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ANALYSIS AND MODELLING OF THE EFFECTS OF MICELLAR SOLUBILIZATION ON THE DEGRADATION RATES OF N-ALKANES.

BY

SCOTT JOSEPH BURY

A THESIS SUBMITTED
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE
DOCTOR OF PHILOSOPHY

APPROVED, THESIS COMMITTEE

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May, 1996
ABSTRACT

Analysis and Modelling of the Effects of Micellar Solubilization on the Degradation Rates of n-alkanes.

by

Scott Joseph Bury

The transport, uptake and degradation of hydrocarbons by microorganisms has been a subject of interest for many years. The inherent low solubility of most hydrocarbons has been thought to be one of the limiting factors in the overall rate of degradation of hydrocarbons. The ability of surfactants to form micelles and increase the solubility of hydrocarbons to many times their normal solubility may overcome this limitation. Designed experiments with well defined surfactant systems of known phase behavior were done to investigate the effects of micellar solubilization by nonionic, ionic, and mixed nonionic and ionic surfactants on the degradation of n-alkanes by pure cultures of three strains of Gram-negative bacteria. It was found that solubilization by nonionic surfactants greatly increased the growth rates and accompanying oxidation of alkanes for two of the three bacterial strains. It also appeared, from initial experiments, that the inhibitory effect of the ionic micelles could be mediated by the addition of nonionic surfactants to form mixed micelles. A mathematical model that treated the solubilized alkanes as soluble substrates via a Monod expression with competitive enzyme interaction successfully described the experimental data. Nonlinear parameter estimation using a maximum likelihood method indicated that $\mu_{\text{max}}$ was constant for a particular bacterial strain, and independent of surfactant concentration and alkane. The variation in observed growth rates was reflected in the variation of the $K_s$ parameter which was found to be a function of surfactant type and alkane. The variation appears to represent differences in the rates of transport of the alkanes through the cell membranes.
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The author would like to thank C. A. M. for his fine direction (and patience) as thesis advisor.

This dissertation is dedicated to K.L.S.B.
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1.0 Introduction

1.1 Microorganisms and Oil

The ability of microorganisms to degrade straight-chain alkanes has long attracted interest in the petroleum industry and of researchers working in the area of production of single-cell proteins. More recently there has been a great deal of research in exploring the role of microorganisms in the clean-up of contaminated soils and aquifers. Utilization of alkanes with limited aqueous solubility presents a challenging transport problem for microbes. The patterns of growth on hydrocarbons are substantially different from those on hydrophilic substrates and are a reflection of the microbial processes of uptake and transport to intracellular sites for degradation (1).

The actual mechanism for the uptake of hydrocarbons has been a source of controversy, but it seems reasonable that the natural mechanisms are directed at providing contact between the hydrocarbon and the substrate. This may be in the form of direct contact with hydrocarbon drops (sub-micron or larger), facilitated by lipophilic cell membrane components or it may be due to metabolites produced by the microbes which appear to complex with the hydrocarbons (2, 3, 4, 5).

The recent review, by Rouse et. al.,(6) points out that the efforts to enhance bioremediation have renewed interest in the microbial transport and oxidation of organic compounds especially in the presence of surfactants. The unique ability of surfactants to act as emulsifiers or solubilizers has appeared to enhance the availability of insoluble materials to some microbes in some cases, but to other microbes and in other cases it has appeared to be inhibitory. From the review, it is clear that the surfactants can affect the biodegradation process in different ways that are dependent on the hydrocarbon, the microorganisms and the surfactant.

The complex nature of aquifer contamination results in multiple phase locations of organic contaminants. This complex system is also reflected in the complex nature of the remediation process. The organic may become adsorbed to soil particles, trapped as a
liquid in the pore space, dissolved in the aqueous phase or occupy the vadose zone as a vapor phase. The first two also provide long term, slow release source of dissolved contaminants (7, 8). The physicochemical and hydrodynamic forces prevent easy removal or remediation of the tightly adsorbed and trapped materials. It is often not possible to develop the required water velocities to mobilize the trapped material using traditional pumping techniques (9). As has been done in enhanced oil recovery, surfactants may be used to decrease the capillary forces allowing the trapped drops to be mobilized. The ability of particular surfactant solutions to solubilize organic materials can also be exploited by solubilizing liquid phase material or tightly adsorbed material such as phenanthrene (8, 10).

The ability to desorb material into micelles greatly reduces retardation. Johnson and Pankrow concluded that enhancement of water solubility of the [chlorinated] solvent (e.g. with a micelle forming surfactant) will accelerate the removal of pools of chlorinated solvents (11). The technology of aquifer flushing or chemically enhanced pump-and-treat is still developing, (12, 13) but an important consideration is the impact of the surfactant on the naturally occurring biodegradation that is often found at contaminated sites.

There is much conflicting evidence as to the effects of surfactants on the uptake and subsequent oxidation of hydrocarbons. Natural and synthetic surfactants appear to have different effects and modes of action. To confound this problem, the chemistry and phase behavior of the systems investigated are not always clear. Early work (14) confused emulsification with micellar solubilization by synthetic surfactants. Other investigations have not adequately accounted for bacteria colonizing the solid organic phase (15) or interacting with the bulk oil (3). We proposed that by removing these confounding effects and using a well characterized surfactant system, we would shed light on the role of solubilization in the degradation of hydrocarbons.
1.2 Thesis Statement

The main hypothesis of this thesis was that solubilizing normal alkanes in small synthetic surfactant micelles increases the oxidation rate of the alkanes by bacteria. Crucial to removing the ambiguity found in previous studies of surfactants and bacteria was the design of a clean and well-defined experimental system. It was proposed to study the oxidation of alkanes, \( C_3-C_{16} \), that were completely solubilized in a micellar system. This required addressing the following issues; selection of suitable surfactants, phase behavior studies and system characterization, toxicity testing, biodegradation studies, mathematical modelling and testing of the model.
2.0 **Surfactant Chemistry Background**

2.1 **Introduction**

The many unusual and interesting properties of "SURFaced" "ACTive" agents make them useful in a wide range of applications. Where there is a surface or more generally where there is an interface there is an opportunity to apply a surfactant. The creation of interfaces, the destruction of interfaces and the modification of interfaces all can be accomplished with surfactants. There are many reviews covering the numerous applications of surfactants to specific industries and processes. Selection of the surfactants can also be made with the aid of vendor literature. The rest of this chapter will cover those properties of surfactants that are important for understanding and interpreting this work.

2.2 **Types of Surfactants**

2.2.1 **The classes**

Surfactants are divided into three broad classifications depending on their charge, negative, neutral or positive. Anionic surfactants have a negatively charged hydrophilic group. Cationic surfactants have a positive charged hydrophilic group. Nonionic surfactants carry no charge.

2.2.2 **Cationic Surfactants**

The positive charge of cationic surfactants creates some unusual behavior which typically makes their use different than the other two classes. One of the most notable is bactericidal action. This makes them particularly useful in hospital cleaning agents and home disinfection products such as Lysol™. This bacterial action precludes their use enhanced biodegradation experiments. The use of cationics in hair conditioners, fabric softeners etc., to counter the normal negative charges of many surfaces does make the biodegradability and bactericidal issues important for municipal water treatment systems.
2.2.3 Anionic Surfactants

Commonly found in detergent formulations and personal care products anionic surfactants have also been indicated as having bactericidal action. The formation of micelles of anionic surfactants is hindered by the electrical repulsion of the head groups. The addition of salts can make the formation of micelles easier.

2.2.4 Nonionic Surfactants

Nonionic surfactants come in wide variety of types. The characteristic hydrophilic head group is the ethoxyl group. Again these surfactants are widely used in different products.

2.2.5 Characteristics

A primary characteristic of surfactants is their ability to form aggregates called micelles in aqueous solutions. The formation of these micelles occurs when the critical micelle concentration (CMC) is exceeded. Micelles are an arrangement of surfactant molecules formed by the hydrophobic tail groups coming together to create a thermodynamically favorable hydrocarbon (HC) pseudophase† with a hydrophilic exterior. Below the CMC, surfactants in solution exist solely as individual molecules or monomers. Above the CMC a nearly constant monomer concentration is maintained in equilibrium with the micelles (16). This thermodynamically stable environment has the further characteristic of being able to solubilize insoluble compounds, such as alkanes. Discussion of the thermodynamics of this system can be found in a number of reviews (17, 18).

†. The term pseudophase comes from the approximation that the CMC is a point value rather than a narrow band. This approximation then treats all of the micelle cores as a separate phase into which organics can partition. This approximation is satisfactory for many purposes, but it is not rigorous from a thermodynamic standpoint. It is important to understand that micellar solutions are thermodynamically stable, single phases and the solubilization of the organics does bring normally insoluble material into a solubilized state.
A general definition of solubilization is "the preparation of a thermodynamically stable isotropic solution of a substance normally insoluble or very slightly soluble in a given solvent by the introduction of an additional amphiphilic compound or component" (19). There are three proposed forms of solubilization: 1) non-polar molecules are dissolved in the core, 2) polar molecules, like long-chain alcohols, are incorporated into the micelle with the hydrocarbon tails partitioned in the core and the hydrophilic groups in the micelle periphery, 3) other molecules that exhibit low solubility in either aqueous or hydrocarbon media may adsorb to the surface of the micelle. When systems can solubilize very large amounts of organic, the micelles are often said to be swollen and are larger than what are found in micellar solutions. These systems are referred to as "microemulsions". The regions were microemulsions exist are typically bounded by small changes in composition and temperature (18).

Micelles are dynamic and respond to the addition of a solubilize and to increases in temperature. A micelle may change shape as increasing amounts of different solubulizates are incorporated. Increasing amounts of lipophilic alcohols, for instance, force the micelle to become more and more asymmetric transforming from spherical to cylindrical, eventually becoming lamellar in shape (20). In contrast, adding sufficient hydrocarbon can transform cylindrical micelles to spherical microemulsion drops. The following diagram (Figure 2.1) shows how different environmental factors influence micelle structure. For the majority of systems used in this work, the micelles were in the range of normal spherical to normal cylindrical. Heating aqueous solutions of oxyethylated nonionics to the cloud point temperature causes the system to become cloudy, following which there is a phase separation. The phases consist of an almost micelle-free dilute solution at the surfactant CMC and a surfactant-rich micellar phase, which only appears above the cloud point. The phase separation is reversible, that is, cooling the mixture to below the cloud point temperature restores the the single-phase micellar solution (20).
Another characteristic common to surfactants is their ability, under certain conditions, to enhance the formation and stability of emulsions (suspensions of fine droplets of one liquid in another) between two immiscible liquids. In some cases, a surfactant can cause an extreme drop in interfacial tension, which may result in spontaneous emulsification. Although surfactants often act as emulsifiers, not all emulsifiers are surfactants. An important difference between micellar solutions and emulsion is that emulsions are not thermodynamically stable. However, some emulsions do not separate over very long times as a result of energy barriers hindering coalescence of drops, e.g., barriers due to electrical repulsion when charged emulsifiers are used.

**Figure 2.1** Effect of environmental factors on micellar structure. The interconversion of normal and reverse lamellar micelles only involves small changes in distances between hydrophilic and hydrophobic groups.

3.0 Biological Background

This chapter reviews some basic physiology of bacteria with particular emphasis on membrane structure and alkane metabolism.

3.1 Outer Membrane Structure & Transport

3.1.1 Porins et al

Walls define a building. The length, breadth and depth of the walls all serve to separate what is inside from what is outside the building. But without the interior of the building, the walls are only a shell and the building is less than before. In the same way, biological membranes define both eukaryotic and prokaryotic cells. Membranes protect the contents of the cells from the environment, yet act as doorways and windows through which cells gain or dispose of nutrients and metabolic wastes as needed. That is an understatement; cell membranes function as the origin of many, if not most of the vital functions of living cells (21). The maintenance of concentration gradients, the generation of energy in the form of ATP and the assembly of proteins are some membrane functions. In eukaryotic cells, membranes also form the many intracellular organelles, which permits a greater diversity of functions than is found in prokaryotes (21). Varied molecules such as proteins and phospholipids endow membranes with these remarkable features. Constituents are complex molecules with associated complex chemical behavior. The organization and assembly of these materials in membranes are under thermodynamic control. A first approximation represents thermodynamic control as a search by each structural molecule for the state of lowest chemical potential (22).

The hydrophobic effect, described more accurately as an entropic effect, might seem out of place in the dynamic world of the living cell. However, one may consider that the cellular processes take place in the framework that is essentially at equilibrium. The equilibrium is, of course, subject to the usual constraints, in the form of physical and kinetic barriers (22). The influence of the hydrophobic effect goes beyond driving the organization of membrane. It also affects the membrane functions and plays a role in
metabolism.

There is a multitude of amphiphiles other than phospholipids and proteins. The hydrophobic effect also controls the formation of traditional detergent micelles and bilayers. The dual nature of detergents makes them ideally suited to the study of biological membranes and their components. It is a field of active research. Each year, researchers publish hundreds of papers on membrane and detergent interactions.

It is the goal of this section is to describe a small area of this broad field. The section will give first a description of the hydrophobic effect, followed by interactions of detergents with membranes and finally, some thoughts about insoluble substrate transport to bacteria.

3.1.2 The Hydrophobic Effect

Many consider the definition of chemical potential, \( \mu \), to be one of the greatest achievements of Gibbs. This deceptively simple concept allows one to describe precisely the state of equilibrium of a complex system.

Tanford (22, 23) has elegantly covered how to describe the equilibrium of the various phases in a biological system by the chemical potential. Moreover, the nature of the hydrophobic effect becomes clear.

Before delving into the interactions of phospholipids and proteins with water, let us backtrack a bit to the solubility of hydrocarbons in water. The low solubility of hydrocarbons in water was once thought to be a result of the "like–like" attraction of the hydrocarbon chains for themselves. However the effect is mostly an entropic effect resulting from the disruption of the isotropic structure of water. When a hydrocarbon molecule is present in the water, the water molecules must form an ordered pocket (cage) for the hydrocarbon molecule.

It is possible to express the hydrophobicity of straight chain hydrocarbons in terms of the standard chemical potential difference for the transfer of a hydrocarbon molecule from water to a pure hydrocarbon solvent. For straight chain alkanes, the free energy
of transfer is a linear function of the number of -CH₂ groups in the molecule. This is approximately proportional to the area of the cavity formed in the water (23). It is important to use a unitary scale for the chemical potential expression; i.e., the concentrations are in mole fraction units:

For a hydrocarbon molecule in water:

\[ \mu_w = \mu^* + RT \ln X_w + RT \ln f_w \]

where \( X_w \) is the concentration in mole fraction units

\( f_w \) is the activity coefficient at \( X_w \) and

\( \mu^* \) is the standard potential at infinite dilution

A similar expression can be developed for a hydrocarbon in the pure liquid or in another nonpolar solvent. The advantage of using this expression is that \( RT \ln X_w \) is the correct expression (in very dilute systems) for the cratic part of the chemical potential that is the purely statistical contribution to the chemical potential. This arises from the entropy of mixing of solvent and solute molecules. The standard chemical potential thus only represents the internal free energy of the solute molecule and its free energy of interaction with the solvent molecules (22, 23).

An analysis of available experimental data provides the following empirical relationship for the transfer of a hydrocarbon molecule from water to a hydrocarbon solvent:

\[ \mu^*_{HC} - \mu^*_W = -2436 - 884\text{nc} \]

\( \text{nc} \) is number of carbon atoms

It is noteworthy that the addition of double bonds affects the absolute magnitude of \( \mu^*_{HC} - \mu^*_W \) but not the functional dependence on the number of carbon atoms. Also, this relationship breaks down for larger molecules. Possibly the larger molecules fold upon themselves and reduce the interaction area or perhaps more conformations are available to the water molecules with increased hydrocarbon chain length.

Again note that the negative entropy results from the local ordering of the water
molecules near the hydrocarbon. Very little heat is associated with solubilizing hydrocarbons. Thus, the hydrogen bonds regenerate when the water molecules arrange themselves to form a cage around the hydrocarbon molecule. The lowering of free energy upon removal of the hydrocarbon has little to do with the affinity between alkyl chains. Indeed, studies indicate that induced dipole attraction between H₂O and alkyl chains may be slightly greater than the dispersion forces between alkyl chains. The dominant player is the H₂O-H₂O self-attraction. Using surface tensions of pure liquids and interfacial tensions at the H₂O-HC interface, Tanford (22) showed that the free energy of attraction at 25 °C between water and hexane or octane is about -40 erg/cm² of contact area and the free energy of attraction of the hydrocarbons for themselves is also about -40 erg/cm²; however, the water self-attraction is -144 erg/cm². The thermodynamic driving force is clearly the water self attraction. Literally squeezing out the hydrocarbon molecule maximizes the water-water interaction. Tanford graciously points out this correct interpretation was given by Hartley in 1936 on micelle formation, Frank and Evans (1945) and Kanzmann (1959), in discussions on the stability of isolated proteins.

Amphiphiles under proper conditions will aggregate to form micelles. Prima facia, this may seem to be an increased ordering but is a higher entropy state due to the increase in local disorder obtained by the segregation of the hydrocarbon chains. Thus the hydrophobic effect favors the formation of micelles. The opposition and size limitations on micelle formation are from electrostatic repulsion in ionic and steric hindrance and hydration in nonionic surfactant systems (18, 23). Micelles take on various shapes and sizes, often dictated by geometry of the molecules. Amphiphiles with two alkyl chains, such as phospholipids form bilayers.

3.1.3 Membranes

As stated earlier, membranes do more than define the cell boundaries. They act as gate keepers, selectively allowing certain molecules to pass in and out of the cell while preventing others from crossing. This is a complex task and requires specialized proteins
and cooperation between molecules, in particular proteins and lipids.

Although eukaryotic cells and prokaryotes differ, they share many of the same cell membrane constituents. These molecules are amphiphilic in nature. It is not surprising that our early soaps came from animal fats (18). We will consider some of the basic molecules found in most cells and give some increased coverage to the outer membrane of Gram-negative bacteria that are dominant soil bacteria. This outer membrane contains molecules (lipopolysaccharide) with a hydrocarbon tail, polar groups and a carbohydrate moiety. These LPS molecules give some unique characteristics to Gram-negative bacteria.

3.1.4 Components

The most widely characterized groups of membrane components are the phospholipids. Two nonpolar hydrocarbon chains are esterified to a glycerol that is esterified to a phosphate in 3' position. Attachment of the alcohol choline leads to phosphatidylcholine (PC) which is one of the most common eukaryotic phospholipids. For many bacteria phosphatidylethanolamine is the dominant lipid. The straight-chain fatty acids range from C12:0 (Lauric) to C24:0 (Lignocenic). Unsaturated fatty acids include Palmitoleic to Arachidonic acid.

Sphingolipids are structurally similar to phospholipids, in particular PC, because the esterified alcohol is choline. The molecule has only one fatty acid chain that is esterified to sphingosine backbone. Sugars added to the sphingosine alcohol form cerebrosides. Brain tissue contains sulfate derivatives. Cholesterol and Cholesterol Esters are essential constituents of mammalian membranes. They are generally not present in bacterial membranes. Their role is not well understood. The presence of sugars characterizes the last class of membrane lipids, amphipathic glycolipids. A widely studied group of glycolipids is the lipopolysaccharides of Gram-negative bacteria. The LPS molecule has two alkyl chains esterified to an oligosaccharide backbone to which the "O-specific" carbohydrate moiety is attached.
3.1.5 Membrane Structure And Organization

Under certain conditions the hydrophobic effect may drive amphiphiles to form micelles or bilayers. Remarkably, these are a higher entropy state and thus are thermodynamically stable. Under physiological conditions, the hydrophobic effect is the driving force behind the formation of biological membranes (22). Typical solubilities for phospholipids are $10^{-10}$ to $10^{-8}$ M, above which they form phase continuous, parallel bilayers, separated by water layers.

The fluid mosaic model of Singer and Nicolson is a useful heuristic model of the general membrane structure. It proposes that the lipids form a bilayer interspersed with membrane proteins. Designated intrinsic membrane proteins, these proteins may span the width of the membrane (Figure 3.1).
Figure 3.1 Membrane models

A

Globular protein
Phospholipid matrix

B

Hydrophilic
Hydrophobic
Hydrophilic

Porins
Outer membrane
(3 nm)
Periplasmic space
(5-7 nm)
Lipoprotein
Peptidoglycan
Lipoprotein
Phospholipid
Lipopoly saccharide
Cytoplasmic membrane
An important feature of the membrane is its fluidity. The membrane is deformable. This is in contrast to substances that form rigid crystalline structures. Also included are proteins whose structures tend to be non-deformable. The functional state of biological membranes is a liquid crystal state. The gel-liquid crystal transition generally occurs at temperatures much below growth conditions. This is fortuitous because some membrane fluidity is necessary for normal cellular functions. Because there are not strong attractive forces between the alkyl chains, the membrane bilayer is fluid. Although the driving force behind the membrane formation is a repulsive force, the membrane structure is well suited for insertion of membrane protein and other molecules with hydrophobic domains. It would be virtually impossible to achieve a typical membrane structure if the formation of the bilayer was based on specific attractive forces, “a brick and mortar” approach (22).

It is interesting that the location of double bonds at the 9-10 carbon of phospholipids maximizes the effect of unsaturation because ordering is more difficult and the transition temperature is lowered. Elegant studies have been done on A. laidlamil using scanning differential calorimetry (23).

Bacteria contain a cytoplasmic (inner) membrane as do eukaryotic cells. However, they also contain a rigid protein-sugar cell wall. Gram-negative bacteria take it one step further with an outer membrane which, in part, leads to many of the unique characteristics of these bacteria. In addition to membrane proteins and phospholipids, the outer membrane contains lipopolysaccharides. These are important in immune response, toxicity cell-host interactions, antibiotic resistance and for our interest, permeation barriers. The lipid A component of a LPS anchors it to the bacterial cell. The polysaccharide is usually subdivided into two subregions; the O-specific chain and the core oligosaccharide.

A tentative model (24) shows that the LPS do form a bilayer with phospholipids. Some of the proposed characteristics of this model are:
1. LPS exhibits a remarkably high state of order compared with natural phospholipids arrangements found in cytoplasmic membranes. This ordering results from the lipid A component and is a rigid arrangement.

2. The O-specific chains assume a heavily coiled conformation. Intermingling of the carbohydrate chains is still in question.

3. The hydrophilic region of the lipid A component, the bis-phosphate glucosamine disaccharide, seems to be oriented at 45 degrees to the surface.

4. Ordered domains persist.

The conformational properties of isolated LPS may also contribute to its function as a vital constituent of the outer membrane of Gram-negative bacteria. Furthermore, the high state of order may be the key role in the function of the outer membrane as a permeation barrier restricting the entrance of hydrophobic molecules.

Another interesting aspect of the outer membrane is the existence of protein oligomers known as porins. Porins function as passages through the outer membrane for certain molecules which are generally polar and can be up to \( \approx 600 \) daltons. Workers have observed that the exclusion limit in \( P. \text{aeruginosa} \) is \( 3,000-9,000 \) daltons. Others have suggested that these might permit the entrance of small micelles or hydrophobic molecules surrounded by a "cage" of water molecules (25).

3.1.6 Detergent-Protein-Lipid Interactions

The study membrane structure and functions requires dissociating the membrane into its components (26). Most amphiphiles in biological membranes including phospholipids, steroids, and membrane proteins are insoluble amphiphiles and would form liquid crystals or insoluble precipitates alone in aqueous media. Detergents are soluble amphiphiles and above a critical concentration and temperature form micelles of various sizes and shapes. Much of the recent progress in membrane research is due to the formation of thermodynamically stable isotropic solutions of membrane compounds in the presence of detergents. This process known as solubilization involves the transformation of lamellar phases into mixed micelles (27). Essentially, membranes are disrupted and vesicles or mixed micelles are formed to facilitate the study of the membrane components.
Both ionic (e.g. SDS) and nonionic (e.g. Triton X-100) detergents are used. Nonionics are milder, thus preserving the biological activity of the membrane constituents. Nonionic detergents are often preferred for this reason.

Lasch et. al.(28) have pointed out that the sequence of liposome solubilization proposed by Helenius and Simons in 1975 is generally accepted as correct.

Stage I: Detergent is incorporated into the bilayer and causes changes in its physical properties.

Stage II. Lamellar-micelle phase transition. When the bilayers contain sufficient amounts of detergent, mixed micelles begin to form, eventually resulting in complete phase transition. The phase transition is encouraged by increased surface curvature caused by the introduction of the detergents into the membrane.

Stage III. Size decrease of mixed micelle. After complete phase transition, the detergent/phospholipid ratio in mixed micelles increases and their size decreases.

Detergents ease the study of intrinsic membrane proteins (proteins that transverse, or are strongly anchored in the membrane). Detergents effectuate solubilization of membrane proteins by binding to the hydrophobic domain of the protein and creating a detergent micelle (23). The detergent essentially replaces the lipid. There are proteins that are too large to be solubilized in a micelle or have only a small hydrophobic portion. Here monolayer binding is the accepted model (26).

The binding of anionic and nonionic detergents is different. SDS is a well known "denaturing" detergent that causes drastic conformational changes in the proteins brought on by cooperative binding. This means that as more detergent binds to the protein more sites appear. The most studied case is serum albumin. This protein contains a large number of high affinity binding sites. In contrast, most nonionics are considered "mild" detergents that do not grossly disturb the proteins (29, 30). These well understood physicochemical principles are the basis for the analysis of protein and detergent association. The main source of information concerning protein association in membranes come from these types of analysis (11).

Results from various studies (29, 30, 31) indicate membrane proteins exist as oli-
gomers. The explanation is that the proteins form a hydrophilic passage when associated with each other. This is a popular theory and at least for bacteriorhodopsin is correct (23).

Although nonionics are considered gentle on protein-protein interactions, studies have shown nonionics can perturb the lipid-protein interactions (32, 33). Sussman et al. noted that low concentrations of Triton-X 100 (0.5%) enhanced the enzymatic activity but at higher concentrations when the protein was completely solubilized, the enzyme lacked activity.

One must consider that the above studies were all in vitro, as most membrane studies are. Further, the systems are usually two or three component systems as compared to the complex nature of actual biomembranes. However, the same principles apply with certain modifying factors. Asymmetry of the membrane prevents homogeneous distribution of lipids and proteins. Different regions of the membrane may have different physical states (gel vs. l.c.). Protein-Lipid interactions may cause local changes. Carbohydrate surfaces or dense protein networks may also affect the penetration and effects of detergents on membranes (26). For example, nonionics generally solubilize the cytoplasmic membrane of bacteria effectively. However, the outer membranes of Gram-negative bacteria are very resistant to detergents, presumably because of protein-protein interactions and the high state of order of the LPS hydrophobic chains (34).

3.2 Alkane Metabolism

3.2.1 Biochemistry

The late sixties and early seventies saw extensive research into the actual biochemical pathways of alkane metabolism. Charkavarty identified the OCT plasmid as being responsible for octane metabolism in Pseudomonas. The following figure illustrates the location and function of the enzyme system in the bacteria. It has both cytoplasmic membrane bound enzymes and unbound constituents.
3.2.2 Uptake of Alkanes

In spite of extensive work on hydrocarbon feedstocks in industrial microbial processes, many questions remain on how bacteria take up sparingly soluble substrates. The three mechanisms traditionally proposed in the literature are: (1) interaction of cells with hydrocarbon dissolved in the aqueous phase; (2) direct contact of cells with hydrocarbon drops considerably larger than the cells; and (3) interaction of cells with “solubilized”, “pseudosolubilized” or “accommodated” hydrocarbon in entities much smaller than the cells. Note that “pseudosolubilization” or “accommodation” need not be into a classical surfactant micelle as described above, but instead into the lipophilic regions of proteins or other polymeric molecules produced and excreted by cells. In any case the solubilized material dispersed in the small entities is in a thermodynamically stable state. In contrast, the much larger drops of mechanism two (22) above are thermodynamically unstable with respect to coalescence into a single, large hydrocarbon lens although the presence of surfactant may cause this process to be very slow.

The first mechanism cannot account for the observed rates of growth of long-chain alkanes due to their low solubility (35). However, it can explain many results for aromatics and gaseous hydrocarbons, which have greater solubilities in water (35).

Direct contact between cells and macroscopic hydrocarbon drops has been observed in many studies (27, 29), especially those involving yeast. If hydrocarbon uptake occurs by this mechanism, the surface area available for contact may be a limiting factor for cell growth. Often, formation of emulsions having small drops is a useful device in promoting growth by providing a larger surface area. Direct contact is not limited to liquid droplets. One study found that Mycobacterium cells can colonize phenanthrene crystals (36, 37).

The third mechanism gained acceptance during the 1980’s although workers had proposed this type of interaction in the early seventies (14). H.D. Singh’s and J.N. Baruh’s group in India has carefully studied this mechanism. They have shown that often
a metabolite produced by a microorganism can cause sufficient pseudosolubilization of hydrocarbon to account for the observed growth rates. However, even within the same bacterial genus, e.g., *Pseudomonas*, the predominant mode of hydrocarbon uptake may vary. A strain they called M1 produced no extracellular metabolite and direct contact was considered the chief uptake mechanism. However, another strain termed N1 did produce an extracellular material and pseudosolubilization was believed to be dominant (3, 4).

There is some ambiguity in previous work with liquid hydrocarbons because it was conducted with both aqueous and oil phases present. Adding surfactants not only facilitates emulsification of the oil with a resulting increase in interfacial area, but also provides micelles for solubilization. Thus, both mechanisms 2 and 3 are possible.

The recent review by Rouse et. al summarizes the previous work with commercial surfactants and biodegradation.

As discussed earlier, integral membrane proteins and the membrane lipids are responsible for the control of the passage of materials into and out of the cell. Of particular interest is the uptake of insoluble substrate at a rate sufficient to sustain growth. A number of theories are present in the literature with "pseudosolubilization" and uptake of dissolved molecules as the leading schools of thought. Several authors (24, 34, 38, 39, 40) discussed the dominant role that the outer membrane plays in substrate uptake by Gram-negative bacteria. Hancock et al. (25) went so far as to say that the porins may even allow for the passage of small micelles. It is also important to note that certain yeasts can also consume hydrocarbons. Their cell membranes are vastly different from a *Pseudomonas*. Thus, it is not obvious what the appropriate uptake mechanism is or if a generalization is even possible.

Those disclaimers aside, it does seem reasonable to consider substrate transport into the cell by way of micelles. Many microorganisms produce surface-active agents and the use of added surfactants to enhance utilization has been mentioned(18). The last study involved a genus known as *Mycobacterium* that is neither Gram-negative nor Gram-pos-
itive. They would stain Gram-positive. However, their outer membranes contain sugars and fatty acids and an adjacent layer of lipid that makes staining impossible. The cell wall contains of up to 60% lipid as compared to 20% for Gram-negative and 1-5% for (41).

The unanswered question is how the increased solubility translates to increased availability to the bacteria. Do the micelles bind to the cell membranes and enhance the transport by forming a pore through the hydrophilic outer portion or do surfactant molecules line the hydrophilic porins to change it to a hydrophobic passage. Furthermore, should not the surfactant disrupt the cell membrane when incorporated if it forms micelles and solubilizes the substrate. There appear to be no satisfactory answers to these questions as yet.
Figure 3.2  Alkane enzyme system in Pseudomonas
4.0 Experimental Methods and Materials

4.1 Bacteria and Culture Media

The experiments in this work used three different species of Gram-negative bacteria, *Pseudomonas aeruginosa* (ATCC 15528) and *Pseudomonas* (*Ochrobactrum*) *anthropi* (ATCC 21909) and *Pseudomonas putida* (27-G). The 21909 strain was originally identified as a *Pseudomonas*, but has recently been reclassified by the ATCC. This genus, *Ochrobactra*, was proposed and described by Holmes and coworkers (69).

Professor C.H. Ward of Rice University generously provided the strain 27-G which was isolated from a fuel spill site in Orange County, California. Professor Ward's group has found this strain to be an effective biosurfactant producer (42).

Glycerol stocks were made of the two ATCC strains and stored at -70 °C. Fresh working cultures on half-strength Nutrient Broth\(^\dagger\) slants were started every month from these glycerol stocks. This was done to minimize the chance that the results would become biased from the adaptation of the bacteria to the particular system at the expense of not growing in other systems. The subculturing flow sheet is shown in the accompanying figure (Figure 4.1). Culture purity was checked periodically using standard microbiological methods. However, these stocks were lost during a clean-out and subsequent relocation of the freezer. Replacement stocks were ordered from the ATCC and were used in all the anionic, mixed anionic/nonionic and mixed oil experiments described in Chapter 5.0. There was no detectable difference between results obtained with the original stock and the subsequent replacement stock. We chose a *Pseudomonas* strain because *Pseudomonads* are common soil bacteria, Gram-negative and well known to use a wide range of substrates, including hydrocarbons. Half-strength Nutrient Broth(Difco) cultures were used to inoculate half-strength Nutrient agar slants and these were incubated at 30°C for 24 hours and then stored at 4°C. Liquid cultures were started from these slants and

\(^\dagger\) Regular strength NB is 3 g/L Beef Peptone and 1.5 g/L Beef Extract. The half-strength is just half the above amounts. Hereinafter references to Nutrient Broth (NB) are half-strength recipes. 1.5%wt Agar (Difco) is added for the agar recipe.
used as the inoculum for the growth experiments. This method of propagation and storage replaced an earlier method of starting cultures from liquid stocks stored at 4°C.

The growth experiments consisted of four types: (I) free phase hydrocarbon, (II) solubilized hydrocarbon, (III) surfactant only, and (IV) modified type III. These experiments used mineral salts media either MSM or MSM2 (Table 4.1). MSM2 was developed for use with the anionic surfactant experiments because the LAS precipitated in the MSM medium. In addition to having a lower ionic strength the MSM2 also originally lacked calcium. However this was found to retard growth and the final recipe had 40 mg/L calcium†. Otherwise, both media formulations gave identical results. The type I medium was prepared as follows: Filtered hydrocarbon was added to 200 ml. of sterile MSM in a flask. This mixture was shaken for 24 hours at 30°C prior to inoculation. The type II medium was prepared by weighing the required amount of hydrocarbon into a sterile, capped tube. The aliquot of sterile 10% surfactant stock was added to this and gently turned for 12 hours at 30°C. The resulting solution was then transferred to the flask containing the remainder of the MSM. In all cases, the result was an optically clear, single-phase, micellar solution. The hydrocarbon was completely solubilized in the micelles. The type

† See section 5.3.8 on page 59
III medium consisted of surfactant in MSM only. This was also a transparent, single-phase solution. Type IV experiments are explained in Chapter 5.0. All growth experiments were conducted at 30°C on a rotary shaker in 1L culture flasks. The flasks were acid washed as required. Cell growth was monitored optically using a Brinkman Probe Colorimeter at 600 nm. The optical density (OD$_{600}$) was correlated with dry weight measurements. OD readings from 0.05 to 1 were used. At higher cell densities the samples were diluted with sterile MSM or MSM2. The dry weight curve is shown in Figure 4.2. For the various micellar solutions the optical density did not differ from that of distilled water and this was used to blank the probe.

<table>
<thead>
<tr>
<th>Component</th>
<th>MSM</th>
<th>MSM2</th>
</tr>
</thead>
<tbody>
<tr>
<td>KH$_2$PO$_4$</td>
<td>2.42 g</td>
<td>0.5 g</td>
</tr>
<tr>
<td>K$_2$HPO$_4$</td>
<td>5.6 g</td>
<td>1.74 g</td>
</tr>
<tr>
<td>(NH$_4$)$_2$SO$_4$</td>
<td>2.0 g</td>
<td>2.0 g</td>
</tr>
<tr>
<td>MgSO$_4$·7H$_2$O</td>
<td>0.6 g</td>
<td>0.15 g</td>
</tr>
<tr>
<td>CaCl$_2$·2H$_2$O</td>
<td>0.040 g</td>
<td>0.040 g</td>
</tr>
<tr>
<td>MnSO$_4$·7H$_2$O</td>
<td>0.0045 g</td>
<td>0.0045 g</td>
</tr>
<tr>
<td>CuSO$_4$·5H$_2$O</td>
<td>100 µg</td>
<td>100 µg</td>
</tr>
<tr>
<td>FeSO$_4$·7H$_2$O</td>
<td>100 µg</td>
<td>100 µg</td>
</tr>
<tr>
<td>Reagent Grade H$_2$O</td>
<td>1 Liter</td>
<td>1 Liter</td>
</tr>
</tbody>
</table>

The n-alkanes were purchased from Aldrich. They were filtered through a 0.22 µm filter before use. The Neodol™ surfactants were ethoxylated alcohols supplied by Shell Development Company. They were used without further purification. The LAS was

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†. Trade Mark of the Shell Chemical Company
supplied by Vista Chemical and was 34% active. 10% wt/vol stocks of the surfactants in MSM or MSM2 were made and autoclaved separately. We used Neodol™ 25-9, 25-7 and 25-3. The first number in the Neodol™ name designates the average range of alkyl chain lengths, i.e., 25 represents a distribution from C_{12} to C_{15}. The second number is the average number of ethylene oxide (EO) groups, i.e., 7 represents a distribution around seven EO groups per molecule. The stock solutions were used for both the phase behavior and growth experiments.

**Figure 4.2** Dry Weight vs. Optical Density

\[ y = 1.442x + 0.144 \]

\[ R^2 = 0.94 \]
4.2 Phase Behavior and Solubilization Determination

The colorimeter probe was also used to determine the solubilization limits for hydrocarbons in the surfactants. 100 ml. of sterile MSM or MSM2 surfactant solution were placed in a beaker and mixed via a homogenizer. No air was entrained and the vortex was minimal. The probe was placed well below the free surface. Hydrocarbon was then introduced in known quantities. The percent transmittance was followed by a strip chart recorder. A return to baseline of the percent transmittance indicated complete solubilization of the hydrocarbon. When the solution remained turbid, the solubilization limit had been reached.

This procedure was improved by the purchase of a non-aerating mixer and the modification of a 100 ml. three-necked flask to allow for the insertion of the mixer through the center neck as shown in Figure 4.3. the non-aerating mixer provides better mixing while imparting less localized heating and shear. The three neck flask also minimizes evaporative losses and simplifies oil addition.
Figure 4.3  Three-necked mixer set-up

Electric Motor

Oil Addition Port

Non-Aerating Mixer

100 ml 3-neck flask

Colorimeter

Chart Recorder
4.3 Gas Chromatography

The disappearance of the n-alkanes during the growth experiments was monitored by GC with a FID (flame ionization detector). The column used was a 15-meter SP-1 fused silica Mega-Bore™ column with a 2-meter guard attached. Results were quantified using an internal standard of n-dodecane (C₁₂). 0.5 milliliters of the sample was added to 0.5 ml of acidified (pH 2) surfactant solution containing solubilized C₁₂. This was centrifuged for 10 minutes and 0.1 μl of the supernatant was then injected directly onto the column (Conditions: inj: 200°C; oven: 110°C for 8 minutes then temperature program to 250°C at 2°C/min, hold at 250°C for 1 minute; det: 220°C. The peaks were integrated on a HP-1330A plotting integrator. This method had a lower detection limit of 0.01 g/l and had an average recovery efficiency of 92-105%.

4.3.1 Solvent Extraction

The above method was developed after solvent extraction of fermentation media was attempted and failed. It is generally preferable not to expose hydrophobic GC columns to water. Also the solvent extraction might prevent the passage of the nonionic surfactant through the column. Traditional GC solvents such as carbon tetrachloride, chloroform, and methyl chloride were tried. The sample was placed in a centrifuge tube with an equal volume of the solvent. This was vigorously mixed and then centrifuged. The early samples, i.e., before substantial cell growth, resulted in a two phase system. Later samples however resulted in a three phase system consisting of an aqueous phase, a solvent phase and an unbreakable emulsion phase. The major problem with this approach was the lack of reproducibility of the results. The variation in the results was greater than 20%. It appeared that not all of the alkane could be liberated from the surfactant micelles. In order to overcome this possibility the sample was diluted to 100 to 500 times depending on the surfactant concentration. This brought the surfactant concentration below the CMC. This was then extracted. However this also proved to be unsuccessful as well as very time consuming.
4.3.2  Direct Injection

As described above, the samples were first combined with an equal volume of the internal standard and then centrifuged to remove the cells. The low pH stopped any further microbial degradation of the alkane. The resulting supernatant was then directly injected onto the column. The major disadvantage of this method was that the analysis time was increased to 25 minutes. The increase was due to the slow elution of the surfactant and the cooling of the column after the ramped heating to 275°C. However, the major benefit was the reproducibility of the results. Samples were reproducible to within 2%. Other benefits were elimination of the production of waste solvent and the shorter and simpler sample preparation.
5.0 Results & Discussion

This chapter contains the results and discussion of the work focused on exploring the central hypothesis of this dissertation: that solubilization of hydrocarbons by micellar solutions will promote hydrocarbon oxidation by bacteria. The chapter is organized as follows.

1. Phase Behavior Determination
2. Free Phase Biodegradation Experiments
3. Micellar Systems Biodegradation Experiments
4. Kinetic Expression Development
5. Mathematical Model Description
6. Parameter Estimation Determination
5.1 Phase Behavior Determination

5.1.1 Introduction

An understanding of the basic phase behavior of the surfactant systems is necessary before carrying out the growth phase experiments. To this end, attempts were made to determine the cloud point of nonionic systems and the Krafft point of anionic systems. For the mixed surfactant systems the cloud points were not determined. All the determinations were done using stock surfactant solutions that were prepared as in the growth experiments. (See “Bacteria and Culture Media” on page 28.)

The straight-chain ethoxylated alcohol surfactants used in this work have very low critical micelle concentrations (the concentration above which micelles form from individual surfactant molecules dissolved in solution) but are sensitive to temperature. An aqueous solution of nonionic surfactant will separate into two liquid phases, with different surfactant concentrations, when heated above its cloud point temperature. The degree of ethoxylation strongly affects the cloud point. For example, the cloud points of nearly pure surfactants are about 10°C for C12E4, about 30°C for C12E5, and about 50°C for C12E6 (18). By C12E4 we mean an ethoxylated alcohol with an alkane chain of length of twelve and four ethoxyl groups. Since the cloud points of pure C12E4 and its commercial counterparts are below ambient temperature, ordinary small micelles do not exist in mixtures of these surfactants with water. Indeed, in this particular case, a dispersion of macroscopic particles of the lamellar liquid crystalline phase exists at room temperature in water (67). The lamellar phase consists of many parallel sheets of surfactant bilayers separated by water layers (67).
Table 5.1 below gives some basic information from Shell Chemical Company's literature on the physical properties of the commercially available Neodol™ Surfactants and some cloud point tests done using a 1% surfactant system in MSM1 (see Table 4.1 on page 30). Although electrolyte effects are typically thought of as having importance only in anionic surfactant systems, certain salts, e.g., sodium sulfate and sodium carbonate, can have significant impact on the cloud point at 5%wt salt. Sodium carbonate at this concentration lowers the cloud point of a 1%wt solution of N25-7 to 15°C from 50°C. Consistent with the water structure forming nature of the PO₄⁻³ and sulfate ions present in the MSM matrix (20), the electrolytes in the MSM lowered the cloud point of the surfactants by a small amount as seen from Table 5.1.

<table>
<thead>
<tr>
<th>Property</th>
<th>N25-3</th>
<th>N25-7</th>
<th>N25-9</th>
</tr>
</thead>
<tbody>
<tr>
<td>EO groups/alcohol, mole/mole avg.</td>
<td>3</td>
<td>7.2</td>
<td>9</td>
</tr>
<tr>
<td>Estimated Molecular Weight</td>
<td>336</td>
<td>519</td>
<td>610</td>
</tr>
<tr>
<td>EO Content%wt</td>
<td>40</td>
<td>61</td>
<td>67</td>
</tr>
<tr>
<td>HLB&lt;sup&gt;A&lt;/sup&gt;</td>
<td>7.9</td>
<td>12.2</td>
<td>13.3</td>
</tr>
<tr>
<td>Cloud Point 1% aqueous soln.</td>
<td>partially insoluble</td>
<td>50</td>
<td>74</td>
</tr>
<tr>
<td>Cloud Point 1% aqueous soln., 5% Na₂SO₄</td>
<td>p. insoluble</td>
<td>30</td>
<td>49</td>
</tr>
<tr>
<td>Cloud Point 1% aqueous soln., MSM</td>
<td>p. insoluble</td>
<td>48</td>
<td>67</td>
</tr>
</tbody>
</table>

<sup>A</sup> HLB (Hydrophilic-lipophilic balance) The balance between the hydrophilic and lipophilic portions of the molecule. Lower numbers are more lipophilic. (Rosen 1989)
The cloud points for the mixtures of the surfactants used for the growth experiments were determined (Table 5.2). It appeared that a mixture of 80% N25-9 and 20% N25-3, by weight, (hereafter called N80/20)† was the lower limit for a N25- 9/3 mixture for use at 30°C. While the cloud point of a mixture of S71/29 was below 20°C the addition of an equal amount, by weight, of decane produced a microemulsion at 30°C. This system could only be prepared from stock surfactant that had been autoclaved only once. This system while thermodynamically stable at 30°C, would phase separate rapidly with a few degrees change in temperature or decreased oil concentration.

Mixture HLB numbers were calculated on a weighted average, that is, \( f \cdot \text{HLB}_{\text{Surf1}} + (1-f) \cdot \text{HLB}_{\text{Surf2}} \). The HLB number for the N80/20 system is nearly the same as that of the N25-7 system but the cloud point is eight degrees lower. This finding is consistent with published reports of cloud point depression by a broader distribution of ethoxyl chain lengths (19). The N80/20 mixture has essentially two EO chain distributions, one for the N25-9 and another for the N25-3.

**Table 5.2** HLB and cloud point of surfactant solutions used in this work.

<table>
<thead>
<tr>
<th>System</th>
<th>Approximate HLB</th>
<th>Cloud Point 1%wt, MSM</th>
</tr>
</thead>
<tbody>
<tr>
<td>90% N25-9, 10% N25-3</td>
<td>12.76</td>
<td>51°C</td>
</tr>
<tr>
<td>80% N25-9, 20% N25-3</td>
<td>12.22</td>
<td>40°C</td>
</tr>
<tr>
<td>75% N25-9, 25% N25-3</td>
<td>11.95</td>
<td>&lt;23°C</td>
</tr>
<tr>
<td>60% N25-9, 40% N25-3</td>
<td>11.14</td>
<td>&lt;23°C</td>
</tr>
<tr>
<td>N25-7</td>
<td>12.2</td>
<td>48°C</td>
</tr>
<tr>
<td>95% N25-7, 5% N25-3</td>
<td>11.98</td>
<td>&lt;30°C</td>
</tr>
<tr>
<td>71% N25-7, 29% N25-3</td>
<td>10.95</td>
<td>&lt;20°C</td>
</tr>
</tbody>
</table>

†. Similarly the mixture of 90% Neodo\textsuperscript{©} 25-9 and 10% Neodo\textsuperscript{©} 25-3 is referred to as N90/10. This naming convention is used for all the mixtures of the Neodo\textsuperscript{©} 25-9 and 25-3 surfactants. For the mixtures of N25-7 and N25-3 the naming convention is similar but with an "S", e.g. 71% N25-7 and 29% N25-3 is S71/29.
5.1.2 Solubilization

Solubilization limits of two hydrocarbons were determined for two nonionic surfactants in the aqueous mineral salts medium described in chapter 4.0. The experiments were conducted at 30°C, a temperature well below the surfactant cloud points. Furthermore, 30°C was the temperature used for all the growth experiments. The solubilization power, $W_s$, is a mass percent based on the ratio of the mass of alkane to the mass of the surfactant. The other measure is the solubilization density called $\rho_{sol}$ which is useful for comparing experimental runs. This describes the amount of hydrocarbon solubilized by the micelles as a concentration. Alternatively, as proposed by Sterns in 1947, the solubilization capacity or solubilization power can be defined as the number of moles solubilized per mole of micellized surfactant [=(C-CMC)*V, where $V$ is the volume of the solution expressed in the same volume unit as the molar concentration C and CMC]. It often remains constant over a wide concentration range above the CMC (20). Other researchers (15, 68) have reported their solubilization results in terms of mole ratio. I did not to use this method because of the inherent heterogeneity of the commercial surfactants used in this research. The basic relationship for solubilization power is:

$$W_s = \frac{\text{mass alkane}}{\text{mass surfactant}} \quad \text{Eqn (1)}$$

The solubilization density is given by:

$$\rho_{sol} = \frac{\text{mass alkane [g]}}{\text{volume of medium [L]}} \quad \text{Eqn (2)}$$

Experimental surfactant concentrations are reported as follows:

$$[S] = \frac{\text{mass of surfactant [g]}}{\text{total volume [L]}} \quad \text{Eqn (3)}$$
The following is an illustrative example. An experiment carried out with 1% Neodol™ 25-7 (referred to from hereon as N25-7), and a $\rho_{\text{sol}} = 1.5$ g/L decane in a one liter flask with a total medium volume of 200 ml would have the following composition: two grams of N25-7 and 300 mg. of $C_{10}$ in sufficient MSM to give 200 ml.

Thus $W_s = \frac{300 \text{ mg}}{2000 \text{ mg}} = 15\%$ or 1/4 of the maximum amount of decane that can be solubilized by N25-7, according to Figure 5.1

The most complete solubilization studies were done with $C_{10}$ and $C_{14}$ in both N25-7 and N90/10. The results are shown as a plot of the $\rho_{\text{sol}}$ vs. the surfactant concentration, $S$, in Figure 5.1. Note that $W_s$ can be obtained from the slope of the line

$$W_{s}^{\text{max}} = \frac{\rho_{\text{sol}}}{S} \quad Eqn (4)$$

As Figure 5.1 indicates, maximum solubilization was a linear function of surfactant concentration in these systems where values of the critical micelle concentration (CMC) were very small and well below the surfactant concentration range investigated. This linear dependence is consistent with the solubilization literature. We also found the expected greater solubilization capacity of the less hydrophilic surfactant (N25-7) for both hydrocarbons and greater solubilization of n-decane than of n-tetradecane by both surfactants. The linear relationship is valid over the small range of concentrations used in the experiment. This method of reporting solubilization allows for quick calculation of the upper mass limit for the alkane in the system of interest.

Maximum solubilization was not rigorously determined for $C_{12}$ and $C_{16}$. However, it did appear that maximum solubilization by a micellar solution of N25-7 was approximately 48% and 15%, respectively. These data are roughly fit by the straight line (Figure 5.2):

$$W_{s}^{\text{max}} = 60\% - 15\% \times \left( \frac{n - 10}{2} \right) \quad Eqn (5)$$

where $n$ is the alkyl chain length.
Figure 5.1  Solubilization Densities
Figure 5.2  Relationship Between $W_s$ and Chain Length
The amount of oil solubilized was a function of the surfactant HLB and the chain length of the alkane. The more lipophilic surfactant micelles were able to solubilize greater amounts of alkanes. The amount solubilized decreases as the alkane chain length increases. It is noteworthy that, even in the experimental system with the highest solubilization, the maximum weight of hydrocarbon solubilized was only about 60% of the weight of the surfactant in the micelles. The solubilization powers of the micellar solutions, even for C_{16}, are orders of magnitude above the solubilities of the hydrocarbons in the absence of surfactants—about 1 \times 10^{-5} \text{ g/L} for n-decane and even lower for the other alkanes. Owing to the low hydrocarbon contents, we refer to the surfactant-containing growth media as micellar solutions rather than microemulsions, which typically have much greater amount of hydrocarbon solubilized.

Solubilizing amounts of oil less than 25% of the maximum was rapid, taking less than two hours of gentle mixing. However, amounts approaching \( W_f^{\text{max}} \) took eighteen to twenty-four hours to solubilize. This effect was inconsequential with regard to biodegradation run preparation but may have negatively impacted the solubilization determination when the homogenizer was used. The new non-aerating mixing method described in section 4.2 should minimize this problem. An example of increasing alkane incorporation versus time is shown in Figure 5.3. The slope of the return to baseline can be found and this shows the decreasing rate of solubilization. After the first addition the slope is 0.054 hr^{-1}. This decreases to 0.02 hr^{-1}, 0.011 hr^{-1}, 0.008 hr^{-1}, 0.0071 hr^{-1} and finally 0.0003 hr^{-1} after the last addition.
Figure 5.3  Solubilization response of tetradecane addition to 2% N25-7 at 30°C in MSM.
5.1.3 Phase Behavior Discussion

The ability to adjust the nature of our surfactant systems while maintaining the understanding of the location of the solubilized oil is a unique and important characteristic of this work. Our systems were clean compared to other work involving synthetic surfactants and biodegradation of sparingly soluble organics. Two key areas, which differed from other work, were no excess hydrocarbon phase (14, 43-45) nor the confounding presence of a solid soil phase (15, 36, 46).

The experiments in this work used a variety of surfactant systems. They ranged from nonionic systems with a single EO distribution to mixed micelle systems made up of nonionic and anionic surfactants. The general characteristics of the phase behavior for such surfactants are known but specific features such as cloud points and solubilization power, are usually not known for a particular surfactant system a priori. Consequently, determining such phase behavior for the surfactant systems used here was a significant part of the overall investigation.

Using our understanding of the phase behavior, we chose systems yielding single phase micellar solutions of nonionic surfactants that met the following criteria; favorable solubilizing power, up to 60%wt/wt, and a cloud point greater than 30°C. This ensured a single, thermodynamically stable phase as the growth medium for the bacteria.

It is interesting to compare the system used in this work with some recent work on polycyclic aromatic hydrocarbons, namely phenanthrene (47) In that work phenanthrene was solubilized in various nonionic surfactants (Triton N101, Triton X100, and Brij30) at solubilization densities significantly lower than used in this work. Typical levels used were $7.6 \times 10^{-4}$ g/L phenanthrene compared to the lowest used in this work of 0.375 g/L alkane. The value is actually less than the aqueous solubility of phenanthrene which is reported as $1.29 \times 10^{-3}$ g/L (48). In this work the lowest solubilization density of 0.375 g/L was four orders of magnitude larger than the aqueous solubility of decane.
According to the model of solubilization given by McKay, for a fixed temperature, pressure and electrolyte composition, once the CMC is reached, there exists an average aggregation number, i.e., the number of surfactant molecules per micelle. In general, the maximum amount of alkane per micelle is constant. Consequently, as the concentration of the surfactant is increased the total amount of oil solubilized also increases. The aggregation number has been found to increase with the addition of a solubilizate and with temperature. The maximum solubilization is a function of temperature as shown in the following table (Table 5.3) from Shinoda and Takeda (49).

**Table 5.3  Maximum Solubilization of Decane by C$_{10}$E$_{12}$CH$_{3}$**

<table>
<thead>
<tr>
<th>Temperature °C</th>
<th>MAC$^A$</th>
<th>Surfactant Aggregation Number</th>
<th>Solubilizate/Surfactant$^B$</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>2.6</td>
<td>78</td>
<td>0.13</td>
</tr>
<tr>
<td>30</td>
<td>4.4</td>
<td>85</td>
<td>0.21</td>
</tr>
<tr>
<td>50</td>
<td>8.7</td>
<td>97</td>
<td>0.42</td>
</tr>
<tr>
<td>60</td>
<td>13.5</td>
<td>127</td>
<td>0.66</td>
</tr>
</tbody>
</table>

$^A$ Maximum Additive Concentration, wt% = $w^\text{max}_A$

$^B$ Moles of n-decane per mole of surfactant in micelles

The procedures used in this work for preparing the solutions and determining maximum solubilization were consistent with the above findings. The linear relationship between the total amount of alkane solubilized and the surfactant concentration shown in Figure 5.1 was consistent the model of micellerization described above. This solubilization behavior is not limited to straight chain alkanes. Edwards and Luthy found it for multiringed aromatics such as phenanthrene solubilized in non-ionic surfactants (8).
The $W_s$ of 60% achieved with N25-7 and decane was orders of magnitude higher than normal solubility of decane in water. Yet it was still far below what can be achieved in microemulsion systems which can have a $W_s > 100\%$. As was expected from the known phase behavior of microemulsions in nonionic surfactant systems we able to formulate a microemulsion that was stable over a relatively narrow range of oil contents for a fixed surfactant concentration and temperature.

The low solubilization power and precipitation problems of the anionic surfactants investigated here was also disappointing and increased the difficulty in assessing the effect of the anionic surfactants. Only LAS was found to be suitable by itself for growth experiments. SDS and N25-3S were not suitable (see Appendix B). In addition to the LAS only N25-3S could be tested in combination with nonionic surfactants. Other anionic surfactants need to be explored to get a higher solubilizing power. A more lipophilic or less charged anionic surfactant might be more favorable in the biodegradation studies also. This matter is discussed further later in this chapter.

A notable problem with the nonionic surfactants is the short shelf life of the prepared sterilized solutions. This is probably due to accelerated oxidation brought on by the autoclaving process. However, future microemulsion work notwithstanding, any added benefit gained from filter sterilizing the media would be minimal. Making small batches of 10% stock solutions and storing them at room temperature for no longer than two weeks prior to use proved to be satisfactory. The surfactant behavior and the growth characteristics of the culture were stable and consistent following this method.
5.2 Free Phase Biodegradation Experiments

5.2.1 Summary

The ability of the microorganisms to grow on "free phase" alkane was assessed in these experiments. Most notable was the lower limit for growth given by a minimum amount of free alkane. This observation was found in the initial experiments which used small levels of the alkanes C\textsubscript{10} and C\textsubscript{14}. At these levels of 1 g/L or less, the alkane does not cover the free surface of the quiescent medium, however it is readily dispersed into fine droplets by agitation. This limiting volume may be related to a minimum required surface area. For strain 15528 the minimum value was 1/2\%v/v or a ρ\textsubscript{sol} = 3.5 g/L, for the all the alkanes. For strain 21909 the minimum value was 1\%v/v for decane, and no growth was obtained for up to 5\% volume/volume for tetradecane and hexadecane. Based on results obtained with strain 27-G, which required 15\% to 20\% v/v (approximately 120 g/L), to get growth on hexadecane, strain 21909 might grow at a higher volume fraction of free phase tetradecane and hexadecane. However, such an amount of free substrate is substantial especially in comparison to levels found in the solubilization experiments described later.

In addition to exhibiting a reluctance to grow with lower volumes of free phase alkanes, the specific growth rates that were obtained were low. All were less than 0.05 hour\textsuperscript{-1} (t\textsubscript{d} ≥ 13.86 hours). This result was independent of shaking speeds from 200 to 300 rpm (the maximum for the equipment). The lower speed was sufficient to disperse the alkanes into fine droplets. Some growth curves for strain 15528 are given in Figure 5.4. The optical density is plotted as a function of run time and is proportional to the dry cell mass. Accurate measurements required that the oil droplets first be allowed to collect on the surface of the medium and then a sample of the free cells was taken from the aqueous phase. The decrease in the observed growth rate may have resulted from the increasing attachment of the cells to the oil droplets (and hence fewer free cells to measure in the aqueous phase) as described below.

\[ t = \frac{ln2}{\mu} \]

\[ t. \text{This is the doubling time for the bacteria: } t_d = ln2\mu \]
Typically as the run progressed, the oil droplets coalesced less. This behavior was due, in part to the attachment of cells to the oil droplets, as found qualitatively by microscopic examination, and in part to the presence of an extracellular material. This phenomenon was especially apparent for strain 15528 growing on hexadecane. The resulting flocculation produced macroscopic particles made up of cells, oil droplets and extracellular material. While the decane droplets were merely covered, the hexadecane flocs were larger and not uniform. The addition of small glass beads ranging in size from 45 to 70 micron increased the floc formation in both the decane and hexadecane systems. The growth rates are summarized in Table 5.4

**Table 5.4 Free Phase Summary Table**

<table>
<thead>
<tr>
<th>Strain</th>
<th>Alkane</th>
<th>Concentration g/L</th>
<th>Observed $\mu$</th>
</tr>
</thead>
<tbody>
<tr>
<td>15528</td>
<td>Decane</td>
<td>&lt; 3.0</td>
<td>ND$^A$</td>
</tr>
<tr>
<td>15528</td>
<td>Decane</td>
<td>3.5 - 14</td>
<td>0.05</td>
</tr>
<tr>
<td>15528</td>
<td>Dodecane</td>
<td>NA$^B$</td>
<td>NA</td>
</tr>
<tr>
<td>15528</td>
<td>Tetradecane</td>
<td>&lt; 3.0</td>
<td>ND</td>
</tr>
<tr>
<td>15528</td>
<td>Tetradecane</td>
<td>3.5 - 14</td>
<td>0.02</td>
</tr>
<tr>
<td>15528</td>
<td>Hexadecane</td>
<td>&lt; 3.0</td>
<td>ND</td>
</tr>
<tr>
<td>15528</td>
<td>Hexadecane</td>
<td>3.5 - 15</td>
<td>growth$^C$</td>
</tr>
<tr>
<td>21909</td>
<td>Decane</td>
<td>&lt; 6.0</td>
<td>ND</td>
</tr>
<tr>
<td>21909</td>
<td>Decane</td>
<td>6.5</td>
<td>0.02</td>
</tr>
<tr>
<td>21909</td>
<td>Tetradecane</td>
<td>&lt; 37.5</td>
<td>ND</td>
</tr>
<tr>
<td>21909</td>
<td>Hexadecane</td>
<td>&lt; 37.5</td>
<td>ND</td>
</tr>
<tr>
<td>27-G</td>
<td>Decane</td>
<td>1 - 120</td>
<td>ND</td>
</tr>
<tr>
<td>27-G</td>
<td>Hexadecane</td>
<td>120</td>
<td>growth$^D$</td>
</tr>
</tbody>
</table>

$^A$ No growth detected  
$^B$ Experiment not attempted  
$^C$ Large and randomly sized flocs made OD measurements unreliable  
$^D$ Large volume of free phase alkane prevented quantitative determination
**Figure 5.4** Free Phase Experiments

- + — Strain 15528  Free C\textsubscript{10} = 14 g/L
- ● — Strain 15528  Free C\textsubscript{10} = 3.5 g/L
- ■ — Strain 15528  Free C\textsubscript{14} = 7 g/L

OD\textsubscript{600} vs Run Time (hours)
5.2.2 *Free Phase Discussion*

As a baseline for the study of surfactant enhanced biodegradation the ability of the microorganisms to degrade the alkanes on their own was assessed in the free phase experiments. It is generally recognized that microorganisms have the ability to uptake insoluble substrates in a variety of ways from direct contact to producing bioemulsifiers to help accommodate the material. It is well known that bioavailability can be limited by surface area (50,51). This appears to be true for our studies. All strains required that a significant amount of free phase alkane be present before they grew. The exception of course was the 27-G strain which did not utilize either the free phase alkane or solubilized alkane. The Groundwater Ecology Laboratory at Rice has had success in growing the 27-G strain on hexadecane and decane in free phase systems. They also found similar high volume ratios (42) Their medium contained some additional trace materials such as cobalt. Use of their medium was not pursued in our lab.

It is difficult to compare the lower free phase volume to an absolute lower limit in the solubilized systems as it appeared that even small quantities of the alkanes, <0.1 g/L, were readily used by the bacteria. The difference is consistent though with different physical states that exist in the two systems. In the free phase system the hydrocarbon exists almost entirely as a separate phase which is dispersed in water by agitation. In the solubilized systems the hydrocarbon exists as a solubilized substrate without the surface area limitations of droplet size.

Researchers have shown that drop size can be a significant factor in promoting rapid growth on alkane in batch reactor systems (35,50). The smaller the average drop size the greater the available (total) surface area for a constant volume of oil. This can be extended to a surface area limitation by virtue of there just not being a large enough volume of oil to have sufficient surface area. The restriction comes from the limitation of the mixing used in this work. Although the mixing was sufficient to disperse the oil into a cloud of fine droplets, below a certain volume of oil, the mixing action apparently did not
impair sufficient energy to produce droplets small enough to create enough surface area so that growth could be observed. The addition of more oil increased the available interfacial area to the point that growth was supported. Indeed, the first experiments with the 15528 strain indicated that it would not grow on decane at all. However, the addition of more decane to values equal to 1/2%v/v to the flasks allowed growth to occur.

Whereas more oil volume for the alkanes greater than decane was favorable, free phase octane seemed to be toxic to both the 15528 and 21909 strains even at very low concentrations ~0.1g/L. Although there are species of Pseudomonas and other microorganisms that can grow quite well on octane and lower alkanes, this tends to be the exception (1,35, 51). However, even with the greater aqueous solubility of octane, the ability to provide good mixing is considered very important (35).

Considering the case of alkanes contaminating a soil matrix, the oil may exist as a pool on the water table or it may have been dispersed into discrete ganglia and occupy discontinuous pore space (7). In any event the surface area available to the bacteria will be limited to the water and oil interface at the mouth of the pores. It is unlikely that microorganisms would exist on the walls of the oil occupied pore space. Consequently there would seem to be a unavoidable surface area limitation for oil trapped in the pore space. This would in turn limit the amount of bacteria which could attach and grow at the interface. Additional limitation might also arise from the formation of a biofilm at the interface. The diffusion of nutrients from the aqueous side through the biofilm might be slow (52-54).

†. See Appendix C for more information
5.3 Micellar Systems Biodegradation Experiments

5.3.1 Summary

The distinguishing characteristics of the batch experiments using nonionic surfactants were the rapid growth and oxidation of the alkanes, and the lack of cell flocculation. A comparison between growth on free phase decane and solubilized decane is shown in Figure 5.6. The difference in growth rates is clear. The observed $\mu_{\text{max}}$ for the micellar system is 0.44 hr$^{-1}$ and for the free phase system it is 0.05 hr$^{-1}$. Even more dramatic is the case for 21909 growing on solubilized tetradecane. Strain 21909 did not demonstrate any appreciable growth on free phase C$_{14}$ at similar solubilization densities but grew with $\mu_{\text{max}} = 0.29$ hr$^{-1}$ on the solubilized form. This was greater than the 0.09 hr$^{-1}$ for the surfactant alone (both N25-7 and N90/10). The findings of the anionic experiments were negative in contrast, that is, solubilization in anionic micelles did not promote the growth on or oxidation of alkanes. The data do suggest that the addition of nonionic surfactants to form mixed micelles can result in favorable growth conditions. The remainder of this section presents some interesting results from the various facets of the micellar system experiments. The main presentations of the experimental conditions, results, kinetic values and comparisons with numerical simulations for the nonionic systems are given in sections 5.5 and 5.6.
5.3.2 Toxicity testing

The surfactants were screened for toxicity using a plate spread method. A lawn of Nutrient Broth grown cells was spread, using an ethanol flame glass hockey stick, on an Nutrient agar plate. Sterile filter disks were soaked in sterilized 2% surfactant solutions and placed on agar plates. Disks soaked in sterile distilled water were used as a control. All plates showed confluent growth including overgrowth of the soaked disks. This indicated that the surfactants were not toxic to the cells. This was also confirmed by growing the cells in Nutrient Broth supplemented with surfactant at the 2% level. Comparison of the growth rates obtained for the Nutrient Broth and the Nutrient Broth supplemented with surfactant showed no significant difference at the 95% confidence level. This shown in the Figure 5.5 and Tables 5.5 and 5.6.
Figure 5.5  Means Comparison of the growth of Strain 15528 on Nutrient Broth with and without Neodol Surfactant present.

Table 5.5  Means and Standard Deviations

<table>
<thead>
<tr>
<th>Level</th>
<th>Number</th>
<th>Mean</th>
<th>Std Dev</th>
<th>Std Err Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neodol</td>
<td>5</td>
<td>1.25149</td>
<td>0.069986</td>
<td>0.03130</td>
</tr>
<tr>
<td>No Surfactant</td>
<td>7</td>
<td>1.31772</td>
<td>0.181941</td>
<td>0.06877</td>
</tr>
</tbody>
</table>
### Table 5.6  Means Comparisons

<table>
<thead>
<tr>
<th>Dif=Mean[i]-Mean[j]</th>
<th>No Surfactant</th>
<th>Neodol</th>
</tr>
</thead>
<tbody>
<tr>
<td>No Surfactant</td>
<td>0.000000</td>
<td>0.066234</td>
</tr>
<tr>
<td>Neodol</td>
<td>-0.06623</td>
<td>0.000000</td>
</tr>
</tbody>
</table>

**Alpha= 0.05**

**Comparisons for each pair using Student's t**

<table>
<thead>
<tr>
<th>t</th>
<th>2.22815</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abs(Dif)-LSD</td>
<td>No Surfactant</td>
</tr>
<tr>
<td>No Surfactant</td>
<td>-0.17593</td>
</tr>
<tr>
<td>Neodol</td>
<td>-0.12649</td>
</tr>
</tbody>
</table>

Positive values show pairs of means that are significantly different.

**Tests that the Variances are Equal**

<table>
<thead>
<tr>
<th>Level</th>
<th>Count</th>
<th>Std Dev</th>
<th>MeanAbsDif to Mean</th>
<th>MeanAbsDif to Median</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neodol</td>
<td>5</td>
<td>0.0699857</td>
<td>0.0569452</td>
<td>0.0569648</td>
</tr>
<tr>
<td>No Surfactant</td>
<td>7</td>
<td>0.1819411</td>
<td>0.1204880</td>
<td>0.1064971</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Test</th>
<th>F Ratio</th>
<th>DF Num</th>
<th>DF Den</th>
<th>Prob&gt;F</th>
</tr>
</thead>
<tbody>
<tr>
<td>O'Brien[.5]</td>
<td>0.7694</td>
<td>1</td>
<td>10</td>
<td>0.4010</td>
</tr>
<tr>
<td>Brown-Forsythe</td>
<td>0.5002</td>
<td>1</td>
<td>10</td>
<td>0.4955</td>
</tr>
<tr>
<td>Levene</td>
<td>1.1733</td>
<td>1</td>
<td>10</td>
<td>0.3042</td>
</tr>
<tr>
<td>Bartlett</td>
<td>3.1438</td>
<td>1</td>
<td>*</td>
<td>0.0762</td>
</tr>
</tbody>
</table>

Variances are equal, observed significance are > 0.05
5.3.3 *Surfactant as Substrate*

Selecting surfactants for groundwater remediation involves more than just selecting a surfactant that is suitable for the contaminant and aquifer matrix; the biodegradability and toxicity of the surfactant are also important (12, 55, 68). For enhanced pump-in-treat remediation or *in situ* processes the issue of level of recalcitrance to biodegradation is important as a surfactant must survive long enough to perform its intended function (contaminant transport, enhancement of bioavailability and so forth) (68). However, Rouse *et al.* point out that eventual biodegradability is important for the residual surfactant in the subsurface (6). This influenced our initial selection of the linear ethoxylated alcohols which have good biodegradation properties (56). As expected, the bacteria were able utilize the Neodol™ surfactants as a sole carbon source. The rate and susceptibility of degradation increases with decreasing number of EO groups and increasing alkyl chain length. The linearity of the alkyl chain is also significant as branched and unsaturated chains tend to make the molecules more difficult to degrade.

The only exception was the failure of strain 27-G to utilize the Neodol™ surfactants. However it did grow well in NB supplemented with 2% N25-7. This indicates that the surfactant was not used as a substrate but was also not toxic.

All batch runs using the surfactant alone exhibited a lag phase of up to 10 hours before exponential growth would occur. This lag phase was not alleviated even when the inoculum cultures were supplemented with alkanes. No experiments were done with surfactant only systems using an inoculum culture supplemented with surfactant. Table 5.7 shows the summary of surfactant only runs. The growth rates are the average of at least four runs.
Table 5.7  Growth rates for surfactant only runs

<table>
<thead>
<tr>
<th>Strain</th>
<th>Surfactant</th>
<th>Surfactant Concentration</th>
<th>Observed $\mu_{\text{max}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>15528</td>
<td>90/10</td>
<td>1.0%</td>
<td>0.16±0.02</td>
</tr>
<tr>
<td>15528</td>
<td>90/10</td>
<td>2.0%</td>
<td>0.15±0.02</td>
</tr>
<tr>
<td>15528</td>
<td>N25-7</td>
<td>0.25%</td>
<td>0.12±0.02</td>
</tr>
<tr>
<td>15528</td>
<td>N25-7</td>
<td>0.5%</td>
<td>0.13±0.03</td>
</tr>
<tr>
<td>15528</td>
<td>N25-7</td>
<td>1.0%</td>
<td>0.15±0.02</td>
</tr>
<tr>
<td>15528</td>
<td>N60/40</td>
<td>2.0%</td>
<td>0.15±0.04$^A$</td>
</tr>
<tr>
<td>21909</td>
<td>90/10</td>
<td>1.0%</td>
<td>0.09±0.02</td>
</tr>
<tr>
<td>21909</td>
<td>N25-7</td>
<td>1.0%</td>
<td>0.09±0.02</td>
</tr>
<tr>
<td>21909</td>
<td>N60/40</td>
<td>2.0%</td>
<td>0.09±0.05$^B$</td>
</tr>
<tr>
<td>27-G</td>
<td>90/10</td>
<td>0.1-1.0%</td>
<td>ND$^B$</td>
</tr>
<tr>
<td>27-G</td>
<td>N25-7</td>
<td>0.1-1.0%</td>
<td>ND</td>
</tr>
</tbody>
</table>

$^A$ Average of two runs.
$^B$ ND = Not detected

5.3.4  Solubilized Decane Systems

The growth and oxidation of solubilized decane by the three bacteria strains was studied. As described in Chapter 4 the decane was completely incorporated into the surfactant micelles. The range of surfactant concentrations used was from 0.25% to 2% and the amount of decane solubilized was from 0.375 g/L to 10 g/L. This last amount was obviously in the 2% surfactant system and represented a $W_s$ of 50% and 83% of the maximum for the N25-7 system. Figure 5.6 shows the dramatic increase in the growth rate of strain 15528 when the hydrocarbon was solubilized in micelles. This was a consistent finding for all the runs done with 15528 and with 21909. The 27-G strain did not utilize the solubilized decane. As mentioned above, it did not appear that the surfactant was toxic to the organism (See Section 5.3.3 on page 53). The medium may also have lacked a required micronutrient.
Figure 5.6  Comparison of free phase growth and growth on solubilized substrate

Non-ionic Surfactant
2.0% 90/10
ρ_sol = 4 g/L
μ_max = 0.44 hr⁻¹

Growth on Free liquid Decane (NO Surfactant)
μ = 0.05 hr⁻¹  SIGNIFICANTLY SLOWER THAN FOR THE SURFACTANT SYSTEMS
For the strains 15528 and 21909, the growth was dependent on the type of surfactant, and the solubilization density but appeared to be independent of the surfactant concentration. Some recent studies with phenanthrene have shown that the apparent bioavailability of the hydrocarbon decreases with increasing surfactant concentration (47). Basically the same hydrocarbon was then distributed among a greater number of micelles. Of course accompanying this is a decrease in the chemical potential of the oil in the micelles, i.e., as the surfactant concentration is increased, \( W_s \) moves away from \( W_s^{max} \) and thus the chemical potential of the oil in the micelles decreases. Such changes in surfactant concentration did not appear to change the bioavailability of the alkanes in our experiments. This may be due to the difference in solubilization location, surfactants, type of contaminant or the bacteria used.

5.3.5 *Determination of Abiotic Losses*

The possibility of volatilization losses was examined using cell free controls. Systems shown in Table 5.8 below were prepared in duplicate in the identical manner as in growth experiments. The results are plotted in Figure 5.7. The data indicate that the volatilization losses were minimal, less than 5% per 24 hours.

<table>
<thead>
<tr>
<th>Surfactant</th>
<th>Concentration</th>
<th>Oil</th>
<th>( P_{sol} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>N90/10</td>
<td>10 g/L</td>
<td>Decane</td>
<td>1 g/L</td>
</tr>
<tr>
<td>N90/10</td>
<td>20 g/L</td>
<td>Decane</td>
<td>4 g/L</td>
</tr>
<tr>
<td>N25-7</td>
<td>10 g/L</td>
<td>Decane</td>
<td>1 g/L</td>
</tr>
<tr>
<td>N25-7</td>
<td>20 g/L</td>
<td>Decane</td>
<td>4 g/L</td>
</tr>
</tbody>
</table>
Figure 5.7  GC Results for decane / surfactant systems without bacteria shaken at 300 rpm and incubated at 30 ºC as in the growth experiments.
5.3.6 Oxygen Limitations

The rapid rate of growth of the cultures raises the question of oxygen limitations during the experiment, especially at higher cell concentrations. Measurements of the dissolved oxygen using a YSI model 58 polarographic probe indicated that levels of 2-3 ppm were obtained. This level of dissolved oxygen is not growth limiting (57).

5.3.7 Effect of Inoculum Supplements

The oxidative pathways for alkanes may require an induction period as opposed to having a constitutive enzyme system (51). It is possible for the microorganisms to lose their degradative ability without the selective pressure of the substrate, in this case, alkanes (5) To this end, a comparison was made between the batch behavior of inocula supplemented with decane and those just grown on Nutrient Broth. The diminishment or elimination of the lag period is clearly shown in the accompanying figure (Figure 5.8). Both strains of the bacteria responded to alkane supplementation of the inoculum broth with the elimination of the lag period. There did not appear to be a difference in the exponential growth rates however.
5.3.8 Calcium Requirements

While testing modified versions of mineral salts medium for use in the anionic studies described below (See "Anionic Micelles" on page 66.), some nonionic runs were conducted using a calcium free medium. The effect was a decrease in the growth rate and the production of a green pigment by the 15528 strain and yellow pigment by the 21909 strain. It was found that at greater than 12 mg./L of CaCl$_2$•H$_2$O in the medium the growth rates were unchanged. Later analysis of the type discussed in section 5.5, showed that there was an increase in the apparent $K_S$ value to greater than 1.2 (from about 0.1) in the calcium lean medium. Unfortunately there were not enough studies done to fully evaluate this observation. Thus the amount of calcium (40 mg./L) present in the modified MSM was more than sufficient to allow full growth. The a comparison plot is given in Figure 5.9
Figure 5.8  The effect of inoculum supplements.
System: Strain 15528, 10 g/L N90/10 and 1 g/L Decane
Figure 5.9  Calcium Requirements
System: Strain 15528, 20 g/L N90/10, 4 g/L Decane
5.3.9  *Tetradecane Solubilization*

The next most extensive experimentation was done on solubilized tetradecane. As stated earlier the bacteria demonstrated a reluctance to grow on C14. Although the specific growth rates obtained were not as high as those for decane, they were substantially higher than those for the free phase systems. The results are summarized in Table 5.18-Table 5.20.

**Table 5.9  Summary Table for Octane**

<table>
<thead>
<tr>
<th>Strain</th>
<th>Surfactant</th>
<th>Surfactant Concentration</th>
<th>Solubilization Density</th>
<th>Observed μ</th>
</tr>
</thead>
<tbody>
<tr>
<td>15528</td>
<td>N25-7</td>
<td>1.00%</td>
<td>0.750</td>
<td>0.15</td>
</tr>
<tr>
<td>21909</td>
<td>N25-7</td>
<td>1.00%</td>
<td>0.750</td>
<td>0.1</td>
</tr>
<tr>
<td>15528</td>
<td>None</td>
<td>None</td>
<td>0.50</td>
<td>Not Detected</td>
</tr>
<tr>
<td>15528</td>
<td>None</td>
<td>None</td>
<td>5</td>
<td>Not Detected</td>
</tr>
<tr>
<td>21909</td>
<td>None</td>
<td>None</td>
<td>5</td>
<td>Not Detected</td>
</tr>
<tr>
<td>21909</td>
<td>None</td>
<td>None</td>
<td>0.50</td>
<td>Not Detected</td>
</tr>
</tbody>
</table>

5.3.10  *Octane Solubilization*

A few experiments done with octane appear to indicate that solubilizing this alkane allows growth based on the disappearance of octane according to GC data. However the GC data were not sufficient to do the type of analysis done for the other four alkanes and it is not possible to conclude whether the bacteria were utilizing the surfactant or the alkane. Octane has a significantly higher solubility and volatilization in water than decane and some reports indicate that this can cause toxicity in some species of bacteria. This may have been the reason for the lack of growth on the free phase octane. The results are described in Table 5.9.
5.3.11 Mixed Oil System

The next extension of the nonionic system studies was the use of mixed oil substrates. Two different alkanes were used at the same solubilization density. Consequently the $W_s$ for the longer chain alkane was closer to the solubility limit for that alkane.

All mixed oil system experiments were conducted using equal masses in 1\% N25-7 systems except for the four oil system. The four oil system was conducted using 2\% N25-7 system. The results tabulated in Table 5.10 clearly show that decane is preferentially utilized when it is present in the micelle. The data are not as clear for the other combinations, but they do suggest a preferential utilization of $C_{16}$ over $C_{12}$ and $C_{14}$.

"Parameter Estimation Determination" on page 91 contains the kinetic parameter estimates for these mixed oil systems.

**Table 5.10 Preferential Oil**

<table>
<thead>
<tr>
<th>Strain</th>
<th>System</th>
<th>Preferential Oil</th>
</tr>
</thead>
<tbody>
<tr>
<td>15528</td>
<td>$C_{10}/C_{12}$</td>
<td>$C_{10}$</td>
</tr>
<tr>
<td>15528</td>
<td>$C_{10}/C_{14}$</td>
<td>$C_{10}$</td>
</tr>
<tr>
<td>15528</td>
<td>$C_{10}/C_{16}$</td>
<td>$C_{10}$</td>
</tr>
<tr>
<td>15528</td>
<td>$C_{12}/C_{14}$</td>
<td>Both</td>
</tr>
<tr>
<td>15528</td>
<td>$C_{12}/C_{16}$</td>
<td>Both</td>
</tr>
<tr>
<td>15528</td>
<td>$C_{14}/C_{16}$</td>
<td>$C_{16}$</td>
</tr>
<tr>
<td>15528</td>
<td>$C_{10}/C_{12}/C_{14}/C_{16^A}$</td>
<td>$C_{10}$</td>
</tr>
<tr>
<td>15528</td>
<td>$C_{12}$</td>
<td>$C_{12}$</td>
</tr>
<tr>
<td>15528</td>
<td>$C_{16}$</td>
<td>$C_{16}$</td>
</tr>
<tr>
<td>21909</td>
<td>$C_{16}/C_{16}$</td>
<td>inconclusive</td>
</tr>
<tr>
<td>21909</td>
<td>$C_{16}$</td>
<td>$C_{16}$</td>
</tr>
</tbody>
</table>

$^A$ 2\% N25-7 System
5.3.12 Microemulsions and Systems Above the Cloud Point

The classical microemulsion usually has at least a 1:1 ratio of oil to surfactant. Our system only approached 60% by weight for most runs. Two runs were conducted using a 71% N25-7 and 29% N25-3 mixture at 2% concentration, with a $W_s = 1.05$ with decane. For these cases, the microemulsion was filter sterilized to prevent disruption of the system by the harsh autoclaving process. The growth rates obtained were 0.38 hr$^{-1}$ and 0.45 hr$^{-1}$ and the growth curves are shown in Figure 5.10. Between six and eight hours after the start of the experiment the system turned cloudy. This behavior indicated that the system had crossed out of the one phase region and into the two phase region as would be expected when the oil content is reduced based on the known phases equilibrium of these systems [Shinoda, 1986]. The cells continued to grow in the two phase system. The results were similar to those obtained using a N60/40 system (see footnote page 34 regarding nomenclature).

The distinguishing feature of the N60/40 experiments were the two phase surfactant system and the higher level of the N25-3, i.e., the more lipophilic surfactant. Although the N60/40 mixture would phase separate, this was a slow process taking six to seven days. Consequently, the agitation provided by the rotary shaker kept the surfactant rich and the surfactant poor phases intimately mixed. Both phases are water continuous. This system also contains micelles in the surfactant rich phase and these are larger than those found in the previously described micellar solutions. The resulting cloudiness is due to the refraction or scattering of the light by the surfactant rich phase. The alkane will also partition preferentially in these micelles, i.e., it will not be found in significant concentrations in the dilute phase. The location of the bacteria is not known and could reasonably be expected to be found in either phase.

The inherent turbidity and presence of two phases required a modification of the sampling procedure. The flask to be sampled was kept agitated until the last moment that known volume, usually two milliliters, of the culture medium was withdrawn. This sample
was centrifuged for 10 minutes, the two phase supernatant was decanted and the cell pellet resuspended in enough sterile MSM2 to return to the original volume. The mixture phase separated during centrifugation and as expected decane was found in the upper phase but was not found in the lower clear phase. The limited GC analysis of these systems used uncentrifuged culture medium sample mixed with the internal standard.

**Figure 5.10** Growth in microemulsion system

![Graph showing growth in microemulsion system](image_url)
The matrix of experiments conducted with this system is shown in Table 5.11. Because of the difference in the system from the micellar systems, N90/10 runs were done as controls to eliminate any question about inoculum or strain variation.

**Table 5.11  Cloud Point Systems**

<table>
<thead>
<tr>
<th>Component</th>
<th>High</th>
<th>Low</th>
</tr>
</thead>
<tbody>
<tr>
<td>Strain</td>
<td>15528</td>
<td>21909</td>
</tr>
<tr>
<td>Surfactant</td>
<td>N90/10</td>
<td>N60/40</td>
</tr>
<tr>
<td>Surfactant Concentration</td>
<td>2.0%</td>
<td>0.5%</td>
</tr>
<tr>
<td>( W_s )</td>
<td>20%</td>
<td>5%</td>
</tr>
</tbody>
</table>

The solubilization densities used in these experiments were 4 g/L, 1 g/L, 1 g/L and 0.25 g/L. This is a two level, four factor design. The analysis indicated that the 21909 strain's growth rate was affected by the type of surfactant. The bacteria grew more rapidly in the N60/40 system, average \( \mu_{\text{max}} = 0.39 \text{ hr}^{-1}, K_s=0.15 \) vs. the N90/10 system, average \( \mu_{\text{max}} = 0.32 \text{ hr}^{-1} \) and \( K_s=0.35 \). These values were generated using a double reciprocal plot. The confidence for these estimates is only about 90%. However the Student's t-test at 95% confidence also indicated that this was not the case for the 15528 strain, i.e., differences in growth rates between the N90/10 and N60/40 systems were not statistically significant. The growth rates and oil consumption for the control runs using the 15528 strain in N90/10 were consistent with results obtained in other runs with the same experimental conditions.

5.3.13 **Anionic Micelles**

The positive results obtained with the nonionic surfactants encouraged us to explore anionic surfactant systems. We chose to use LAS (linear alkylbenzene sulfonate) as our model anionic surfactant. It was provided by Vista Chemical Company. LAS is biodegradable, a property that makes it suitable for household laundry formulations. The nature of LAS might offer different types of interactions with the oil and the bacteria. It
also might prove to be more suitable for field use depending on the soil matrix. However anionic surfactants suffer from problems such as precipitation in the presence of divalent cations, i.e., "hard water." This was indeed the case for the original MSM formulation. The MSM2 medium developed for this group of experiments did not cause precipitation of the LAS but was capable of supporting excellent growth in the nonionic systems as previously described (See Section 5.3.8 on page 59).

The mineral salts medium MSM2 developed for use with LAS contained calcium so that the problems mentioned in section 5.3.8 were not encountered. However the divalent ionic strength and overall ionic strength was low enough to prevent precipitation. The LAS had a $W_s^{max} = 5\%$ for decane. This limited the solubilization density considerably at the lower concentrations.

The solubilization of decane in LAS micelles did not promote the growth of cells nor the oxidation of decane. The experiments ranged from LAS at 0.25% with 0.125 g/L decane to 4% LAS and 2 g/L decane, and LAS alone over the same range of concentrations. The run combinations tried are shown in Table 5.12 and Table 5.13. Even after 72 hours the cells showed no sign of growth nor was the consumption of decane apparent as checked by GC analysis. As check for toxicity, 15528 and 27-G cells were grown in 4% LAS and 2% citrate; 4% LAS and 1 g/L Decane and 2% citrate; 1 g/L Decane and 2% Citrate; and 2% citrate alone. The growth rates were identical, 0.15 hr$^{-1}$, 0.17 hr$^{-1}$, 0.15 hr$^{-1}$, and 0.16 hr$^{-1}$ respectively, implying no toxicity. Also NB inoculum cultures supplemented with 2% LAS grew well (see table footnote A. page 69). The lack of toxicity of the LAS is important because of the lack of growth on the solubilized oils in these systems. This negative effect of LAS solubilization was in direct contrast to the previous solubilization experiments and indicates that the anionic micelles have a less than favorable if any interaction with the bacteria cells. Since the species used in this study have a net negative charge, electrical repulsion could be a factor. In the citrate supplemented run with the decane solubilized in the LAS micelles, the decane did not appear to decrease at a rate
greater than that found in bacteria free controls. This finding supports the hypothesis that
the there is not the same cell/micelle interaction found in the nonionic systems.

5.3.14 Mixed Surfactant Systems

To test whether this effect could be mediated by the addition of nonionic surfac-
tants, mixed anionic/nonionic systems were tried. The mixtures and results are given in
the following tables (Table 5.14 and Table 5.15). All the runs listed used a 1% solution
made from the autoclaved 15% stock solutions A, B or C. Growth was detected in the sys-
tems and observed growth rates were determined from a semilog plot of the cell mass
versus time. Gas chromatography of these systems was inconclusive, so it can not be con-
cluded that the alkane was oxidized. However this area of mixed micelles should be pur-
sued in future research.
<table>
<thead>
<tr>
<th>Strain</th>
<th>%LAS</th>
<th>$p_{sol}$</th>
<th>Growth</th>
</tr>
</thead>
<tbody>
<tr>
<td>15528</td>
<td>1.0</td>
<td>0.5</td>
<td>NO</td>
</tr>
<tr>
<td>15528</td>
<td>0.5</td>
<td>0.25</td>
<td>NO</td>
</tr>
<tr>
<td>15528</td>
<td>0.5</td>
<td>0.125</td>
<td>NO</td>
</tr>
<tr>
<td>15528</td>
<td>2.0</td>
<td>1.0</td>
<td>NO</td>
</tr>
<tr>
<td>15528</td>
<td>1.0</td>
<td>0.5</td>
<td>NO</td>
</tr>
<tr>
<td>15528</td>
<td>0.5</td>
<td>0.25</td>
<td>NO</td>
</tr>
<tr>
<td>15528</td>
<td>0.1</td>
<td>0</td>
<td>NO</td>
</tr>
<tr>
<td>15528</td>
<td>1.0</td>
<td>0</td>
<td>NO</td>
</tr>
<tr>
<td>15528^A</td>
<td>0.25</td>
<td>0</td>
<td>NO</td>
</tr>
<tr>
<td>15528^A</td>
<td>2</td>
<td>0</td>
<td>NO</td>
</tr>
<tr>
<td>15528</td>
<td>0.5</td>
<td>0.25</td>
<td>NO</td>
</tr>
<tr>
<td>15528^A</td>
<td>1.0</td>
<td>0.25</td>
<td>NO</td>
</tr>
<tr>
<td>15528^A</td>
<td>2.0</td>
<td>0.25</td>
<td>NO</td>
</tr>
<tr>
<td>15528</td>
<td>3.0</td>
<td>0.25</td>
<td>NO</td>
</tr>
<tr>
<td>15528</td>
<td>4.0</td>
<td>0.25</td>
<td>NO</td>
</tr>
<tr>
<td>15528</td>
<td>4.0</td>
<td>1.0</td>
<td>NO</td>
</tr>
<tr>
<td>15528</td>
<td>4.0</td>
<td>2.0</td>
<td>NO</td>
</tr>
<tr>
<td>15528</td>
<td>4.0</td>
<td>1.0^B</td>
<td>Yes</td>
</tr>
<tr>
<td>15528</td>
<td>4.0</td>
<td>0</td>
<td>NO</td>
</tr>
<tr>
<td>15528</td>
<td>0</td>
<td>0^B</td>
<td>Yes</td>
</tr>
<tr>
<td>15528</td>
<td>0</td>
<td>1.0^B</td>
<td>Yes</td>
</tr>
<tr>
<td>15528</td>
<td>4.0</td>
<td>1.0</td>
<td>NO</td>
</tr>
<tr>
<td>15528</td>
<td>4.0</td>
<td>2.0</td>
<td>NO</td>
</tr>
</tbody>
</table>

^A- The inoculum in these experiments was from Nutrient Broth with 2% LAS as a supplement. The final OD of the inoculum culture was 1.826 compared to 1.716 for the unsupplemented Nutrient Broth. Both were started from a slant culture.

^B- Also contained 1.1 g/L Citrate
<table>
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<th>%LAS</th>
<th>$p_{sol}$</th>
<th>Growth</th>
</tr>
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</tr>
<tr>
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<td>0.25</td>
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<tr>
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<td>NO</td>
</tr>
<tr>
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<td>1.0</td>
<td>NO</td>
</tr>
<tr>
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<td>0.5</td>
<td>NO</td>
</tr>
<tr>
<td>27-G</td>
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<td>0.25</td>
<td>NO</td>
</tr>
<tr>
<td>27-G</td>
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<td>NO</td>
</tr>
<tr>
<td>27-G$^A$</td>
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<td>0</td>
<td>NO</td>
</tr>
<tr>
<td>27-G$^A$</td>
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<td>0</td>
<td>NO</td>
</tr>
<tr>
<td>27-G</td>
<td>0.5</td>
<td>0.25</td>
<td>NO</td>
</tr>
<tr>
<td>27-G$^A$</td>
<td>1.0</td>
<td>0.25</td>
<td>NO</td>
</tr>
<tr>
<td>27-G$^A$</td>
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<td>NO</td>
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<td>NO</td>
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</tr>
<tr>
<td>27-G</td>
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<td>1.0$^B$</td>
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<td>0$^B$</td>
<td>Yes</td>
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<td>27-G</td>
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<td>1.0$^B$</td>
<td>Yes</td>
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<tr>
<td>27-G</td>
<td>4.0</td>
<td>2.0</td>
<td>NO</td>
</tr>
</tbody>
</table>

A. The inoculum in these experiments was from Nutrient Broth with 2% LAS as a supplement. The final OD of the inoculum culture was 0.987 compared to 1.05 for the unsupplemented Nutrient Broth. Both were started from a slant culture.

B. Also contained 1.5 g/L Citrate
Table 5.14  Mixed Surfactant Mixture Table

<table>
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<tr>
<th>Code</th>
<th>N25-7</th>
<th>N25-3</th>
<th>N25-3S</th>
<th>LAS</th>
<th>Volume</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>30g</td>
<td>10g</td>
<td>10g</td>
<td>0g</td>
<td>500ml</td>
</tr>
<tr>
<td>B</td>
<td>30g</td>
<td>3g</td>
<td>0g</td>
<td>10g</td>
<td>500ml</td>
</tr>
<tr>
<td>C</td>
<td>30g</td>
<td>0g</td>
<td>0g</td>
<td>10g</td>
<td>500ml</td>
</tr>
</tbody>
</table>

Table 5.15  Mixed Surfactant Results

<table>
<thead>
<tr>
<th>Solution 1%</th>
<th>Strain</th>
<th>Oil</th>
<th>$\rho_{sol}$</th>
<th>$\mu$</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
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<td>decane</td>
<td>0.375</td>
<td>0.22</td>
</tr>
<tr>
<td>B</td>
<td>15528</td>
<td>decane</td>
<td>0.375</td>
<td>0.22</td>
</tr>
<tr>
<td>C</td>
<td>15528</td>
<td>decane</td>
<td>0.375</td>
<td>0.20</td>
</tr>
<tr>
<td>A</td>
<td>21909</td>
<td>decane</td>
<td>0.375</td>
<td>—</td>
</tr>
<tr>
<td>B</td>
<td>21909</td>
<td>decane</td>
<td>0.375</td>
<td>0.20</td>
</tr>
<tr>
<td>C</td>
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<td>decane</td>
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<td>0.19</td>
</tr>
<tr>
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<td>octane</td>
<td>0.75</td>
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</tr>
<tr>
<td>C</td>
<td>21909</td>
<td>octane</td>
<td>0.75</td>
<td>0.1</td>
</tr>
</tbody>
</table>

^: Run not finished

5.3.15  Discussion of the effect of small micelles

The data presented above demonstrate clearly that when normal alkanes are solubilized in small micelles of synthetic nonionic surfactants, the rate of biodegradation can substantially increase. This finding was true for two strains of bacteria but did not hold for a third strain. While nonionic systems were favorable the use of anionic micelles prevented uptake and utilization. At this point, it appears to be a transport effect rather than an inhibition effect, i.e., interference with the cell biochemistry.
As will be shown later, it was possible, using a mathematical model, to simulate the cell growth and hydrocarbon consumption data for n-alkanes. This suggests that, at least in these situations where individual micelles are much smaller than the bacteria and typically contain no more than few hundred hydrocarbon molecules, the main effect is an effective increase in the solubility of the hydrocarbon in the aqueous phase. The incorporation into the micelles of the alkane is the creation of a single thermodynamic phase. The model of bacteria attaching to oil droplets is no longer valid as there are no longer insoluble oil droplets. The oil now appears as would a soluble substrate. The data indicate that it is possible to increase the growth rate by increasing the concentration of the alkane present in solution. This increases the chemical potential (driving force) for the uptake and consumption of the oil from the micelles.

The results obtained for the cloud point systems also indicate the importance of the general effect of having the oil in a water continuous phase albeit one that is surfactant rich, has larger micelles and is a true separate phase. The closeness of the growth rates obtained indicate that it is the presence of micelles and not necessarily their distribution (uniformly dispersed or concentrated in a surfactant rich phase) that enhances the growth.
Goswami and Singh (5) reported that “pseudosolubilization” of n-hexadecane by glycoproteins produced during growth of Pseudomonas strain N1 caused its growth factor \( \mu \) to be about a factor of two greater than that observed for a similar strain M1 that did not produce molecules capable of incorporating hydrocarbon. They conducted their experiments with bulk n-hexadecane present, in contrast to our procedure, and it is of interest that strain N1 also produced a lipoprotein that facilitated emulsification of the oil. The glycoprotein responsible for pseudosolubilization was rather specific to the particular hydrocarbon present. In our case the surfactant micelles are capable of solubilizing various hydrocarbons though solubilization decreases for longer-chain compounds (Figure 5.1). It is noteworthy that the doubling times reported by Goswami and Singh (5)-- about 5 hours for strain N1 with pseudosolubilization and 10 hours for strain M1 -- are of the same order of magnitude as those given above for our systems.

Miller and Bartha (58) reported that solubilization of long-chain hydrocarbons below their melting points in phospholipid liposomes increased their rate of degradation by a Pseudomonas strain. This use of biosurfactants or bioemulsifiers was continued by Zhang and Miller (59) who have looked at octadecane dispersed by a \textit{Pseudomonas} rhamnolipid. The liposomes used in these two studies were estimated to be 20-50 nanometers in diameter, at least five to ten times larger than our micelles. It is unclear if true micelles were present in their studies. They postulated these aggregates could easily cross the outer membrane of the \textit{Pseudomonas} bacteria used in the experiments. While they did provide data showing the uptake of the alkanes, the evidence did not strongly support the conclusion that the liposomes or micelles crossed the membrane.

The limited data presented in Section 5.3.12 indicate that the bacteria will readily grow in a microemulsion system. The large amount of substrate available then might allow for sustained growth and subsequent oxidation of the substrate at maximal rates. The narrow ranges where microemulsion systems exist provide extra challenges for use in biodegradation experiments. However, microemulsions should not be ruled out for future work as
they present perhaps a way to deliver the maximum amount of hydrocarbon to the bacteria on a weight basis of surfactant.
5.4 Kinetic Expression Development

5.4.1 Single Soluble Substrate Expression

The traditional kinetic expressions used for bacteria growing on a soluble substrate are often based on the empirical relationship developed by Monod. This "saturation" expression has proved to be useful in a variety of cases by other workers and thus provides a good starting point for this work. For growth in a batch system, we can describe the change in cell mass, \( X \), by:

\[
\frac{dX}{dt} = \mu X
\]

Equation (6)

and the change in the substrate, \( S \), by

\[
\frac{dS}{dt} = -\frac{1}{Y} \left( \frac{dX}{dt} \right)
\]

Equation (7)

The growth rate, \( \mu \), in equation 6 is given by

\[
\mu = \mu_{\text{max}} \frac{S}{K_s + S}
\]

Equation (8)

Substituting this into equation 6 gives the following familiar batch mass balance equations:

\[
\frac{dX}{dt} = X \left[ \mu_{\text{max}} \frac{S}{K_s + S} \right]
\]

Equation (9)

\[
\frac{dS}{dt} = -\frac{1}{Y} \left( X \left[ \mu_{\text{max}} \frac{S}{K_s + S} \right] \right)
\]
The units for the cell mass, substrate and \( K_s \) are [g/L]. The units for \( \mu_{\text{max}} \) are hr\(^{-1}\) and the yield, \( Y \), are

\[
\frac{\text{dry cell mass \[g\]}}{\text{substrate consumed \[g\]}}
\]
5.4.2 Dual Substrates with the same enzyme pathway

The general form of the empirical Monod expression is compatible with the Michaelis-Menten expression from enzyme kinetics. The treatment of competitive binding has been done for enzyme systems, and this is the starting point for an analogous development for a system with solubilization of multiple oils. The confidence in this approach is increased as the metabolic pathways for the different hydrocarbons are likely the same, and hence they will be competing for the same metabolic machinery.

Consider the alkB enzyme system, $E$, and two alkane substrates, $S_1$ and $S_2$ and define the following reactions:

\[
\begin{align*}
E + S_1 & \overset{k_1}{\rightleftharpoons} ES_1 \overset{k_3}{\to} E + P_1 \\
\text{and} \quad & \frac{1}{k_2}
\end{align*}
\quad \text{Eqn (10)}
\]

\[
\begin{align*}
E + S_2 & \overset{k_4}{\rightleftharpoons} ES_2 \overset{k_6}{\to} E + P_2 \\
\text{and} \quad & \frac{1}{k_5}
\end{align*}
\quad \text{Eqn (11)}
\]

Define the following:

\[
K_{S_1} = \frac{k_2 + k_3}{k_1} \quad \text{and} \quad K_{S_2} = \frac{k_4 + k_6}{k_4}
\quad \text{Eqn (12)}
\]

From Equations 10 and 11 we can write the following mass balances:

\[
\frac{dES_1}{dt} = k_1E \cdot S_1 - k_2ES_1 - k_3ES_1
\quad \text{Eqn (13)}
\]
and

\[
\frac{dES_2}{dt} = k_4E \cdot S_2 - k_3ES_2 - k_6ES_2
\]

_Eqn (14)_

This differential form of the mole balance contains the active intermediate and we would like to eliminate it so that we can obtain a closed-form solution. If we assume that the active intermediates have a high specific reaction rate and are present at small levels, we can invoke the pseudo-steady state hypothesis\(^\dagger\). This approximation says that the rate of formation of the intermediate is equal to its rate of disappearance. This is a common approximation for enzyme kinetics (60). At the pseudo-steady-state, Equation 15, and using the definitions from Equation 12 we have:

\[
\frac{dES_1}{dt} = \frac{dES_2}{dt} = 0
\]

_Eqn (15)_

\[
ES_1 = \frac{E \cdot S_1}{K_{S_1}}
\]

_Eqn (16)_

\[
ES_2 = \frac{E \cdot S_2}{K_{S_2}}
\]

_Eqn (17)_

\(^\dagger\) See R. Aris, Am. Sci., 58, 419 (1970)
From the mass balance on the enzyme system we also know that the total amount of enzyme present is given by:

\[ E_0 = E + ES_1 + ES_2 \quad \text{Eqn (18)} \]

Substituting Equations 16 and 17 into Equation 18 and solving for \( E \) provides the following expression:

\[ E = \frac{E_0}{1 + \frac{S_1}{K_{S_1}} + \frac{S_2}{K_{S_2}}} \quad \text{Eqn (19)} \]

Equation 19 is substituted back into the steady-state relationships to give:

\[ ES_1 = \frac{E_0 \cdot S_1}{K_{S_1}\left(1 + \frac{S_2}{K_{S_2}}\right) + S_1} \quad \text{Eqn (20)} \]

and

\[ ES_2 = \frac{E_0 \cdot S_2}{K_{S_2}\left(1 + \frac{S_1}{K_{S_1}}\right) + S_2} \quad \text{Eqn (21)} \]

From Equation 10 we write the rate of substrate utilization for \( S_1 \) as:

\[ \frac{dS_1}{dt} = -k_1E \cdot S_1 + k_2ES_1 \quad \text{Eqn (22)} \]

Combining equations 22 and 13 gives:

\[ \frac{dS_1}{dt} = -k_2ES_1 \quad \text{Eqn (23)} \]
Invoking Equation 20 results in the following:

$$\frac{dS_1}{dt} = -k_3 \frac{E_O \cdot S_1}{K_{S_1} \left(1 + \frac{S_2}{K_{S_2}}\right) + S_1} \quad Eqn (24)$$

We recognize the form of this expression as that of the single substrate Monod expression

$$\frac{dS}{dt} = -\left(\frac{\mu_{\text{max}}}{Y}\right) X \frac{S}{K_S + S}$$

From this we write:

$$k_3 E_O = \left(\frac{\mu_{\text{max}}}{Y_1}\right) X \quad Eqn (25)$$

and substitute it into Equation 24 to give the following expression for the substrate utilization:

$$\frac{dS_1}{dt} = -\left(\frac{\mu_{\text{ml}}}{Y_1}\right) \frac{S_1 X}{K_{S_1} \left(1 + \frac{S_2}{K_{S_2}}\right) + S_1} \quad Eqn (26)$$
There is a similar expression for the second substrate:

\[
\frac{dS_2}{dt} = -\left(\frac{\mu_{m2}}{Y_2}\right) \frac{S_2 X}{K_{S_2} \left(1 + \frac{S_1}{K_{S_1}}\right) + S_2} \quad Eqn (27)
\]

Growth on the combined substrates is then given by:

\[
\frac{dX}{dt} = X \left[ \mu_{m1} \frac{S_1}{K_{S_1} \left(1 + \frac{S_2}{K_{S_2}}\right) + S_1} + \mu_{m2} \frac{S_2}{K_{S_2} \left(1 + \frac{S_1}{K_{S_1}}\right) + S_2} \right] \quad Eqn (28)
\]
5.4.3 Complete Kinetic Expression

The previous three equations, 26-28, describe three generalized mass balances for the consumption of dual substrates with competitive enzymatic interaction. After some initial analysis, the data with two solubilized hydrocarbons supported replacing $\mu_{m1}$ and $\mu_{m2}$ with the same specific growth rate $\mu_m$. Then differences, if any, between growth on the hydrocarbons can be described with different "half-saturation" constants. It is important to note that these $K_s$ terms are not only describing the enzyme interaction but also the difference in the transport of the individual molecules across the membranes. These are the first two main model assumptions, i.e., that the enzyme pathway used for the hydrocarbon is the same and that the differences in utilization are the consequence of different enzyme binding and mass transfer across the membrane. The next assumption is that the growth on the hydrocarbon is preferential to that of the surfactant and that even small amounts of oil exert an inhibitory effect on the use of the surfactant as substrate. This work did not attempt to determine the nature of the inhibition so it is not possible to say if the inhibition was of the nature of that observed with the lac operon, or if the effect is just to extend the lag period for the consumption of the surfactant due to the presence of a readily degradable substrate. In order to model this observed effect, a mathematical "lag" function was incorporated. Although the use of an empirical expression is less satisfying than description of the actual enzymatic interactions, it did serve its function adequately. The next process is an ongoing endogenous mechanism. The process is difficult to describe but can be viewed as the maintenance energy and death of the cell and the subsequent release of soluble material back into the media. The following three mass balances include the above assumptions and processes. The other major assumptions are that the hydrocarbons are the limiting substrates, that is, oxygen and nitrogen are available at all times, and that the surfactant is in great enough concentration that growth on it is essentially constant:
\[
\frac{dX}{dt} = X \left[ \mu_m \left( \frac{S_1}{K_{S_1} \left( 1 + \frac{S_2}{K_{S_1}} \right) + S_1} \right) + \frac{S_2}{K_{S_2} \left( 1 + \frac{S_1}{K_{S_1}} \right) + S_2} \right] + \frac{k_{bar}}{k_{bar} + \sqrt{S_1 + S_2}} \mu_{surf} - k_D
\]

Eqn (29)

\[
\frac{dS_1}{dt} = -\left( \frac{\mu_{ml}}{Y_1} \right) \frac{S_1X}{K_S \left( 1 + \frac{S_2}{K_{S_2}} \right) + S_1}
\]

Eqn (30)

\[
\frac{dS_2}{dt} = -\left( \frac{\mu_{m2}}{Y_2} \right) \frac{S_2X}{K_{S_2} \left( 1 + \frac{S_1}{K_{S_1}} \right) + S_2}
\]

Eqn (31)

The "kbar" term in equation 29 is the mathematical switching function that serves to turn on the surfactant growth when the hydrocarbon is depleted. The square root of the substrate concentration delayed the switch over a longer period than a linear term did and this produced better optimization results than did the linear term. This is shown in the following figure comparing two different switching functions. The top figure is for a single alkane; the bottom figure is for a multiple alkane system. A single hydrocarbon system reduces to two mass balances, one for the cell mass and the other for the single oil with simplified saturation kinetics.
Figure 5.11 Effect of different forms of the switching function

- Linear Switching Term
- Square Root Switching Term
- Alkane Substrate
5.5 Mathematical Model Description

5.5.1 Numerical and Statistical Approach

In order to test how well the above model system described the experimental data, model testing and discrimination was done using the Simusolv® Software package. This package allows for the parameter estimation of non-linear models using the maximum likelihood method. One of the key features of this method is that it includes an estimated error in the model analysis. The integration method used was Gear's Backward Difference Formula. This method is ideally suited for solving stiff ordinary differential equations such as the ones previous described. The parameter estimates are determined through an optimization routine which attempts to maximize a specified objective function, which for these analyses is the log likelihood function (LLF). The algorithm integrates the system of equations and then performs the statistics comparing the output of integration to the experimental data. Complete details can be found in the SimuSolv manual (61). It performs a separate integration for each of the data sets using the initial conditions for the cell mass, hydrocarbon, sample times and termination time. This procedure is repeated until the optimum, that is the maximum value for the objective function is located.
The first attempts at parameter estimation looked at individual data sets at the same bacteria, surfactant and alkane combinations. The results indicated that the surfactant concentration had little impact on the parameter estimates. The decision was made to group all the data according to bacteria, surfactant and alkane. The groupings are shown in Table 5.16. These data were then used to develop the final parameter estimates. The groups vary in the number of experimental sets depending on the number of different conditions tested. The estimates were done using the results of at least four experiments for each set listed in the table. The model definition programs are shown on the next two pages. The programs use the same algorithm and are set up in the same way. The primary difference is that the single hydrocarbon program has only two mass balances and the kinetic expression has been mathematically simplified. However it is clear that the single hydrocarbon program is the result of simplifying the multiple substrate program when the concentration of the second oil is set to zero.
PROGRAM -Multiple Hydrocarbon
VARIABLE TIME, TIME0 = 0.0
ALGORITHM IALG = 2
CONSTANT TSTOP = 20. $ 'LENGTH OF EXPERIMENT'
CONSTANT POINTS = 50. $ 'NUMBER OF OUTPUT POINTS'
CONSTANT KS1=0.1, Y1=1, GRM1=0.43, X0=0.05, S10=1.0, KD=0.05
CONSTANT GRSURF=0.13, LB =0.0, UB = 100
CONSTANT KBAR=0.01, KS2=0.3, S20=1.0, Y2=1.
INITIAL

CINT = TSTOP / POINTS $ 'SPECIFY COMMUNICATION INTERVAL'

END

DYNAMIC

DERIVATIVE

XS1=-(1/Y1)*X*(ST1*GRM1/(KS1*(1+ST2/KS2)+ST1))
XS2=-(1/Y2)*X*(ST2*GRM1/(KS2*(1+ST1/KS1)+ST2))
XA=X*((ST1*GRM1/(KS1*(1+ST2/KS2)+ST1)) ... +GRSURF*(KBAR/(KBAR+sqrt(ST1+ST2)))-KD)
S1=INTEG(XS1,S10)
S2=INTEG(XS2,S20)
ST1 = BOUND(LB,UB,S1) $'Prevent negative numbers to sqrt'
ST2 = BOUND(LB,UB,S2)
X=INTEG(XA,X0)

END

TERM(TIME .GE. TSTOP ) $ 'DEFINE TERMINATION CONDITION'

END

TERMINAL

END

END
PROGRAM - Single Hydrocarbon

VARIABLE TIME, TIME0=0.0
ALGORITHM IALG =2
CONSTANT TSTOP = 20. $ 'LENGTH OF EXPERIMENT'
CONSTANT POINTS = 50. $ 'NUMBER OF OUTPUT POINTS'
CONSTANT KS1=0.1,Y1=1.,GRM1=0.43,X0=0.05,S10=1.0,KD=0.05
CONSTANT GRSURF=0.130, LB =0.0 , UB = 100.
CONSTANT KBAR=0.01.

INITIAL

CINT = TSTOP / POINTS $ 'SPECIFY COMMUNICATION INTERVAL'

END

DYNAMIC

DERIVATIVE
XSL1=-(1/Y1)*X*(ST1*GRM1/(KS1+ST1))
X= X*( (ST1*GRM1/(KS1+ST1))...
+GRSURF*(KBAR/(KBAR+sqrt(ST1)))-KD)
S1=INTEG(XS1,S10)
ST1 = BOUND(LB,UB,S1)
X=INTEG(XA,X0)

END

TERMT( TIME .GE. TSTOP ) $ 'DEFINE TERMINATION CONDITION'

END
TERMINAL
END

END
<table>
<thead>
<tr>
<th>Group</th>
<th>Set</th>
<th>Strain</th>
<th>Surfactant</th>
<th>Conc [g/L]</th>
<th>Oil 1</th>
<th>Oil 2</th>
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<th>S2 [g/L]</th>
<th>Statistical Output</th>
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<td>90/10</td>
<td>5</td>
<td>C_{10}</td>
<td></td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
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<td>3</td>
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<td>90/10</td>
<td>5</td>
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5.6 Parameter Estimation Determination

5.6.1 Section Description

This section presents further discussion of the estimation process and the significant features of the statistical process used. This is followed by a results summary which presents the summarized the main findings of the parameter estimation. Finally, the detailed fitting logs are presented along with plots of the simulated and experimental data. The fitting logs provide the statistical information used in generating the results summary.

5.6.2 Process Description

While the process of nonlinear fitting and parameter estimation is made substantially easier with the use of optimization algorithms, there is still a great deal of manual work involved in the process. Additionally, attention must be paid to the physical reality of the determined constants. In this case the main check was the observed yield. The process is an iterative one that involves determining the initial guesses for the parameters and then running a simulation using the parameters and finally doing a “visual” determination of fit, that is, looking at the predicted curves and the experimental data. This manual tweaking is important because it is possible for an optimization algorithm to fail due to lack of convergence or to arrive at a local maximum. This can occur when the initial guess is too far from the optimal value. Also, an understanding of the model behavior as a function of the parameters can be gained. Once a good manual fit has been achieved, the optimization routine is invoked. As mentioned before, it performs numerous integrations and parameter adjustments while attempting to maximize the objective function, in this case, the log likelihood function. After the parameters are estimated, a statistical report is generated that is used to determine the goodness of the estimation as well as red flag possible problems with the model. This output is used to determine if the results should be accepted or further refinement (including a new model formulation) is required.

The statistical output describes the optimization results, and it also contains graphical comparisons of the simulation results and the data, i.e., a residual plot. The
output has the parameter estimates, the maximized value of the log likelihood function for
the multivariate case, the standard deviation for each estimate, and the statistical summary.
The results of the integration using the optimized parameter estimates and the comparison
with the experimental values and the residual plots for all the data sets analyzed are
included in the appendices. The statistical summary shows the associated error and the
percentage of variation explained as well as the correlation matrix. Tables of the results
are presented later in this chapter.

The correlation matrix is a way of representing the stability of the each of the
parameter estimates. In general, correlations above 0.99 in absolute value are a red flag
that further investigation is needed (62). One or more of the following can be happening.
First, this can be an indication of too much variability in the data. Second, the model may
be overspecified and the model may have nuisance parameters. Third the model may not
be formulated correctly and therefore the parameters are coupled. This work we used a
conservative value of 0.8 for the correlation matrix values. When indicated by the above,
further statistical tests were done to verify that the appropriate model

The following three plots show how the determination of the model fit was
made. They show plots of the LLF as functions of model parameters. In a good fit there is
a well defined maximum. The plots are from the Group 1 data set and show that param-
eter estimation is well behaved.
PLEASE NOTE

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The following groups were dual substrate runs and subject to testing using the Non-inhibited model.
5.6.3  Results Summary

The use of the statistical fitting capabilities of SimuSolv® allowed for the verification of the kinetic models proposed in Section 5.4. Nonlinear regression was used by Miller and Bartha to determine $\mu_{\text{max}}$ and $K_s$ for solubilization enhancement of octadecane (58). They do not describe the method used in their regression. Guha and Jaffé (48) have also used the maximum likelihood function for analysis of their nonlinear transport equations.

The generally good agreement of the proposed models and the observed growth behavior supports the conclusion that the solubilization of alkanes in small micelles actually presents the oil to the bacteria as a soluble substrate versus macroscopic bulk oil drops. This is a fundamental change in the interaction between the bacteria and the previously insoluble substrate. Furthermore there is good support for the conclusion that the net growth rate of the bacteria on a particular alkane is controlled by the a combination of enzyme binding and different transport rates across the membrane. That is, the maximum specific growth rate $\mu_{\text{max}}$ would have been observed if the supply was not limited by membrane transport and enzyme binding reflected by variations in the $K_s$ term.

An alternative interpretation of the Monod equation in terms of mass transfer has recently been proposed (63). This interpretation is similar to ours and has been used by others to describe their surfactant influenced biodegradation (47,48). One significant difference between our model and Guha's is that we assumed that bulk mass transfer to the cell was not limiting, all the solubilized hydrocarbon was available, and that the limiting mass transfer was across the membrane. In addition we also still include substrate enzyme interactions including inhibition which the Merchuk proposal would ignore.
The correlation matrix reported in the statistical output also provides insight into the goodness of fit and validity of the model. If there was evidence of high correlation, then investigation of reduced models was carried out. This was accomplished through trying to fit the experimental data with a reduced parameter model. To do this a particular parameter like $k_D$ is set to zero and the data are fit as before but with the reduced set of parameters. The values of the LLF are then compared using a a chi-square test. By multiplying the competitive interaction terms $\frac{S_1}{K_{S1}}, \frac{S_2}{K_{S2}}$ by the integer value 0, the model is reduced to a dual substrate Monod model without interaction. The results are shown in Table 5.17. The table contains the values for the LLF function using the “best” estimates for the full model, the model less the surfactant growth, the model less the decay and the model less both the surfactant and decay terms. For the dual substrate systems the LLF values are also included for the non-inhibited reduced model. The reduced model LLF values are compared to the full model LLF value using a chi-squared test ($\chi^2 = -2 \times \text{LLF}_R - \text{LLF}_{\text{Full}}$). The confidence level reported for each level is our confidence that the full model describes the data better than the reduced model.

Overall the full model was the best in describing the data. However there were cases where this was not true. This was most likely due to a limited amount of data, i.e., not enough information to allow for the model discrimination. In particular, it occurred when the run times were not long enough to show growth on the surfactant or significant decay. However, the data do support the use of the general form of kinetic expression used in the model for the uptake and oxidation of the alkanes. One notable success was the ability of the inhibition model to describe the data better for all mixed oil systems except for group 8. In this case it was possible to fit the data using the non-inhibited model. This was probably due to the nearly identical kinetic constants for these two alkanes. The suppression of growth on the surfactant by the presence of available hydrocarbon is also indicated by the results.
The next three tables summarize the results of the parameter estimation. These represent the analyses of all the sets of data as grouped in Table 5.16. The results for strain 15528 are in Table 5.18. The results for strain 21909 are in Table 5.19. The results for mixed oil testing are in Table 5.20. The data presented are the parameter estimates for $\mu_{\text{max}}$, $K_S$, yield, $\mu_{\text{surfactant}}$, and the decay coefficient, $k_D$. The standard deviations of each estimate are also included. The standard deviations represent how much variability exists for each estimate. As the data population increases standard deviations can get quite small as seen in the estimates for group 1. Consequently, we do not judge the models by standard deviations alone.

The first noteworthy feature of the results is consistency of the values for $\mu_{\text{max}}$ obtained for each of the strains. Strain 15528 had a mean value of $0.45 \text{ hr}^{-1} \pm 0.01$ with a normal distribution of values. Strain 21909 had a mean value of $0.30 \text{ hr}^{-1} \pm 0.01$ also with a normal distribution of values. The variation in growth rates is reflected the values obtained for $K_S$. These show a strong dependence on the type of surfactant and the alkane. The strain 15528's values for $K_S$ increased for the oils as follows; $C_{10} < C_{16} < C_{12} = C_{14}$. This was true in both N90/10 and N25-7 systems and in the mixed oil systems where the values obtained for $K_S$ matched those obtained for the single oil systems. Surprisingly, the values appeared to be independent of the solubilization density and surfactant concentration and hence $W_S$. This indicates that bulk mass transfer, i.e., the availability of the micelles to the bacteria is not limiting. The strain 21909's values for $K_S$ increased for the oils as follows; $C_{16} < C_{10} < C_{14}$. The low $K_S$ value obtained for hexadecane is interesting and may be due to better enzyme interaction. The consistency of the $\mu_{\text{max}}$ and $K_S$ values between the single hydrocarbon and mixed hydrocarbon systems supports the model assumption that transport across the membrane is different for different alkanes and that different alkanes can interfere with each other. This is shown in group 13 where decane was used faster than the three other alkanes all present at the same concentration. An interesting experiment would be use a high solubilizing system so that a slower utilized alkane
could be present at a significantly higher solubilization density than the faster utilized alkane. This experiment might elucidate the relative importance of the enzyme interactions compared to mass transfer.

The yield parameter estimates obtained were slightly higher than those determined in the experiments which was to be expected as the model incorporates a decay term. Consequently what we are estimating is a true yield vs. an observed yield (57). The yield values did appear to follow an increasing trend as the alkane chain length increased. This result was consistent with what other workers have observed (1, 14,57,64).

The estimates of the decay term and $\mu_{\text{surf}}$ were the more difficult parameters to obtain. This is reflected in results from the reduced model comparison in Table 5.17. The estimate for the $\mu_{\text{surf}}$ term used only the observed growth of the bacteria and was cast as a first order term, since we had no method available to measure the change in concentration of the surfactant during the batch run. Percentage change was probably minimal in any case, with the large surfactant concentrations we used. Further the experiments had to be run long enough to demonstrate growth on the surfactant. This was especially true for the runs with dodecane and tetradecane as even small amounts of hydrocarbon appeared to inhibit the growth on the surfactants. The decay term was included to model the flat or declining cell densities observed in some of the experiments. Some examples of this can be seen in Figures 5.43 through 5.46. Further discussion of the individual run results are given in the fitting logs that follow the tables.
### Table 5.18: Summary of Kinetic Parameters for Strain 15528

<table>
<thead>
<tr>
<th>Group</th>
<th>Surfactant</th>
<th>Hydro-carbon</th>
<th>$\mu_{\text{max}}$</th>
<th>$\text{SD}$</th>
<th>$K_S$</th>
<th>$\text{SD}$</th>
<th>Yield</th>
<th>$\text{SD}$</th>
<th>$K_D$</th>
<th>$\text{SD}$</th>
<th>$\mu_{\text{surf}}$</th>
<th>$\text{SD}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>90/10</td>
<td>C_{10}</td>
<td>0.465 ±7E-07</td>
<td>0.094 ±9E-07</td>
<td>1.23 ±5E-06</td>
<td>0.052 ±3E-07</td>
<td>0.11 ±5E-07</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>14</td>
<td>90/10</td>
<td>C_{12}</td>
<td>0.458 ±0.01</td>
<td>0.63 ±0.05</td>
<td>1.37 ±0.052</td>
<td>0.050 ±0.004</td>
<td>0.12 ±0.04</td>
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<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>11</td>
<td>90/10</td>
<td>C_{14}</td>
<td>0.444 ±0.002</td>
<td>0.60 ±0.01</td>
<td>1.52 ±0.008</td>
<td>0.05 ±0.001</td>
<td>0.09 ±0.022</td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>90/10</td>
<td>C_{16}</td>
<td>0.448 ±0.004</td>
<td>0.30 ±0.005</td>
<td>1.48 ±0.015</td>
<td>0.049 ±0.0004</td>
<td>0.09 ±0.026</td>
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<tr>
<td>2</td>
<td>25-7</td>
<td>C_{10}</td>
<td>0.450 ±0.0003</td>
<td>0.21 ±0.0002</td>
<td>1.14 ±0.0014</td>
<td>0.056 ±4E-6</td>
<td>0.13 ±0.0003</td>
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<tr>
<td>3</td>
<td>25-7</td>
<td>C_{12}</td>
<td>0.462 ±0.0077</td>
<td>0.69 ±0.02</td>
<td>1.46 ±0.02</td>
<td>0.055 ±0.007</td>
<td>0.088 ±0.0055</td>
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<tr>
<td>12</td>
<td>25-7</td>
<td>C_{14}</td>
<td>0.444 ±0.004</td>
<td>0.725 ±0.027</td>
<td>1.52 ±0.026</td>
<td>0.05 ±0.003</td>
<td>0.11 ±0.0014</td>
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</tr>
<tr>
<td>4</td>
<td>25-7</td>
<td>C_{16}</td>
<td>0.438 ±0.008</td>
<td>0.393 ±0.017</td>
<td>1.58 ±0.04</td>
<td>0.048 ±0.004</td>
<td>0.12 ±0.022</td>
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### Table 5.19: Summary of Kinetic Parameters for Strain 21909

<table>
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<tr>
<th>Group</th>
<th>Surfactant</th>
<th>Hydro-carbon</th>
<th>$\mu_{\text{max}}$</th>
<th>SD</th>
<th>$K_s$</th>
<th>SD</th>
<th>Yield</th>
<th>SD</th>
<th>$K_D$</th>
<th>SD</th>
<th>$\mu_{\text{surf}}$</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>16</td>
<td>90/10</td>
<td>C\textsubscript{10}</td>
<td>0.312</td>
<td>±0.0021</td>
<td>0.35</td>
<td>±0.012</td>
<td>1.15</td>
<td>±0.016</td>
<td>0.036</td>
<td>±0.002</td>
<td>0.074</td>
<td>±0.0026</td>
</tr>
<tr>
<td>18</td>
<td>90/10</td>
<td>C\textsubscript{14}</td>
<td>0.286</td>
<td>±0.002</td>
<td>0.518</td>
<td>±0.0093</td>
<td>1.48</td>
<td>±0.012</td>
<td>0.028</td>
<td>±0.0005</td>
<td>0.066</td>
<td>±0.002</td>
</tr>
<tr>
<td>17</td>
<td>25-7</td>
<td>C\textsubscript{10}</td>
<td>0.301</td>
<td>±0.001</td>
<td>0.369</td>
<td>±0.005</td>
<td>1.14</td>
<td>±0.009</td>
<td>0.036</td>
<td>±0.087</td>
<td>0.07</td>
<td>0.002</td>
</tr>
<tr>
<td>19</td>
<td>25-7</td>
<td>C\textsubscript{14}</td>
<td>0.289</td>
<td>±0.005</td>
<td>0.521</td>
<td>±0.006</td>
<td>1.48</td>
<td>±0.007</td>
<td>0.025</td>
<td>±0.0001</td>
<td>0.06</td>
<td>0.0016</td>
</tr>
<tr>
<td>20</td>
<td>25-7</td>
<td>C\textsubscript{16}</td>
<td>0.296</td>
<td>±0.005</td>
<td>0.083</td>
<td>±0.0045</td>
<td>1.60</td>
<td>±0.04</td>
<td>0.04</td>
<td>±0.003</td>
<td>0.07</td>
<td>0.001</td>
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### Table 5.20: Summary of Kinetic Parameters for Mixed Systems

All Groups used Strain 15528 except Group 21 which used Strain 21909

<table>
<thead>
<tr>
<th>Group</th>
<th>Surfactant</th>
<th>Oil</th>
<th>$\mu_{\text{max}}$</th>
<th>SD</th>
<th>$K_s$</th>
<th>SD</th>
<th>Yield</th>
<th>SD</th>
<th>$K_D$</th>
<th>SD</th>
<th>$\mu_{\text{surf}}$</th>
<th>SD</th>
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<tr>
<td>5</td>
<td>$C_{10}$</td>
<td>25-7</td>
<td>0.446</td>
<td>±0.001</td>
<td>0.238</td>
<td>±0.0004</td>
<td>1.2</td>
<td>±0.0006</td>
<td>0.049</td>
<td>±0.0001</td>
<td>0.09</td>
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<tr>
<td></td>
<td>$C_{12}$</td>
<td></td>
<td></td>
<td></td>
<td>0.667</td>
<td>±0.0007</td>
<td>1.38</td>
<td>±0.0005</td>
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<tr>
<td>6</td>
<td>$C_{10}$</td>
<td>25-7</td>
<td>0.451</td>
<td>±0.0004</td>
<td>0.248</td>
<td>±0.002</td>
<td>1.19</td>
<td>±0.005</td>
<td>0.049</td>
<td>±0.0001</td>
<td>0.09</td>
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<tr>
<td></td>
<td>$C_{14}$</td>
<td></td>
<td></td>
<td></td>
<td>.743</td>
<td>0.005</td>
<td>1.40</td>
<td>±0.002</td>
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<tr>
<td>7</td>
<td>$C_{10}$</td>
<td>25-7</td>
<td>0.447</td>
<td>±0.00078</td>
<td>0.216</td>
<td>±0.002</td>
<td>1.12</td>
<td>±0.01</td>
<td>0.052</td>
<td>±0.0003</td>
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<tr>
<td></td>
<td>$C_{16}$</td>
<td></td>
<td></td>
<td></td>
<td>0.386</td>
<td>±0.0045</td>
<td>1.61</td>
<td>±0.02</td>
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<td>8</td>
<td>$C_{12}$</td>
<td>25-7</td>
<td>0.425</td>
<td>±0.011</td>
<td>0.667</td>
<td>±0.073</td>
<td>1.33</td>
<td>±0.176</td>
<td>0.044</td>
<td>±0.002</td>
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<tr>
<td></td>
<td>$C_{14}$</td>
<td></td>
<td></td>
<td></td>
<td>0.737</td>
<td>±0.113</td>
<td>1.39</td>
<td>±0.167</td>
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<tr>
<td>9</td>
<td>$C_{12}$</td>
<td>25-7</td>
<td>0.437</td>
<td>±0.006</td>
<td>0.657</td>
<td>±0.132</td>
<td>1.41</td>
<td>±0.275</td>
<td>0.051</td>
<td>±0.003</td>
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<tr>
<td></td>
<td>$C_{16}$</td>
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<td></td>
<td></td>
<td>0.382</td>
<td>0.053</td>
<td>1.50</td>
<td>±0.210</td>
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<tr>
<td>10</td>
<td>$C_{14}$</td>
<td>25-7</td>
<td>0.431</td>
<td>±0.0067</td>
<td>.653</td>
<td>±0.053</td>
<td>1.49</td>
<td>±0.092</td>
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<tr>
<td></td>
<td>$C_{16}$</td>
<td></td>
<td></td>
<td></td>
<td>0.360</td>
<td>±0.015</td>
<td>1.52</td>
<td>±0.081</td>
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<tr>
<td>13</td>
<td>$C_{10}$</td>
<td>25-7</td>
<td>0.445</td>
<td>±0.00005</td>
<td>.244</td>
<td>±0.0001</td>
<td>1.2</td>
<td>±0.025</td>
<td>0.049</td>
<td>0.000013</td>
<td>0.07</td>
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<tr>
<td></td>
<td>$C_{12,14,16}$</td>
<td></td>
<td></td>
<td></td>
<td>0.617</td>
<td>±9E-05</td>
<td>1.42</td>
<td>±0.003</td>
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<tr>
<td>21</td>
<td>$C_{10}$</td>
<td>25-7</td>
<td>0.302</td>
<td>±0.0004</td>
<td>0.315</td>
<td>±0.0002</td>
<td>1.28</td>
<td>±0.0002</td>
<td>0.03</td>
<td>±0.00001</td>
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<tr>
<td></td>
<td>$C_{16}$</td>
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<td>0.104</td>
<td>±0.0002</td>
<td>1.5</td>
<td>±0.0002</td>
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</table>
5.6.4 Fitting Log for Group 1: Strain 15528 and Decane, N90/10 System

Group 1 consisted of the most extensively studied system. The group contains ten different sets of experimental conditions as described in the earlier table (see Table 5.16 on page 89) and represents the fifty-six separate experimental runs. The value of the log likelihood function is the greatest for this group due to the large number of data. The simulation results and residual plots are in the appendix. The statistical output is shown in the following table. Selected plots of the data and corresponding simulation with the best estimate parameters follow the table.

The results from these experiments showed remarkably rapid consumption of the decane, followed by a small lag, and then growth on the surfactant. The growth rate estimate for the surfactant was lower than that found in the surfactant only systems, 0.11 hr\(^{-1}\) and 0.16 hr\(^{-1}\) respectively. This might reflect the increasing importance of the decay term as the cell concentration increased. It is possible that another nutrient became limiting but this seems unlikely.
### Table 5.21 Statistical Output for Group 1

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<thead>
<tr>
<th>DESCRIPTION</th>
<th>INITIAL</th>
<th>FINAL</th>
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<tr>
<td>LOG LIKELIHOOD FUNCTION</td>
<td>3279.4</td>
<td>3744.0</td>
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<tr>
<td>GRM1</td>
<td>0.44000</td>
<td>0.46502</td>
</tr>
<tr>
<td>K5</td>
<td>0.10000</td>
<td>9.40775E-02</td>
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<tr>
<td>Y1</td>
<td>1.2000</td>
<td>1.2331</td>
</tr>
<tr>
<td>KD</td>
<td>5.00000E-02</td>
<td>5.24402E-02</td>
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<tr>
<td>GRSURF</td>
<td>0.11000</td>
<td>0.11235</td>
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**STATISTICAL SUMMARY**

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<tr>
<th>MAXIMIZED</th>
<th>WT RESID</th>
<th>WEIGHTED</th>
<th>STANDARD</th>
<th>PERCENTAGE</th>
<th>LOG LIKELIHOOD</th>
<th>SUM OF RESIDUAL</th>
<th>ERROR OF VARIATION</th>
<th>WEIGHTING</th>
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<tr>
<td>FUNCTION</td>
<td>SUM OF SQUARES</td>
<td>SUM</td>
<td>ESTIMATE</td>
<td>EXPLAINED PARAMETER</td>
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<td>OVERALL</td>
<td>3744.2</td>
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<td>X</td>
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<td>2.45</td>
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<tr>
<td>S1</td>
<td>3148.2</td>
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<td>13.0</td>
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<td>92.723</td>
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**CORRELATION MATRIX**

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<tr>
<th></th>
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<th>Y1</th>
<th>KD</th>
<th>GRSURF</th>
</tr>
</thead>
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<td>GRSURF</td>
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**VARIANCE-COVARIENCE MATRIX**

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RESULT TIME = 0.700 SECONDS
Figure 5.15  Plot from Group 1  Set 1. 0.5%N90/10, 1 g/L decane

Figure 5.16  Plot from Group 1  Set 1. 0.5%N90/10, 1 g/L decane
Figure 5.17  Plot from Group 1  Set 2. 0.5%N90/10, 2 g/L decane

Figure 5.18  Plot from Group 2  Set 1. 0.5%N90/10, 2 g/L decane
Figure 5.19  Plot from Group 1  Set 5. 1.0%N90/10, 2 g/L decane

Figure 5.20  Plot from Group 1  Set 5. 1.0%N90/10, 2 g/L decane
Figure 5.21  Plot from Group 1  Set 5. 1.0% N90/10, 2 g/L decane

Figure 5.22  Plot from Group 1  Set 8. 2.0% N90/10, 2 g/L decane
Figure 5.23  Plot from Group 1  Set 8. 2.0%N90/10, 2 g/L decane

Figure 5.24  Plot from Group 1  Set 9. 2.0%N90/10, 4 g/L decane
Figure 5.25  Plot from Group 1  Set 9. 2.0%N90/10, 4 g/L decane

Figure 5.26  Plot from Group 1  Set 9. 2.0%N90/10, 4 g/L decane
Figure 5.27  Plot from Group 1  Set 9. 2.0%N90/10, 4 g/L decane

Figure 5.28  Plot from Group 1  Set 9. 2.0%N90/10, 4 g/L decane
5.6.5 *Fitting Log for Group 2: Strain 15528 and Decane, N25-7*

Group 2 consisted of 4 different sets of experimental conditions as described in the earlier table (see Table 5.16 on page 89). The simulation results and residual plots are in the appendix. The statistical output is shown in the following table. Selected plots of the data and corresponding simulation with the best estimate parameters follow the table.
Table 5.22  Statistical Output for Group 2

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STATISTICAL SUMMARY

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<th>PERCENTAGE EXPLAINED</th>
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CORRELATION MATRIX

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VARIANCE-COVARIANCE MATRIX

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<td>-1.4988E-09</td>
<td>-4.6949E-10</td>
<td>-2.3080E-11</td>
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**Figure 5.29** Plot from Group 2 Set 1. 0.5%N25-7, 1 g/L decane

**Figure 5.30** Plot from Group 2 Set 1. 0.5%N25-7, 1 g/L decane
Figure 5.31  Plot from Group 2 Set 1. 0.5%N25-7, 1 g/L decane

Figure 5.32  Plot from Group 2 Set 1. 0.5%N25-7, 1 g/L decane
Figure 5.33  Plot from Group 2 Set 1. 0.5%N25-7, 1 g/L decane

Figure 5.34  Plot from Group 2 Set 1. 0.5%N25-7, 1 g/L decane
Figure 5.35  Plot from Group 2 Set 3. 2.0% N25-7, 5 g/L decane

Figure 5.36  Plot from Group 2 Set 3. 2.0% N25-7, 5 g/L decane
5.6.6 Fitting Log for Group 3: Strain 15528, Dodecane, N25-7

Group 3 consisted of 2 different sets of experimental conditions as described in the earlier table (see Table 5.16 on page 89). The simulation results and residual plots are in the appendix. The statistical output is shown in the following table. Selected plots of the data and corresponding simulation with the best estimate parameters follow the table.

The limited amount of data for this group, eight runs, and the short run times are reflected in the fact that the full reduced model (i.e., no growth on surfactant and no decay) was able to also adequately represent the data based on the chi-square comparison of the LLF's. The parameter estimates did not change with the exclusion of the surfactant growth term but \( \mu_{\text{max}} \) decreased from 0.46 to 0.45 hr\(^{-1} \) and \( K_s \) decreased from 0.69 to 0.66.
Table 5.23  Statistical Output for Group 3

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STATISTICAL SUMMARY

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<th>STANDARD ERROR OF VARIATION</th>
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CORRELATION MATRIX

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VARIANCE-COVARIANCE MATRIX

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RESULT TIME = 0.140 SECONDS
Figure 5.37  Plot from Group 3 Set 1. 1.0%N25-7, 1 g/L dodecane

Figure 5.38  Plot from Group 3 Set 1. 1.0%N25-7, 1 g/L dodecane
5.6.7 Fitting Log for Group 4: Strain 15528 and Hexadecane, N25-7 System

Group 4 consisted of 2 different sets of experimental conditions as described in the earlier table (see Table 5.16 on page 89). The simulation results and residual plots are in the appendix. The statistical output is shown in the following table. Selected plots of the data and corresponding simulation with the best estimate parameters follow the table.
Table 5.24  Statistical Output for Group 4

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STATISTICAL SUMMARY

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CORRELATION MATRIX

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VARIANCE-COVARIANCE MATRIX

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**Figure 5.39** Plot from Group 4 Set 2. 2.0%N25-7, 0.75 g/L hexadecane

**Figure 5.40** Plot from Group 4 Set 2. 2.0%N25-7, 0.75 g/L hexadecane
Figure 5.41  Plot from Group 4 Set 2. 1.0%N25-7, 0.375 g/L hexadecane

Figure 5.42  Plot from Group 4 Set 2. 1.0%N25-7, 0.375 g/L hexadecane
5.6.8 Fitting Log for Group 5: Strain 15528, Decane and Dodecane, N25-7

Group 5 consisted of one set of experimental conditions as described in the earlier table (see Table 5.16 on page 89). The simulation results and residual plots are in the appendix. The statistical output is shown in the following table. Selected plots of the data and corresponding simulation with the best estimate parameters follow the table.
### Table 5.25 Statistical Output for Group 5 (One Run)

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### STATISTICAL SUMMARY

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<th>STANDARD ERROR OF ESTIMATE</th>
<th>PERCENTAGE VARIATION</th>
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### CORRELATION MATRIX

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### VARIANCE-COVARIANCE MATRIX

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### Table 5.26  Statistical Output for Group 5 (Four All Four Runs)

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**Figure 5.43** Plot from Group 5 Set 1. 1.0%N25-7, 0.375 g/L decane, 0.375 g/L dodecane

**Figure 5.44** Plot from Group 5 Set 1. 1.0%N25-7, 0.375 g/L decane, 0.375 g/L dodecane
Figure 5.45  Plot from Group 5 Set 1. 1.0%N25-7, 0.375 g/L decane, 0.375 g/L dodecane

Figure 5.46  Plot from Group 5 Set 1. 1.0%N25-7, 0.375 g/L decane, 0.375 g/L dodecane
5.6.9 Fitting Log for Group 6: Stain 15528, Decane and Tetradecane, N25-7

Group 6 consisted of one set of experimental conditions as described in the earlier table (see Table 5.16 on page 89). The simulation results and residual plots are in the appendix. The statistical output is shown in the following table. Selected plots of the data and corresponding simulation with the best estimate parameters follow the table.
Table 5.27  Statistical Output for Group 6

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VARIANCE-COVARIANCE MATRIX

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Figure 5.47  Plot from Group 6 Set 1. 1.0%N25-7, 0.375 g/L decane, 0.375 g/L tetradecane

Figure 5.48  Plot from Group 6 Set 1. 1.0%N25-7, 0.375 g/L decane, 0.375 g/L tetradecane
Figure 5.49  Plot from Group 6 Set 1. 1.0%N25-7, 0.375 g/L decane, 0.375 g/L tetradecane

Figure 5.50  Plot from Group 6 Set 1. 1.0%N25-7, 0.375 g/L decane, 0.375 g/L tetradecane
5.6.10 Fitting Log for Group 7: Stain 15528, Decane and Hexadecane, N25-7

Group 7 consisted of one set of experimental conditions as described in the earlier table (see Table 5.16 on page 89). The simulation results and residual plots are in the appendix. The statistical output is shown in the following table. Selected plots of the data and corresponding simulation with the best estimate parameters follow the table.
### Table 5.28  Statistical Output for Group 7

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Figure 5.51  Plot from Group 7 Set 1. 1.0%N25-7, 0.375 g/L decane, 0.375 g/L hexadecane

Figure 5.52  Plot from Group 7 Set 1. 1.0%N25-7, 0.375 g/L decane, 0.375 g/L hexadecane
**Figure 5.53**  Plot from Group 7 Set 1. 1.0%N25-7, 0.375 g/L decane, 0.375 g/L hexadecane

**Figure 5.54**  Plot from Group 7 Set 1. 1.0%N25-7, 0.375 g/L decane, 0.375 g/L hexadecane.
5.6.11 Fitting Log for Group 8: Strain 15528, Dodecane and Tetradecane, N25-7

Group 8 consisted of one set of experimental conditions as described in the earlier table (see Table 5.16 on page 89). The simulation results and residual plots are in the appendix. The statistical output is shown in table 5.30. Selected plots of the data and corresponding simulation with the best estimate parameters follow the table.

As mentioned earlier the closeness of the $K_S$ values for these two hydrocarbons made it difficult to determine a stability set of estimates. Consequently a “non-inhibition” model was able to adequately describe the data. However the parameter estimates were very different for the non-inhibited model as shown in

<table>
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<th>Parameter</th>
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<th>Non-Inhibited</th>
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<tr>
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<td>$K_{S2}$</td>
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<td>$Y_2$</td>
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<td>$K_D$</td>
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<tr>
<td>$H_{\text{surf}}$</td>
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Table 5.30  Statistical Output for Group 8

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STATISTICAL SUMMARY

| MAXIMIZED MAXIMIZED | WT RESID WT RESID | WEIGHTED WEIGHTED |
| LOG LIKELIHOOD LOG LIKELIHOOD | SUM OF SUM |
| FUNCTION FUNCTION | SQUARES SQUARES | RESIDUAL RESIDUAL |
|                   | SUM | SUM | ERROR OF ERROR OF |
|                   | ESTIMATE | EXPLAINED | VARIATION |
|                   | PARAMETER | PARAMETER |
| OVERALL           | 578.2 | 0.140 | -0.456 | 99.343 |
| X                 | 121.9 | 0.104 | -0.155 | 2.934E-02 | 98.616 | 0.61 |
| S1                | 234.2 | 1.195E-02 | -0.115 | 3.170E-03 | 99.800 | 0.72 |
| S2                | 222.1 | 2.432E-02 | -0.186 | 3.577E-03 | 99.691 | 0.90 |

CORRELATION MATRIX

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<th>KS2</th>
<th>Y1</th>
<th>Y2</th>
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VARIANCE-COVARIANCE MATRIX

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<th>KS2</th>
<th>Y1</th>
<th>Y2</th>
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</table>
**Figure 5.55** Plot from Group 8 Set 1. 1.0% N25-7, 0.375 g/L dodecane, 0.375 g/L tetradecane

**Figure 5.56** Plot from Group 8 Set 1. 1.0% N25-7, 0.375 g/L dodecane, 0.375 g/L tetradecane
Figure 5.57  Plot from Group 8 Set 1. 1.0%N25-7, 0.375 g/L dodecane, 0.375 g/L tetradecane

Figure 5.58  Plot from Group 8 Set 1. 1.0%N25-7, 0.375 g/L dodecane, 0.375 g/L tetradecane
5.6.12 Fitting Log for Group 9: Strain 15528, Dodecane and Hexadecane

Group 9 consisted of one set of experimental conditions as described in the earlier table (see Table 5.16 on page 89). The simulation results and residual plots are in the appendix. The statistical output is shown in the following table. Selected plots of the data and corresponding simulation with the best estimate parameters follow the table.
### Table 5.31  Statistical Output for Group 9

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**STATISTICAL SUMMARY**

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<th>STANDARD ERROR OF VARIATION</th>
<th>PERCENTAGE WEIGHTING</th>
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**CORRELATION MATRIX**

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<th>KS2</th>
<th>Y1</th>
<th>Y2</th>
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**VARIANCE-COVARIANCE MATRIX**

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| KD       | 6.3442E-06 |        |        |        |        |
Figure 5.59 Plot from Group 9 Set 1. 1.0%N25-7, 0.375 g/L dodecane, 0.375 g/L hexadecane.

Figure 5.60 Plot from Group 9 Set 1. 1.0%N25-7, 0.375 g/L dodecane, 0.375 g/L hexadecane.
Figure 5.61  Plot from Group 9 Set 1. 1.0% N25-7, 0.375 g/L dodecane, 0.375 g/L hexadecane.

Figure 5.62  Plot from Group 9 Set 1. 1.0% N25-7, 0.375 g/L dodecane, 0.375 g/L hexadecane.
5.6.13 Fitting Log for Group 10: Strain 15528, Tetradecane and Hexadecane, N25-7

Group 10 consisted of one set of experimental conditions as described in the earlier table (see Table 5.16 on page 89). The simulation results and residual plots are in the appendix. The statistical output is shown in the following table. Selected plots of the data and corresponding simulation with the best estimate parameters follow the table.
Table 5.32  Statistical Output for Group 10

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CORRELATION MATRIX

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<th>Y1</th>
<th>Y2</th>
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VARIANCE-COVARIANCE MATRIX

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Figure 5.63  Plot from Group 10 Set 1. 1.0%N25-7, 0.375 g/L tetradecane, 0.375 g/L hexadecane

Figure 5.64  Plot from Group 10 Set 1. 1.0%N25-7, 0.375 g/L tetradecane, 0.375 g/L hexadecane
**Figure 5.65**  Plot from Group 10 Set 1. 1.0%N25-7, 0.375 g/L tetradecane, 0.375 g/L hexadecane

**Figure 5.66**  Plot from Group 10 Set 1. 1.0%N25-7, 0.375 g/L tetradecane, 0.375 g/L hexadecane
5.6.14 Fitting Log for Group 11: Strain 15528, Tetradecane, N90/10 System

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CORRELATION MATRIX

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VARIANCE-COVARIANCE MATRIX

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<td>-2.3179E-06</td>
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<tr>
<td>KS1</td>
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<td>6.7991E-05</td>
<td>5.7771E-06</td>
<td>6.1907E-06</td>
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<td>5.7771E-06</td>
<td>6.1907E-06</td>
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<td>6.7991E-05</td>
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5.6.15 Fitting Log for Group 12: Strain 15528, Tetradecane, N25-7 System

Group 12 consisted of two sets of experimental conditions as described in the earlier table (see Table 5.16 on page 89). The simulation results and residual plots are in the appendix. The statistical output is shown in the following table. Selected plots of the data and corresponding simulation with the best estimate parameters follow the table.
Table 5.33  Statistical Output for Group 12

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<tr>
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STATISTICAL SUMMARY

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<th>VARIATION</th>
<th>PERCENTAGE</th>
<th>WEIGHTING</th>
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<td>SUM</td>
<td>ESTIMATE</td>
<td>EXPLAINED</td>
<td>PARAMETER</td>
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CORRELATION MATRIX

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<th>Y1</th>
<th>KD</th>
<th>GRSURF</th>
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VARIANCE-COVARIANCE MATRIX

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<th>Y1</th>
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<th>GRSURF</th>
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</table>
Figure 5.67  Plot from Group 12 Set 1. 1.0%N25-7, 1.5 g/L tetradecane.

Figure 5.68  Plot from Group 12 Set 1. 1.0%N25-7, 1.5 g/L tetradecane.
Figure 5.69  Plot from Group 12 Set 1. 1.0% N25-7, 1.5 g/L tetradecane.
5.6.16 Fitting Log for Group 13: Strain 15528, Decane, Dodecane, Tetradecane, and Hexadecane.

Group 13 was the combination experiment. In four runs, all four of the five alkanes (no octane) used in this work were solubilized. The “S2” oil here is the sum of the measured values for dodecane, tetradecane and hexadecane. Due to the nature of the model and the limited amount of data, it was not practical to try and determine individual $K_S$ 's for these alkanes. The simulation results and residual plots are in the appendix. The statistical output is shown in the following table. Selected plots of the data and corresponding simulation with the best estimate parameters follow the table.

The low percentage explained for the decane, (S1), is due to numerical error. The experimental data was zero due to detection limits but numerically the value was only approaching zero via the integration and thus for 18 hours there a was slowly unchanging offset that SimuSolv® viewed as unexplained variation. A better lower banding procedure would prevent this numerical problem.
**Table 5.34  Statistical Output for Group 13**

<table>
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**STATISTICAL SUMMARY**

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<th>STANDARD ERROR OF VARIATION</th>
<th>PERCENTAGE WEIGHTING</th>
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**CORRELATION MATRIX**

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<th>Y1</th>
<th>Y2</th>
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**VARIANCE-COVARIANCE MATRIX**

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<th>Y1</th>
<th>Y2</th>
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</table>
Figure 5.70  Plot from Group 13 Set 1. 1.0% N25-7, 0.375 g/L decane, 0.375 g/L dodecane, 0.375 g/L tetradecane, 0.375 g/L hexadecane

Figure 5.71  Plot from Group 13 Set 1. 1.0% N25-7, 0.375 g/L decane, 0.375 g/L dodecane, 0.375 g/L tetradecane, 0.375 g/L hexadecane
Figure 5.72  Plot from Group 13 Set 1. 1.0%N25-7, 0.375 g/L decane, 0.375 g/L dodecane, 0.375 g/L tetradecane, 0.375 g/L hexadecane

Figure 5.73  Plot from Group 13 Set 1. 1.0%N25-7, 0.375 g/L decane, 0.375 g/L dodecane, 0.375 g/L tetradecane, 0.375 g/L hexadecane
5.6.17 Fitting Log for Group 14:  Fitting Log: Strain 15528, Dodecane, N90/10 System

Group 14 consisted of two sets of experimental conditions as described in the earlier table (see Table 5.16 on page 89). The simulation results and residual plots are in the appendix. The statistical output is shown in the following table. Selected plots of the data and corresponding simulation with the best estimate parameters follow the table.

The data from this group of experiments had some of the highest levels of scatter. This is reflected in the correlation matrix.
### Table 5.35  Statistical Output for Group 14

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<th>STANDARD ERROR OF ESTIMATE</th>
<th>PERCENTAGE VARIATION EXPLAINED</th>
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</table>
Figure 5.74  Plot from Group 14 Set 1. 1.0%N90/10, 0.375 g/L dodecane

Figure 5.75  Plot from Group 14 Set 1. 1.0%N90/10, 0.375 g/L dodecane
**Figure 5.76**  Plot from Group 14 Set 2. 2.0%N90/10, 0.75 g/L dodecane

**Figure 5.77**  Plot from Group 14 Set 1. 2.0%N90/10, 0.75 g/L dodecane
Group 14 Set 2

$\square = S_1$ Hydrocarbon [g/L]

$\circ = X$ Cell Mass [g/L]

TIME

0 4 8 12 16 20

0.0 0.2 0.4 0.6 0.8

Group 14 Set 2

$\square = S_1$ Hydrocarbon [g/L]

$\circ = X$ Cell Mass [g/L]

TIME

0 2 4 6 8 10 12 14

0.0 0.2 0.4 0.6 0.8
Figure 5.78  Plot from Group 14 Set 2. 2.0%N90/10, 0.75 g/L dodecane

Figure 5.79  Plot from Group 14 Set 1. 2.0%N90/10, 0.75 g/L dodecane
5.6.18 Fitting Log for Group 15: Strain 15528, Hexadecane, N90/10 System

Group 15 consisted of two sets of experimental conditions as described in the earlier table (see Table 5.16 on page 89). The simulation results and residual plots are in the appendix. The statistical output is shown in the following table. Selected plots of the data and corresponding simulation with the best estimate parameters follow the table.
### Table 5.36  Statistical Output for Group 15

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**STATISTICAL SUMMARY**

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**CORRELATION MATRIX**

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**VARIANCE-COVARIANCE MATRIX**

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Figure 5.80  Plot from Group 15 Set 2. 2.0%N90/10, 0.75 g/L hexadecane

Figure 5.81  Plot from Group 15 Set 2. 2.0%N90/10, 0.75 g/L hexadecane
Figure 5.82  Plot from Group 15 Set 2. 2.0%N90/10, 0.75 g/L hexadecane

Figure 5.83  Plot from Group 15 Set 2. 2.0%N90/10, 0.75 g/L hexadecane
5.6.19 Fitting Log for Group 16: Strain 21909, Decane, N90/10

Group 16 consisted of two sets of experimental conditions as described in the earlier table (see Table 5.16 on page 89). The simulation results and residual plots are in the appendix. The statistical output is shown in the following table. Selected plots of the data and corresponding simulation with the best estimate parameters follow the table.

Although the model results predict the data very nicely, the runs were not long enough to discriminate between the full model and reduced models.
### Table 5.37  Statistical Output for Group 16

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#### CORRELATION MATRIX

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#### VARIANCE-COVARIANCE MATRIX

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Figure 5.84  Plot from Group 16 Set 1. 1.0%N90/10, 2 g/L decane

Figure 5.85  Plot from Group 16 Set 2. 1.0%N90/10, 1 g/L decane
Figure 5.86  Plot from Group 16 Set 2. 1.0%N90/10, 1 g/L decane

Figure 5.87  Plot from Group 16 Set 2. 1.0%N90/10, 1 g/L decane
5.6.20 Fitting Log for Group 17: Strain 21909, Decane, N25-7 System

Group 17 consisted of three sets of experimental conditions as described in the earlier table (see Table 5.16 on page 89). The simulation results and residual plots are in the appendix. The statistical output is shown in the following table. Selected plots of the data and corresponding simulation with the best estimate parameters follow the table.
Table 5.38  Statistical Output for Group 17

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CORRELATION MATRIX

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VARIANCE-COVARIANCE MATRIX

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Figure 5.88  Plot from Group 17 Set 1. 0.5%N25-7, 1.5 g/L decane

Figure 5.89  Plot from Group 17 Set 1. 0.5%N25-7, 1.5 g/L decane
Figure 5.90  Plot from Group 17 Set 2. 1.0\%N25-7, 1.0 g/L decane

Figure 5.91  Plot from Group 17 Set 2. 1.0\%N25-7, 1.0 g/L decane
Figure 5.92 Plot from Group 17 Set 3. 2.0%N25-7,2.0 g/L decane

Figure 5.93 Plot from Group 17 Set 3. 2.0%N25-7,2.0 g/L decane
5.6.21 Fitting Log for Group 18: Strain 21909, Tetradecane, N90/10 System

Group 17 consisted of three sets of experimental conditions as described in the earlier table (see Table 5.16 on page 89). The simulation results and residual plots are in the appendix. The statistical output is shown in the following table. Selected plots of the data and corresponding simulation with the best estimate parameters follow the table.
Table 5.39  Statistical Output for Group 18

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VARIANCE-COVARIANCE MATRIX

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Figure 5.94  Plot from Group 18 Set 1. 0.5%N90/10, 1.0 g/L tetradecane.

Figure 5.95  Plot from Group 18 Set 1. 0.5%N90/10, 1.0 g/L tetradecane.
Figure 5.96  Plot from Group 18 Set 3. 1.0%N90/10, 1.0 g/L tetradecane.

Figure 5.97  Plot from Group 18 Set 3. 1.0%N90/10, 1.0 g/L tetradecane.
Figure 5.98  Plot from Group 18 Set 3. 1.0%N90/10, 1.0 g/L tetradecane.

Figure 5.99  Plot from Group 18 Set 3. 1.0%N90/10, 1.0 g/L tetradecane.
5.6.22 Fitting Log for Group 19: Strain 21909, Tetradecane, N25-7

Group 19 consisted of three sets of experimental conditions as described in the earlier table (see Table 5.16 on page 89). The simulation results and residual plots are in the appendix. The statistical output is shown in the following table. Selected plots of the data and corresponding simulation with the best estimate parameters follow the table.

The stability of the estimates for this optimization is lower than one would like because of short run times and some larger scatter in the data. This is reflected in the high correlations and the low confidence level determined in the reduced model testing. On the other hand the model did explain a high percentage of the variation.
Table 5.40  Statistical Output for Group 19

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1.604E-03 STATISTICAL SUMMARY

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VARIANCE-COVARIANCE MATRIX

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Figure 5.100 Plot from Group 19 Set 1. 0.5%N25-7, 1.5 g/L tetradecane

Figure 5.101 Plot from Group 19 Set 1. 0.5%N25-7, 1.5 g/L tetradecane
**Figure 5.102** Plot from Group 19 Set 2. 1.0% N25-7, 0.75 g/L tetradecane

**Figure 5.103** Plot from Group 19 Set 2. 1.0% N25-7, 0.75 g/L tetradecane
Figure 5.104 Plot from Group 19 Set 3. 2.0%N25-7, 4.0 g/L tetradecane

Figure 5.105 Plot from Group 19 Set 3. 2.0%N25-7, 4.0 g/L tetradecane
**Figure 5.106** Plot from Group 19 Set 3. 2.0%N25-7, 4.0 g/L tetradecane

**Figure 5.107** Plot from Group 19 Set 3. 2.0%N25-7, 4.0 g/L tetradecane
Group 19 Set 3

$S_1 = \text{Hydrocarbon [g/L]}$

$X = \text{Cell Mass [g/L]}$

TIME

$0 \quad 4 \quad 8 \quad 12 \quad 16 \quad 20$

$0.0 \quad 1.0 \quad 2.0 \quad 3.0 \quad 4.0 \quad 5.0$

Group 19 Set 3

$S_1 = \text{Hydrocarbon [g/L]}$

$X = \text{Cell Mass [g/L]}$

TIME

$0 \quad 2 \quad 4 \quad 6 \quad 8 \quad 10$

$0.0 \quad 0.4 \quad 0.6 \quad 0.8 \quad 1.0 \quad 1.2$

$0.0 \quad 0.4 \quad 0.8 \quad 1.2 \quad 1.6 \quad 2.0$
5.6.23 Fitting Log for Group 20: Strain 21909, Hexadecane, N25-7

Group 20 consisted of one set of experimental conditions as described in the earlier table (see Table 5.16 on page 89). The simulation results and residual plots are in the appendix. The statistical output is shown in the following table. Selected plots of the data and corresponding simulation with the best estimate parameters follow the table.

The stability of the estimate for the $\mu_{\text{surf}}$ term is low because short run times prevented collection of meaningful data. This is reflected in the high correlation with $\mu_{\text{max}}$ and the low confidence level determined in the reduced model testing.
### Table 5.41  Statistical Output for Group 20

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#### CORRELATION MATRIX

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#### VARIANCE-COVARIANCE MATRIX

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Figure 5.108 Plot from Group 20. 1.0%N25-7, 0.375 g/L hexadecane

Figure 5.109 Plot from Group 20. 1.0%N25-7, 0.375 g/L hexadecane
Figure 5.110 Plot from Group 20. 1.0% N25-7, 0.375 g/L hexadecane

Figure 5.111 Plot from Group 20. 1.0% N25-7, 0.375 g/L hexadecane
5.6.24 Fitting Log for Group 21: Strain 21909, Decane and Hexadecane, N25-7

Group 21 consisted of one set of experimental conditions as described in the earlier table (see Table 5.16 on page 89). The simulation results and residual plots are in the appendix. The statistical output is shown in the following table. Selected plots of the data and corresponding simulation with the best estimate parameters follow the table.

The significant finding in this group was that hexadecane was utilized faster than decane. The fitting of the data was good. The stability of the estimates was high and consistent with those for the single hydrocarbon runs.
Table 5.42  Statistical Output for Group 21

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Figure 5.112 Plot from Group 21 Set 1. 1.0%N25-7, 0.375 g/L decane, 0.375 g/L hexadecane

Figure 5.113 Plot from Group 21 Set 1. 1.0%N25-7, 0.375 g/L decane, 0.375 g/L hexadecane
Figure 5.114 Plot from Group 21 Set 2. 1.0%N25-7, 0.375 g/L decane, 0.375 g/L hexadecane

Figure 5.115 Plot from Group 21 Set 2. 1.0%N25-7, 0.375 g/L decane, 0.375 g/L hexadecane
6.0 Proposed Models, Conclusions and Recommendations

6.1 Proposed Models

Researchers have long been interested in the structure and nature of the Gram-negative outer membrane. Some of its unusual properties have been described in section 3.1. One of the most important is the formidable barrier to the passage of hydrophobic materials. It has been long established that the enteric species of *E. coli* have asymmetric outer membranes. The outside part of the bilayer is made of exclusively LPS and membrane proteins. The inside layer is phospholipid and protein. This presents a bit of a paradox for the other Gram-negative bacteria which can readily use hydrocarbons and other lipophilic materials as a food source. The material has to cross the outer membrane to the cytoplasmic membrane bound enzymes responsible for the oxidation process (51). Based on what is believed about the structure of outer membranes we can propose some mechanisms for the enhanced micellar transport of the hydrocarbon to the enzyme system. We can then attempt to narrow the possibilities. The caveat is that it is not known how hydrophobic materials such as alkanes cross the membrane under normal conditions, i.e., when not solubilized in micelles. This makes the task of determining an appropriate model more difficult. As a first step we can identify two micelle-cell interactions which differ in a one fundamental aspect; whether or not the micelles cross the membrane intact.

There are two plausible models based on extensive membrane studies of Gram-negative bacteria. The first considers that there are significant patches of phospholipids on the outer side of the membranes of hydrocarbon degraders. It is well known that hydrophobic substances can partition and pass through phospholipid bilayers. The second is that the hydrocarbon passes through multiple protein structures known as porins. These have been found to have diameters of a few nanometers. Let’s consider these two models.
The first involves transport of the alkane only through the phospholipid patches. A micelle interacts with the phospholipid and releases the alkane. The alkane crosses the bilayer and passes through the periplasmic space to the oxidizing enzymes. In the second mode the intact micelles pass through the phospholipid patches into the periplasmic space. Here the micelles may be disrupted due the local concentration being less than the CMC or by the interaction with the inner membrane. Both these models would be consistent with the observed Monod kinetics in this work and that of the above mentioned researchers (58, 59) However, it seems very unlikely that the ordered structure of the LPS can be sufficiently disturbed to allow passage of the micelles or larger vesicles for that matter. Further consideration of the use of the surfactant as substrate supports the first mode. While it is possible that the intact micelles could also cross the phospholipid patches, one would expect the surfactant molecules to partition into the phospholipid. This is a well known phenomenon and the basis for protein solubilization for membranes (26).

The second model involves the passage of the hydrocarbon through porins. These multiple protein structures have been identified as important for the transport of different soluble substrates (24, 65) However, there is not any evidence that they play a part in the assimilation of hydrocarbons. While the idea of small passages designed for alkanes is appealing, the first model involving passage of the alkanes through the membrane is preferred.

The actual uptake and fate of the micelles could be determined by using radiolabelled surfactants and also by NMR studies to determine if there are any changes in the state of the membranes brought on by incorporation of the surfactant into the membrane. SEM techniques similar to those used by Kennedy et. al. (66) might also allow for morphological studies of membrane changes if any that occur when the micelles and bacteria interact.
Of course this model also appears to apply only to the nonionic micelles used in this work. As described in Chapter 5.0 the solubilization of the oil in LAS micelles prevented the oxidation of the oil. Both the bacteria and the micelles have net negative charges under the conditions used in this work. Mutual repulsion due to this like-like charge interaction would serve to limit the ability of the micelles to interact with the bacteria and not pass through the membrane. This conclusion is supported by the results given in section 5.3.14 which demonstrate that mixed micelles can promote the uptake and oxidation of decane. The anionic surfactant in these runs was present at only 25% by weight. This would translate to 0.25% in the 1% growth solutions. Recall that even at this low level there was no growth detected in the LAS only systems. If the LAS was interfering with the metabolism of the bacteria one would expect that this would have been evident in these mixed surfactant systems as well. Further exploration of this idea should be carried out by examining different mixtures of nonionic and anionic surfactants to determine at what level nonionic surfactants can reduce or remove the limiting effects of anionic surfactants such as LAS.
6.2 Conclusions

The main hypothesis of this thesis was that solubilizing normal alkanes in small synthetic surfactant micelles increases the oxidation of the alkanes by bacteria. Crucial to removing the ambiguity found in previous studies of surfactants and bacteria was the design of a clean and well-defined experimental system. It was proposed to study the oxidation of alkanes, \( C_8\text{-}C_{16} \), that were completely solubilized in a micellar system. This required addressing the following issues; selection of suitable surfactants, phase behavior studies and system characterization, toxicity testing, biodegradation studies, mathematical modelling and testing of the model.

This work supported the main hypothesis stated above. In particular it found that for two strains of Gram-negative bacteria, micellar solubilization significantly enhanced the transport, uptake and oxidation of decane, dodecane, tetradecane and hexadecane. The findings also support the assertion that solubilization is a more efficient transport mechanism than the attachment of cells to oil droplets. The development of a mathematical model to describe this process was also successful. This model treated the solubilized hydrocarbon as a soluble substrate. The model also allowed for different rates of mass transport and enzyme inhibition both in a competitive form for the alkanes and a suppression of the growth on the nonionic surfactants when hydrocarbon was present.
6.3 Recommendations for further research

The continued interest in surfactant enhanced bioremediation is indicative of the many possibilities and unknowns in the field. In terms of this work there is certainly opportunity to expand the anionic and mixed micelle work. Improvements in our ability to determine oxidation rates and cell/micelle interactions is also an area for work. As mentioned previously, NMR studies of the changes in the cell membranes may give crucial insight. The use of specific types of mutants defective in various aspects of the outer membrane may also be an effective tool for determining more about the cell/micelle interactions. Various chemical treatments of the cell membranes, including the exposure of cells to EDTA, may also provide information about the nature of the outer membranes (24). In addition to different surfactants systems, the use of Gram-positive microorganisms is also of interest.

The use of continuous cultures is an intriguing possibility. The main drawback would seem to be aeration. The use of air spargers and agitation would cause prohibitive foaming. One possible way around this would be to use oxygen membranes as is done in mammalian cell cultures. This would allow for high oxygen transfer without the introduction of gas bubbles that in addition to foaming would strip some of the alkanes or other hydrocarbon. The use of membranes also opens up the possibility of biofilm or other plug-flow systems.

The findings of this work on the role of $K_S$ and the recent papers on the alternative interpretation of the Monod expression (48, 63) in terms of mass transfer indicate that this type of modelling analysis should be continued and expanded as a way to describe the transport, uptake and oxidation of the hydrocarbons in surfactant systems.
7.0 References


VOLUME II

ANALYSIS AND MODELLING OF THE EFFECTS OF MICELLAR SOLUBILIZATION ON THE DEGRADATION RATES OF N-ALKANES.

by

SCOTT JOSEPH BURY
A.0 Testing of alternative anionic surfactants

The two main obstacles in using common anionic surfactants such as LAS and SDS are low solubilization power and precipitation in hard water. All together I examined three anionic surfactants for possible use in the growth experiments. They were SDS, LAS and N25-3S. The last is a sulfonated linear ethoxylated alcohol which is derived from the nonionic N25-3.

Both the SDS and N25-3S were not soluble in either MSM or MSMII and hence could not be used for the growth experiments. There are of course many variations of anionic surfactants and these should explored
B.0  **Surface Area of Droplets**

Consider a volume of a completely immiscible oil and water such that when undisturbed the oil floats as a layer on the surface of the water. The equilibrium state is said to have minimum free energy. Next put a certain amount of energy into the system as shaft work (i.e., mixing) sufficient to disperse the oil layer into droplets. Because we have increased the area of the system by the formation of droplets, the free energy of the system also has risen. The droplets will attempt stay as large as possible thereby minimizing the area. Because the free energy of the system is a function of the surface area at constant volume, more work is required to achieve ever smaller droplets. This shown graphically in the next figure. The total surface area (surface area of each drop * the number of droplets) is plotted against the number of droplets. This is an increasing function and hence the free energy of the system also increases as the number of droplets increase. In addition it also becomes more difficult to develop velocity gradients (have a large enough Weber Number) to actually shear small droplet into smaller droplets.
Figure A.116 Total Surface Area at constant volume as a function of the number of drops of equal radius.
C.0  Group 1 Log File

This and the following twenty appendices (D-W) contain the complete fitting logs for the optimizations described in Chapter 5. The experimental data is listed in the observed column starting with X, the cell mass. The data is sequential based on the sets contained within the larger groups. After all the cell mass data, S1 (then S2 for dual systems), the alkanes data is presented. TIME = 0.0000E+00 represents an individual data set.

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| 22.00 | 1.7200E-02 | 1.3732E-02 | 20.16 | 0.874 | *** |
| 24.00 | 1.0900E-02 | 8.0516E-03 | 26.13 | 0.877 | *** |
| 26.00 | 6.3700E-03 | 4.8766E-03 | 23.44 | 0.582 | ** |
| 28.00 | 0.0000E+00 | 3.0493E-03 | 0.00 | -1.64 | ****** |
| 30.00 | 0.0000E+00 | 1.9637E-03 | 0.00 | -1.28 | ****** |
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| 4.000 | 0.3330 | 0.3186 | 4.33 | 0.987 | *** |
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| 8.000 | 0.2040 | 0.1831 | 10.23 | 1.77 | ****** |
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| 4.000 | 0.3510 | 0.3628 | -3.37 | -0.780 | *** |
| 6.000 | 0.3570 | 0.3500 | 1.95 | 0.462 | ** |
| 8.000 | 0.3570 | 0.3289 | 7.88 | 1.87 | ****** |
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- **Observed** and **Predicted** columns indicate the observed and predicted values, respectively.
- **% Error** shows the percentage error between observed and predicted values.
- **Standardized Residual** indicates the standardized residual for each observation.
- Observations with ******* indicate significant deviations from the predicted values.
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**T.0 Group 18 Log File**

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