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AUTHOR   Cowan, Christina E.
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ABSTRACT
                 This module is part of a series designed to be used
by life science students for instruction in the application of
physical theory to ecosystem operation. Most modules contain computer
programs which are built around a particular application of a
physical process. This module explores some of the characteristics of
aquatic organisms which can be explained in terms of pressure and
buoyancy. Emphasis is placed on physical laws which illustrate how
organisms interact with their environment. The two physical
properties of primary concern are density and viscosity. The effects
of pressure caused by the density of water and the problems of
flotation and buoyancy in static water are discussed. A problem set
illustrates and extends ideas presented in the text. An accompanying
computer program, BUOY, permits the student to investigate the
sinking of plankters. A knowledge of calculus and differential
equations is presumed. (Author/CS)

PRESSURE AND BUOYANCY

IN AQUATIC ECOSYSTEMS

by

Christina E. Cowan

CENTER FOR QUANTITATIVE SCIENCE IN

FORESTRY, FISHERIES AND WILDLIFE

University of Washington

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3

PREFACE

This module explores some of the characteristics of aquatic organisms which can be explained in terms of pressure and buoyancy. Emphasis is placed on physical laws which illustrate how organisms interact with their environment. A set of hand-worked problems follows to illustrate and extend ideas presented in the text. Furthermore, an accompanying computer program, BUOY, allows the user to investigate the sinking rates of plankters. The module is intended for college undergraduates interested in aquatic biology who have some understanding of calculus and differential equations.

4

CONTENTS

INTRODUCTION

Aquatic life forms show many adaptations to the physical and
chemical characteristics of the water in which they live. The chemical
composition of the water is important because the water transports minerals
and foodstuffs dissolved in it, making them available to the inhabitants.
The physical properties of the water are important because they influence
the shape, size and distribution of aquatic organisms. In this module, we
will deal with the physical properties of still water, a portion of the more
general subject termed fluid statics.

Two physical properties of fluids will be of primary concern:
density and viscosity. One effect of fluid density is manifested in terms
of the pressure exerted on an immersed object. The greater the depth of
immersion, the greater is the resultant pressure on the body. Also, the
greater the fluid density, the greater the pressure for a given depth of
immersion. The density of water, ρ_w, is 775 times that of air. This creates
enormous hydrostatic pressures in the depths of the seas and lakes which
creates physiological "problems" for the organisms living there. Another
important effect of fluid density is the buoyancy force. The volume of
fluid displaced by an immersed object gives rise to this force, which is
proportional to the density of the fluid. As a result, the buoyancy force
exerted by water on an organism is 775 times that in air, the same ratio as
the densities of water and air. Compare the structure of a tree with that
of a large kelp plant. A tree must "use" much of its mass holding the
photosynthetic surfaces high to compete for light. On the other hand,
a kelp plant being about the same density as sea water is not "concerned"
with holding itself up but instead must be able to withstand the forces of

water currents. It is actually thicker at the top than at the bottom. Similarly, the greater buoyancy of water will allow most people to float, a feat quite impossible in the air.

The second physical property of interest is fluid viscosity. The frictional resistance to movement in a fluid is due to its viscosity, which is caused by cohesive forces between molecules. Since the viscosity (μ) of water is 100 times that of air, there is greater resistance to the movement of an object through the water as compared to movement through air. This increased resistance keeps plankton from sinking too rapidly but also retards movement of motile organisms. These animals adapt by assuming certain shapes for which the resistance is reduced. Thus stream-lined forms become more important and more common in aquatic organisms than in terrestrial ones.

In this module, then, we discuss briefly the effects of pressure caused by the density of water and the problems of flotation and buoyancy in static water. Limnologists and marine biologists seek to understand how pressure and flotation have influenced the characteristics and distribution of aquatic organisms. They ask questions such as: What effects can high pressures have on organisms? How do organisms adapt to these high pressures? How do sudden changes in pressure affect organisms? In terms of flotation, they are interested in such things as the velocity at which organisms sink, adaptations that might influence the sinking rate, and evolutionary advantages in sinking. Many of these questions can be approached by examining the underlying physical principles and relating these to biological observations.

PRESSURE

Terrestrial organisms experience a maximum pressure caused by the
weight of the air above them of 1.01325×10^6 dynes cm^{-2} (defined as
1 atmosphere). This pressure decreases with altitude, as does the density
because air is compressible. Aquatic organisms, however, must endure not
only the atmospheric pressure at sea level but also an increased pressure
caused by the weight of the column of water above them. The hydrostatic
pressure exerted on an aquatic organism at depth h can be computed as

$$P = P_o + \rho_w gh , \tag{1}$$

where P_o is the atmospheric pressure (at sea level given above), ρ_w is the
density of the water (1 g cm^{-3}), g is the gravitational constant,
980.665 cm s^{-2}, and h is the depth below the surface (here to keep the
units consistent, it is given in cm). The first term, P_o, represents the
atmospheric pressure at sea level and the second term represents the
pressure caused by the mass of water above the organism at depth h.
This hydrostatic pressure increases by approximately 1 atm for every
10 meters of depth, exceeding 1000 atmospheres in some deep marine tranches.
In general, the density of water is a function of both temperature and
pressure, but these effects are small, and the value of 1 g/cm^3 is
commonly used.

In natural environments, fish generally experience pressures
ranging from 0.5-500 atmospheres. Very few freshwater species encounter
hydrostatic pressures greater than 40 atms because only 18 of the world's
lakes have depths below 400 meters. Generally speaking, most fresh water
fish experience even less pressure since few live below 100-200 meters.
Marine fish, in contrast, are abundant down to 5000 meters with fewer

collected below this depth. Special forms have been found as far down as 7579 meters.

The question of how the aquatic organisms manage to adapt to these pressures was explored around 1891 by the French scientist Regnard. Surprisingly, he found that pressures up to 100 atmospheres had little or no effect on organisms and that the effects of pressures up to 1000 atm were often reversible--the organisms returning to normal after a short recovery period at normal pressures. The observed effects were functions of both the pressure and the time of exposure. After this pioneering work by Regnard, studies were neglected for 30 years until they were taken up by Fontaine in 1920 in France. In the 1930's and again in the 1960's, a resurgence in research on the effects of pressure changes occurred in Germany and the United States. This research determined that one of the effects of the increased pressure occurs at the cellular or molecular level where the pressure seems to cause protein denaturization. Thus, organisms living permanently at great depths probably have adapted by changing proteins to forms that are not readily denatured by the intense pressure.

Another effect of increased pressure of biological importance is related to the behavior of gases. The equation of state for a perfect gas is

$$PV = RT$$

where P is the pressure, V is the volume, T is the temperature and R is the universal gas constant (equal to 8.314 J g^{-1} $mole^{-1}$ K^{-1}). At low pressures, real gases tend to obey the perfect gas law. At pressures of less than 200 atmospheres, the error is typically less than 10% for atmospheric gases. Thus, the perfect gas law can be used to represent the

behavior of gases with which we will be concerned. If the temperature

is regarded as constant, the equation (2) becomes simply

$$PV = constant$$

which is Boyles' law. The volume of gaseous spaces in organisms such as

swim bladders in fish can change dramatically as the organisms rise or

sink in the water. A rapid decrease in pressure can cause expansion of

internal gases and explosion. Fish rapidly brought to the surface by a

trawling rig can have greatly distended swim bladders. Fish that are

forced from deep reservoirs through power turbines to shallow ponds run

similar risks. This explosion is also experienced by divers when

ascending too rapidly and causes damage to the lungs. Nitrogen bubble

formation in the bloodstream, known as "the bends," can cause paralysis

or even death. The increased pressure also causes changes in the quantity

of gases dissolved in the tissues. As pressures increase, the volume of

gases decreases, causing implosion under drastic conditions. Gases can

come out of solution and can cause toxic effects. The most familiar of

these effects is nitrogen narcosis. Nitrogen gas has an intoxicating

effect on the nervous system.

At the extreme depths of some deep lakes, the pressure may reach

high levels (especially in comparison to terrestrial values), but on the

whole pressure is considered a minor problem in lakes and rivers. This

may be due not to true insensitivity but simply to lack of research in

that area. For example, certain aquatic insects which use spiracular

gills for respiration have been shown to be sensitive to pressure changes

caused by the increase in water depth due to flooding. At high pressures

the gills collapse or become completely wetted. Thus these sensitive species

do not occur in areas where floods cause water depth changes (Hynes 1972).

BUOYANCY OF ORGANISMS

As we have seen in the previous section, some fishes use swim
bladders to maintain neutral buoyancy. Denton (1960) has described two
other intriguing mechanisms used by marine organisms to regulate their
depth. The cuttlefish changes its density with an osmotic pump connected
to the cuttlebone. The animal is limited to depth above about 260 meters
because hydrostatic pressure will overcome the osmotic potential. The
deep-sea squid regulate density by filling the coelomic cavity with a
fluid containing ammonium ions, a by-product of metabolism, which is less
dense than sea water. This mechanism has the advantage that it is not
influenced by changes in static pressure but it takes up a large volume
of the animal. In contrast to these methods some fish such as sharks and
tuna just swim all the time. This short paragraph reviews some of the
mechanisms used by animals to stay afloat. In the rest of the module we
will concentrate on smaller life forms of the marine and aquatic environ-
ments.

The plankton represents a community that is completely dependent
on water as a place to live. In order for the plankton to exist in this
unique way, they must be able to remain suspended or at least be able to
maintain their position in the photosynthetic region long enough to grow
and reproduce. In still water, the plankter is unable (without an external
force) to remain truly suspended without movement but instead is actually
sinking slowly because its density is greater than that of the water.

Continuous residence within the euphotic zone may be neither a
necessary nor a practical requirement for successful planktonic existence.
Successful growth and survival only require that the residence time in

11

the euphotic zone permit enough photosynthesis to counterbalance respiration and permit some growth. The rate of growth will be influenced in part by the actual time spent in the euphotic zone each day. While full appreciation of the total planktonic distribution must ultimately include consideration of the gross effects of water movement (waves, convection, turbulence), treatment of buoyancy and flotation mechanisms in static water can give valuable insights.

Before proceeding we need to discuss the Reynolds number concept. This will help the student interpret the results from the following sections on terminal velocity of resistive forces on, and biological responses of sinking plankters.

The Reynolds Number

The Reynolds number, Re, is used to distinguish between two very different types of flow regimes--laminar and turbulent. Laminar or streamline flow is characterized·by the orderly motion of fluid particles in essentially parallel paths. A thin dye tracer will not diffuse significantly in laminar flow but will form a thin line parallel to the flow axis. Turbulent flow on the other hand is characterized by random motion, in which a dye tracer will rapidly diffuse throughout the fluid. Thus, if the Reynolds number is low (Re < 1.0) the flow is laminar and if it is high (Re > 10.0) the flow is turbulent (in between is a transition zone). The Reynolds number is defined as

$$Re = \frac{v \; d \; \rho_w}{\mu}$$

where v is the fluid velocity, d is the characteristic dimension such as the diameter of a sphere or cylinder, ρ_w is the density of the water and μ is the viscosity of the water. It was derived by non-dimensionalizing

the governing equations. Thus the distinction between laminar and turbulent

flow can be made independent of size and velocity since they are included

in the calculation of Re. Check to see that Reynolds number is a dimension-

less quantity.

Motion and Dynamic Equilibrium

Consider a passive plankter (such as algae) sinking in a column of

water. The forces acting on this plankter are 1) the force of gravity acting

downward, 2) a buoyant force equal to the weight of the fluid displaced by

the plankter acting upward, 3) the force associatd with the acceleration

of the plankter downward in the y direction, and 4) a force representing the

resistance of the medium to the movement of the plankter acting upward. This

is shown diagramatically below:

Resistive force, R·   Buoyant force, B

ma   Gravitational force, G
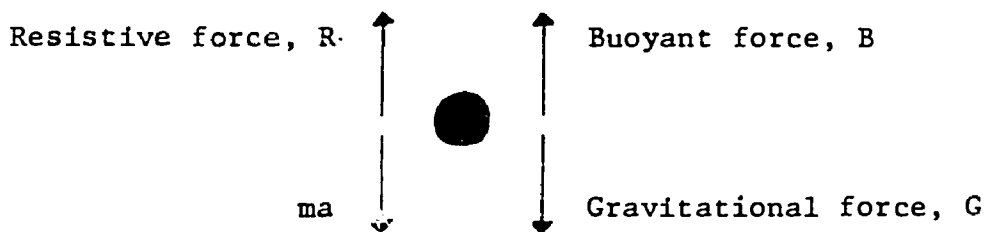
The buoyant and gravitational forces can be considered constant for a given

plankter. (However, many organisms, e.g. blue-green algae, form gas vacuoles

and can thus control buoyant forces.) Usually the gravitational force is

greater than the buoyant force, therefore the plankter is sinking. The

resistive force is not constant but is proportional to the velocity of the

plankter and increases as the plankter accelerates. Viewing the spherical

plankter as a point mass, we can sum up the forces of the "free body diagram"

and set them equal to zero for dynamic equilibrium ($\Sigma F=0$.). Taking the down-

ward direction as positive we have [1,2]

$$-ma + G - B - R = 0 \quad . \tag{4}$$

To proceed with the analysis each component of equation 4 will be discussed.

Since the mass is equal to the density times the volume the gravitational force, G, is equal to mg = ρ_B V g.

The buoyant force is proportional to the fluid density, as described earlier. It turns out that this force is just equal to the weight of the fluid displaced by the body which can be written ρ_w V g, where ρ_w is the water density, V the plankter volume, and g the gravitational constant. This "law of buoyancy" is known as Archimedes' principle. If the plankter is spherical, its volume is 4/3 πr^3, where r is the radius. Consequently, the gravitational force, G, and the buoyant force, B, are respectively 4/3 $\pi r^3 \rho_B$g and 4/3 $\pi r^3 \rho_w$g for a spherical plankter. The resistive force may take a variety of forms depending on the velocity at which the sphere is sinking. For the low velocities at which most plankters sink, the resistive force has been found to be directly proportional to the velocity and can be represented by Stokes' law, which is developed and discussed later in this module. Stokes' law states that the resistive force is

$$R = k\pi r v$$

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[1] I have chosen ma as negative because the particle is decelerating. It is possible to assign arbitrary direction to this force but the solution will determine which way the object is moving. Here this choice facilitates a solution.

[2] Alternatively this same equation may be derived by applying Newton's Second Law, which states that the acceleration of a body is directly proportional to the resultant summation of the forces acting on the body.

where k is a constant of proportionality equal to 6π for spherical objects,
μ is the viscosity of the fluid, and v is the velocity at which the body
is sinking.

Finally, recalling that the acceleration is the time rate of change
of velocity, we can substitute each term back into equation to get equation
5.

$$-m \frac{dv}{dt} + \frac{4}{3} \pi r^3 \rho_B g - \frac{4}{3} \pi r^3 \rho_w g - 6\pi \mu r v = 0 \quad . \tag{5}$$

Using the volume-mass relationship again to substitute for $\frac{4}{3} \pi r^3$
and rearranging, we have

$$-\frac{dv}{dt} - \frac{6\pi\mu r}{m} v + g(1-\frac{\rho_w}{\rho_B}) = 0.$$

This is a differential equation of 1st order which can be solved by separa-
tion of variables to determine the velocity at any time when we include the
initial condition that at t = 0, v = 0.

The solution is

$$v = [Cg(1 - \frac{\rho_w}{\rho_B})](1 - e^{-t/C}) \tag{6}$$

where

$$C = \frac{m}{6\pi r \mu} \quad .$$

This solution has the general form illustrated in the following
diagram.

velocity

time

15
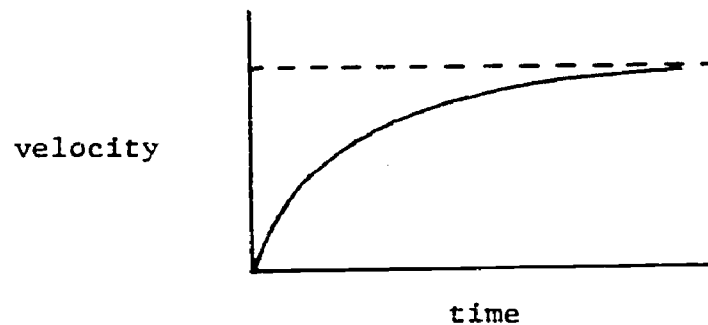
The time constant, C, which is based on the geometric and material traits of the plankter, characterizes the rate at which the velocity of the plankter approaches the limiting value. The larger the value of the time constant, the slower the approach and conversely as illustrated below:
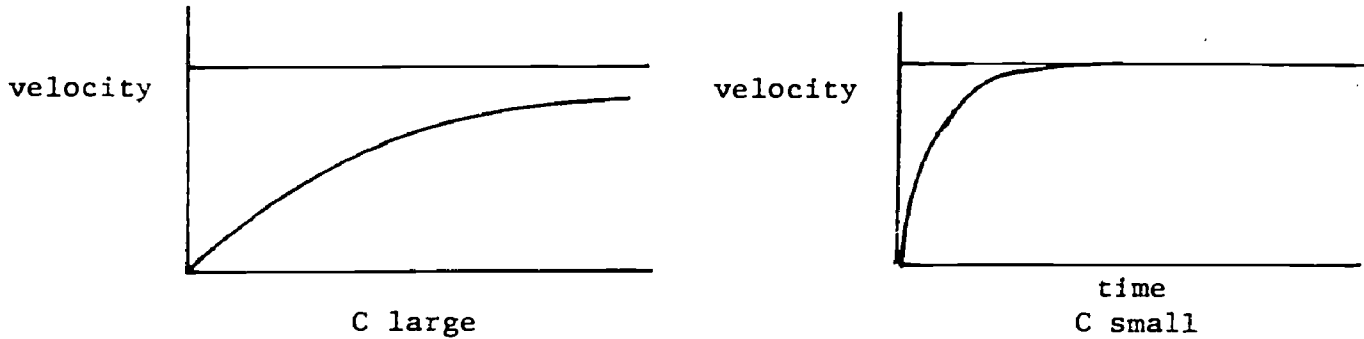
C large

time
C small

Terminal Velocity of a Sinking Plankter

The limiting value that is approached as the time interval gets larger (i.e., as $t \to \infty$) is

$$v_t = Cg \left(1 - \frac{\rho_w}{\rho_B}\right) \quad . \tag{7}$$

This is called the terminal velocity, which represents the velocity at which the acceleration is equal to zero, i.e., $\frac{dv}{dt} = 0$. To understand this phenomenon, consider a body initially at rest which is suddenly released. Under the influence of gravity, the body begins to accelerate downward, i.e. $\frac{dv}{dt} \neq 0$. Looking at (4), one can see that this must be due to an imbalance of forces--- in this case, the resistive force is smaller than the combined gravitational and buoyant forces. However, as the velocity of the body increases, so does the resistive force, until there is zero acceleration and no change in momentum. The result is a constant rate of fall.

For very small objects, the terminal velocity is approached so rapidly that the period of accelerational can be ignored. To demonstrate this solve

equation 6 for the time (t_c) that it takes for the plankter to reach a fraction x of the terminal velocity v_t.   Thus

$$xv_t = v_t(1 - e^{t_c/C})$$

$$e^{t_c/C} = 1 - x$$

$$t_c = C \ln(1 - x) \quad . \tag{8}$$

Consider a small plankter whose radius is r = 20 microns and density of $\rho_B = 1.02$ g cm^{-3}.   The viscosity of the water is 1 x 10^{-2} dyne s cm^{-2}.   The terminal velocity is $v_t = 1.73$ x 10^{-3} cm s^{-1}.   The time it takes to reach a velocity of 1.56 x 10^{-3} cm s^{-1} or 90% of the terminal velocity is 2 x 10^{-4} s. Thus the period of acceleration is so small that, for most computations, it can be ignored.

Resistive Forces on Sinking Plankters

As stated previously, the equation representing the resistive force may have a variety of forms depending on the velocity, unlike the gravitational and buoyant forces.   It is known, for the examples considered here, that the resistive force at low velocity is a function of 1) the surface area of the body in contact with the water, 2) the speed of the water moving by the body or the speed of the body moving through the water, and 3) constants which are related to the nature of the fluid and its temperature (the viscosity and density of the fluid are dependent on temperature).   Using functional notation, we write

$$R = f(A, v, \mu, \rho_w)$$

where A is the surface area of the plankter body, v is the velocity, μ is the viscosity of the water, and ρ_w is the density of the water.

17

Assuming that our analysis of the relevant variables determining R has been complete, we are left with the problem of determining the exact functional form of $f(A, v\ \mu, \rho_w)$. A common tool of fluid mechanics useful in this regard is that area of mathematics known as dimensional analysis. This is based upon the fact that an equation expressing a physical relationship between quantities must have the same dimensions on both sides. The process involves combining the independent variables $(A, v, \mu$ and $\rho_w)$ in such a way that the result yields dimensions identical to those of R. Since the dimensions of the independent variables are in general not the same, their addition or subtraction is not possible, hence the most general form of equation possible is a combination of products of powers of the relevant variables.

In this case, A is assumed to be some power function of the radius, r, therefore

$$R = K' r^n v^q \rho_w^u \mu^s \tag{9}$$

where K' is a constant of proportionality. (Notice that independent variables of this function are the same ones that form the Reynolds number.) Each of these quantities is now replaced by its dimensional form in terms of mass, M; length, L; and time, T. Dimensionally, (9) becomes

$$MLT^{-2} = (L^n)(L^q T^{-q})(M^u L^{-3u})(M^s L^{-s} T^{-s}) \ .$$

Now equating the powers of each dimension on the two sies of the equation, we get

$$M: \quad 1 = u + s$$

$$L: \quad 1 = n + q - 3u - s$$

$$T: \quad -2 = -q - s$$

Since there are four unknowns and three equations, we can solve simultaneously for n, u, s in terms of q, and the power of the velocity, Equation (9) becomes

$$R = K'r^q v^q \rho_w^{q-1} \mu^{2-q} \tag{10}$$

Thus, if the above assumption holds and R varies as some unknown powers of r, v, ρ_w and μ, then a general form for the resistive force has been found. The coefficients n, u, s were expressed in terms of q, the power of the velocity, because experimentation has shown that the resistive force is proportional to some power of the velocity. For small velocity values, it is proportional to the first power; for large velocity values to the second power; and for intermediate velocity values some intermediate power. With these experimental results in mind, values for q of 1, 1.5, and 2 are chosen for discussion.

It should be emphasized here that dimensional analysis is an experimental technique, useful in that it allows intelligent formulation of experiments leading to a maximum amount of information from a minimum of experimentation. The reader is referred to Vennard and Street (1975) for a complete discussion. Analytical determination of R is also possible through a consideration of the basic equations of motion for a fluid, which is beyond the scope of this module. The interested reader is referred to Batchelor (1970). Were an analytical solution not available, verification

19

of the usefulness of the functional form derived by dimensional analysis would be possible only by comparison with experiment.

If we assume q = 1 in (10), i.e., that the resistive force is proportional to the first power of the velocity, then

$$R = K'rv\mu \quad . \tag{11}$$

This expression is the same as that derived by Stokes in 1851 by classical hydrodynamic (i.e. analytical) methods given earlier in the text and is commonly called Stokes' Law. Thus, the two methods, dimensional analysis and classical hydrodynamic methods, have led to the same results, indicating the strength of dimensional analysis.

This relationship is important in the study of the sinking of small plankton because in general, for biological objects less than 0.5 mm in diameter, passive sinking rates fall in the range within which Stokes' law is valid. Bacteria, noncolonial algae, many species of colonial algae, nearly all protozoa, and most rotifers fall in this range, but the larger crustacea and some nonspherical forms do not. Thus, if the Reynolds number

$$Re = \frac{2\ r\ v\ \rho_w}{\mu} \quad < \quad 1.0 \quad ,$$

then Stokes' law is valid because the flow is laminar.

Next, if we assume that q = 3/2 in (10) then R becomes

$$R = K'r_c^{3/2}v^{3/2}\rho_w^{1/2}\mu^{-1/2} \quad . \tag{12}$$

This equation, called Allen's law, was derived in 1900 for spheres in the transition zone between laminar and turbulent flow (1.0 < Re < 10.0). Allen's

law can be used to describe the resistance for large crustacea and plankters. Note that the term r_c is not the radius but computed linear dimension. Allen (1900) and Hutchinson (1967, p. 272) show how to compute r_c.

Finally, if we assume that q = 2 in (10) then

$$R = K'r^2v_t^2\rho_w \quad . \tag{13}$$

This relationship is credited to Newton and is valid when the flow is completely turbulent (i.e. Re > 10). It is useful in the present context when considering the sedimentation of heavy materials. It also describes the resistive forces experienced by fish and birds as they swim or fly. In this connection, it is termed drag. See problem 10 for further development of these ideas.

Biological Responses

Now that the general physical principles regarding the passive sinking of a spherical plankter have been discussed, let's go back and examine some biological responses to the problem of flotation. Examining Stokes' law and Allen's law, we see that the dependence of the terminal velocity on the excess density, $(\rho_B - \rho_w)$, is very important. Indeed, if the plankter were able to decrease this difference to zero, i.e., make its body density equal to the density of the medium, the terminal velocity would be zero and thus the organism would not sink at all. Any reduction of the excess density would cause a decrease in the terminal velocity. Many organisms do include gases or fatty and oily materials to reduce the overall density and retard sinking, or even provide for positive buoyancy.

Density changes on a daily basis may partially account for diurnal migration. *Daphnia pulex* has been shown to exhibit a diurnal variation in

21

sinking speed with the greatest value occurring after sunrise when the
Daphnia have finished feeding and are sinking into the deeper waters during
the day. Many organisms exhibit density changes during their life history
with dispersal stages or feeding stages being lighter than other stages.
Calanus finmarchius and Calanus plumchius show gradual density decreases
from eggs to Copepodite stages and an increase in the adult forms. It is
interesting to note that the Copepodite feed on phytoplankton near the sur-
face whereas the adults do not feed. Not only does density change diurnally
and during the life history but for algal forms the density increases with
age and disease causing older forms to sink faster out of the photosynthetic
zone. Since the density of the medium changes with temperature, the organ-
isms must adapt their internal density with the season in order to maintain
the constant terminal velocity. For example, assuming extreme temperatures
of 0 and 25°C, a salt water salinity of 35% and an excess density of 0.05,
the sinking rates for a 20 micron cell calculated from Stokes' law would be
0.023 and 0.045 mm s^{-1} at the two extremes. Similar results can be found
for fresh water populations. It has often been assumed that cyclomorphic
changes in some organisms or differences between the forms of tropical and
temperate plankton may be due to adaptations to these density changes, but
no conclusive proof exists for either confirmation or refutation.

Empirical Results

The above physical theory was developed to describe the sinking of
inanimate objects such as metal spheres. Biological limnologists and
oceanographers have shown that use of these physical principles to describe
the sinking of biological organisms gives reasonable results.

Because of the considerable technical difficulty in obtaining re-

liable data, the information on the density and sinking rate of freshwater organisms is extremely meager. Experimental data does, however, show that nearly all freshwater diatoms and most phytoplanktonic organisms except certain species of blue-green algae are slightly denser than the medium and sink when undisturbed. Results of experiments by Fritz (1935), as reported in Hutchinson (1967), using *Cyclotella bodanica* (diameter 32-62μ mean 49μ), *Fragilaria Crotonensis* (mean 68μ) and *Asterionella formosa* (mean 68μ) are given in the following table.

TABLE 1. Observed and Computed Sinking Speeds
of Diatoms in Quiet Water[1]

	Temperature (°C)	Viscosity (Poise)	Sinking Speed (10^{-3} cm s^{-1}) Observed	Calculated[2]
Cyclotella bodanica	6	0.0147	17.0	25.0
	20	0.0101	21.0	
Asterionella formosa	6	0.0147	8.6	12.6
	20	0.0101	11.1	
Fragilaria crotonensis	6	0.0147	5.9	8.6
	20	0.0101	10.5	

[1]Table from Hutchinson (1967), p. 276.
[2]Calculated using Stokes' law.

Possible reasons for the small discrepancies between observed and calculated sinking speeds include inadequate geometrical description of the diatoms and distrubances by small turbulent currents in the experimental appartus. Other work by Grim (1951) and Lund (1959), as reported in Hutchinson (1967), give similar ranges of values although their actual results are different.

Most importantly, Grim (1939), as reported in Hutchinson (1967), concluded that living specimens of small species of *Cyclotella* do not sink

appreciably when alive but sink 7-8 m day^{-1} when dead or less healthy. He also observed that *Fragilaria crotonensis* sank at rates of up to 7 to 9 m day^{-1} and *Synedraacus delicatissima* sank 3-20 m day^{-1}. Thus the range for one species of organisms may be considerable depending on the health and density of the organisms, supporting previous speculation.

The gaps in our knowledge of the zooplankton density and sinking rates are not as great as that of phytoplankton. For example, densities of many planktonic forms of zooplankton have been computed and typically the excess density, $\rho_B - \rho_w$, lies between 0.015 and 0.025. The value for *Gammarus pulex*, given in the accompanying table, is much higher because it is commonly a benthic form.

TABLE 2. Densities of Freshwater Animals

Rotatoria (Luntz 1928)

Euchlanis triquetra, reared at 8°C	1.025 at 18°C
Euchlanis triquetra, reared at 25°C	1.020 at 18°C
Euchlanis triquetra, wild, taken in summer	1.025 at 18°C
Brachionus quadridentatus, wild, taken in summer	1.025 at 18°C
B. quadridentatus f. *rhenanus*, wild, taken in spring	1.025 at 18°C
B. quadridentatus f. *rhenanus*, reared at 8°C	1.025 at 18°C
B. quadridentatus f. *rhenanus*, reared at 25°C	1.020 at 18°C

Crustacea (Lowndes 1938, 1942; Hamilton 1958)

Chirocephalus diaphanus	1.011 at 11.3°C
Daphnia pulex	1.017 at 7.0°C
Holopedium gibberum	1.0015 at 18°C
Holopedium gibberum	1.014 at 18°C
Eudiaptomus gracilis	1.023 at 8.0°C
Gammarus pulex	1.066-1.088 at 20°C
Candona candida	1.025 at 7.4°C

Chordata

Gasterosteus aculeatus	1.003 at 10°C
Gasterosteus aculeatus	1.002 at 20°C
Rana temporaria tadpole	1.014 at 9.6°C

Table from Hutchinson (1967), p. 249.

The rate of sinking of some small zooplankton has been computed. For small rotifers such as *Euchlanis triquetra* and *Brachionus quadridentatus*, Stokes' law is valid (see section on Resistive Forces) and the results are given on the following page.

TABLE 3. Observed and Computed Sinking Speeds of Rotifers

	Density (ρ_B)	Average Terminal Velocity (V_t)
Euchlanis triquetra	1.025	0.0862 cm s^{-1}
	1.020 obs.	0.0658 cm s^{-1}
	1.020 calc.= 0.0862 x 20/25	0.0690 cm s^{-1}
Brachionus quadridentatus f. *rhenanus*	1.025	0.0495 cm s^{-1}
	1.020 obs.	0.0386 cm s^{-1}
	1.020 calc.= 0.0495 x 20/25	0.0396 cm s^{-1}

Table from Hutchinson (1967), p. 278.

Experimentation on various Daphnia species illustrates that the larger specimens do indeed fall at a velocity that would be predicted by Allen's relationship with *Daphnia pulex* falling at a rate of between 0.4 cm s^{-1} and *Daphnia magna* falling at a rate of approximately 0.8 cm s^{-1}. Data on marine phytoplankton (especially diatom) species is abundant. Smayda (1970) gives a very good table of values for size and sinking rate observations for many diatoms and flagellates including various life stages. Once again, these observations agree very well with the theoretical calculations.

Thus the experimental work does suggest that the relationships developed above do hold approximately for a variety of phytoplankton and zooplankton species and sizes.

FURTHER CONSIDERATIONS

The development thus far has assumed a spherical plankter shape. In fact, many plankters are not spherical or have a gelatinous sheath to change the terminal velocity from that calculated above. This section discusses the sinking velocity for plankters exhibiting the above complications. The effects of other factors (such as water movement) are not considered, but see problem 11, which considers swimming.

Non-spherical Form

The theory developed above was based on the case of a plankter that was spherical, but few aquatic organisms are spherical in form and the true spherical shape is conspicuously absent in phytoplankton. One reason for this may be found by examining the relationships for the buoyant and resistive forces. The buoyant force is proportional to the volume and the resistive force is proportional to the surface area. Increasing surface area with respect to a given volume would mean increased resistance and slower terminal velocity. Thus, departures from the spherical form are important in aiding a plankter to keep from sinking. These changes from spherical form may involve flattening, various forms of asymmetry, formation of colonies, and the addition of various projections such as spines, hairs, cilia, etc. The simplest way to deal with the effect of these changes in shape on the resistive force and terminal velocity is to suppose that the new shape can be formed by deforming a sphere of radius r_s.

The original resistance for the sphere with radius r_s at terminal velocity, assuming Stokes' law (11) applies, is

$$R_s = 6\pi\mu r_s v_{ts}$$

and the resistance at terminal velocity for the new shape is

$$R_a = 6\pi\mu\phi_r r_s v_{ta}$$

where ϕ_r is the coefficient of form resistance which relates the change in resistance to changes in the amount of surface area relative to the sphere. Since the volume and density of the body are unchanged by the deformation, the gravitational and buoyant forces are respectively $\rho_B \pi\frac{4}{3}r_s^3 g$ and $\rho_w \pi\frac{4}{3}r_s^3 g$. Substituting into Equation 5 with the resistance for the new body, and the velocity assumed constant, we get:

$$\rho_B \frac{4}{3}\pi r_s^3 g - \rho_w \frac{4}{3}\pi r_s^3 g - 6\pi\mu\phi_r r_s v_{ta} = 0.$$

Now, solving for the terminal velocity of the new form, v_{ta}, yields

$$v_{ta} = \frac{2}{9} g r_s (\rho_B - \rho_w)\phi_r^{-1}\mu^{-1}$$

Forming the ratio of the velocity of the sphere and the new body, we get

$$\phi_r = \frac{v_{ts}}{v_{ta}} \quad . \tag{23}$$

Further, we find that if a sphere can be constructed with radius d_B which falls at the rate v_{ta}, then

$$\phi_r = \frac{r_s^2}{r_B^2} , \tag{24}$$

where r_B is called the nominal radius. This latter expression in terms of the radius will prove useful because the planktologist usually wants to

know the new terminal velocity and can measure the various linear dimensions

to estimate d_B. Then, substituting in (23) we obtain

$$v_{ta} = \frac{r_B^2}{r_s^2} v_{ts} .$$

Thus, a fairly convenient method exists for determining the terminal velocity

of general nonspherical forms. The experimental results of Luntz (1928,

1929) as reported in Hutchinson (1967) demonstrate the importance of just

such changes from the spherical form. He showed that *Branchionis quadri-*

dentatus rhenonus without spine and a density of 1.025 sank at a rate of

0.05 cm s^{-1} whereas the typical form *Branchionis quadridentatus* with spine

and density also 1.025 sank at a rate of 0.041 cm s^{-1}.

For simple solid forms such as ellipsoids and disks, a fairly rigor-

ous theoretical and experimental method is possible. The reader is referred

to Hutchinson (1967, p. 260-272) for details. In general, both ellipsoids

and disks sink slower than spherical objects of the same volume (i.e. ϕ_r

will be greater than one). Somewhat surprisingly, the elongated prolate

form is usually more efficient than the more flattened oblate form in re-

ducing sinking velocity. It should be noted that for ellipsoids within a

certain small class of dimensions, $\phi_r < 1$, so that it is not possible to

say that a sphere will always sink faster than an equivalent ellipsoid. A

disk shape, however, which can be regarded as the extreme form of an oblate

spheroid, no matter what its orientation, will descend slower than an equi-

valent sphere for Re ≤ 7. For a disk one hundred times as wide as it is

thick, the time taken to fall a given distance broadside down is 4.3 times

that taken of a like sphere. In contrast, cylindrical organisms with

diameters less than 0.01 cm, oriented horizontally, will fall roughly 10 times as fast as a sphere of equal diameter. Thus the cylindrical form is not efficient in reducing the terminal velocity, especially if the cell walls are very dense such as in diatoms.

The latter statement brings up the important point of considering density differences between various geometrics of identical volume which we might be comparing. For example, one can by reducing the diameter and increasing the length make a cylinder that will fall slower than a sphere of the same volume. However, in all likelihood, the added structural material would cause such a cylinder to be denser than the equivalent sphere, increasing the gravitational force and probably offsetting any gain. Similar considerations are pertinent in the case of ellipsoids, also. The extra surface area of an ellipsoid, as compared with an equal volume sphere, will probably give the former a greater density. For example, in the case of diatoms, part of the advantage of increased form resistance is obliterated by increased density since diatoms have external skeletons.

In conclusion, it is important to consider the observation that a body moving in a liquid will tend to take up an orientation with its greatest area of projection normal to the direction of motion to minimize the forces acting on them. A small body may have no preferred orientation. However, slight asymmetries in the body shape and the presence of surface area projections will aid the plankter in attaining the preferred orientation with its greatest sectional area normal to the direction of motion. Thus an organism will normally orientate so that the resistive force will be greatest for that body shape.

Gelatinous Sheath

One other structural adaptation remains that warrants discussion.
This is the gelatinous sheaths in phytoplankton and many nonmotile planktonic
algae such as the blue-green algae. Although the gelatinous capsules may
increase the difficulty of zooplankton attempting to eat them, they are
undoubtedly important in the problem of flotation. Not only does the sheath
mean an increase in diameter and the corresponding decrease in sinking
speed, but it also aids in reducing the organism's overall density due to
the low density of the gelatinous sheath.

To determine the effect of the gelatinous sheath on the resistance
and sinking speed of the plankter, we will proceed in a manner similar to
that of the previous section. Consider a spherical organism of radius r
and density ρ_B whose terminal velocity by Stokes' law is

$$v_{t1} = \frac{2}{9} gr^2(\rho_B - \rho_w)\mu^{-1} \quad .$$

Now add a gelatinous sheath of density ρ_s to the outside of the
organism. The new radius is increased to ar where a > 1. The new volume
is then $\frac{4}{3} \pi r^3 a^3$, the new mass $\frac{4}{3} \pi r^3 [\rho_B + (a^3 - 1)\rho_s]$ and the new density
therefore $[\rho_s + (\rho_B - \rho_s)/a^3]$. The new terminal velocity then becomes

$$v_{t2} = \frac{2}{9} gr^2 a^2 [\rho_s - \rho_w + \frac{1}{a^3}(\rho_B - \rho_s)]\mu^{-1}$$

where $[\rho_s - \rho_w + \frac{1}{a^3}(\rho_B - \rho_s)]$ represents the excess density.

Comparing the terminal velocities thus achieved and relating to
the coefficient of form resistance ϕ_r, we obtain

$$\phi_r = \frac{v_{t1}}{v_{t2}} = \frac{a(\rho_B - \rho_w)}{a^3(\rho_s - \rho_w) + (\rho_B - \rho_s)} \ .$$

Assuming $\phi_r > 1$, i.e., that the gelatinous sheath does reduce the sinking rate, and collecting like density terms, factoring out $(a-1)$ and rearranging, we end up with

$$\frac{\rho_B - \rho_s}{\rho_s - \rho_w} > a(a + 1) > 2$$

since $a > 1$. Thus, in order for the sheath to be effective in reducing the sinking rate, the difference in density between the sheath and the plankton body must be at least twice as great as the density difference between the sheath and the medium. Indeed, if the jelly and the medium have the same density, the sinking speed may be reduced to any degree by merely increasing the thickness of the sheath. In nature, this is unlikely to occur since the greater thickness would interfere with the metabloic exchanges of the cell with the medium.

We have considered the many ways in which a single celled organism can reduce its sinking velocity by decreasing its density, changing shape or acquiring a gelatinous sheath. All or one may act to help the organism achieve the desired goal to remain in the photosynthetic zone until it has at least accomplished its objective of growth and reproduction.

Multiple Plankters

When two or more spheres are sinking through a liquid in the vicinity of each other, they cause a change in each other's sinking speed. In small groups they also tend to take up specific orientations with respect to each other which can be predicted. Although the theory is not well developed

for more than two spheres (even that of two spheres is intractable for the purposes of this work), some interesting observations have been made. They will proceed to arrange themselves in a regular polygon on the same horizontal plane if the cluster contains three to six spheres. Clusters of seven or more do not tend to form any regular grouping. The effect on the terminal velocity is related to the number of spheres in the vicinity, their orientation and the distance between the spheres as compared to their diameter (Jayaweero et al., 1964). Generally speaking, spheres close to each other decrease the terminal velocity by an amount dependent on the angle between the spheres and their distance of separation, as shown below. The velocity ratio $\frac{v_t}{v}$ (where v_t represents the predicted terminal velocity of the sphere alone and v represents the velocity with other spheres) caused by the mutual interaction between the sinking spheres is a linear function of the ratio $\frac{2r}{D}$ when the two spheres are sinking directly beside each other and a quadratic function of the same ratio at other angular orientations (Eveson, et al., 1959). Other researchers have noted that the spheres tend to rotate slowly as they are falling and may separate slightly when the distance between the centers is very small (Mathew and Smith, 1960). Although this theory was developed for spheres under conditions that may not occur for plankter, other results do suggest that the presence of other plankters will affect the ultimate sinking rate. Thus, when dealing with organisms in a natural setting, it may be expected that their terminal velocity will be less than that predicted by the theory given above, especially if the density of organisms in an area is high.

WHY DO ORGANISMS SINK?

As the previous discussion and examples have illustrated, aquatic organisms do not have the same density as the medium and do indeed sink. Obviously continuous sinking even at very small velocities would eventually cause all the phytoplankton community to sink out of the photosynthetic zone. Field observations have shown that this is not the case. Turbulent movement in the photosynthetic zone no doubt plays an important role in resuspension. Why not just adjust the internal density to be equal to that of the media? In other words, why sink at all? This subject was approached in a very unusual way by Munk and Riley (1952) in what is now a classic paper. They not only present an interesting insight into the possible reasons for sinking but also provided alternative explanations for the presence of spines and irregular shapes.

Firstly, they suggest that an increased sinking rate would allow for increased absorption of nutrients from the water. They argue that if an organism were to remain stationary that it would soon use up the nutrients in its vicinity. Movement would allow renewal of nutrients in the vicinity of the organism and thus aid growth. By applying the physical laws of heat absorption of inanimate objects through diffusion and forced convection to a theoretical analysis of phytoplankton nutrient absorption, they have been able to predict rates of sinking, excess density and other characteristics of the populations for waters with different nutrient levels. They have also argued that morphological adaptations are not necessarily aids to suspension but are mechanisms to permit twisting and vertical movements. They then suggested that specialization can be understood as responses

to problems of flotation, nutrient absorption and predation. More recently Garvis (1976) has reformulated Munk and Riley's (1952) work to incorporate the physiology of the phytoplankton. It is now known that nutrient uptake rates are controlled by biological characteristics of the plants unlike the passive diffusion phenomenon that Munk and Riley modeled. Garvis (1976) shows that the diffusion limitations can be important for uptake rates at low nutrient concentrations but less so for corresponding growth rates. Nonetheless competitive interactions should favor small size in nutrient depleted waters. The inter-relationships between ecological problems and available morphological adaptations has led to a general theory based on all sizes, namely:

Cell Size	Chief Problem	Adaptation
Large	Flotation	Large vacuoles -- lead to low cell nutrient concentration and low cell densities
	Nutritional absorption	
Intermediate	Predation	Formation of chains which endangers nutrient absorption and flotation
Small	Predation	Chain formation: nutrient absorption and flotation not endangered

Parsons and Takahasi (1973), Smayda (1974), Pasciak and Garvis (1975) and Titman and Kilham (1976) provide more recent experimental results on this general topic. The interested reader will also wish to read the summaries provided by Hutchinson (1967, Chapter 20) and Smayda (1970).

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PROBLEMS

1. a. Pressure is given in units of atmospheres and dynes cm^{-3}. Name at least two other systems of units and give conversion factors.

   b. That the hydrostatic pressure increases by 1 atm for every 10 meters at depth was given as a rule of thumb. At 10 meters what is the percent change in pressure as compared with the surface? At what depth would there be a 1 atm error using this rule of thumb?

   c. How will the density of water change as a function of dissolved solids, temperature and pressure?

2. In the discussion section of this module, mention was made of the effects on fish and other aquatic organisms of sudden changes in the hydrostatic pressure due to changes in depth.

   What would be the absolute pressures and the pressure change experienced by a fish which lived at 25 meters and was suddenly brought to the surface (0 meters)? What if it were brought to the surface from 100 meters?

3. Many of the higher fish, _Teleostei_, contain closed air bladders which serve as a means for reducing the overall density of the fish to that of the surrounding water. The air bladder regulation is very slow so changes in the gas content due to regulation will be ignored. Now assume that the fish in the example above had an air bladder which was cylindrical with diameter 1/2 cm and length 6 cm. What is the volume at the living depth? What would be the volume at the surface for each case? What would be the volume

37

change in each case? What can you say about the relationships be-
tween the depth changes, pressure changes and volume changes?

4. The overall density of the fish consists of the density of the body
mass of the fish and the density of the air bladder, in proportion
to the volume occupied by each component. Since the volume of the
air bladder changes with pressure and depth, the overall density of
the fish changes also.

Imagine a salmon at a depth of 100 meters. The volume of the
air bladder is 5 cm^3 and the remaining body mass volume is 95 cm^3.
The density of the gases in the air bladder is .00125 gm/cm^{-3} and
that of the remaining body mass is 1.053 gm/cm^{-3}. Confirm this.

If the salmon is now raised 50 meters, what would happen to the
overall density? What would this mean to the fish? What if instead
the fish were lowered 50 meters?

5. In the above examples the fish had no means of controlling the
volume change. What if instead of the salmon we placed a diver at
100 meters? If his lung volume is 500 cm^3 at 100 meters, what would
be the volume at the surface? What is the volume change? How can
he deal with this volume change?

6. What disadvantages are there to swim bladders? What kinds of fish
would you expect not to have them?

7. Assume that you are studying a population of small spherical plankters
that occur in the ocean. You collect a sample of them and measure
the radius and density. The average values you obtain are .001 cm

radius and density $\rho_B = 1.001$. Assuming the standard values for ρ_w and μ what would be the terminal velocity if Stokes law for the resistance can be assumed to hold? If the plankter continued to sink at this rate for a full day, how far would it sink? If the radius were 10 times as big, what effect would it have on v_t and how far would it fall in a day? Would we expect this plankter to keep sinking under natural conditions? What might influence the distance that the plankter sinks?

8. Using equations (7) and (8) compute v_t and t_c for 90% of v_t for the given values of ρ_B and r.

$$\rho_B = 1.0001 \quad 1.001 \quad 1.0001$$
$$r = .005 \quad .005 \quad .05$$

Sketch curves of v_t and t_c vs. r and $\rho_B - \rho_w$.

With r constant what does a 10 fold increase in $\rho_B - \rho_w$ do to v_t and what does the corresponding change in ρ_B do to t_c? With ρ_B constant what does a 10 fold increase in r do to v_t and t_c?

9. For the water temperatures of 1, 15, 25 and 40 °C, what is the density and the viscosity? Which is more important for determining the sinking velocity? At what temperature would a plankter sink fastest?

10. In equations 11 through 13 the resistance force is derived using dimensional analysis. Assuming that the acceleration is zero for equation 4 in the text, derive the terminal velocity for Stokes',

Allen's and Newton's resistance terms. Assume a spherical plankter. Also leave the solution in terms of r_c for Allen's form.

11. Not all plankters are passive organisms. Many possess means of swimming which may help in maintaining or at least regaining position. Such organisms as the small crustacea may be quite powerful swimmers whereas others have only limited success with cilia or flagella. For example, species of dino-flagellates have been shown to have swimming speeds ranging from $0.05-3$ cm min^{-1}.

Write down a force balance equation to include the swimming term, S, using Stokes law. If the acceleration is zero, what is the terminal velocity.

PROBLEM SOLUTIONS

1. a. Table of Conversions

PRESSURE

	atm	dyne/cm²	inch of water	cm Hg	NT/METER²	lb/in.²	lb/ft²
1 atmosphere =	1	1.013×10^6	406.8	76	1.013×10^5	14.70	2116
1 dyne per cm² =	9.869×10^{-7}	1	4.015×10^{-4}	7.501×10^{-5}	0.1	1.450×10^{-5}	2.089×10^{-3}
1 inch of water at 4°C =	2.458×10^{-3}	2491	1	0.1868	249.1	3.613×10^{-2}	5.202
1 centimeter of mercury at 0°C =	1.316×10^{-2}	1.333×10^4	5.353	1	1333	0.1934	27.85
1 NEWTON per METER² =	9.869×10^{-6}	10	4.015×10^{-3}	7.501×10^{-4}	1	1.450×10^{-4}	2.089×10^{-2}
1 pound per in.² =	6.805×10^{-2}	6.895×10^4	27.68	5.171	6.895×10^3	1	144
1 pound per ft² =	4.725×10^{-4}	478.8	0.1922	3.591×10^{-2}	47.88	6.944×10^{-3}	1

* Where the acceleration of gravity has its standard value 9.80665 meters/sec².

1 bar = 10⁶ dyne/cm²   1 millibar = 10³ dynes/cm²

From Halliday, D. and R. Resnick, 1962. Physics, part II. Appendix
G, p. 44.

1. b. At 10 meters the change in pressure is 0.980665 x 10⁶ dynes/cm⁻³ of

96.78% of the 1 atmosphere estimated. The depth where there is a

1 atm error using this rule is calculated as

$$\frac{.0322 \text{ atm error}}{10 \text{ m}} = \frac{1 \text{ atm error}}{x \text{ m}}$$

x = 310.56 m

1. c. Density increases with increasing pressure and increasing dissolved

solids. Distilled water has a minimum density at about 4 °C.

Pressure

2) $P = P_0 + \rho_w gh$

$\quad = 1.01325 \times 10^6 \text{ dynes/cm}^3 + 1 \text{ g cm}^{-3} \times 980.665 \text{ cm s}^{-2} \times 25$

$\quad\quad \times 10^2 \text{ cm} =$

$P_{25} = 3.4649 \quad 10^6 \text{ dynes/cm}^3 = 3.42 \text{ atm}$

$P_0 = 1.01325 \times 10^6 + 0 = 1.01325 \times 10^6 \text{ dynes/cm}^3 = 1 \text{ atm}$

$P_{25} - P_0 = 2.452 \times 10^6 \text{ dynes/cm}^3 = 2.42 \text{ atm}$

$P_{100} = 1.01325 \times 10^6 + 9.8 \times 10^6 = 10.82 \times 10^6 \text{ dynes/cm}^3 = 10.68 \text{ atm}$

$P_{100} - P_0 = 9.8 \times 10^6 \text{ dynes/cm}^3 = 9.68 \text{ atm}$

3) $\pi r^2 = \pi(.25)^2 = .196 \text{ cm}^2 \quad , \quad \pi r^2 \ell = .196(6) = 1.18 \text{ cm}^3$

$PV = C \quad , \quad P_{25} \cdot V_{25} = P_0 \cdot V_0 \quad , \quad V_0 = \dfrac{P_{25}}{P_0} V_{25}$

$4.04 \text{ cm}^3 = \dfrac{3.42}{1} \cdot 1.18 \quad , \quad \Delta V = 2.86 \text{ cm}^3$

$\dfrac{P_{100}}{P_0} \cdot V_{100} = V_0 \qquad\qquad \dfrac{10.68}{1} 1.18 = 12.60 \text{ cm}^3$

$\qquad\qquad\qquad\qquad\qquad \Delta V = 11.42 \text{ cm}^3$

$\dfrac{\Delta P_{25}}{\Delta V_{25}} = \dfrac{\Delta P_{100}}{\Delta V_{100}} = .846 \qquad \therefore \qquad \Delta P = .846 \Delta V$

$\dfrac{\Delta P_{25}}{\Delta D_{25}} = \dfrac{\Delta P_{100}}{\Delta D_{100}} = .10 \qquad \therefore \qquad \Delta P = .10 \ \Delta D$

4) $$V_{air \atop bladder} \times \rho_{air \atop bladder} + V_{body} \times \rho_{body} = V_{total} \times \rho_{total}$$

$$5 \times .00125 + 95 \times 1.053 = 100 \times \rho_{total}$$

$$\rho_{total} = \frac{.00625+100.04}{100} \doteq 1.00 \text{ gm/cm}^3$$

$$P_{50} = 1.01325 \times 10^6 + 4.903 \times 10^6 = 5.9166 \times 10^6 \text{ dynes/cm}^3$$
$$= 5.839 \text{ atm}$$

$$P_{100} V_{100} = P_{50} V_{50}$$
$$V_{50} = \frac{10.68(5)}{5.839} = 9.14 \text{ cm}^3, \ V_{total} = 95 + 9.14 = 104.14$$

$$\rho_{total} = \frac{9.14(.00125)+100.04}{104.14} = .96 \text{ gm/cm}^3.$$

The fish is now lighter than the water and will rise.

$$P_{150} = 1.01325 \times 10^6 + 14.71 \times 10^6 = 15.723 \times 10^6 \text{ dynes/cm}^3$$
$$= 15.52 \text{ atm}$$

$$P_{100} V_{100} = P_{150} V_{150}$$
$$V_{150} = \frac{10.68(5)}{15.52} = 3.44 \text{ cm}^3, \ V_{total} = 95 + 3.44 = 98.44 \text{ cm}^3$$

$$\rho_{total} = \frac{3.44(.00125)+100.04}{98.44} = 1.02 \text{ gm/cm}^3.$$

The fish is heavier than the water and will sink.

5) $$V_0 P_0 = V_{100} P_{100}$$
$$V_0 = \frac{10.68(500)}{1} = 5340.0 \text{ cm}^3$$
$$\Delta V = 4840 \text{ cm}^3$$

The diver must decrease the volume in his lungs by exhaling deeply as he rises

so that his lung volume will remain at 500 cm^3. This is in contrast to the

fish which cannot easily increase or decrease the air bladder volume voluntarily.

6) A fish must change the volume of its swim bladder to achieve neutral buoyancy. This would be a disadvantage if the animal were changing depths quickly as does a tuna. Fishes inhabiting shallow waters might not need them.

Buoyancy

7) $v_t = \frac{2}{9} \frac{g}{\mu} d^2 (\rho_B - \rho_w)$

$g = 980.665 \text{ cm/s}^2$ $\mu = .01 \text{ g/cm-s}$

$d = .001 \text{ cm}$ $\rho_B = 1.001 \text{ g/cm}^3$

$(\rho_B - \rho_w) = .001 \text{ g/cm}^3$

$v_t = 21.793 \ d^2$

$= 2.1793 \times 10^{-5} \text{ cm/s}$ $d = .001$

Distance travelled in 1 day $= v_t \times$ # of seconds in 1 day

$= 2.1793 \times 10^{-5}(8.64 \times 10^4) = 1.883 \text{ cm}$

$v_t = 2.1793 \times 10^{-3} \text{ cm/s}$ $d = 0.01$

Distance $= 2.1793 \times 10^{-3}(8.64 \times 10^4)$

$= 188.3 \text{ cm.}$

Thus a 10 times increase in d causes a 100 times distance increase in both the terminal velocity, v_t, and the distance.

Under natural conditions, turbulent water conditions would cause the plankton to be carried to the upper surface again.

The plankton could also change its density to change the sinking rate, v_t, and the distance it falls.

8) $v_t = 2.792.556 \ d^2 (\rho_B - \rho_w)$ $t_c = 51.17 \rho_B d^2$

a) $\rho_B = 1.0001$ $\rho_B - \rho_w = .0001$ $d = 0.005$

$v_t = 5.45 \quad 10^{-5} \text{cm/s}$

$t_c = 1.28 \quad 10^{-3} \text{s}$

b) $\rho_B = 1.001$ $\rho_B - \rho_w = 0.001$ $d = 0.005$

    $v_t = 5.45 \times 10^{-4}$ cm/s

    $t_c = 1.28 \times 10^{-3}$ s

c) $\rho_B = 1.0001$ $\rho_B - \rho_w = .0001$ $d = .05$

    $v_t = 5.45 \times 10^{-3}$ cm/s

    $t_c = 1.28 \times 10^{-1}$ s
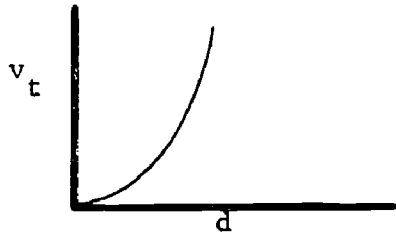
100 fold increase in v_t for 10 fold increase in d
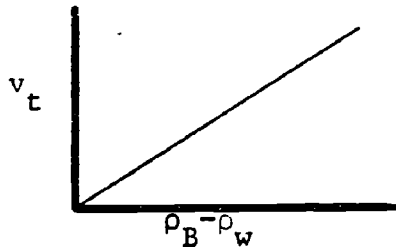
10 fold increase in v_t for 10 fold increase in $\rho_B - \rho_w$
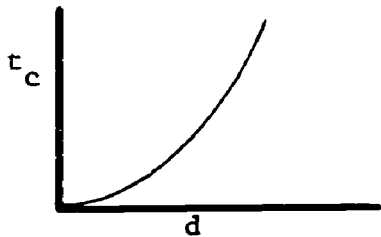
100 fold increase in t_c for 10 fold increase in d
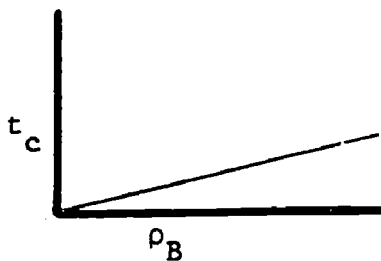
10 fold increase in t_c for 10 fold increase in ρ_B.

9)

Water temperature (°C)	1	15	25	40
Density (g cm^{-3})	0.9996	0.9993	0.9969	0.9923
Viscosity (g cm^{-1}s^{-1})	0.01724	0.01138	0.00890	0.00650

Viscosity is more important than density in determining sinking rates. A plankter will sink faster in warmer water.

10) Using Stokes' law and substituting into equation 4 with acceleration zero we have

$$mg - \rho_w Vg - K'rv_t\mu = 0 .$$

Assuming that the plankter is spherical, this becomes

$$\frac{mg(\rho_B - \rho_w)}{\rho_B} - 6\pi rv_t\mu = 0 .$$

Solving for v_t, we get

$$v_t = \frac{m}{6\pi r\mu} g(1 - \frac{\rho_w}{\rho_B}) = \frac{2}{9} gr^2(\rho_B - \rho_w)\mu^{-1}$$

which is identical to the solution found in the module.

Likewise for Allen's law, we get

$$mg - \rho_w Vg - kr_c^{3/2} v_t^{3/2} v_t^{3/2} \rho_w^{1/2} \mu^{-1/2} = 0$$

$$v_t = 1/2 \, r_c g^{2/3} (\rho_B - \rho_w)^{2/3} \rho_w^{-1/3} \mu^{1/3}$$

where

$$r_c = r - 2/5 \, d$$

and

$$r = \sqrt[3]{\frac{9\mu^2}{2g\rho_w(\rho_B - \rho_w)}}$$

Similarly for Newton's law, we find that

$$v_t = \sqrt[2]{krg(\rho_B - \rho_w)\rho_w^{-1}}$$

Notice that in all cases the terminal velocity is dependent on the term $\rho_B - \rho_w$ called the excess density.

11) $m \dfrac{dv}{dt} = mg \dfrac{(\rho_B - \rho_w)}{\rho_B} - 6\pi r \mu v - S$

$\therefore v_t = \dfrac{2\ r^2\ g}{9\mu} \dfrac{(\rho_B - \rho_w)}{\rho_B} - \dfrac{S}{6\pi r \mu}$

47

APPENDIX I. SYMBOLS, UNITS AND DIMENSIONS

Symbol	Quantity	Units	Dimensions	S.I. Equivalent
A	area	cm^2	L^2	m^2
a	constant	dimensionless	--	--
C	constant	seconds	T^{-1}	--
D	distance between sinking spheres	cm	L	m
G	force of gravity	Dynes	MLT^{-2}	N
g	gravitational constant	980. $cm\ s^{-2}$	LT^{-2}	$m\ s^{-2}$
h	height	cm	L	m
k	coefficient	dinensionless	--	--
k'	coefficient	dimensionless	--	--
m	mass	g	μ	kg
n	exponent	dimensionless		
P	pressure	dynes cm^{-2}	$ML^{-1}T^{-2}$	$N\ m^{-2}$
P_o	atmospheric pressure	dynes cm^{-2}	$ML^{-1}T^{-2}$	$N\ m^{-2}$
q	exponent	dimensionless	--	--
R	resistance	dynes	MLT^{-2}	N
R	gas constant	8.314 J g^{-1} $mole^{-1}\ K^{-1}$	$L^2T^{-2}\theta^{-1}$	--
Re	Reynolds number	dimensionless	--	--

Symbol	Quantity	Units	Dimensions	S.I. Equivalent
R_a	resistance of new shape	dynes	MLT^{-2}	N
R_s	resistance of sphere	dynes	MLT^{-2}	N
r	radius	cm	L	m
r_B	nominal radius	cm	L	m
r_c	critical radius (Allen's law)	cm	L	m
r_s	radius of sphere	cm	L	m
S	swimming force	dynes	MLT^{-2}	N
T	temperature	°C	θ	--
t	time	seconds	T	--
t_c	time to reach	seconds	T	--
u	fraction x exponent	dimensionless		
V	volume	cm^3	L^3	m^3
v	velocity	$cm\ s^{-1}$	LT^{-1}	$m\ s^{-1}$
v_t	terminal velocity	$cm\ s^{-1}$	LT^{-1}	$m\ s^{-1}$
v_{ta}	terminal velocity at new form	$cm\ s^{-1}$	LT^{-1}	$m\ s^{-1}$
v_{ts}	terminal velocity of sphere	$cm\ s^{-1}$	LT^{-1}	$m\ s^{-1}$
v_{t1}	terminal velocity of 1	$cm\ s^{-1}$	LT^{-1}	$m\ s^{-1}$
v_{t2}	terminal velocity of 2	$cm\ s^{-1}$	LT^{-1}	$m\ s^{-1}$

Symbol	Quantity	Units	Dimensions	S.I. Equivalent
X	fraction	dimensionless		
ρ	density	g cm^{-3}	ML^{-3}	kg m^{-3}
ρ_B	density of the body	g cm^{-3}	ML^{-3}	kg m^{-3}
ρ_s	density of gelatinous sheath	g cm^{-3}	ML^{-3}	kg m^{-3}
ρ_w	density of water	g cm^{-3}	ML^{-3}	kg m^{-3}
μ	viscosity	g cm^{-1} s^{-1}	ML^{-}T^{-1}	kg m^{-1} s^{-1}
ϕ_r	coefficient of form resistance	dimensionless		

COMPUTER PROBLEMS

Program BUOY is described in detail in the section titled "User's Guide to Program BUOY." It contains a line printer graphics subroutine named PRNT3D (Gales, 1978) which displays all of the output generated by the program. In each exercise the user must input certain parameter values according to the rules and restrictions listed in the user's guide.

1. Plankter can alter its sinking rate by adopting different strategies of size and density. Consider, for example, a hypothetical plankter of radius = 0.01 cm. How does the theory, explained in the accompanying text, predict that the terminal velocity varies with density (use density values between 1.09 and 1.2)? In particular, is there any difference in the functional relationship for the regions where Stokes' law or Allen's law are valid? Why might these differences occur?

2. Further exploring the strategies of planktonic organisms in regulating their sinking rates, consider a hypothetical plankter of density 1.01 g/cm^3. How does theory predict that the terminal velocity varies with radius (use radius values between .01 cm and .05 cm)? Are there any differences in the functional relationships for the regions when Stokes' law and Allen's law are valid?

3. Combining the results from questions (1) and (2), find a set of radius and density values that results in a terminal velocity of 8.7 x 10^{-2} cm/s. Verify that these values are correct. Find other combinations of radius and density values which yield the same terminal velocity. These results suggest that an infinite number of combinations of radius and density will give a given terminal velocity. In nature, only a few of these combinations are actually seen. Why?

4. Many hydrodynamics texts plot the graphical representation of radius or density versus terminal velocity on log paper. This is done typically because the range of values is very large and some detail is lost. Using the log plot option and the values used for questions (1) and (2), compare the current plots with those obtained previously.

5. In the previous example, the water temperature and, consequently, the viscosity of the water were considered constant. In nature, the temperature and viscosity change with the season of the year and with depth. Consider the hypothetical plankter; find a set of radius and density values such that in the summer the plankter doesn't sink any faster than 2.0 x 10^{-2} cm/s. What effect does this combination of values have on the sinking rate during the winter? Now choose a set of values that results in a winter sinking rate of approximately 2.0 x 10^{-2} cm/s. What effect does the combination of values have on the summer sinking rate? What strategy is generally adapted by aquatic plankters?

USER'S GUIDE FOR PROGRAM BUOY

Identification

BUOY   -A Program Which Displays the Effects of Plankter Radius,
       Plankter Density, and Water Temperature on the Terminal
       Velocity of a Sinking Plankter.

Authors -Christina E. Cowan and Mark Bailey, Center for Quantitative
         Science in Forestry, Fisheries, and Wildlife, University
         of Washington, Seattle. May 1979.

Purpose

Program BUOY is the computer supplement to the module

"Pressure and Buoyancy in Aquatic Ecosystems" by Christina E. Cowan.

The program is designed to let the student investigate the effects

of plankter radius, plankter density, and water temperature (acting

only through water viscosity and not water density) on the sinking

velocity of the organism. Two different water resistance formula-

tions, associated with the names of Stokes and Allen, are used depend-

ing on the value of the Reynold's number.

Operation

Several explicit and implicit factors control the operation of

program BUOY by way of the formulation of the resistance function and

the selection and format of the output.

The resistance function depends on the value of the Reynold's

number, which in turn is a function of user-input. Stoke's law is used

if the Reynold's number is less than 0.5; Allen's law is used if it

exceeds 0.5.

A list of user-assigned options named OPLIST controls the
selection of output. Each option in the list may take on the values
1 through 10 and the list may contain up to 10 unique elements. The
options are divided into four classes, as follows:

Option 1: Perform calculations for a single (radius,
density, temperature) triple and print out the associated
Reynold's number, resistance, and terminal velocity.

Options 2, 3, 4: Hold density and temperature constant
and plot radius versus a) Reynold's number (option 2),
b) terminal velocity (option 3), and/or c) resistance
(option 4).

Options 5, 6, 7: Hold radius and temperature constant and
plot density versus Reynold's number (5), terminal velocity
(6), and/or resistance (7).

Options 8, 9, 10: Hold radius and density constant and plot
temperature versus Reynold's number (8), terminal velocity
(9), and/or resistance (10).

For example, OPLIST = 1,3,5,7 invokes options 1,3,5, and 7 in a single
run. Variables held constant for a set of plots are specified by a
single value, whereas variables which form a plot axis are specified
by two values and indicate a value range. For example, in options
5, 6, or 7, the input

RADIUS = 0.07,

TEMP   = 10,

DENSTY = 1.09, /TQ/ 1.2

indicate that RADIUS (0.07) and TEMP (10) are to be held constant,

whereas DENSTY is to form a continuous x-axis which varies from 1.09
to 1.2.

BUOY calls a printer plot package named PRNT3D to generate
the plots for options 2 through 10. The plot formats (e.g. size, shape,
scale (log or linear) etc.) are controlled by a large number of user-
assignable parameters which are described in the User's Guide for
PRNT3D (Gales, 1978). These parameters may be included along with
the above mentioned input for BUOY; however, BUOY itself assigns de-
fault values which are adequate for most purposes (one common exception:
setting NY = -45 instead of + 45 generates plots with a logarithmic
y-axis scale).

Program Organization

The program is organized around the following flow chart:

```
                              ╳
                              │
                              ▼
              ┌──────────────────────────────┐      Yes
              ⟨      NODFLT = TRUE?      ⟩ ──────────────┐
              └──────────────────────────────┘          │
                              │ No                       │
                              ▼                          │
                ┌──────────────────────────┐            │
                │ Read default values for  │            │
                │ all variables from the   │            │
                │ built in default file    │            │
                └──────────────────────────┘            │
                              │                          │
                              ▼◄─────────────────────────┘
                ┌──────────────────────────┐
                │ Read in the next         │
                │ user-supplied data set   │
                └──────────────────────────┘
                              │
                              ▼                  Yes    ┌──────────────┐
              ⟨      FINIS = TRUE?      ⟩ ──────────────▶│ Terminate    │
                              │ No                       │ program      │
                              ▼                          └──────────────┘
                ┌──────────────────────────┐
                │ Check for errors in      │
                │ the input set just read  │
                └──────────────────────────┘
                              │
┌──────────────┐  Yes         ▼
│ Output       │◄──────────⟨   Errors found?   ⟩
│ appropriate  │                  │ No
│ error        │                  ▼
│ messages     │   ⟨ Is OPLIST exhausted? ⟩ ────── Yes ──────┐
└──────────────┘                  │ No                       │
      ▲                           ▼                          │
      │                                           ┌──────────────────────┐
      │           ⟨   OPLIST(I) = 1?   ⟩ ── Yes ─▶│ Calculate values     │
      │                           │ No            │ for a single point   │
      │                           ▼               │ and print out        │
      │           ┌──────────────────────────┐    └──────────────────────┘
      │           │ Calculate all points     │              │
      │           │ in a plot, and flag      │              │
      │           │ any error conditions     │              │
      │           └──────────────────────────┘              │
      │                           │                          │
      │      Yes                  ▼                          │
      │  ├─────────────────⟨   Errors?   ⟩                   │
      │                           │ No                       │
      │                           ▼                          │
      │           ┌──────────────────────────────┐          │
      │           │ Write out x,y coordinates     │          │
      │           │ plus plot titles.  Call the   │          │
      │           │ printer plot routine QQI R3D  │          │
      │           │ which generates the plot      │          │
      │           └──────────────────────────────┘          │
      │                           │                          │
      │                           ▼◄─────────────────────────┘
      │                ⟨   I = I + 1   ⟩
      │                           │
      └───────────────────────────┘
```

Input

All input is handled by a format free input package (Gales and Anderson, 1978) which permits a user to assign values to variables by a "name=value" convention. Not all variables need be explicitly assigned by the user, however, as unassigned variables automatically assume default values. The input consists of any number of data sets, each of which is terminated by a dollar sign ($). Comments in an input set are enclosed within slashes (/). Each data set may generate a number of separate printer plots.

The input for BUOY is divided into three classes: a) variables having biological significance or related to program options: NPOINT, OPLIST, RADIUS, DENSTY, and TEMP; b) variables which control certain program operations, such as program termination or the handling of default input: IPRINT, ECHO, NODFLT, and FINIS; and c) variables which control the printer plots (default values are in parentheses): XMIN (0), XMAX (0), YMIN (0), YMAX (0), ZMIN (0), ZMAX (9), XRICH (0), YRICH (0), DFAULT (0), OVPRNT (.F.), AVE (.F.), INT2D (.F.), NX (60), NY (45), and ZMAP (0,1,2,3,4,5,6,7,8,9). The variables in the first two classes are explained in the following INPUT TABLE, whereas the printer plot variables are explained in the user's guide for PRNT3D (Gales, 1978).

INPUT TABLE

Name	Type and Dimensions	Range Limits	Description
NPOINT	Integer	[2,99]	The number of points calculated for each curve. Default value is: NPOINT = 12
OPLIST	Integer(10)	[1,10]	A list of up to 10 unique options which control the output. The options are as follows: 1: Perform calculations for a single (RADIUS, DENSTY, TEMP) triple and print out the associated Reynold's number, resistance, and terminal velocity 2: Hold (DENSTY, TEMP) constant and plot RADIUS vs. Reynold's number 3: Hold (DENSTY, TEMP) constant and plot RADIUS vs. terminal velocity 4: Hold (DENSTY, TEMP) constant and plot RADIUS vs. resistance 5: Hold (RADIUS, TEMP) constant and plot DENSTY vs. Reynold's number 6: Hold (RADIUS, TEMP) constant and plot DENSTY vs. terminal velocity 7: Hold (RADIUS, TEMP) constant and plot DENSTY vs. resistance 8: Hold (RADIUS, DENSTY) constant and plot TEMP vs. Reynold's number 9: Hold (RADIUS, DENSTY) constant and plot TEMP vs. terminal velocity 10: Hold (RADIUS, DENSTY) constant and plot TEMP vs. resistance If OPLIST(I) = 0 for some I, then no action is taken for the I-th option. Default values are: OPLIST = 1,0,0,0,0,0,0,0,0,0

60

Input Table Cont.

Name	Type and Dimensions	Range Limits	Description
RADIUS	Real(2)	[0.001,1.0]	The radius of a plankter, in centimeters. For options 1,5,6,7,8,9 and 10, RADIUS is specified by a single number(or the first number only in a pair); for options 2,3 and 4, it is specified by a pair of numbers which indicate a range of values (e.g. RADIUS = 0.1, /TO/ 0.3). Default values are: RADIUS = 0.01, /TO/ 1.0.
DENSTY	Real(2)	[1.001,2.0]	The density of a plankter, relative to water (= 1.000). For options 1,2,3,4,8,9 and 10, DENSTY is specified by a single number (or the first number only in a pair); for options 5,6 and 7, it is specified by a pair of numbers which indicate a range of values. Default values are: DENSTY = 1.09, /TO/ 2.0
TEMP	Real(2)	[0,30]	The water temperature, in degrees centigrade. For options 1,2,3,4, 5,6 and 7, it is specified by a single number (or the first number only in a pair); for options 8,9 and 10 it is specified by a pair of numbers which indicate a range of values. Default values are: TEMP = 0.0, /TO/ 30
IPRINT	Logical	.F., .T.	A Logical value which causes the current values for all input variables (default as well as current user input) to be printed. Default value is: IPRINT = .F.
ECHO	Logical	.F., .T.	A Logical value which causes the user's input to be echoed if ECHO = .T., or suppresses echoing if ECHO = .F. Default value is: ECHO = .T.
NODFLT	Logical	.F., .T.	A Logical value which suppresses the input of default values if NODFLT = .T. Default value is: NODFLT = .F.

Input Table Cont.

Name	Type and Dimensions	Range Limits	Description
FINIS	Logical	.F., .T.	A Logical value which causes program termination if and only if FINIS = .T. Default value is: FINIS = .F.

The last four variables deserve special mention.

1. The logical variable IPRINT controls the output of all input variables which are currently in effect (default values as well as those specified in the current input set). Setting IPRINT=TRUE (or T or .T.) displays the current values for all input variables; setting IPRINT= FALSE (or F or .F.) suppresses the display.

2. The logical variable ECHO controls the echoing of the input cards. Setting ECHO=TRUE causes the subsequent input set to the echoed; setting ECHO=FALSE suppresses the echo for the subsequent input set.

3. The logical variable NODFLT can be used to inhibit the automatic assignment of default values to input variables. If NODFLT is set TRUE in the current input set, then the current input set is assigned default values as usual, but all subsequent input sets merely accumulate more input values. In effect, the input values which exist after the i-th input set is read, become the default values for the (i+1)-th input set. The standard default values may then be restored by setting NODFLT=FALSE, but, again, the effects of this change are delayed until the next input set is read. To a limited extent, NODFLT permits a user to set up his own default values and can be very useful for executing a number of input sets which differ only in a few parameters. Consider the following example in which a user wishes to produce a number of radius versus terminal velocity plots with different values for temperature:

```
/INPUT SET 1:  THE FOLLOWING VALUES BECOME THE/
/DEFACTO DEFAULTS FOR ALL SUBSEQUENT INPUT SETS:/
     NODFLT = TRUE,  NPOINT = 15, OPLIST = 3,
     RADIUS = 0.001, /TO/ 0.5,  TEMP = 0, DENSTY = 1.3, $
```

```
/INPUT SET 2:  UP THE TEMPERATURE/

     TEMP = 2, $

/INPUT SET 3:  UP IT AGAIN/

     TEMP = 4, $

/INPUT SET 4:  AND AGAIN/

     TEMP = 6, $

/INPUT SET 5:  FRY IT TO A CRISP/

     TEMP = 30, $

/INPUT SET 6:  STOP IT NOW/   .

     FINIS = TRUE, $
```

4. The logical variable FINIS controls program termination. The user

    must add the card:

    FINIS = TRUE, $

    as the very last input set. If FINIS is not set, the program will

    terminate abnormally.

Output

BUOY produces a small table of values for option 1, and a maximum

of nine plots for the full set of options 2 through 10, in a single run.

Each plot contains a set of titles at the top of the plot, x and y axis

annotation, x and y axis numeric labels, and a plot legend which speci-

fies scale factors for the numeric labels. The parts of a plot are

best explained by an example. Consider the first plot in the set of

sample runs. The plot title consists of the four lines:

    HYDRAULIC PROPERTIES OF PLANKTON

RANGE OF X (.0100, .0400), RANGE OF Y (.0138, .8805)

        DENSITY = 1.0100

        TEMPERATURE = 0

64

, The x- and y-axis annotations are:

REYNOLDS NUMBER   (y-axis)

RADIUS (CM)   (x-axis)

The x and y numeric labels, along with the first line of the plot legend, enable the user to interpret the plot numerically. For example, the point in the extreme upper right corner (designated with a "1" character) is at coordinates (x = 4.000, y = 8.805). Since the scale factor for x is E - 02 (i.e. 10^{-2}) and the scale factor for y is E - 01 (i.e. 10^{-1}), the true coordinates are (x = 4 x 10^{-2}, y = 8.805 x 10^{-1}) = (x = 0.04, y = 0.8805). Note that the y-axis is plotted on a logarithmic scale. The last two lines in the plot legend show the number of points mapped to each of 10 z-axis levels (this information is more useful for programs which generate a number of different curves on a single page, each one identified by a single z-axis level). In this case, a large number (> 99) were mapped to z level 0 and show up as blanks, 20 were mapped to z level 1 and show up as 1's, and none were mapped to any other z level.

Restrictions

The user must restrict all input variables according to the range limits listed in the input table, in order to avoid unrealistic physical values.

Error Messages

There are four types of errors which may occur when attempting to execute program BUOY:

1. Syntax errors in the user's input

2. Range check errors

3. Calculation errors

4. Plot parameter errors

```
XBUOY,T15,P2.
ACCOUNT,9XM08C00,███████
COMMENT.
COMMENT.    **************************************************************
COMMENT.    * THE FIRST CARD SPECIFIES THE JOB NAME, -XBUOY-, THE        *
COMMENT.    * CENTRAL PROCESSOR TIME, -T20- (IN SECONDS), AND THE JOB    *
COMMENT.    * PRIORITY, -P2-. THE SECOND CARD SPECIFIES THE BUDGET AND   *
COMMENT.    * PASSWORD.                                                  *
COMMENT.    **************************************************************
COMMENT.
ATTACH,BBUOY,ID=BBUOY.
ATTACH,BFF,ID=BFF.
ATTACH,BPR3D,ID=BPR3D.
COMMENT.
COMMENT.    **************************************************************
COMMENT.    * THE ABOVE CARDS ATTACH THE PROGRAM BUOY, -BBUOY-, AND THE  *
COMMENT.    * SUPPORT ROUTINES FREE FORM INPUT, -BFF-, AND PRNT3D,       *
COMMENT.    * -BPR3D-. THEY ARE ALL IN BINARY FORM.                      *
COMMENT.    **************************************************************
COMMENT.
LOAD,BBUOY.
LOAD,BFF.
LOAD,BPR3D.
EXECUTE,BUOY.
COMMENT.
COMMENT.    **************************************************************
COMMENT.    * THE ABOVE CARDS LOAD THE PROGRAM AND SUPPORT ROUTINES,     *
COMMENT.    * AND PASS CONTROL TO BUOY FOR EXECUTION.                    *
COMMENT.    **************************************************************
COMMENT.
*EOR
/                                                                        /
/                                                                        /
/ THE FOLLOWING DEFAULT VALUES ARE ASSUMED UNLESS OVERRIDDEN BY          /
/ INPUT VALUES                                                           /
/                                                                        /
/    OPLIST = 1                                                          /
/    NPOINT = 12                                                         /
/    DENSTY = 1.09,2.0                                                   /
/    RADIUS = 0.001,1.0                                                  /
/    TEMP = 0.0,30.0                                                     /
/    ECHO = .T.                                                          /
/    FINIS = .F.                                                         /
/    NODFLT = .F.                                                        /
/    IPRINT = .F.                                                        /
/                                                                        /
/                                                                        /
/*****************************RUN 1*******************************/
/                                                                        /
/    OPLIST=1, RADIUS=0.007, DENSTY=1.01, $                              /
/                                                                        /
/                                                                        /
/*****************************RUN 2*******************************/
/                                                                        /
/    OPLIST=2,3,4, NPOINT=20, RADIUS=0.01, /TO/ 0.04, NY= -45,           /
/    DENSTY=1.01, $                                                      /
/                                                                        /
/*****************************RUN 3*******************************/
```

```
     OPLIST=5,6,7, NPOINT=15, DENSTY=1.09, /TO/ 1.2, S
/                                                                          /
/**************************************RUN 4********************************/
/                                                                          /
     OPLIST=8,9,10, NPOINT=12, DENSTY=1.01, RADIUS=0.04, S
/                                                                          /
/**************************STOP PROGRAM*************************************/
/                                                                          /
     FINIS = .T., S
*EOR
```

68

     OPLIST=5,6,7, NPOINT=15, DENSTY=1.09, /TO/ 1.2, S

```
OGRAM -BUOY- READY FOR INPUT

/   THE FOLLOWING DEFAULT VALUES ARE ASSUMED UNLESS OVERRIDDEN BY
/   INPUT VALUES
/
/       OPLIST = 1
/       NPOINT = 12
/       DENSTY = 1,09,2.0
/       RADIUS = 0.001,1.0
/       TEMP = 0,0,30.0
/       ECHO = .T,
/       FINIS = .F.
/       NODFLT = .F.
/       IPRINT = .F.
/
/***********************************RUN 1***************************/
/
        OPLIST=1, RADIUS=0.007, DENSTY=1.01, S
```

```
:US                     .70000E-02
SITY                    .10100E+01
ERATURE                      0
NOLDS NUMBER            .47190E-02
STANCE                  .14069E-04
MINAL VELOCITY          .59964E-02
```

69

/   /
/***************************************RUN 2***************************************/
/
    OPLIST=2,3,4, NPOINT=20, RADIUS=0.01, /TO/ 0.04, NY= -45,
    DENSTY=1.01, S

70

    OPLIST=2,3,4, NPOINT=20, RADIUS=0.01, /TO/ 0.04, NY= -45,
    DENSTY=1.01, S

HYDRAULIC PROPERTIES OF PLANKTON
-RANGE OF X (.0100, .0400), RANGE OF Y (.0138, .8805)
DENSITY = 1.0100
TEMPERATURE = 0

```
          1.000      1.458      1.966      2.475      2.983      3.492      4.000
          X----------X----------X----------X----------X----------X----------X
8.805Y                                                                      1
     I                                                                  1
     I                                                              1
     I                                                          1
     I
5.489Y                                                     1
     I
     I                                                1
     I
3.422Y                                            1
     I
     I                                        1
     I
2.133Y                                   1
     I
     I                               1
     I
1.330Y                           1
     I
     I                       1
     I
 .829Y                    1
     I
     I               1
     I
 .517Y           1
     I
     I        1
 .322Y     1
     I
     I
     I
 .201Y  1
     I
     I
 .138Y1
      X----------X----------X----------X----------X----------X----------X
   1.000      1.458      1.966      2.475      2.983      3.492      4.000
                                 RADIUS (CM)
```

SCALE FACTORS = X-AXIS: E-02   Y-AXIS(LOG): E-01   Z-AXIS: E+00
Z0-Z4=   0(-9);   1.000(20);   2.000(0);   3.000(0);   4.000(0)
Z5-Z9= 5.000(0);   6.000(0);   7.000(0);   8.000(0);   9.000(0)

71
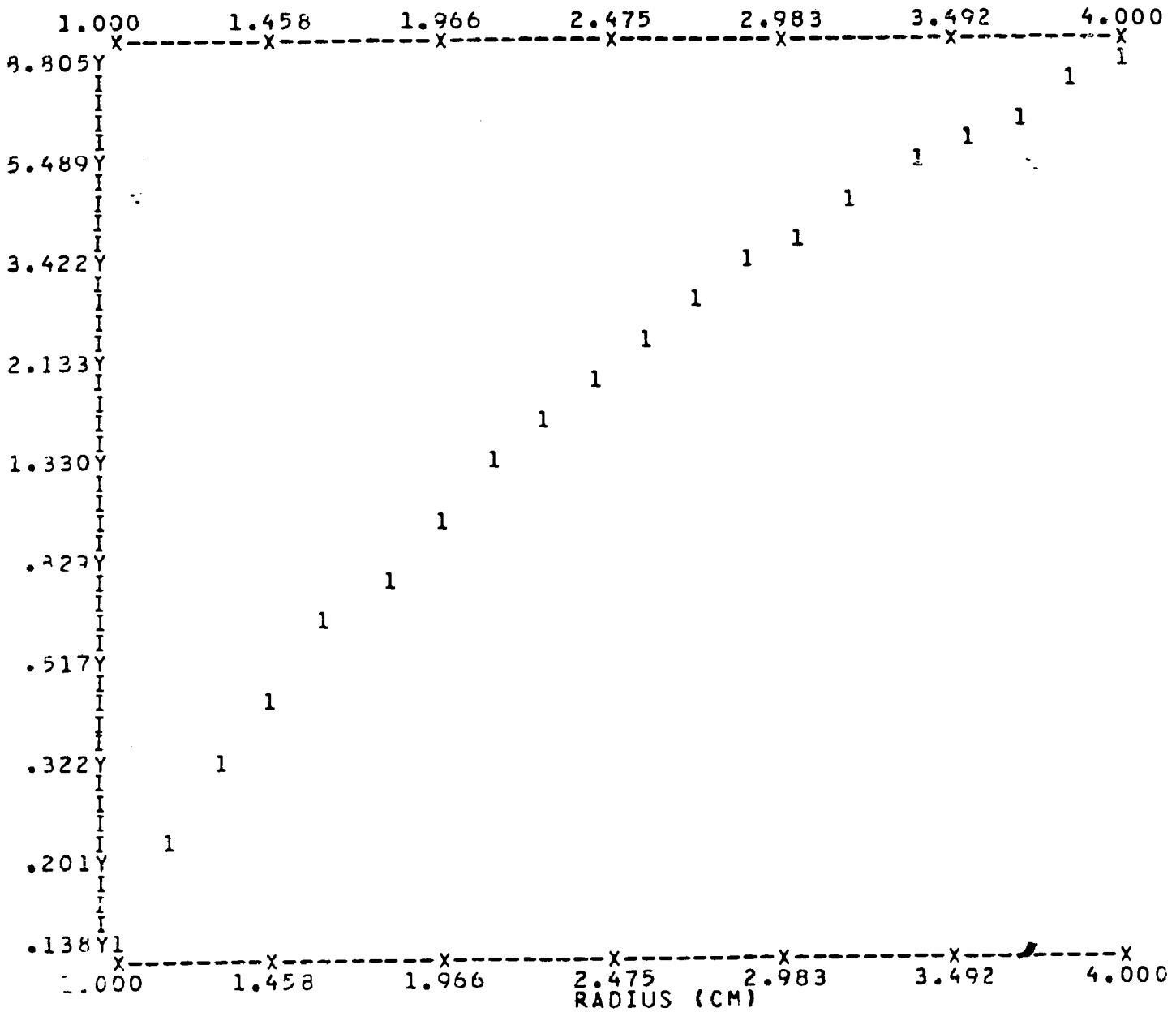
HYDRAULIC PROPERTIES OF PLANKTON
RANGE OF X (.0100, .0400), RANGE OF Y (.0122, .1665)
DENSITY = 1.0100
TEMPERATURE =   0

```
           1.000      1.458      1.966      2.475      2.983      3.492      4.000
             X----------X----------X----------X----.--.--X----------X----------X
       1.665Y                                                                  1
           I                                                              1
           I                                                         1
       1.238Y                                                   1    1    1
           I                                          1    1              1
           I                                     1
       .920Y                                1
    T      I                           1
    E      I                      1
    R  .684Y                 1
    M      I            1
    I      I       1
    N  .508Y    1
    A      I 1
    L      I
    .378Y       1
    V      I 1
    E      I
    L  .281Y  1
    O      I
    C      I
    I  .209Y  1
    T      I
    Y      I
    ( .155Y    1
    C      I
    M      I
    / .122Y1
    S      X----------X----------X----------X----------X----------X----------X----X
    E    1.000      1.458      1.966      2.475      2.983      3.492      4.000
    C                                    RADIUS (CM)
```

SCALE FACTORS = X-AXIS: E-02   Y-AXIS(LOG): E-01   Z-AXIS: E+00
Z0-Z4=   0(-9); 1.000(20); 2.000(0); 3.000(0); 4.000(0)
Z5-Z9=   5.000(0); 6.000(0); 7.000(0); 8.000(0); 9.000(0)

72

HYDRAULIC PROPERTIES OF PLANKTON
RANGE OF X (.0100, .0400), RANGE OF Y (.0000, .0487)
DENSITY = 1.0100
TEMPERATURE = 0

SCALE FACTORS = X-AXIS: E-02, Y-AXIS(LOG): E-02 Z-AXIS: E+00
Z0-Z4= 0(-9), 1.000(20), 2.000(0), 3.000(0), 4.000(0)
Z5-Z9= 5.000(0), 6.000(0), 7.000(0), 8.000(0), 9.000(0)

PROGRAM -BUOY- READY FOR INPUT

```
/********************************RUN 3********************************/
/
      OPLTST=5,6,7, NPOINT=15, DENSTY=1.09, /TO/ 1.2, S
```

74

HYDRAULIC PROPERTIES OF PLANKTON
RANGE OF X (1.0900, 1.2000), RANGE OF Y (.1238, .2752)
RADIUS = .0100
TEMPERATURE = 0

SCALE FACTORS = X-AXIS: E+00   Y-AXIS: E-01   Z-AXIS: E+00
Z0-Z4=   0(-9),   1.000(15),   2.000(0),   3.000(0),   4.000(0)
Z5-Z9=   5.000(0),   6.000(0),   7.000(0),   8.000(0),   9.000(0)

RANGE OF X (1.0900, 1.2000), RANGE OF Y (.1101, .2448)
RADIUS = .0100
TEMPERATURE = 0

```
          1.090      1.107      1.125      1.144      1.163      1.181      1.200
          X----------X----------X----------X----------X----------X----------X
  2.448Y                                                                     X
        I                                                                    1
        I
        I                                                              1
  2.295Y
        I                                                         1    .
 T      I
 E 2.142Y                                                    1
 R      I
 M      I                                              1
 I      I
 N 1.989Y                                        1
 A      I
 L      I                                  1
        I
 V 1.836Y                            1
 E      I
 L      I                       1
 O      I
 C 1.683Y                  1
 I      I
 T      I             1
 Y      I
  1.530Y         1
 (      I
 C      I       .
 M      I
 / 1.377Y    .    1
 S      I
 E      I    1
 C      I
 ) 1.224Y
        I   1
        I
  1.101Y1
        X----------X----------X----------X----------X----------X----------X
          1.090      1.107      1.125      1.144      1.163      1.181      1.200
                              DENSITY (GM/CM**3)
```

SCALE FACTORS = X-AXIS: E+00   Y-AXIS: E-01   Z-AXIS: E+00
Z0-Z4=   0(-9);   1.000(15);   2.000(0);   3.000(0);   4.000(0)
Z5-Z9= 5.000(0);   6.000(0);   7.000(0);   8.000(0);   9.000(0)

76

```
                    HYDRAULIC PROPERTIES OF PLANKTON
      RANGE OF X ( 1.0900, 1.2000), RANGE OF Y ( .0004,  .0008)
                         RADIUS =     .0100
                         TEMPERATURE =        0

        1.090        1.107        1.125        1.144        1.163        1.181        1.200
          X------------X------------X------------X------------X------------X------------X
  8.203Y                                                                               1
        I
        I                                                                        1
  7.691Y
        I                                                                  1
        I
R 7.178Y                                                             1
E       I
S       I
I       I                                                      1
S 6.665Y
T       I                                                1
A       I
N 6.152Y                                           1
C       I
E       I                                     1
( 5.640Y
G       I                                1
M       I
/ 5.127Y                            1
C       I
M       I
/ 4.614Y                      1
S       I
E       I                1
C 4.102Y
*       I           1
*       I
2 3.691Y1
)         X------------X------------X------------X------------X------------X------------X
        1.090        1.107        1.125        1.144        1.163        1.181        1.200
                              DENSITY (GM/CM**3)
```

SCALE FACTORS = X-AXIS: E+00   Y-AXIS: E-04   Z-AXIS: E+00
Z0-Z4=   0(-9),   1.000(15),   2.000(0),   3.000(0),   4.000(0)
Z5-Z9= 5.000(0),   6.000(0),   7.000(0),   8.000(0),   9.000(0)

77
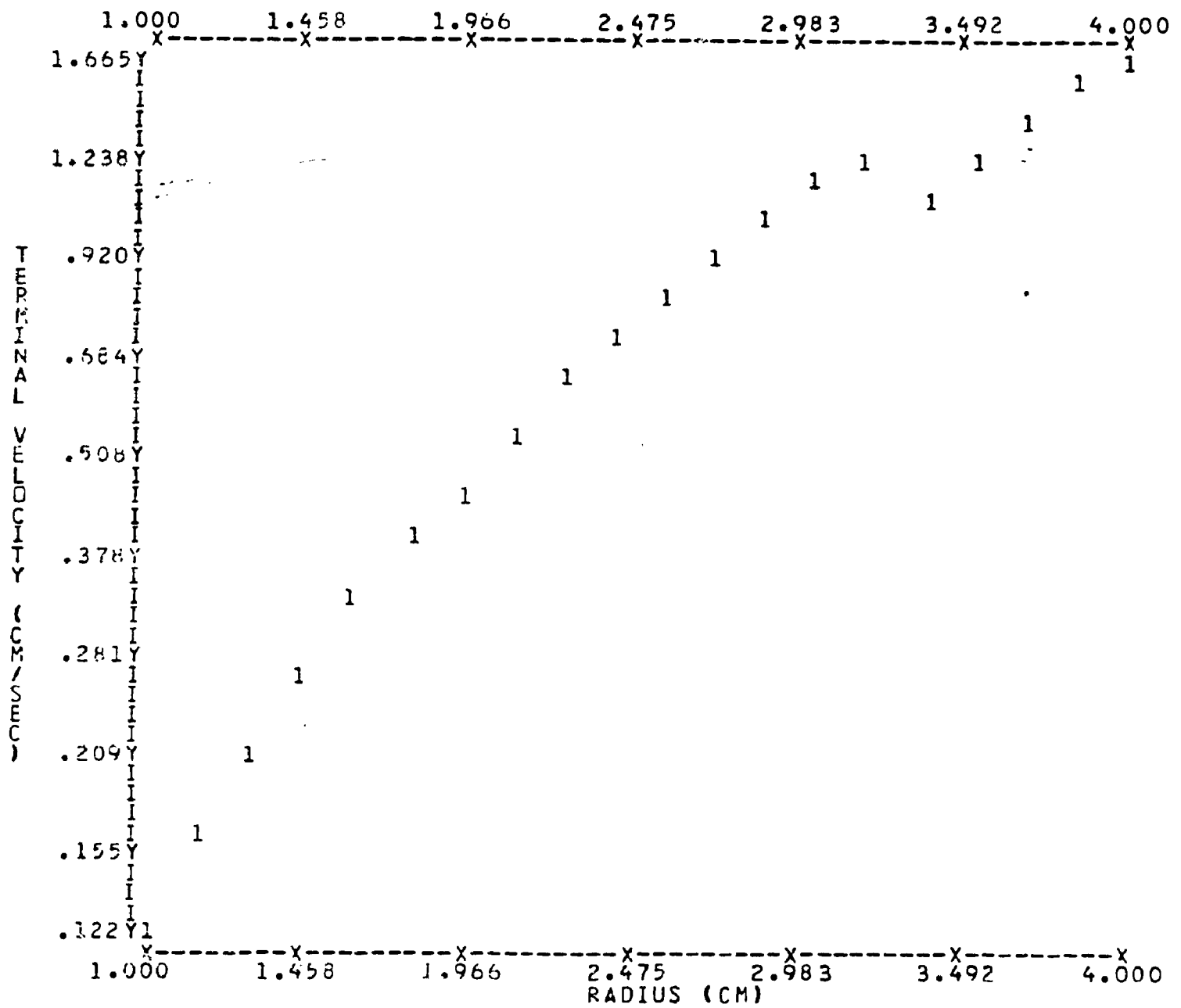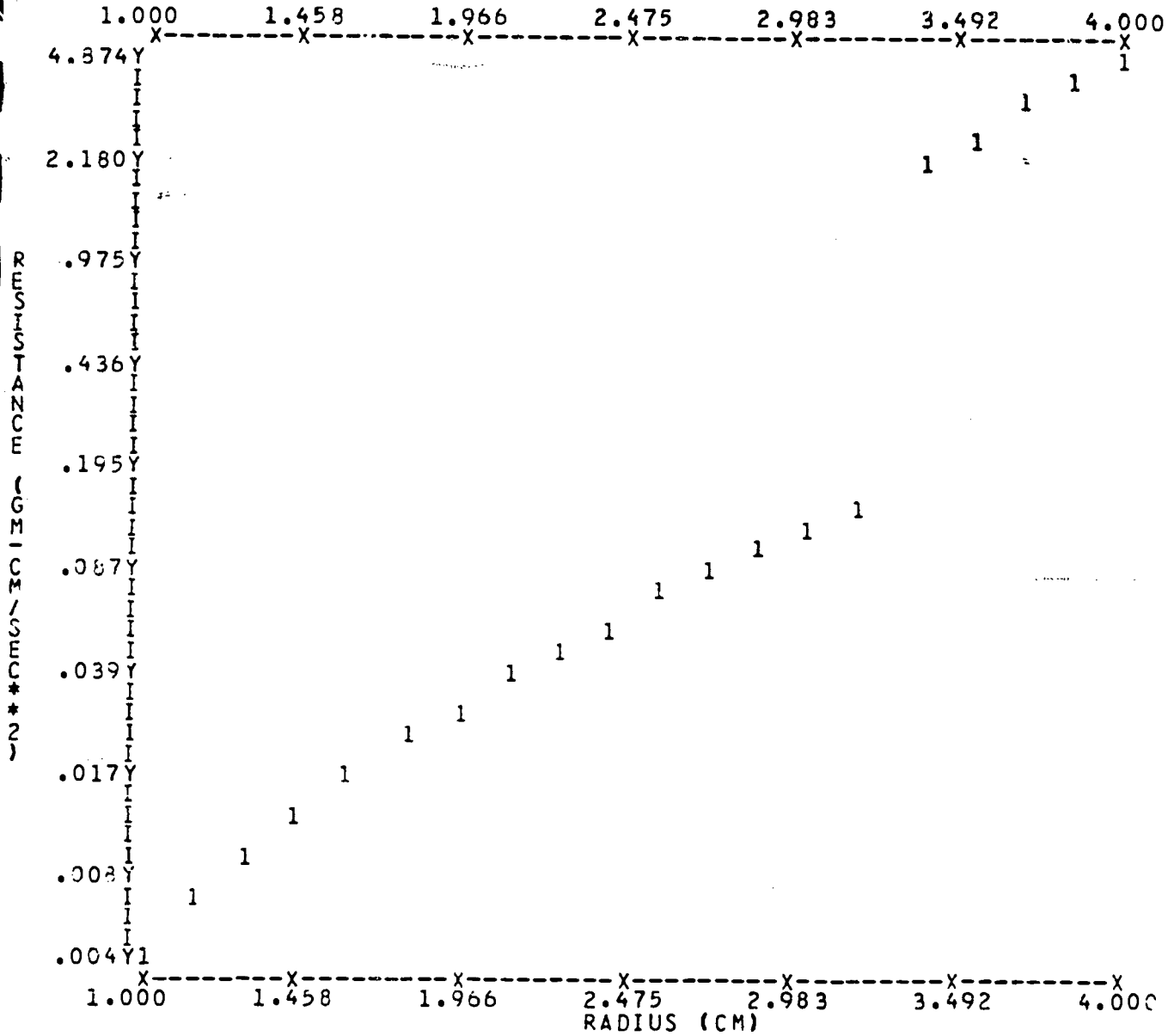
PROGRAM -BUOY- READY FOR INPUT

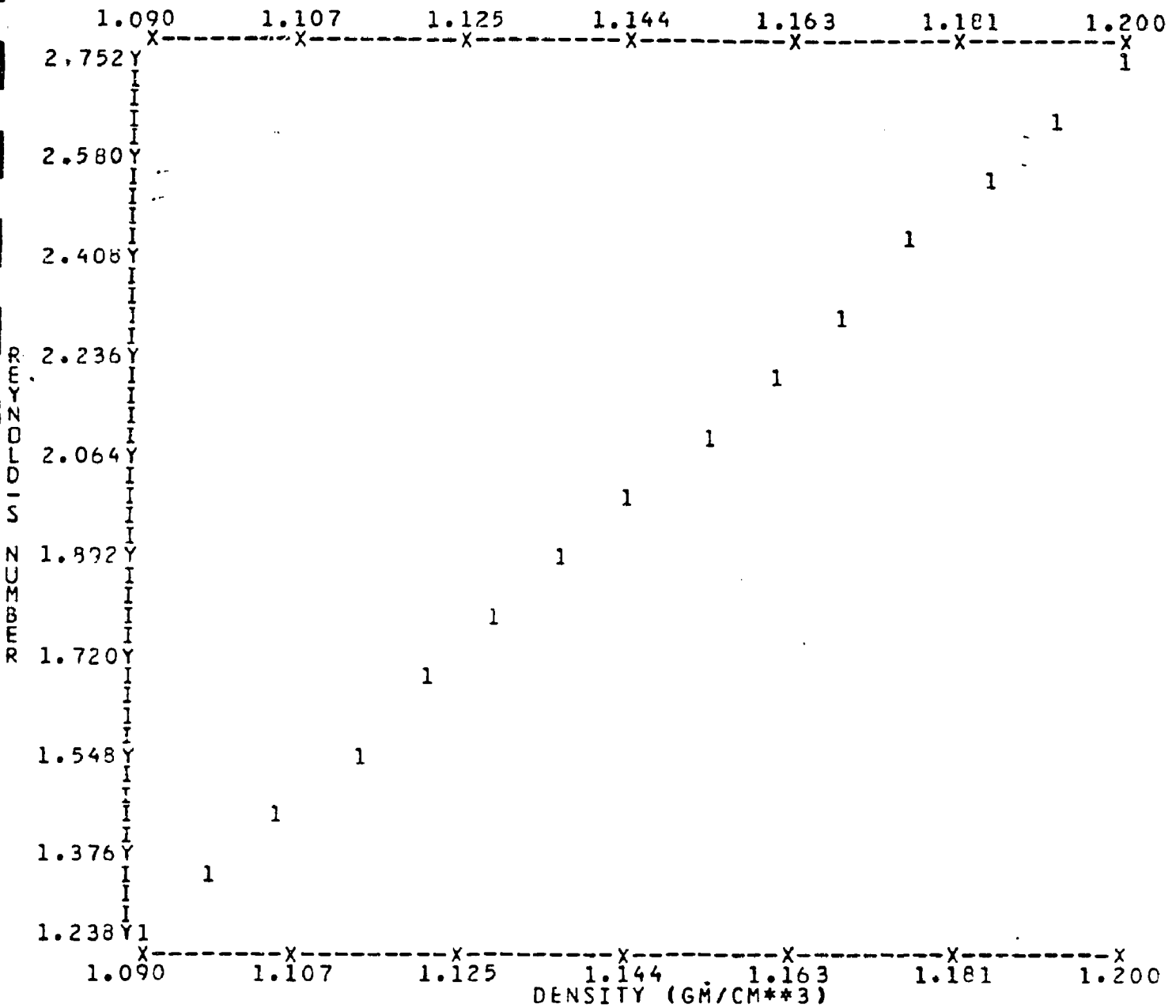/*******************************RUN 4*******************************/

    OPLIST=8,9,10, NPOINT=12, DENSTY=1.01, RADIUS=0.04, S

HYDRAULIC PROPERTIES OF PLANKTON
RANGE OF X (0,30.0000), RANGE OF Y (.8805, 4.3187)
RADIUS = .0400
DENSITY = 1.0100

```
          0        .458       .966      1.475      1.983      2.492     3.000
       X---------X----------X----------X----------X----------X---------X
4.319Y                                                                   1
     I
     I
3.928Y
     I                                                         =1
     I
3.537Y
     I
R    I                                                 1
E 3.147Y
Y    I
N    I                                         1
O 2.756Y
L    I
D    I                                   1
S 2.365Y
     I
N    I                             1
U 1.974Y
M    I                        1
B    I
E 1.584Y
R    I                   1
     I
1.193Y              1
     I
     I        1
 .861Y1
     X---------X----------X----------X----------X----------X---------X
          0        .458       .966      1.475      1.983      2.492     3.000
                              TEMPERATURE (CELSIUS)
```

SCALE FACTORS = X-AXIS: E+01   Y-AXIS: E+00   Z-AXIS: E+00
Z0-Z4=   0(-9),   1.000(12),   2.000(0),   3.000(0),   4.000(0)
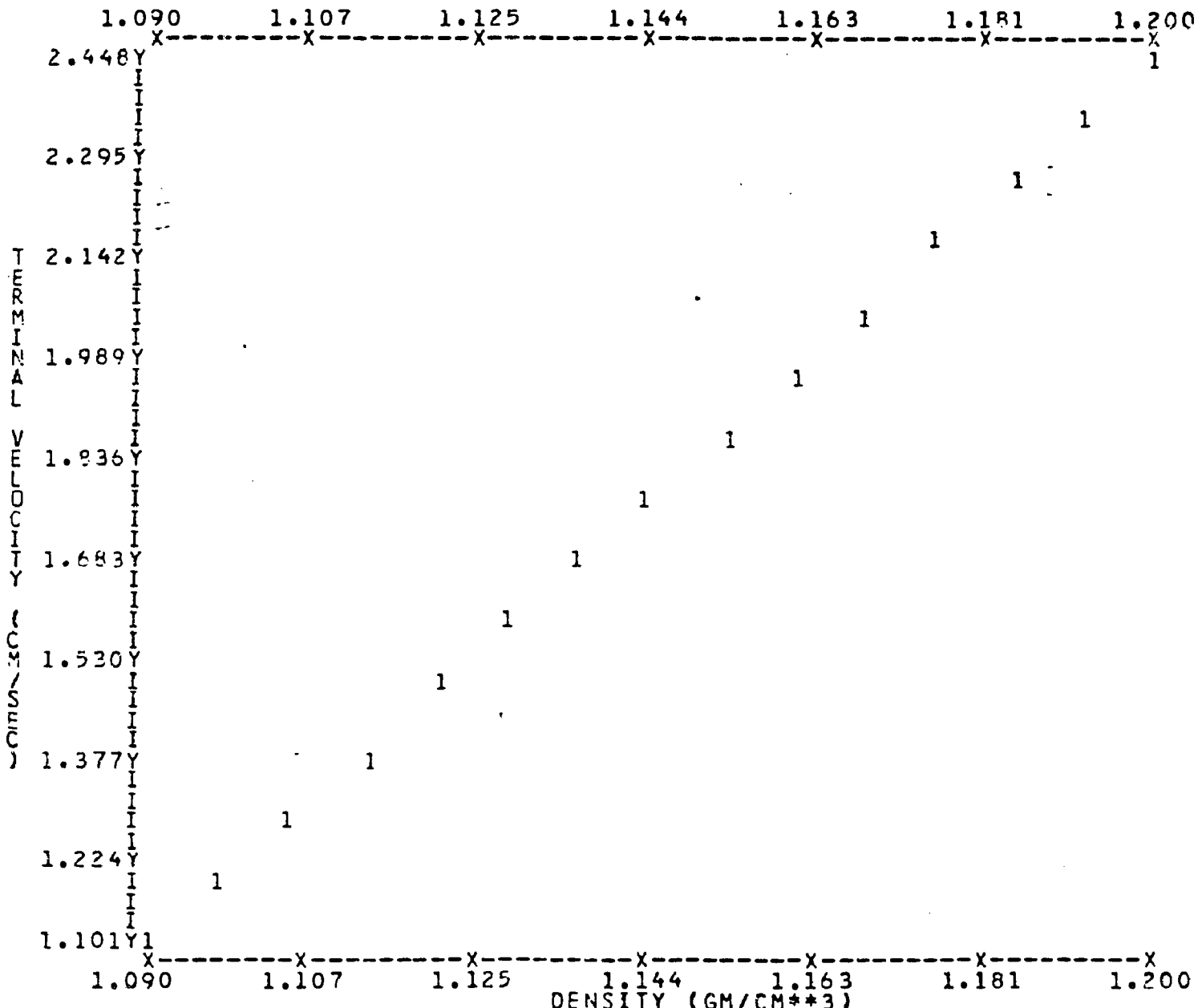Z5-Z9= 5.000(0),   6.000(0),   7.000(0),   8.000(0),   9.000(0)

HYDRAULIC PROPERTIES OF PLANKTON
RANGE OF X (0,30.0000), RANGE OF Y (.1665,   .3160)
RADIUS =   .0400
DENSITY = 1.0100

```
             0        .458        .966       1.475      1.983      2.492     3.000
          X---------X---------X---------X---------X---------X---------X
   3.160Y                                                              X
        I                                                              1
        I
        I                                                         1
   2.990Y
        I
        I
        I
   2.820Y                                                   1
   T    I
   E    I
   R    I                                              1
   M    I
   I    I
   N  2.650Y                                       1
   A    I
   L    I
        I                                     1
   V    I
   E  2.480Y
   L    I                                 1
   O    I
   C    I
   I    I                            1
   T  2.311Y
   Y    I
        I
   (    I                        1
   C  2.141Y
   M    I                   1
   /    I
   S    I
   E    I
   C  1.971Y              1
   )    I
        I
        I
        I
   1.801Y         1
        I
        I
        I
   1.665Y1
          X---------X---------X---------X---------X---------X---------X
             0        .458        .966       1.475      1.983      2.492     3.000
                              TEMPERATURE (CELSIUS)
```

SCALE FACTORS = X-AXIS: E+01   Y-AXIS: E-01   Z-AXIS: E+00
Z0-Z4=   0(-9);   1.000(12);   2.000(0);   3.000(0);   4.000(0)
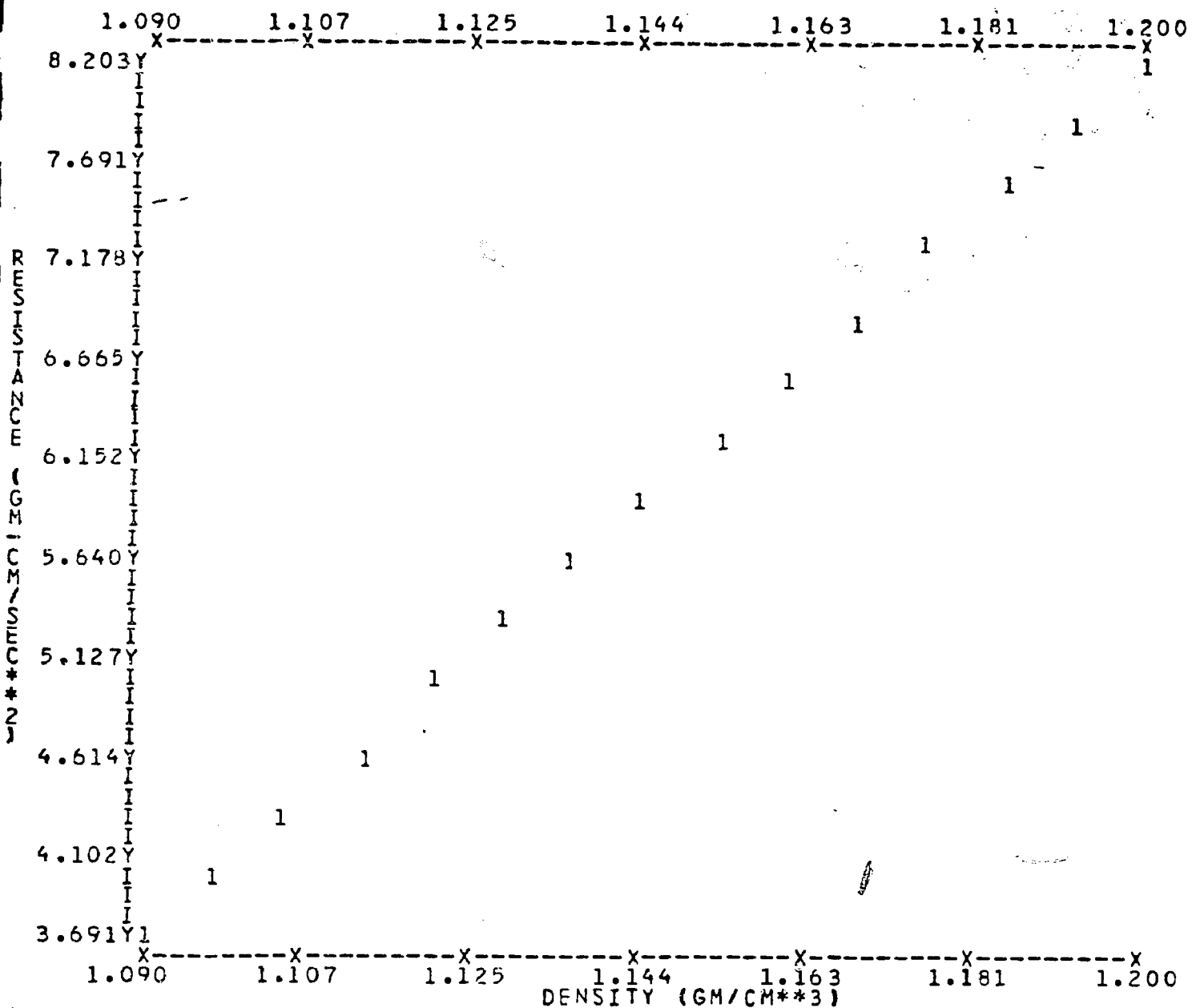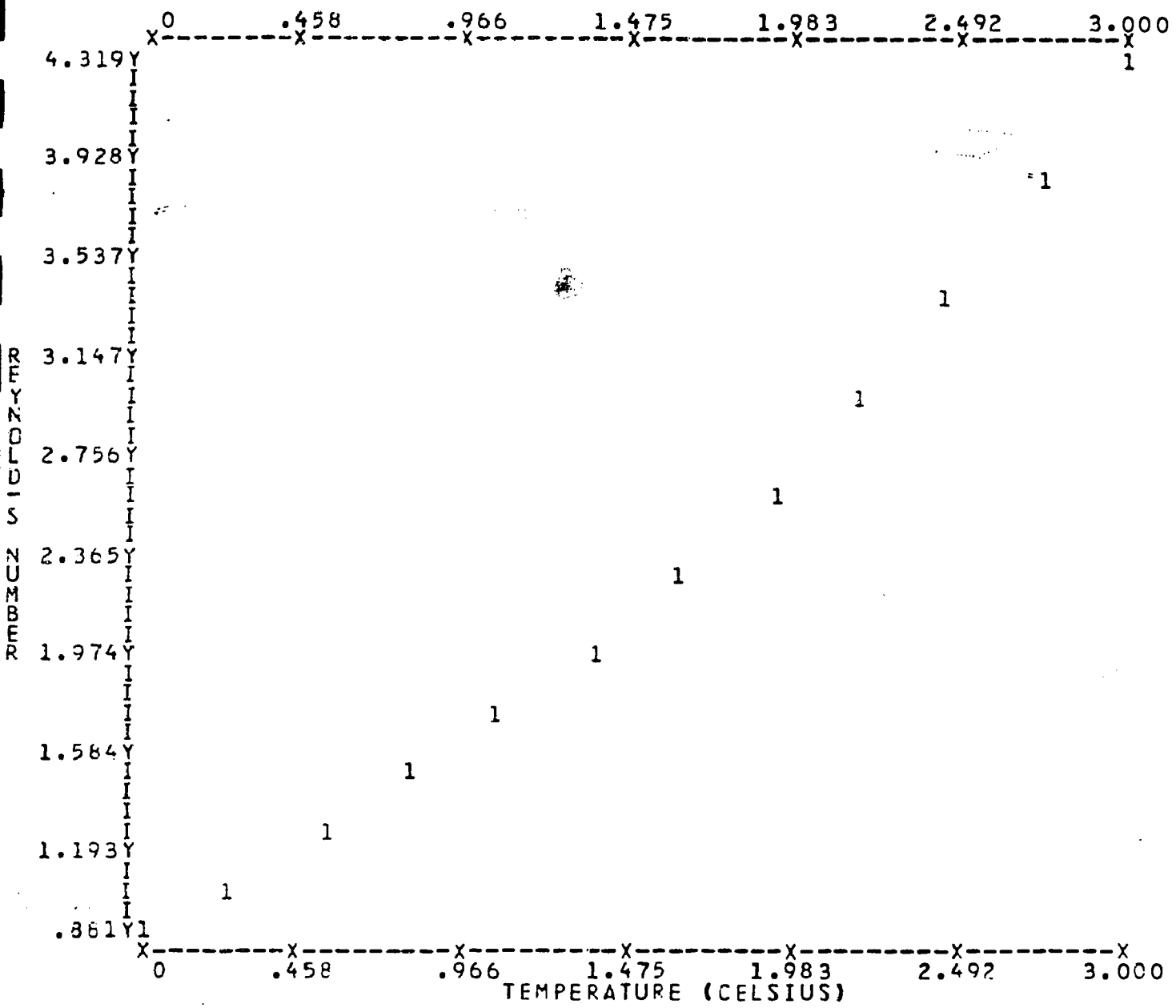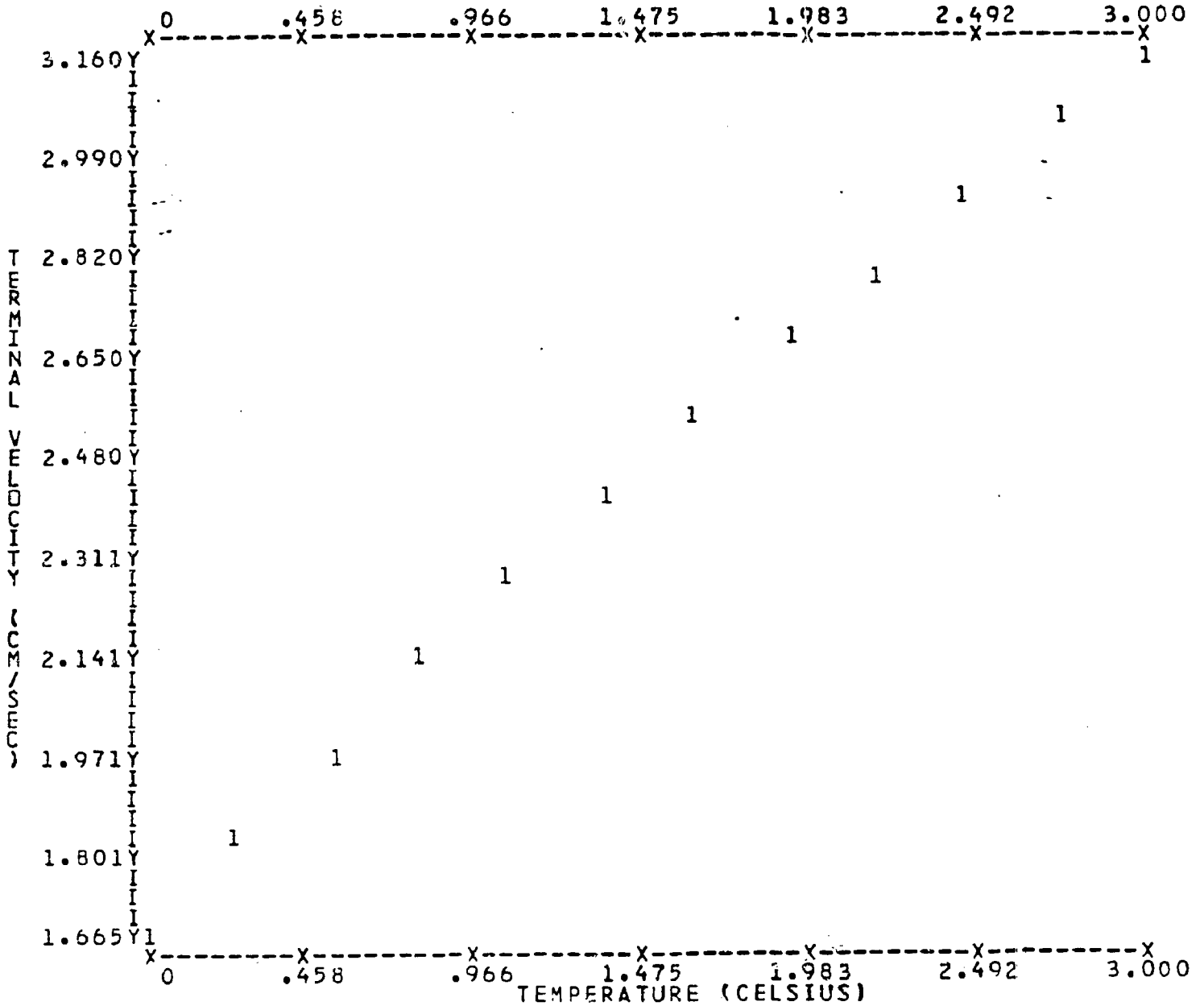Z5-Z9= 5.000(0);   6.000(0);   7.000(0);   8.000(0);   9.000(0)

80

HYDRAULIC PROPERTIES OF PLANKTON
RANGE OF X (0,30.0000), RANGE OF Y (.0487, .1896)
RADIUS = .0400
DENSITY = 1.0100

```
            0         .458        .966       1.475       1.983       2.492       3.000
          X----------X-----------X-----------X-----------X-----------X-----------X
    1.896Y|                                                                      1
          I
          I
          I
    1.736Y|                                                                 1
          I
          I
   R      I
   E 1.576Y|                                                          1
   S      I
   I      I
   S      I
   T 1.416Y|                                                    1
   A      I
   N      I
   C      I
   E 1.256Y|                                              1
   (      I
   G      I
   M      I
   - 1.096Y|                                        1
   C      I
   M/     I
   S      I
   E  .936Y|                              1
   C      I
   *      I
   *      I
   2  .776Y|                        1
   )      I
          I
          I
     .615Y|              1
          I
          I
          I
     .487Y1
          X----------X-----------X-----------X-----------X-----------X-----------X
            0         .458        .956       1.475       1.983       2.492       3.000
                                  TEMPERATURE (CELSIUS)
```
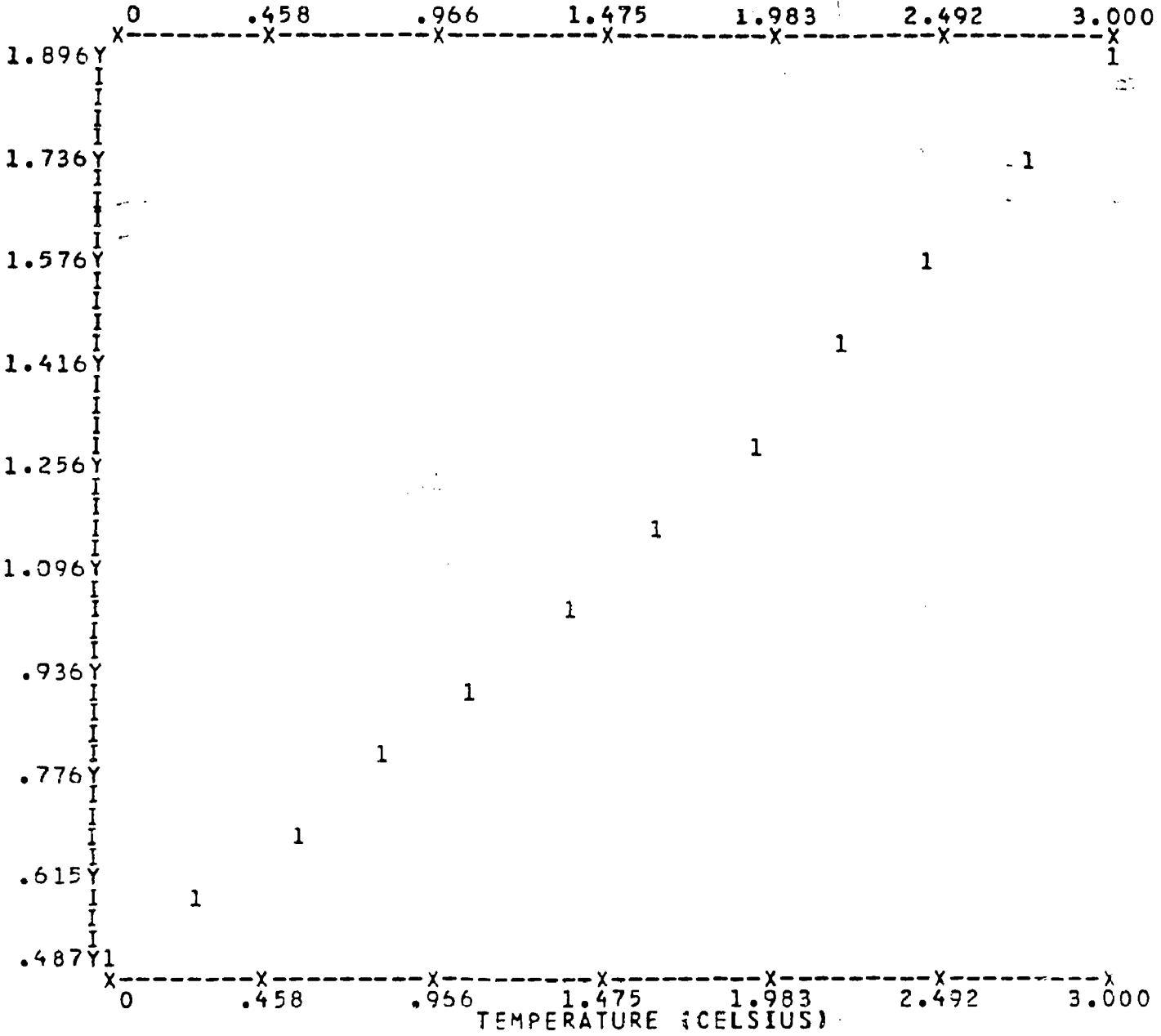
SCALE FACTORS = X-AXIS: E+01   Y-AXIS: E-01   Z-AXIS: E+00
Z0-Z4=   0(-9);   1.000(12),   2.000(0),   3.000(0),   4.000(0)
Z5-Z9= 5.000(0),   6.000(0),   7.000(0),   8.000(0),   9.000(0)

PROGRAM -BUOY- READY FOR INPUT
/   /
/*************************STOP PROGRAM*****************************/
/   /.
        FINIS = .T., S

PROGRAM -BUOY- TERMINATED
EOR

82

References

Gales, L. E. 1978. User's guide for subroutine PRNT3D. Center for Quantitative Science in Forestry, Fisheries, and Wildlife, University of Washington, Seattle, Washington.

Gales, L. E. and L. Anderson. 1978. User's guide for subroutine FFORM: a format free input system. Center for Quantitative Science in Forestry, Fisheries, and Wildlife, University of Washington, Seattle, Washington.