P. aeruginosa} PA01 is a significant event in biofilm development: Clearly $1/3$ of new cells do not stay located near the parent cell. This result lends support to the finding by O'Toole and Kolter (1998a) that microcolonies develop as result of "recruitment" and not lineage of cellular division.

This study made an effort to quantify the rates of movement of bacterial cells, the time to division or emigration of a cell and the probability of a cell to emigrate. These results can be useful inputs for rules governing cell behavior in biofilm models.
CHAPTER 4

CONCLUSION

This research project was an effort to evaluate the importance of the initial events in biofilm formation. This purpose was accomplished by monitoring the behavior of both the cells which transition from a planktonic state to a biofilm state and the progeny which arise from this original population. The original population of biofilm cells, primary cells, actually undergo a change in phenotype as they become sessile organisms. An apparent lag time in replication is associated with the attachment event.

Once primary cells emerge from this lag stage, they proceed to populate their chosen substratum and form a biofilm. During this period of biofilm growth, it is evident that *Pseudomonas aeruginosa* PA01 cells retain their ability to move around within the biofilm. This constant movement of cells away from their “birth” location serves to disperse the cells to colonize all reaches of a substratum.

This study showed that biofilm development is a very dynamic process with cells varying in growth rate depending upon their point of origin. Cells also vary in the amount of locomotion they exhibit depending upon whether the cell is destined to emigrate or remain in the general area. The most surprising result from this
project was that there were no forming microcolonies observed. All cells as they
replicated, moved away from their original location. Therefore, the cells which
appear to be closely associated with one another in these biofilms were not
necessarily of the same lineage. GFP+ cells which were clumped together were
more likely a result of either colonization or recolonization events, rather than
subsequent generations.

Another useful result of this project was the quantification of cell behaviors such
as time to division and emigration, movement rates, and probability of detachment.
This information can be directly used to refine modeling parameters or to compare
with modeling results.

Finally, the methods used in this research will be invaluable when used to
investigate other biofilm questions. For instance, the same techniques can be
used to assess movement rates of non-motile bacteria in biofilms. This will
elucidate how much movement is a result of a “popcorn” effect and not from
motility. Also, reattachment of GFP cells can be visualized on a non-GFP biofilm.
This type of work will allow researchers to investigate how organisms become
entrained into an established biofilm. Another very interesting question to
investigate is whether or not detached biofilm phenotype cells endure a similar lag
phase upon reattachment. This type of research could possibly vary the length of
times that “biofilm” cells were in a planktonic environment before a surface
associated lag time occurs.
REFERENCES CITED


Modeling: Application for Growth in Gel Beads. Biotechnology and Bioengineering 57, 718-731.


Pulcini, E. The Effects of Initial Adhesion Events on the Physiology of Pseudomonas aeruginosa. (UnPub) Montana State University-Bozeman.


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- Surface 3: Step 0.486

**Miscellaneous:**
- 8 of 8 objects in range
- Intensity: 80...255
- Area: .01 - 7.5
- Added by manually splitting objects

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- **Intensity**: 80...255
- **Area**: 0.01 - 7.5
- **10 of 10 objects in range**
- **Surface 1**
- **Step**: 0.486

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**Nov21-Cell Tracking (AOI#1)**

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11 of 12 objects in range added by manually splitting objects

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| 3 | 0.75 | 51.63 | 49.52 | 0.486 | 4.5 | 3 | 0.75 | 51.43 | 49.69 | 0.486 | 4.5 |
| 4 | 0.57 | 54.48 | 50.82 | 0.729 | 5 | 5 | 0.66 | 54.18 | 50.45 | 0.972 | 5.5 |
| 6 | 0.82 | 52.99 | 53.39 | 0.486 | 4.5 | 7 | 0.48 | 50.56 | 51.70 | 0.729 | 5 |
| 7 | 0.67 | 51.93 | 54.04 | 0.3645 | 4.25 | 8 | 0.65 | 49.37 | 51.94 | 0.486 | 4.5 |
| 8 | 0.83 | 53.46 | 54.95 | 0.3645 | 4.25 | 9 | 0.85 | 52.84 | 53.31 | 0.486 | 4.5 |
| 9 | 0.78 | 56.99 | 54.94 | 1.458 | 6.5 | 10 | 0.69 | 51.71 | 53.93 | 0.3645 | 4.25 |
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| T3 | 53.18 | 51.42 | 1.458 | 6.5 | T2 | 53.08 | 51.32 | 1.458 | 6.5 |
| T4 | 53.76 | 51.81 | 0.243 | 4 | T3 | 53.47 | 51.91 | 0.243 | 4 |
| T5 | 52.59 | 52.49 | 0.243 | 4 | T4 | 52.30 | 52.49 | 0.243 | 4 |
| T6 | 52.10 | 52.39 | 2.187 | 8 | T5 | 51.91 | 52.30 | 1.944 | 7.5 |

Nov21-Cell Tracking(AOI#2)
Object #s
### Nov21-Cell Tracking (AOI#2)

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- Surface: 1.25
- Step: 0.486

**Area:** 0.5 - 2.5

8 of 14 objects in range
6 added by manually splitting objects

**Intensity:** 80...255

7 of 10 objects in range
6 added by manually splitting objects

**Surface:** 0.5

**Step:** 0.486
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Nov21-Cell Tracking(AOI#2)

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### Nov21-Cell Tracking(AOI#2)

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### Intensity Map

- **Intensity**: 80...255
- **Area**: 0.1 - 7.5
- **Surface**: 8 of 12 objects added by manually splitting objects
- **Step**: 0.486

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**Additional Information**

- Number of objects in range: 8 of 12
- Number of objects added by manually splitting: 6
- Surface step 0.486

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- 12 of 15 objects in range
- 7 added by manually splitting objects

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- 10 of 12 objects in range
- 10 added by manually splitting objects

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1 of 6 objects in range

- added by manually splitting objects

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- added by manually splitting objects

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- **Intensity:** 80...255
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Nov21-Cell Tracking(AOI#3)  
Object #s
### Nov21-Cell Tracking(AOI#3)

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- **4 of 5 objects in range** added by manually splitting objects
- **5 of 6 objects in range** added by manually splitting objects

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Nov21-Cell Tracking(AOI#3)
Object #s
### Nov21-Cell Tracking(AOI#3)

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**Graph #s**

**Intensity:** 0.01 - 2.5

12 of 13 objects in range

7 of 10 objects in range

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**Surface**

- 3.5
- 2

**Step**

- 0.486
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Nov21-Cell Tracking(AOI#3)
Object #'s
### Nov21-Cell Tracking(AOI#3)

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#### Intensity: 80...255

#### Area: 0.01 - 2.5

5 of 7 objects in range added by manually splitting objects

8 of 8 objects in range added by manually splitting objects
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- **Objects in range**: 8 of 8
- **Surface**: 0.5
- **Step**: 0.486

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**Nov21-Cell Tracking(AOI#3)**

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### Nov21-Cell Tracking(AOI#3)

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**Area:** .01 - 7.5

2 of 4 objects in range

3 added by manually splitting objects
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11 of 12 objects in range
added by manually splitting objects

Substatum: 1
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Oct21-Cell Tracking
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19 of 20 objects in range
22 of 23 objects in range

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Oct21-Cell Tracking
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### Oct21-Cell Tracking

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- **Center-X, Center-Y, Center-Z**: These columns represent the center coordinates of each object within the image. The coordinates are given in integer values, indicating the pixel position of the object's center.

**Range**: The range data provided indicates the encompassing area (e.g., `Area: 0.01 - 7.5`) and pixel values (`Range: 90...255`). This suggests the document is analyzing cell tracking results from a biological or medical experiment, focusing on the spatial distribution and characteristics of objects within the specified area and range.
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