Quantitative Approaches to Organismal Biology

Selected topics and executable examples

Daniel Grünbaum

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Contents

Part I

Introduction

Chapter 1

Why use models in Organismal Biology?

Organismal Biology is, historically, a mostly experimental disciplne. Organismal Biologists have frequently pushed experimental technological boundaries. Examples include confocal microscopy and other computerized imaging techniques; molecular techniques to identify taxa, measure population connectivity and understand patterns of development; and many other areas. This innovative spirit has not reached similar levels in applying quantitative approaches like mathematical modeling and computer simulations to Organismal Biology. Mathematical models have so far made only modest contributions to Organismal Biology. The potential of mathematical tools to contribute to Organismal Biology, however, is much broader and deeper than the current literature reflects.

One reason thinking about and using models can benefit Organismal Biologists is that much of what we do already *implicitly* assumes some type of modeling framework. For example, all statistics are based on underlying models about probability distributions and random processes that emerge from them (independent events, normal distributions, *etc.*). Nearly all measurements of environmental characteristics (temperature, pH, salinity, *etc.*) are based on electrical measurements as proxies for the quantity being measured. The resistance or voltage being measured is translated into the environmental quantity using models. Even more broadly, most experimental design is based (often on an unspoken, intuitive level) on assumptions about how a measurement or manipulation carries implications for a biological process – in other words, a model.

A great many scientists who undertake statistical tests, use environmental sensors or design experiments have little awareness of the ways their work is based solidly on modeling. Better awareness of the modeling already involved in their work, especially if they also approach their investigations with a quantitative framework in mind, could result in a very satisfying synergy: Modelers who also undertake experiments can design more innovative and insightful models. Experimentalists equipped with a modeling perspective can have insights that enable them to design better, more compelling experiments. The best modeling of all is *modeling while experimenting*, when moving quickly between the computer and the laboratory or field site makes the connections between nature and models especially thought-provoking.

Disseminating some of the background knowledge and experience for using models, and the understanding of why using models is a productive adjunct to traditional approaches in Organismal Biology, is a primary objective of this book. A future Organismal Biology in which the potential of models to enhance discovery is more fully exploited – in which quantitative models are freely interdigitated among empirical methods and observations where each approach can best contribute – would be a more interesting, productive and impactful discipline.

Some of the reasons Organismal Biologists might be interested in quantitative models are:

Models are tools for inferring the logical consequences of specific assumptions.

The emphasis here is on the "specific assumptions" as much as on the "logical consequences". In a career of modeling biological processes in which I believed I was well versed, and of helping other biologists to formulate models in their own areas of expertise, I have consistently encountered two phenomena:

- Formulating a mathematical model requires *specificity* in details that are easy to overlook in conceptual thinking: Exactly *how* is a process like morphogenesis, synchronized spawning, predator avoidance or gene flow regulated? In what way are an egg, an early embryo, a larva and an adult "individuals" in a population model? I have been frequently flummoxed (and delighted) while modeling to discover basic aspects I had never thought about in organismal systems I thought I knew well. Writing down a quantitative model, even if results are never calculated, exposes these details and the intriguing new insights and questions that arise from them.
- Different scientists, especially scientists from different disciplines, use the *same word with very different meanings*. This means that interdisciplinary collaborations, which are necessary and productive in Organismal Biology, are frequently derailed by misunderstandings between two experts who have firm, well-founded (but different) interpretations of the subject at hand. An example is "memory". To a mathematician or statistician, a "memoryless system" is one in which the current state determines the probabilities of future events, without regard to how the current state was brought about. Thus, a mathematician could happily formulate a "memoryless" model of the human brain. Clearly, this would not be a biologist's interpretation. Confounding vocabulary and other vagueness in terminology are usually clarified when the relevant biological mechanisms are expressed in mathematical form.

Models are tools for inferring what we want to know from what we can measure.

Organismal Biology is frequently hampered by quantities and characteristics that we want to know but cannot directly measure. What are the fitness implications of variants we observe in morphology, size, behavior, geography, or seasonality? What are the mechanisms responsible for patterns in speciation and extinction, for species range expansion and contraction, or for the prevalence or rarity of different life history strategies? How is recruitment of a juvenile cohort limited or enhanced by each of the numerous biotic and abiotic environmental variables at a given time and place? How are environmental signals transduced by sensory and regulatory processes into reproductive, foraging or mortality events?

All of these questions, and many more, involve unknowns that are difficult or impossible to measure. Modeling provides approaches to infer quantities that cannot be measured. For example, it is in most cases impractical to measure the mortality rates of organisms in most terrestrial and marine environments. Direct measurements would involve unobtrusive observations following a large sample size of individuals, recording whether and how they died. In most cases, this is not possible to carry out. An alternative is to track cohorts of juveniles, measuring changes in abundance, age- and stage- structure, and geographic distribution. From cohort data, *combined with a modeling framework that provides quantitative predictions based on alternative mortality regimes*, inferences can be made regarding plausible rates and mechanisms of mortality in the observed juvenile population (e.g. **?**).

Another way in which observations are constrained is in considering the consequences of hypothetical alternatives to observed characteristics such as morphology or life history. Organisms that do not exist cannot be observed, but models that correctly reflect the key underlying mechanisms can give quantitative assessments of how hypothetical variation of extant organisms might function. These models could give insight into *why* these variant don't exist, in the context of implied changes in performance or distribution, or evolutionary costs and benefits.

Models are tools for communicating biological knowledge across organizational levels.

Another way in which models can contribute to insights in Organismal Biology is by integrating specialized knowledge from different disciplines. For example, biologists investigating maternal allocation to reproduction – how many eggs of what size mom should make each year – may focus on the physiology of egg production, the energy inputs and outputs of mature females, and coordination of spawning to maximize fertilization success. However, they would not be able to draw inferences about the costs and benefits of the traits they observe without context: What are the functional consequences of smaller or larger juveniles in terms of habitat selection, food capture and predator avoidance? What are the geographic implications of shorter or longer dispersal phases, and do those have implications for maintaining viable self-sustaining populations? How do impacts in present environments compare to historical environments, or future environments affected by climate change?

Each of these questions draws in the expertise of other scientists, whose understanding can be

exploited by investigators of an organism's reproductive biology. Biomechanical models may provide them with specific estimates of how locomotion and sensory performance is likely to differ in smaller or larger offspring. Demographic models may offer quantitative insight into the consequences of variations in maturation time and dispersal. Geophysical circulation models may predict the transport of propagules in winds, tides and currents, and environmental characteristics such as temperature, oxygen, chlorophyll and pH that may affect recruitment. Climate models may specify the environmental conditions in relevant to past and future environments. In all these cases, quantitative models formulated at one biological or environmental level can be leveraged by investigators at another level. Leveraging models in this way provides a mechanisms for community level collaborations, in which investigators make their discoveries available in the form of publicly available and easily used toolkits. This approach would mark a change for Organismal Biology, but would be following the productive pathways of other disciplines such as statistics, geophysical modeling and molecular biology.

Models let you make scientific discoveries anytime, anywhere.

Beyond all of these reasons, one additional point which has given me satisfaction is worth mentioning: Many interesting and important organisms are available only at narrowly constrained times and places, commonly a certain interval in spring or early summer, at a field station, marine lab or offshore location. Experimental work in Organismal Biology grinds to a halt outside this very limited window in space and time. Modeling is portable and extends the productive working season of a Organismal Biologist to year-round. A novel insight in Organismal Biology, even if obtained on a computer rather than a microscope, is equally thrilling in the dark winter months!

Chapter 2

How to use this book

This book is organized into Parts, each devoted to a different general topic or biological research area (e.g., Biomechanics, Demography, etc.). Each Part contains Chapters that present, in context, one or more models within the general topic. "In context" means that these examples provide brief background (with additional outside references); a working "executable" model; instructions how to use that model and suggested activities for exploring potential implications of the model for interesting questions in Larval Biology.

In most cases, background is presented in short form, often supplemented by separate "Quick Explainer" pages. These pages are intended to be short enough for a reader to internalize the most relevant, essential facts about a topic refered to in a model, without losing continuity of thought while working with that model. Quick Explainers are not intended to be comprehensive, though ideally they may refer to additional sources that provide in-depth perspectives. In many cases the most useful reference is simply a link to Wikipedia, which has proven to usually be comprehensive and accurate in many areas of biology, mathematics, physics, statistics and other disciplines.

Models, instructions on how to use them, and activities applying the models to currently relevant questions in Larval Biology are presented in **Jupyter notebooks**. Jupyter notebooks are among the latest and (so far) best platforms for embedding working computer code with formatted text and graphical content. Jupyter notebooks can be combined and integrated with Markdown and other content in the form of an Executable Book. Jupyter books can be run on a reader's own computer, can be run online on platforms such as Binder, and can be freely exported using a drop-down menu as a static (non-executable) PDF document. With additional setup, Jupyter books can also be exported as a LaTeX document, and then reconverted to a variety of other formats. This flexibility in format and usage makes Jupyter books the best platform, at the time of this writing, for a book aimed at helping Larval Biologists gain experience working with models.

- The **source** documents for the book can be downloaded ("cloned") from GitHub at the book's main repository, **quant-larval-bio**. This repository belongs to the **organismal-systems** organization on GitHub, which is associated with the **Organismal Systems Modeling Network**. The source documents can be used to fully build the book using JupyterBook.
- A **static** (read-only) version of the book constructed with *GitHub Pages* can be viewed online (or downloaded) at the **organismal-systems GitHub Pages site. This version is quick and easy to read, and can be a useful reference alongside executable pages.
- **Online executable models** implemented in Jupyter notebooks are available with a button click through Binder. The great advantage of these models is that they require nothing more than a browser to be running on users' machines. This makes them accessible to nearly everyone everywhere.

  As with most free online resources, though, there are limitations. One is that the execution speed can be slower, especially at peak times, compared to running the same model on a local workstation (it can also be faster, depending on the workstation...). Another is that sessions "expire" after a period of inactivity, freeing computing resources for other users. The session can easily be restarted, however, with the click of a button. In some contexts, Binder implementations also have constraints on reading and writing data files.

- **Executable models running locally on your computer** can be launched from downloaded copies of the source repositories, or from copies of those repositories already in the source materials for this book. Executable Jupyter notebooks containing models (and supporting Python libraries, if needed) are also incorporated into the book as **subrepos** or **submodules**, which it *git* jargon for repositories that are incorporated as components of other repositories. The source repositories for these models are stored elsewhere on GitHub, at links provided in the text. **These repositories are typically forked so that independent copies are retained on the OSYM GitHub site, from which they are linked in the book. These repositories often have their own license requirements, which supercede (for that content) the licensing requirements for the original content of this book.** This structure is necessary for two reasons:

    1. The Jupyter notebooks (and, often, a Python code library in which models are implemented) may be created and updated by different authors. Having a separate repository for these models enables the authors to develop their own codes, avoiding requiring them to separately update a book implementation. It also avoids giving all authors editing access to the entire book content, which is not sustainable in the long run.
    2. Different models require different sets of Python libraries. Some of these libraries are quite voluminous, so requiring a user of one model to install all libraries relevant to any of the other models is problematic. Moreover, Python libraries are updated and modified frequently; it is quite possible for different models in the book to require conflicting, incompatible versions of the same library.

The easiest way to manage the libraries required to build the book on your own computer and to run the executable models in Jupyter Lab is using the miniconda, Anaconda or Mamba package managers. A brief explanation of what these managers do, the differences between them, and how to install and use them is given in the Appendix. The required modules for each repository are listed in a file called *environment.yml*, included with the repository. miniconda, Anaconda and Mamba use this file to automatically recreate the set of packages needed to make the models function correctly.

Chapter 3

Terms of Use

Chapter 4

An example Jupyter notebook

This is an example of a Jupyter notebook. It demonstrates some of the properties that make these notebooks useful for executable books. This notebook can be run online via Binder, by clicking on the button below:

Note that when you open a notebook on Binder, the Python environment in which the notebook runs must be loaded before it can execute. If it hasn't been run recently, Binder has to rebuilt its environment and this can take a few minutes. Rerunning it afterwards is noticeably faster.

Alternatively, it can be run directly on your own machine if you have JupyterLab set up, by cloning the qob-notebooks repository or the source materials for this book.

4.1 Jupyter notebook structure

Jupyter notebooks are composed of *cells*. To execute a cell, make it the active cell by clicking on it, and either type *shift-enter* or select *Run Selected Cells* from the *Run* menu at the top of the page.

The sentences you are reading are in a cell of type "Markdown". This is indicated (and, if need be, selected) in the drop-down menu at the top of the page. As the name suggests, the content of this cell is coded in the formatting language Markdown, and when executed is rendered as a formatted display.

To see the Markdown code, click on the blue vertical bar at left, then type the letter "m" on your keyboard (or just double-click on the cell). The cell will now show the original Markdown code. Now you are able, for example, to edit words and links in the cell.

To re-render it, execute the cell by typing *shift-enter*. Now you see the formatted display.

4.2 Python code cells

The cell below is a *Code* cell, containing Python commands to be run when the cell is executed. You can see what this code does in either of two ways:

1. by selecting its cell and typing *shift-enter*
2. by selecting the *Run Selected Cell* item under the *Run* menu at the top left of this page

Many notebooks are set up for your use by running all the code cells. This is easy to do using the *Run All Cells* item under the *Run* menu.

Try changing the numbers in the cell below, then executing it by clicking on it and typing *shift-enter*:

```
# This is a simple test of whether your notebook is executing correctly:
# Change the value of a or b and shift -enter.
# The output should reflect your updated addition calculation.
a = 2
b = 3
print('{} plus {} equals {}'.format(a,b,a+b))
```

```
2 plus 3 equals 5
```

4.2.1 Code cell visibility

In Jupyter Lab, the commands in code cells can be hidden by clicking on the blue vertical bar at left, leaving only three small dots visible. The output remains visible below in its own cell.

For example, the cell below is a *hidden code cell*. Even though the code isn't initially visible, you can still execute it by selcting it and typing *shift-enter*.

```
2 times 3 equals 6
```

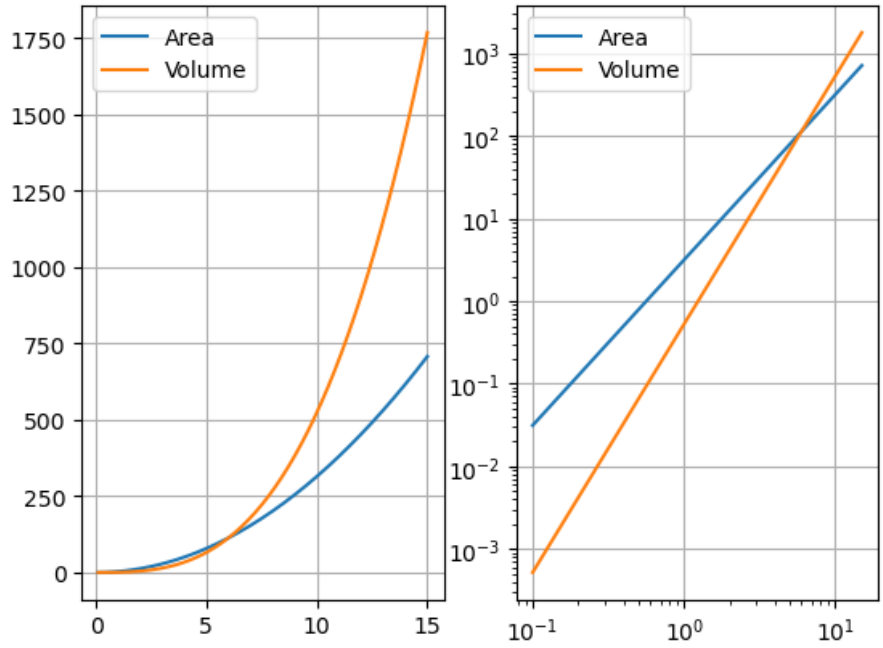
You can see hidden code any time you want. In an active notebook (e.g., on Binder) you can show or hide code by clicking on the blue bar at the left. In the static version, you can click on the "Source" bar to show or hide the code.

This is convenient when there is a lot of code that would be distracting in ordinary usage of the notebook. For example, the parameters in many models are set in textboxes (called "widgets"). This means users can use the models without having to interact directly with the code. However, there is distracting amount of code needed to set up the widgets. Hiding that code makes using the model more intuitive and visually appealing. To make the code visible, click on the blue vertical bar again.

The output can also be hidden and exposed by clicking on the vertical bar.

```
# This cell shows an example of defining a Python class, in this case representing a
# spherical egg, with some calculated geometrical properties relevant to respiration,
# heat content and other processes.
from math import pi # import the value of pi from the math module
class Egg():
    """ An example of a class definition in Python, that facilitates calculating
        the surface area and volume of a spherical egg given its diameter.
        If the parameter d is not supplied, it defaults to d=1
    """
    def __init__(self,d=1):
        """ Create an Egg instance.
        """
        self.d = d            # save the diameter as an attribute of the egg
        self.r = d/2          # calculate the radius
        self.A = pi * d**2    # calculate the surface area
        self.V = pi/6 * d**3  # calculate the volume

# An example of using an instance of the Egg class.
egg = Egg(d=2)
print(f'The surface area of an egg of diameter {egg.d} is {egg.A} and its volume is {egg.V}')

The surface area of an egg of diameter 2 is 12.566370614359172 and its volume is 4.18879020478

# Now let's look at some plotting examples. Here is an example of making a list of diameters,
# using that to make lists of volumes and areas, and then making a plot of area and volume as
# functions of diameter.
import matplotlib.pyplot as plt # import the pyplot graphics library
plt.ion()                       # use interactive plotting mode
ds = [0.1*(d+1) for d in range(150)]
As = [Egg(d).A for d in ds]
Vs = [Egg(d).V for d in ds]
# Create a plot object, and add the first subplot
fig = plt.figure()
# Plot area and volume against diameter, on a linear axis
```

```
ax1 = fig.add_subplot(1,2,1)
ax1.plot(ds,As,label='Area')
ax1.plot(ds,Vs,label='Volume')
ax1.legend()
ax1.grid()
# Plot area and volume against diameter, on a log axis
ax2 = fig.add_subplot(1,2,2)
ax2.plot(ds,As,label='Area')
ax2.plot(ds,Vs,label='Volume')
ax2.set_xscale('log')
ax2.set_yscale('log')
ax2.legend()
ax2.grid()
```



The plots above demonstrate several things. First, if they are visible, they show your Jupyter notebook is executing correctly.

Secondly, they provide examples of using a model (in this case, a very simple model of egg characteristics) to make a systematic study of variation of key model results across a range of input variables. This sytematic use of models to understand cause and effect, analogous to systematic variation of parameters in experimental design, is one of the most important yet widely underappreciated uses of models.

Thirdly, they illustrate that a very orderly pattern of variation exists in area and volume as functions of diameter – area and volume are simple lines as functions of diameter on a log-log plot – but the simplicity of this variation is obvious only when scaled and plotted in a specific way.

All three of these are important ideas to carry forward in using this book.

Chapter 5

Allometry: How organismal characteristics vary with size

One area in which Organismal Biologists use these ideas is in the study of allometry. Allometry is the study of how organismal traits vary systematically with body length or similar metrics of size. Allometric relationships have been found or hypothesized for many traits, including mass, morphology of limbs and other structures, locomotion and other behaviors, and physiological characteristics such as respiration and nutrient uptake.

A well-known example of an allometric relationshop is Kleiber's law, which posits that the basal metabolic rate of animals varies approximately as the animal's mass raised to the $\frac{3}{4}$ power:

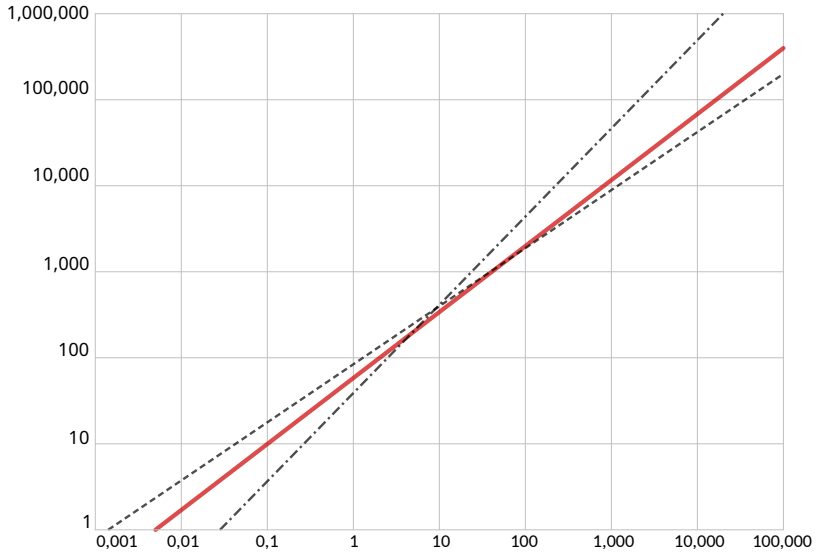


Figure 5.1: A plot of Kleiber's law, relating the metabolic rates of organisms to their sizes across a large range of sizes. See the Wikipedia article on Kleiber's law for details.

Allometric relationships within taxonomic groups are usually determined by statistical analysis of observations across a range of organism sizes within the group. These observations are most commonly plotted on log-log plots, and statistically analyzed to detect trends. A line on a log-log plot represents a power law relationship, which can be expressed mathematically as

$$trait = c\ size^p, \tag{5.1}$$

where c is a constant, and p is an exponent indicating the type of allometry. Taking the log of both sides of [#K1] gives

$$\log trait = \log c + p \times \log size. \tag{5.2}$$

[#K2] shows why power law allometries appear at straight lines on log-log plots.

For example, in Figure 5.1, the trait is Basal Metabolic Rate in watts, BMR, the size metric is mass, M, the constant $c = 70$, and the hypothesized exponent is $p = \frac{3}{4}$, *i.e.*,

$$BMR = 70\ M^{\frac{3}{4}} \tag{5.3}$$

It is useful to distinguish two types of allometry, *isometric scaling* and *allometric scaling*.

5.1 Isometric scaling

Isometric scaling is also known as *geometrical similarity*. In isometric scaling, all linear proportions are held constant as overall size increases or decreases. The spherical egg model in the previous notebook is an example of isometric scaling. In general, a series of isometrically scaled objects follow the so-called square-cube law, stating that surface area is proportional to the length squared, and volume is proportional to length cubed.

5.2 Allometric scaling

In allometric scaling, different organismal traits scale differently with metrics of size. For example, larger animals often have more robust bones than would be predicted by isometric scaling from smaller animals. In a given organism, different traits may reflect either direct or indirect effects of isometric and allometric scaling.

For example, if a set of animals scaled isometrically, their weight might be expected to increase in proportion to the cube of their length. However, following the square-cube law, the cross-sectional area of their bones would increase only in proportion to the square of their length. This is likely to result in much higher loading and risk of breakage in larger animals.

In this case, some traits of these animals might deviate from isometric scaling, and instead follow an allometric scaling. For example, bones might increase in thickness faster than isometrically, or mass might increase slower than isometrically. Either form of allometric scaling would tend to equalize the loading on bones, relative to isometric scaling.

Chapter 6

Scale models and dynamic similarity

Much of the discussion in this book involves scale models. Most of us are familiar with scale models, even if we don't ordimarily think of them using that name. For example, a model boat that a child plays with in a bathtub is a scale model of a full sized boat that floats on the ocean. A doll is a scale model of a human being. An architect often uses a scale model of a building to develop and explain a design. These examples are of large objects made small enough to be practical and inexpensive, but scale models that are enlargements of the original can also be useful. For example, a model of a microorganism or cell can be a useful tool for understanding its morphology and relationship with its surroundings.

These examples reflect **geometric similarity**. That is, the derived objects are scale models because their components have *geometries that are similar in proportion to the originals**.

6.0.1 Dynamic similarity

The concept of similarity can be extended to include forces acting on objects and their surroundings. This concept is called "*dynamic similarity*" or "similitude". Scale models are dynamically similar if, in addition to being geometrically similar in proportion, *the different forces acting on them are also similar in proportion.*

The additional requirement of equal proportional forces means that not all geometrically similar scale models are dynamically similar. We all have an intuitive grasp of this fact. To illustrate this, let's look at video of a scale model of the Titanic sailing on a body of water:

As you watch this video, consider your intuition about how big the model is.

What is your intuitive estimate of the size of this model?

The model in this video is a very detailed scale model of the Titanic. It is geometrically similar in nearly every visible detail, and in a great many that are not visible. There is little direct information about the size of the model (such as a ruler, human hand or other object of known scale) Nonetheless, it is immediately apparent from watching the video that this model is not 267 meters long, like the full sized Titanic was. What is it about the video that makes the model seem smaller?

It is the context of the water motion. The water is behaving as water always does, and the model is geometrically similar. However, the relative motion of the water waves and model are out of proportion with each other, compared to a full sized ship moving in the ocean.

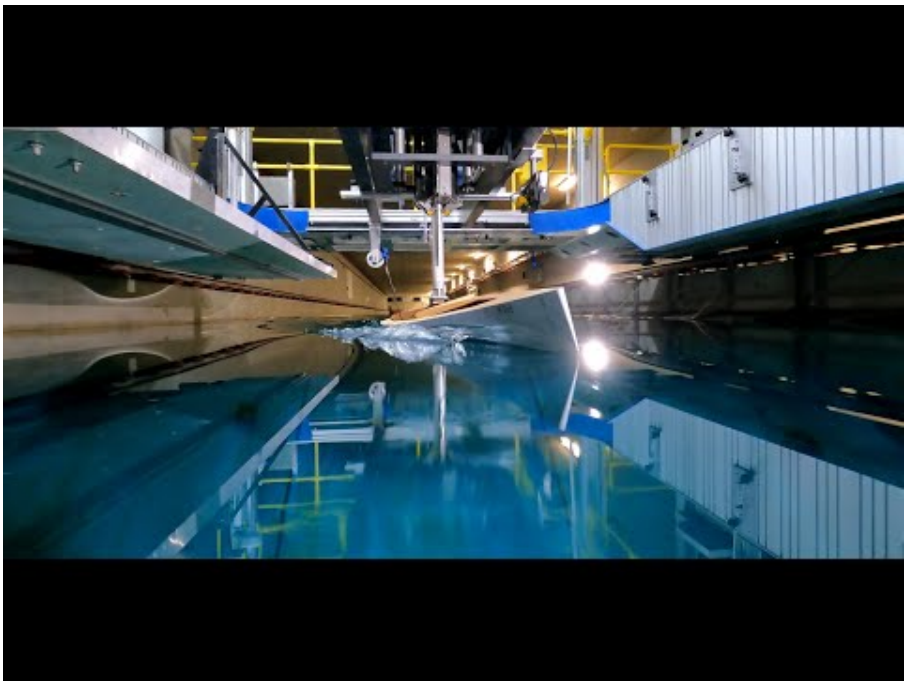
That is, the forces moving the ship and the forces moving the water are not in the proper proportions. Therefore, this geometrically similar model is not dynamically similar.

Our intuition based on many experiences watching lakes, oceans, pools and other water bodies gives us a sense of scale for waves. The model gives little indication of its size, but the size scale suggested by our intuition for the water waves tells us that the model is only about a meter long (it's actually a 1:212 scale model, with a length of roughly 1.25m).

Ship model basins

For comparison, let's take a look at a ship model basin, also known as a "tow tank". A ship model basin is a facility for inferring characteristics of full sized ship, from measurements of motions and forces on much smaller scale models. The video below shows some sequences of scale models being towed in Southhampton University's Boldrewood Towing Tank as part of engineering studies:

```
# This displays a video posted of the [QinetiQ Ship Tank](https://www.qinetiq.com)
display_yotube_video("https://www.youtube.com/watch?v=Q9qZcN5iX2k", width=800, height=600)
```



The video shows a modern ship model basin being used to observe water interactions with the moving ship and boat models in great detail. The bow and stern waves from these models are dramatically more reminiscent of those from a full sized ship than the Titanic video. In fact, if it were not for the people on the moving gantry, it would be difficult to estimate the size of these scale models just by observing their interactions with the water. **The difference betwen the two videos is that the models in the second video are set up by engineers to be dynamically similar, while the first model is not.**

6.1 Establishing dynamic similarity

How did the engineers in the video know how to design the model and set its movement so that it would be dynamically similar?

The criterion an engineer used to determine dynamic similarity is called the Froud number, abbreviated as $\mathcal{F}\nabla$. The Froud number associated with a full sized ship of length L sailing on the ocean at speed U is defined as

- $\mathcal{F}\nabla = \frac{U}{\sqrt{gL}}$

were g is gravitational acceleration.

If a scale model of the ship which has length L_{model} travels at speed U_{model}, its Froud number is

- $\mathcal{F}\nabla_{\text{model}} = \frac{U_{model}}{\sqrt{gL_{model}}}$

When

- $\mathcal{F}\nabla = \mathcal{F}\nabla_{\text{model}}$

the full sized ship and the model are dynamically similar. This is the condition created by the engineers in the second video. As you can see, the resulting water motion resembles that around a real vessel much more than the dynamically dis-similar model in the first video.

6.1.1 Why does the Froud number determine dynamic similarity for ships and ship models?

The Froud number is based on the speed at which water waves travel. This speed is a function of their wavelength, L_w (the distance between neighboring crests): water waves' speed is (in the ideal case) proportional to $\sqrt{L_w}$ (and to g, the gravitational acceleration). The Froud number is the ratio of the full sized ship's speed, divided by the estimated speed of a wave equal in length to the ship.

Why do the relative lengths of the ship and wave matter? It is because a moving ship generates waves traveling around the same speed it's traveling. That means a slow ship is generating slow, short waves. As the ship increases speed, it generates faster, longer waves.

A ship can effectively "straddle" and plow through waves that are much shorter than its hull. However, when a wave starts to get to as long or longer than the hull, the ship's stern gets caught in the trough while the bow is raised in the crest. That means that, in effect, the ship is continuously going uphill! When this happens, an increase in propulsive power just adds to the size of the wave being generated – it has almost no effect on ship speed.

In effect, the length of the hull imposes a "speed limit": the speed of waves as long as the ship. This is known as the *hull speed*. The faster hull speeds of longer vessels is one of the reasons racing shells, hunting kayaks, container ships and many other watercraft for which speed is important tend to be long.

The Froud number, $\mathcal{F}\nabla$, is a ship's speed expressed as a fraction of its hull speed. A model with matching Froud number – that is, traveling at the same fraction of its hull speed – will both in appearance and in the quantitative measures of force and motion match the full sized ship. That is, the ship and model will be dynamically similar.

6.1.2 Nondimensional numbers

The Froud number is a ratio of two quantities – the wave speed and the hull speed of a moving ship or model &ndash that have the same units, $\frac{m}{s}$. Because the units of the numerator and denomenator cancel, the Froud number is dimensionless.

The Froud number is one of many indices in engineering, physics and biology that has this characteristic. These indices are usually referred to with the slightly unintuitive name non-dimensional numbers (also known as "dimensionless quantities"). Nondimensional indices that express the ratio of two lengths, speeds, masses, rates or other characteristics relevant to an organism's biology are often informative about that organism's function.

For example, you may already be familiar with a nondimensional number from epidemiology: the pathogen reproductive number, $\mathcal{R}$. $\mathcal{R}$ is the number of new infections caused by a primary infection

before it is cleared. If $\mathcal{R} < 1$, then each successing round of infection is smaller; the infected population is then decreasing, and an epidemic is not possible. If $\mathcal{R} > 1$, then each successing round of infection is larger; the infected population is increasing and an epidemic can occur.

By summarizing the conditions under which an epidemic is or is not possible, the nondimensional index $\mathcal{R}$ highlights factors that make epidemics more likely (those that incease $\mathcal{R}$, such as high contact rates among susceptibles and poor hygiene) and those that make epidemics less likely (those that decrease $\mathcal{R}$, such as reduction in susceptibility through vaccination and good hygiene).

Because nondimensional numbers play similarly useful roles in many aspects of Organismal Biology, it is worth thinking about them in some detail.

Chapter 7

Non-dimensional numbers

The idea that *similarity of proportions generalized to include both geometries and forces* as required for dynamic similarity is most practical to work with using **non-dimensional numbers**. Dimensions, in this context, refers to measurements in physical units (such as SI units: meters, seconds, kilograms, etc.). "Non-dimensional numbers" is somewhat strange terminology, because by nature pure numbers are not associated with any physical dimensions. In this context, though, "non-dimensional" refers to ratios that have no dimensions because the units of the numerator are the same as the units of the denominator. That is, **non-dimensional numbers are composed of factors with units (lengths, times, masses, etc.) but they are nonetheless non-dimensional because the units of their factors cancel.**

Many non-dimensional numbers have been devised in diverse fields of science. Some of these are listed, together with their physical interpretations, in this Wikipedia page.

Non-dimensional numbers are useful in quantitative sciences for two reasons:

1. Many phenomena are governed by non-dimensional combinations of parameters, which is made explicit in the form of non-dimensional numbers. By using non-dimensional numbers as "meta" parameters, these phenomena can be understood and predicted using far fewer variables than in the original dimensional form.

2. Non-dimensional numbers in which the denominator and the numerator reflect different mechanisms can be indicators of the relative importance of those mechanisms, across variation in important parameters such as size, speed, duration, etc.

Because non-dimensional numbers are not intuitive the first few times they are encountered, it's worth delving into some further explanation of these ideas.

7.1 Characteristic values

A good starting point for thinking about non-dimensional numbers is to consider the fact that adjectives like big, small, fast, slow, etc. are *relative* descriptions.

That is, nothing is big or small except in comparison to something else. In our ordinary thinking, that something else is a standard set of units. For example, the fundamental SI unit for length is the meter. An object a kilometer long is "big" compared to a meter – it's equal to 1000 of them. An object a micron long is "small", because it's only 1/1000th of a meter.

Suppose, instead, we adopt a complementary perspective, in which the basis for comparison comes from the object itself. This depends on finding what are called **characteristic values**. Characteristic values could include a length, speed or duration that emerges from the object or its interations with its surroundings. These characteristic values specify a subset chosen from a set of scale models.

7.1.1 Characteristic dimensions of an egg

Let's begin with an intentionally simplified example, that we completely understand: In a previous page, we considered the surface area, A, and volume, V, of a spherical egg. We could expect that

A and V have signicance for an egg's biology. For example, we might expect its mass to be roughly proportional to its volume; that mass may have functional consequences for respiratory demands, development time, sinking or rising rates, etc. Likewise, we might expect its surface area to be related to gas exchange rates, encounter probability with sperm or pathogens, and other factors. In this simplified example, these serve as a biological motivation for understanding how surface area and volume vary with size.

Because spheres have the same shape, all spheres are geometrical scale models of each other. Across the set of spheres, there is a single parameter, the diameter d, that specifies a unique sphere. Knowing d, we can calculate the surface area A and volume V using familiar formulas:

- $A = \pi d^2$
- $V = \frac{\pi}{6} d^3$

Anticipating more complicated and realistic applications in Organismal Biology, let's suppose we did not know these formulas. In that case, we would expect to conduct a series of observations in which we **measure** the surface area and volume of a series of spheres of various sizes. We could then use interpolation or curve-fitting to estimate the surface area and volume of spheres within the range of our measurements.

Instead, lt's consider using nondimensional ratios to express the formulas for A and V, in a more general form with fewer parameters. We'll start by choosing a characteristic length, L. The geometry of the egg suggests that the most useful choice of characteristic value is the length scale corresponding to the diameter,

- $L = d$. From their units (m^3 for A, m^3 for V) we can anticipate that surface areas of shapes generally scale isometrically with the length scale squared, L^2, while the volume scales with the length scale cubed, L^3. We know this because there is no other way to construct a quantity with the units of area and volume using the only available characteristic dimension, L.

Knowing that $A \propto L^2$ and $V \propto L^3$, we can set about measuring the constants of proportionality. Doing so for a conveniently sized sphere, we find that

- $c_{A_{sphere}} = \frac{A}{L^2} = \pi$
- $c_{V_{sphere}} = \frac{V}{L^3} = \frac{\pi}{6}$

That is, our measurements tell us that the constant of proportionality $c_{A_{sphere}}$ of surface area to L^2 is π, and the constant of proportionality $c_{V_{sphere}}$ of volume to L^3 is $\frac{\pi}{6}$.

Having measured one sphere, we are done. That is, knowing $c_{A_{sphere}}$ and $c_{V_{sphere}}$, we can write down A and V for spheres with *any* L (even those too large or small to measure). That beats making new measurements for tens or hundreds of different-sized spheres!

7.1.2 What did we just do?

In the lines above, we did not create any new formulas or data. All we did was to express the surface area as *relative* to the square of the characteristic length, L^2, and the volume *relative* to L^3. In mathematical jargon, we **nondimensionalized** A and V with the formulas

- $\hat{A} = \frac{A}{L^2} = c_{A_{sphere}}$
- $\hat{V} = \frac{V}{L^3} = c_{V_{sphere}}$

We call $\hat{A}$ the *nondimensional surface area* and $\hat{V}$ the *nondimensional volume*. Thinking in terms of these nondimensional variables,

- All the effects of **size** are encapsulated in the length scale, L.
- All the effects of **shape** are encapsulated in the constants $c_{A_{sphere}}$ and $c_{V_{sphere}}$.

In words, the constants $c_{A_{sphere}}$ and $c_{V_{sphere}}$ are *shape factors*, that together with the basic geometrical scaling of L, tell us the surface area and volume of all spheres.

7.1.3 Nondimensionalization as a general approach

The strategy of nondimensionalization by scaling using appropriate characteristic values is a common one in engineering, mathematics and physics but much less fully employed by Organismal Biologists.

Before moving on, it's worth broadening our perspective with a few take-home points:

1. The logic leading to the shape constants $c_{A_{sphere}}$ and $c_{V_{sphere}}$ did not depend on the spherical shape, or on us having a formula. It depended only on the basic scaling geometry, that areas and volumes of geometrically similar objects must be proportional to their length scale squared and cubed, respectively. If you were to conduct the same measurement on a cube, you would find the same scaling but different shape constants ($c_{A_{sphere}} = c_{V_{sphere}} = 1$). For any other shape – an ellipsiod, a dodecahedron, or a lobster – corresponding pair of shape constants summarize the area and volume across all sizes.

2. The nondimensionalization exploited the fact that all spheres are scale models of each other, so that only one needed to be measured rather than an infinite spectrum of diameters. In mathematical jargon, it reduced the *dimensionality* of the problem. Dimensionality is the number of variable along which we have to measure to characterize a phenomenon. In this simplified case, nondimensionalization reduced the dimensionality from 1 axis (diameter) to none (all spheres have the same constants). Even in this simple case, reducing a hypothetical series of measurements from a series to a single observation represents a significant savings.

As stated, this example started with an extremely simple calculation, which the analysis made still simpler. The real utility of non-dimensionalization is found in application to more complex problems in Organismal Biology, in which there are many independent variables and for which no formulas are available. In these cases, including examples found in the following chapters of this book, a reduction in the number of parameters and an orderly separation of effects of different elements of the problem can be very useful and insightful.

Part II

Biomechanics

7.2 ReSphere

Jupyter notebooks for spheres moving in fluids, calculated using Reynolds numbers

The CdSphere.ipynb notebook can be accessed via Binder using this link:

The RS1.ipynb notebook can be accessed via Binder using this link:

The RS2.ipynb notebook can be accessed via Binder using this link:

The RS3.ipynb notebook can be accessed via Binder using this link:

7.3 Movement of organisms in fluid

7.3.1 Motivation

Many aspects of Organismal Biology are affected, directly or indirectly, by the ways organisms (or parts of organisms) move through fluids. Some of these effects arise from consequences of sinking or floating in air or water. For example, the rate at which carbon dioxide is removed from the atmosphere into the ocean is affected by how fast carbon fixed by phytoplankton sinks into the deep ocean. The sinking rate for a given phytoplankton cell can vary greatly depending on whether it is eaten by zooplankton and excreted into large, fast-sinking fecal pellets or lysed by a viral infection into tiny slow-sinking subcellular fragments. The rate and direction of range shifts by plants in response to climate change, or the ability to colonize new habitat patches, may depend on the sinking rates of windblown or current-borne propagules. For an aquatic microorganism, its position in a water column that varies in temperature, light, nutrient availability and density of predators and prey may depend on its vertical movement relative to the water around it. From a more applied perspective, the "drift" of corn pollen from genetically modified plants into neighboring fields of organic corn depends on the sinking rate of the pollen particles. Generalizing even more, the "footprint" of land contaminated by pollutant particles emitted by a sewage outfall or smokestack, or ocean fertilized by iron in wind-blown dust, depends on how fast these particles sink. You can think of many other examples.

In addition to effects on spatial distributions, movement through fluids can also greatly amplify the effects of key molecular transport mechanisms, especially mass diffusion and heat conduction. You are already familiar with these effects in your daily life. Each time you stir sugar into a cup of tea, blow on a hot spoonful of soup to make it edible, walk outside on a windy day, or stick a finger in the air to assess the wind direction you are experiencing the effects of fluid movement enhancing molecular transport. This enhancement effect has implications for diverse aspects of Organismal Biology, including nutrient uptake, blood physiology, fertilization success, endothermy and many others.

7.4 Organization

This unit provides quantitative tools for understanding the consequences for organsism of movement through fluids. To keep the discussion general, we often refer to "particles" – this refers in specific instances to whole organisms such as microorganisms, propagules such as seeds, or components of organisms such as blood cells or pollen. The tools in this unit facilitate understanding the linkages by organismal characteristics such as size and density to organismal function from subcellular to physiological to ecological scales.

The unit is divided into three related but distinct sections.

1. The first section relates the sizes of particles, their densities, and the gravity and buoyancy forces acting on them to rates of movement through their fluid environment. This section provides worksheets to address questions such as:

    - How does the rate at which fish or invertebrate eggs sink or float depend on egg size and lipid content?
    - How does the rate of transport to the deep ocean of carbon fixed by phytoplankton depend on consumption by zooplankton or infection by viruses?
    - How fast do propagules like seeds, spores or pollen sink?

2. The second section connects particles' sinking or floating rates to ambient winds or currents and turbulence, to understand how organismal characteristics interact with ambient environmental conditions to determine population-level horizontal and spatial distributions. This section provides worksheets to address questions like:

    - How far does wind-borne pollen travel? How does pollination success depend on the distance and height of plants??
    - What does the "plume" of pollution particles look like? What is the likely exposure of organisms given habitat distributions and typical weather patterns?

3. The third section focuses specifically on fluxes of conserved quantities such as nutrients, oxygen and waste products as functions of movement through fluids. This section addresses questions such as:

    - What chemical cues are available to organisms such as bacteria? How does movement affect uptake and release of oxygen in blood cells?
    - In what ways do increases or decreases in size of aquatic microorganisms alter constraints on oxygen and nutrient uptake?
    - How does egg size and content affect fertilization success in aquatic environments?

Each of these section is introduced with background and context, implemented in Jupyter notebooks running on Binder, and followed by activities that develop insights through application to specific questions in Organismal Biology.

7.5 What makes organisms move through fluids (and what slows them down)?

Like all physical objects, immersed particles obey Newton's 2nd Law:

$$sum\ of\ forces = mass \times acceleration \tag{7.1}$$

This Law gives us a tool to calculate the rate at which an object subjected to a force will move in a particular type of fluid. If we know the particle's movement, Newton's Law also gives us a tool with which to calculate the force that must be acting on the particle to cause that movement.

Understanding the factors that cause organisms to move through a fluid environment is easiest if we consider the lefthand side of this equation separately from the righthand side.

7.5.1 The lefthand side: The sum of forces

A situation familiar to many of us is coasting downhill on a bicycle. Starting at a slow speed, we coast faster and faster, accelerated by the force of *gravity*. Eventually we reach a steady speed, when *drag* caused by the air we're pushing aside as we move (along with a bit of friction from the wheels and tires) matches the gravity forces. At that point, the sum of gravity and drag forces are equal and opposite – that is, they sum to zero – so the acceleration rate is also zero.

If we duck down to the handlebars, we reduce the air drag. Then, the gravity force exceeds drag until we accelerate to a new, higher steady speed. If the hill levels out somewhat, the gravity force is reduced. Then, the drag exceeds the gravity force until we slow down to a new, slower steady speed.

This dynamic balance between gravity and drag (and it's application in Newton's 2nd Law) is helpful to keep in mind when we consider the forces acting on particles in fluids.

7.5.2 The righthand side: Mass × acceleration

As we continue on our bicycle ride, we eventually encounter a rise or uphill. At that point, gravity is pulling us backwards, but we do not immediately stop and reverse – we continue to coast uphill for awhile. We continue coasting because we have **momentum**.

Momentum is a familiar experience for all of us, but its name and definition may not be. The momentum of an organism (or any other object) is defined as:

$$momentum = mass \times velocity \tag{7.2}$$

Intuitively, a bigger mass has more momentum than a smaller mass traveling at the same velocity[1]. Likewise, a faster mass has more momentum than the same mass traveling more slowly.

Acceleration is the rate of change in velocity,

$$acceleration = rate\ of\ change\ of\ velocity \tag{7.3}$$

Substituting this expression for acceleration in Newton's Law, and using the definition of momentum, we can state Newton's 2nd Law in a different and possibly more intuitive way,

$$sum\ of\ forces = rate\ of\ change\ of\ momentum \tag{7.4}$$

Hopping onto our bicycles again, this expresses another familiar phenomenon: When we apply force to the pedals, we produce a forward force which increases our momentum (by speeding us up). When we apply brakes, we produce a backwards force which decreases our momentum (by slowing us down).

[1] It's useful to keep in mind that, in science and engineering, the term "velocity" means a **vector**. This means that it has both a *magnitude* and a *direction*. This is distinct from "speed", "celerity" and other terms that have only magnitude (that is, they are **scalars**). For example, a bicycle going 10 mph north has the same speed as a bicycle going 10 mph south, but it has opposite velocity.

7.5.3 Understanding movement through fluids

The elements of Newton's 2nd Law that apply to bicycle riding – gravity and drag forces resulting in changes to velocity and momentum – also apply generally to organisms (or components of organisms) moving in fluids. The next part of this section presents a more in-depth discussion of forces, masses and velocity changes. The ideas in that discussion are then used in assessing *scaling* of forces on organisms immersed in fluids:

- How do forces increase or decrease with organism size and velocity?
- How can we understand consequences of organism *shape*, as opposed to variations in *size*?
- In what ways is being immersed in air different from (or similar to) being immersed in water or another fluid?

The results of the scaling analysis are then used in a worksheet that provides tools to ask more specific questions, such as "How fast will a given organism sink or float in a given fluid?"

7.6 What are the forces acting on immersed particles?

For most particles relevant to Organismal Biology, three types of forces most strongly affect movement[2]:

1. **Gravity forces**: Every particle has mass, M.

   The force gravity exerts on a particle is

   $$F_{gravity} = g \times M \tag{7.5}$$

   where $g = 9.81 \frac{m}{s^2}$ is the gravitational acceleration[3].

2. **Pressure forces**:

   As you know from your ears, if you have dived to the bottom of a swimming pool, pressure increases with depth[4]. That implies that the pressure acting on the bottom surface of a particle is stronger than the pressure acting on the top of that particle (because the bottom is deeper than the top).

   Since the pressure pushing upwards on the bottom of the particle is stronger that the pressure pushing downwards on the top of the particle, the net force of this pressure is an upward force, which we call **buoyancy**. It turns out that this force is always equal to the gravitational force on the mass of fluid that the particle displaces, but opposite in direction (that is, the buoyancy tends to push particles upwards while gravity pulls them downwards).

   This gives us the familiar sinking *vs.* floating phenomena: If a particle is denser than the fluid, its mass is greater than the mass of the displaced fluid, and hence it has a net downward force (gravity exceeds buoyancy). Therefore it sinks. If the particle is less dense than the fluid, buoyancy exceeds gravity, and it floats.

   If the particle is moving,

3. **Viscous forces**:

   Viscosity is a measure of how "thick" a fluid is. In engineering terms, viscosity is the resistance to the motion of two parallel plates sliding past one another (this motion is called **shear**). For example, fluids like honey, molasses and glycerine have much higher viscosity than fluids like water and air.

   This means that dragging a particle through a more viscous fluid like honey at a given velocity requires much more force than dragging the same particle at the same velocity through a less viscous fluid like water or air.

Gravity, pressure (including buoyancy) and viscous forces all contribute to the sum of forces on the *left hand side* of the equation for Newton's 2nd Law, as applied to an immersed particle.

[2] In a few rare but interesting cases, other forces such as magnetism are important!

[3] Note that $F_{gravity}$ is a **vector**, which means simply that it has both a *magnitude* ($9.81 \times M$) and a *direction* (down).

[4] You may also have felt the opposite: "popping" in your ears from the decrease in air pressure as an airplane takes off.

7.7 Momentum changes due to "added mass" and "wake momentum"

As noted, the term on the *right hand side* of Newton's 2nd Law is *mass* × *acceleration*, representing the rate of change of **momentum**[5]. Momentum is the product of mass times acceleration.

One contribution to momentum comes from the mass of the organism or particle. In familiar terms, the mass of a bowling ball is much greater than the mass of a ping-pong ball, so the bowling ball has much more momentum than the ping-pong ball if they are traveling at the same velocity.

In most applications in Organismal Biology, an organism's mass is more or less constant over short periods. In that case, changes in the organism's momentum result from changes in its velocity[6].

However, for organisms immersed in fluids, there is another factor: *To move, an organism or any other particle must also displace fluid around itself.* The water that is moved in concert with an organism must be accounted for in assessing the relationship between forces and movement. There are two primary ways in which moving fluid affects the righthand side terms of Newton's 2nd Law: *Added mass*, and *wake momentum*. Understanding these concepts will be very helpful when thinking about the biomechanics of organism movement in fluids.

7.7.1 Added mass

If you have seen a person rowing a boat (or had a chance to row one yourself) you have seen the shape of an oar. At one end the oar has a handle, where it is gripped by the rower. At the other end, the oar is the "blade", which is wide and flat but quite thin.

To propel the boat, the rower inserts the oar into the water with the blade perpendicular to the direction the boat is moving, before pulling. It is intuitive that this is necessary to row effectively – if the blade were parallel to the direction of motion, it would slice easily through the water and provide very little propulsion.

Despite it being intuitive, few people (including rowers) have thought about *why this is the case*? When an oar is pulled through the water, its mass is the same whether it's perpendicular or parallel to the direction of motion. What then is the difference?

The difference is added mass, the engineering term for fluid that must be moved when an object moves through a fluid. For example, when the oar is pulled in a perpendicular position, water next to the front and back of the blade moves with it. Because the perpendicular blade has a large area in line with its motion, this is a lot of water. This water is the added mass of the oar. Accelerating this added mass of water is what makes the oar effective, and oars are designed specifically to have large added mass when pulled in the perpendicular position.

In contrast, the parallel blade has a small area in line with its motion, so it moves relatively little water. That is, it has little added mass. It is said to be *streamlined*, which means it moves with little resistance through the fluid.

In a well-designed oar, the added mass in its "power" orientation is much larger than the mass of the blade itself. The same is true of many appendages of organisms that propell themselves through water. While other fluid dynamical mechanisms are also operating, thinking in terms of added mass often provides useful insights into the biomechanics of movement through fluids.

7.7.2 Wake momentum

Standing in an exposed spot on a very windy day, you can feel the pressure of the wind pushing you downwind. Since you are stationary and not accelerating, your momentum is constant and its rate of change is zero. Newton's 2nd Law says that if your momentum is not changing, the sum of forces on

[5]Some references refer to inertia as a synonym for momentum. Inertia is defined slightly differently, but is a closely related concept. Some references refer to momentum effects as an inertial force. These effects are is not really a force, but it has units of force, and some references find it convenient to use this shorthand (while keeping in mind its actual interpretation).

[6]In some cases, though, changes in mass during acceleration are important. Examples include the swimming biomechanics of "jet-propelled" animals like squid and jellyfish, in which water that initially is enclosed and moves with the organism is left behind during a muscular contraction to produce thrust.

you must be zero. However there is quite definitely a wind force acting on you. How does this make sense?

It makes sense because, though your body's momentum is not changing, by blocking the wind you are constantly changing the momentum of the air around you. Specifically, you are creating a wake downwind of yourself, and that wake has less momentum than the air that is approaching you from upwind.

To understand the basic mechanism, let's think about a simplified geometry: Let's assume that your have a profile area (perpendicular to the wind) of $1m^2$. The wind speed upwind of you is $10\frac{m}{s}$ (about $11mph$). That means roughly $10m^3$ of air, corresponding to a little over $12kg$, is encountering your body every second. The momentum in that air is $10m^3 \times 12kg$ – a considerable amount.

However your body is blocking that air, so that downstream of you there is a zone in which wind speed is greatly reduced. If the air in this zone has zero velocity (an oversimplification, but still a useful rough estimate) then, by blocking the wind, you are subtracting $120m^3kg$ of momentum each second from the air as it passes you. This requires force, that is the force that you feel as wind pressure and provide by opposing it with your feet.

This idea – that a moving organism creates a wake that requires force to maintain even if its own momentum is constant – is key to understanding both how organisms are shaped by evolution to minimize costs of locomotion and how forces on moving organisms scale with basic characteristics such as size and velocity.

7.7.3 Summary

To sum up, an object moving in a fluid has additional "apparent" contributions to its momentum, as accounted for in Newton's 2nd Law. This is because:

1. When it accelerates, it also accelerates some of the fluid around it; the mass of this fluid is called "added mass".

2. As it moves through the fluid, it leaves behind it a wake of fluid it has accelerated to its own velocity; to continually change the momentum of the fluid it encounters (the "wake momentum") requires force, which the object experiences as drag.

Added mass and wake momentum are continually acting on our own bodies, because we are immersed in a fluid (air). Because our bodies are so much denser than air, we usually don't feel these effects, but under some circumstances (bicycling, swimming, windy days, *etc.*) they become much more noticeable.

7.8 Estimating drag forces, Part 1

In understanding the ways organisms move through fluids, it's useful to distinguish between effects that are due mostly to an organism's size from those associated with its shape. We might ask, for example, "How does swimming speed and cost of locomotion differ between a smaller younger fish and that same fish when it is older and larger but substantially the same shape?" We could also ask, "Is the morphology of this fish streamlined as an adaptation to swimming quickly or for long distances, by comparison to another fish that is equal in size but largely sedentary?"

Here, we focus on understanding the basic effects of size on drag forces acting on organisms moving in fluids. That is, we will ask, "*What are the inherent effects of being large or being small on drag forces?*" Likewise, we will ask, "*What are the inherent effects of moving quickly or slowly on drag forces?*" These questions are posed in generic terms because we are interested in *inherent* effects – those that are largely unavoidable consequences of size or speed.

The answers to these questions will provide us with tools to think more concretely about the effects of specific shapes, behaviors, *etc.* The idea is that factors like size and speed will have strong effects on drag, and that variations in shape, surface properties and other specific traits will be "tweaks" of those strong effects. If we can factor out the effects of size and speed, more subtle effects (like those of shape) will be easier to understand and quantify.

7.8.1 Organismal characteristics

Figure 7.1 is a cartoon of an organism moving through a fluid (in this case, sinking downwards). As it moves, it pushes aside fluid in front of itself, illustrated by the blue "streamlines" moving sideways near the underside of the organism. Immediately adjacent to the organism, fluid is moving with the organism (hence, added mass). The organism leaves a wake behind itself, of fluid that is moving nearly as fast as it is (hence, wake momentum).

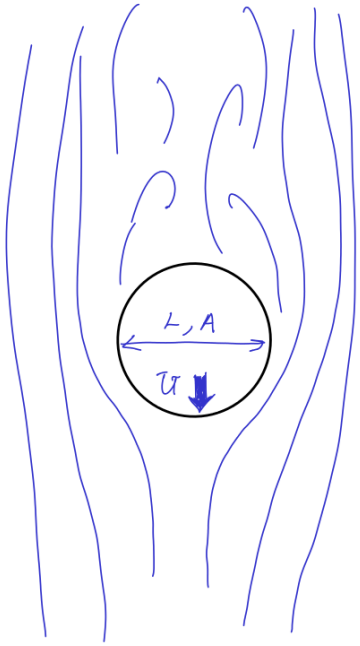


Figure 7.1: A cartoon of a sinking organism. The organism has a linear dimension (diameter) L, frontal area A, and sinking velocity U. The blue lines indicate water flow around the organism, and the wake it leaves behind.

In generic terms, we can describe this organism using **characteristic values** (also see the discussion on Scale models and nondimensional numbers in the Overview). For example, we can consider a **characteristic length**, $\boldsymbol{L}$, as a linear metric that expresses an object size. If the organism is spherical, then an obvious choice for L is the diameter. If the organism is oblong, then there is some ambiguity, but if we choose for L some consistent standard such as maximum dimension or average

of the dimensions, then the analysis will still reflect the differences between larger and smaller (but similarly shaped) particles.

L is the characteristic length. Analogously, we specify a **characteristic area**, $\boldsymbol{A}$. A is an indicator of the approximate magnitude of the organism's projected area. As with length, the exact specification of A is obvious for a sphere, and a little ambiguous for an oblong organism. In general, choosing a simple standard like the square of the characteristic length, $A = L^2$, will capture essential size effects as long as it is used consistently.

We also specify a **characteristic speed**, $\boldsymbol{U}$, which in this case is clearly the sinking rate, as indicated by the blue arrow in Figure 7.1.

7.8.2 Fluid characteristics

The drag on a moving organism depends, of course, on the characteristics of the fluid in which it is immersed. The key fluid properties that affect drag are density and viscosity. You can open worksheet to calculate these properties for freshwater, saltwater and air on Binder by clicking on

The variation of density and viscosity over a range of relevant temperatures for freshwater and saltwater with 35 ppt salinity are shown in Figure 7.2

Density

The density of a fluid is simply the mass of the fluid for a given volume. In SI units, density is expressed in $\frac{kg}{m^3}$ (that is, kilograms per meter cubed). Density is a function of temperature, the concentration of solutes such as salt, and pressure. As an example, the bottom plot of Figure 7.2 shows the variation in density of freshwater (lower line) and 35 ppt saltwater (upper line). This plot show that density is a slowly decreasing function of temperature. [7]

Viscosity

We intuitively understand the difference between a more viscous fluid like honey or molasses and a less viscous fluid like water. If we imagine sliding two plates next to each other in a fluid, viscosity expresses how much force is required to keep them moving. Intuitively, if the fluid is honey, it requires more force than if the fluid is water. Keeping them moving in air requires even less force. Therefore, honey is more viscous than water, and air is less viscous than either water or honey.

There is one slightly confusing aspect of viscosity, however: there are two ways in which visosity is commonly measured: dynamic viscosity and kinematic viscosity.

Dynamic viscosity The **dynamic viscosity** relates to forces, such as the *force* required to keep plates sliding past each other. Dynamic viscosity is often symbolized by the Greek letter μ. The SI units for dynamic viscosity are $\frac{Ns}{m^2}$.

To understand dynamic viscosity, let's think about two plates immersed in water, separated by a distance H. One of these plates is stationary, and the other is sliding past it at velocity $U\frac{m}{s}$. The water touching the stationary plate is stationary, and the water touching the moving plate moves with it at velocity U[8]. The dynamic viscosity is the force acting on each unit area of the moving plate required to keep it moving, divided by the separation distance H and the velocity U. [9]

The velocity U divided by the distance H is a quantity called the **velocity gradient**. Therefore **the dynamic viscosity is the force acting on each unit area of the moving plate normalized by the velocity gradient.**

[7] The curve for freshwater ends at $0C$; that is, at the freezing point of fresh water. The curve for salt water extends to lower temperatures, because its freezing point is lower.

[8] This is because of the **no-slip condition**, which says that fluid molecules in contact with a surface are moved along with that surface.

[9] For "simple" fluids, like water or air, dynamic viscosity does not vary with H or U. These are called *Newtonian fluids*. For some complex fluids relevant to Organismal Biology, such as blood or mucus, dynamic viscosity can differ for different values of H and U. These are called *non-Newtonian fluids*.

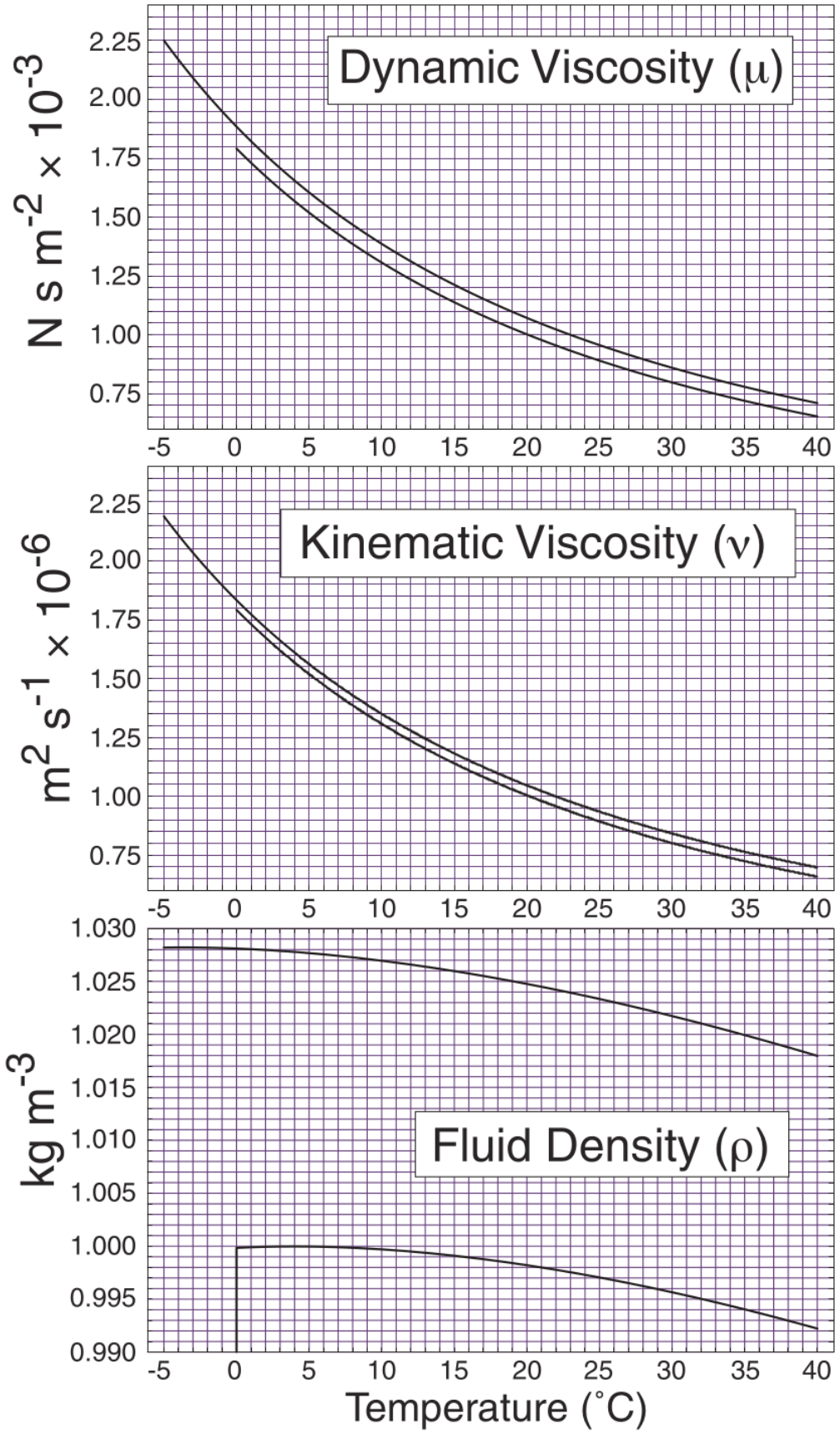


Figure 7.2: These plots show the variation of density, dynamic viscosity and kinematic viscosity across a range of temperatures relevant to aquatic organisms. It is a personal communication from Dr. Pete Jumars, and was calculated using formulas in Jumars, P.A., J.W. Deming, P.S. Hill, L. Karp-Boss, P.L. Yager and W.B. Dade. 1993. Physical constraints on marine osmotrophy in an optimal foraging context. Mar. Microbial Food Webs 7:121-159.

Kinematic viscosity Kinematic viscosity is simply the dynamic viscosity divided by the density. Kinematic viscosity is often symbolized by the Greek letter ν. The SI units for kinematic viscosity are $\frac{m^2}{s}$.

In some ways, since we typically know both the density and the dynamic viscosity, it seems counter-intuitive to also define the kinematic viscosity. The reason it is defined is that dynamic viscosity frequently occurs in formulas divided by the density. Furthermore, the kinematic viscosity has an intuitive interpretation: it characterizes the diffusion of momentum in the same way the diffusion coefficient characterizes the diffusion of a solute, and conductivity characterizes the diffusion of heat. This analogy between diffusion of mass, heat and momentum is often helpful in gaining intuition and in quantitative analysis about organism function.

7.9 Estimating drag forces, Part 2

With the set of organismal and fluid characteristics developed in Part 1, we can now begin to assess the generic effects of size and speed on drag forces acting on organisms. As a reminder, we are deliberately avoiding references to specific morphologies, behaviors or fluids. Instead, we are looking for inherent effects of size, velocity and fluid characteristics that generalize across these specifics. Because we omit specifics, we are aiming here for **order of magnitude estimates**. The intent is, knowing the order of magnitude of the inherent generic effects, we will then be able to focus in detail about possible "tweaks" due to adaptations in morphology, behavior *etc.*

As our case study, we will think about the organism from Part 1 that is sinking at a steady speed in stationary fluid. We will consider two types of forces, drawn from the previous pages:

- *Forces due to momentum*
  Momentum forces on an organism moving at a constant velocity stem from the wake momentum, which is increasing as the length of the wake lengthens over time and requires force to maintain.
- *Forces due to viscosity*
  Viscous forces on an organism moving in a fluid stem from the fluid's viscosity, μ, acting on the organism's surface in proportion to the velocity gradient in flow from the organism's surface (where fluid moves with the organism) to the "free stream" far from the organism, where fluid is undisturbed.

The key question we will address is, "*How do we expect forces due to viscosity and wake momentum to increase with organism size and speed?*"

7.9.1 Forces due to wake momentum

Figure 7.3 is a cartoon of the wake behind the sinking organism.

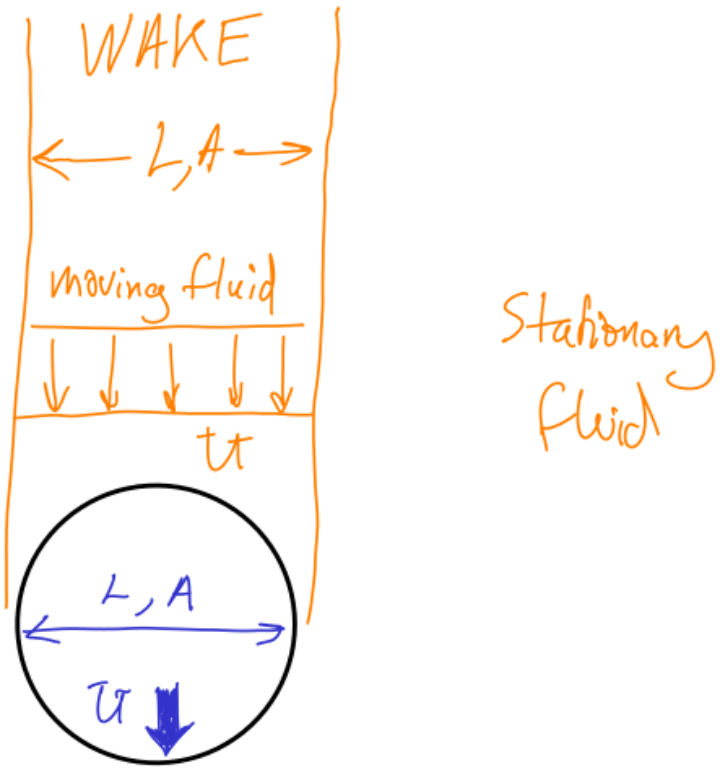


Figure 7.3: Idealized wake behind a sinking particle. The orange lines indicate the wake. For our estimate, we assume the cross section of the wake is equal to A, the projected area of the particle. We also assume water within the wake has velocity U, and that water outside the wake has negligible velocity.

Our estimate of forces on an organism due to wake momentum is based on:

1. The organism's "characteristic" parameters: size, L; area, $A = L^2$; and velocity, U.

2. The fluid's density, ρ.

3. Newton's 2nd Law, which tells us that the force arising from wake momentum, F_{mom}, equals

$$F_{mom} = \textit{rate of increase of wake momentum} \tag{7.6}$$

4. The knowledge that the wake momentum is increasing because fluid mass "swept out" by the organism (approximately at rate $A \times U \times \rho$) is accelerated to the organism's velocity (U).

Putting these observations together, we can estimate the apparent drag force on the organism due to wake momentum as

$$F_{mom} = \rho L^2 U^2 \tag{7.7}$$

In sum, F_{mom} is an order of magnitude estimate of the wake momentum force on an organism, which expresses the inherent effects of size L, velocity U and fluid density ρ, subject to "tweaks" from future consideration of effects from specific details such as the organism's shape.

7.9.2 Forces due to viscosity

Figure 7.4 is a cartoon of the fluid motion to the side of the sinking organism. The cartoon illustrates several features that are important to recognize before estimating the drag forces due to viscosity.

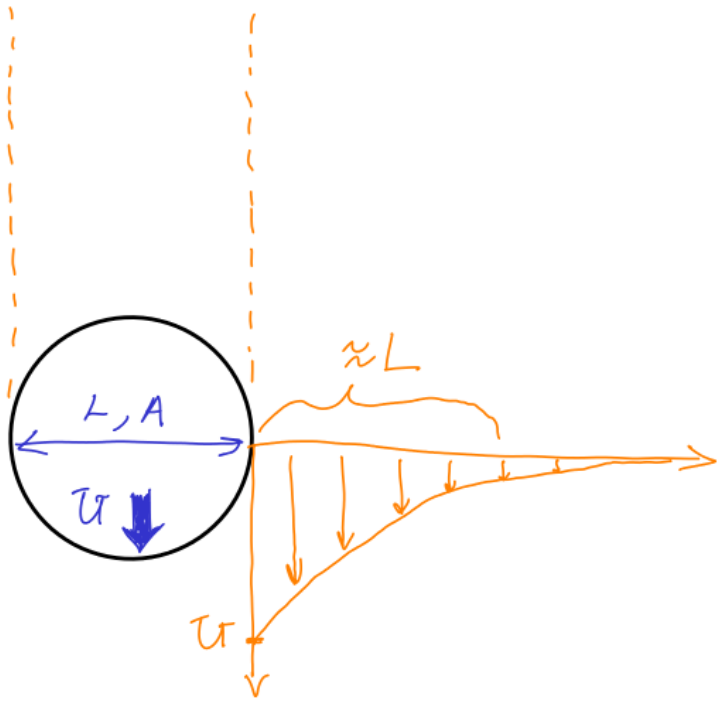


Figure 7.4: Idealized shear layer on a sinking particle. We assume that the velocity grades from U on the particle's surface to close to zero over a distance approximately the size of the particle, L.

The orange curve represents a **velocity profile**, which is simply a plot of velocity as a function of distance from the organism's surface. This velocity profile reflects the fact that, regardless of details about the organism or the fluid, the fluid's velocity at the surface equals the organim's velocity, and the velocity of undisturbed fluid far from the organism is zero.

The velocity profile also illustrates the *velocity gradient* (that is, the rate of change of velocity with distance from the surface). In the cartoon, the velocity gradient is relatively steep near the organism and becomes more gradual further away, which is typical of profiles observed near objects moving

in fluids. The velocity gradient is important because, as we saw in Part 1, the viscous force on the organism's surface is proportional to this gradient.

To estimate the viscous force, then, we need an estimate of the velocity gradient at the organism's surface. As before, because we are deferring consideration of specifics like shape and behavior, we will settle for order of magnitude estimates of the velocity gradient and viscous force. These details can be considered when we better understand the inherent effects of size, velocity and fluid properties.

Our estimate of forces on an organism due to viscosity is based on:

1. The organism's "characteristic" parameters: size, L; area, $A = L^2$; and velocity, U.
2. The fluid's dynamic viscosity, μ.
3. The knowledge (stemming from the way dynamic viscosity is defined and measured) that the viscous force is equal to the velocity gradient adjacent to the organism's surface, multiplied by the dynamic viscosity and the area over which that viscosity acts.
4. The likelihood that the size of the organism, L, is usually a rough indicator of the distance over which it disturbs the surrounding fluid (illustrated by L in Figure 7.4 above the velocity profile.

From these facts we can estimate the drag force due to viscosity, F_v, as

$$F_v = \textit{viscosity} \times \textit{area} \times \textit{velocity gradient} \tag{7.8}$$

In mathematical terms,

$$F_v = \mu L^2 \frac{U}{L} = \mu L U \tag{7.9}$$

where the area is estimated as L^2 and the velocity gradient is estimated as $\frac{U}{L}$.

7.10 Scaling of fluid forces: the Reynolds Number

A deep insight by fluid mechanicists George Stokes and Osborne Reynolds in the mid-19th century is that *the relative magnitude of the inertial and viscous forces* tells us a lot about a flow. That led to the definition of the Reynolds number, abbreviated as $\mathcal{R}$]:

$$\mathcal{R}] = \frac{\text{momentum forces}}{\text{viscous forces}} \tag{7.10}$$

Substituting our order-of-magnitude estimates of drag forces for these forces,

$$\mathcal{R}] = \frac{\rho U^2 L^2}{\mu L U}, \tag{7.11}$$

or, after simplification,

$$\mathcal{R}] = \frac{\rho U L}{\mu}. \tag{7.12}$$

In words: **The Reynolds number, Equation (7.12), states the relative strengths of momentum effects and viscous forces, as inferred from the inherent effects of size, velocity and fluid characteristics.**

Using the Reynolds number, we can list these inherent effects:

- Larger size, L, increases the relative strength of momentum effects compared to viscous forces; smaller size increases the relative strength of viscous forces
- Faster velocity, U, increases the relative strength of momentum effects compared to viscous forces; slower velocity increases the relative strength of viscous forces
- Higher fluid density, ρ, increases the relative strength of momentum effects compared to viscous forces; lower density increases the relative strength of viscous forces
- Higher fluid viscosity, μ, decreases the relative strength of momentum effects compared to viscous forces; lower viscisity decreases the relative strength of viscous forces

It's important to understand that these statements do not imply that increasing L results in smaller viscous forces. Instead, the statements are saying that, as L gets larger, momentum effects and viscous forces both increase, but momentum effects increase *faster* than viscous forces. That can be seen from Equation (7.11), which shows that momentum effects increase in proportion with L^2, while viscous forces increase in proportion with L.

7.10.1 Scale models and dynamic similarity

The Reynolds number gives us an important insight because it tells us that, for any two similarly shaped organisms moving in any Newtonian fluids, the relative magnitudes of inertial and viscous forces are equal if they have equal $\mathcal{R}$]. That is, any two organisms that are similar in shape but that may differ in size, speed and fluid type, are dynamically similar. Dynamic similarity means those organisms (or replicas of organisms) are scale models of each other: measuring the forces, flows and other features of one is equivalent, after appropriate scaling, to measuring those features on the other.

An application of dynamic similarity

As an example, let's consider a tiny organism: a bacterium swimming in water. It is very difficult to measure the fluid forces on a bacterium. Suppose, instead, that we create a tennis ball-sized replica of the bacterium. Instead of water, we immerse the replica in Karo Syrup, which has a much larger kinematic viscosity, ν. Since ν is so much larger, we can make L much larger and (with an appropriate choice of velocity, U) we can still make the replica's Reynolds number match the bacterium's. We can take then take advantage of the replicas large size to measure fluid forces, and rescale them to correspond to forces on the bacterium.

7.10.2 Reynolds number as an analytical tool

The mathematical formulas describing flow of fluids around organisms are called the Navier-Stokes equations. These equations calculate the combined effects of momentum, viscosity and pressure on each part of a moving fluid. Solving the Navier-Stokes equations is often technically difficult, computationally expensive or simply not possible. The Reynolds number provides a route to simplifying the Navier-Stokes equations in many biological applications, to obtain approximations that are usefully accurate and much easier to implement.

The low Reynolds number flow regime: $\mathcal{R}\rceil \ll 1$

A microorganism swimming in water, or a spore or pollen grain drifting in a breeze, is very small and typically moves very slowly. That is, its characteristic length, L, and characteristic velocity, U, are both small. From Equation (7.12), we know this implies its Reynolds number is very small. In mathematical terms:

$$\mathcal{R}\rceil \ll 1 \tag{7.13}$$

We can interpret Equation (7.13) to say that momentum effects are much smaller than viscous effects. If we look for an intuitive comparison for $\mathcal{R}\rceil \ll 1$, we can imagine a human (with much larger L and U) swimming in a fluid with very large μ, such as honey or tar.

Equation (7.13) suggests that we can approximate the Navier-Stokes equations by neglecting momentum effects, and for very small slow organisms we won't lose much accuracy. It turns out that this simplification results in fluid flow equations that are much more tractable than the Navier-Stokes equations. These are called the Stokes equations, and the flow they describe with $\mathcal{R}\rceil \ll 1$ is called Stokes flow. Almost all fluid dynamical analysis of microorganisms is done using the Stokes equations. The model of swimming larvae later in this unit is an example.

As a reminder, the conclusion that flows around small, slow organisms is dominated by viscous forces arose from a very general consideration of the inherent effects of size and velocity. They are not changed by specific morphological or behavioral adaptations.

The high Reynolds number flow regime: $\mathcal{R}\rceil \gg 1$

At the other end of the spectrum, high Reynolds number flows are ones in which momentum effects are much larger than viscous forces.

$$\mathcal{R}\rceil \gg 1 \tag{7.14}$$

There are some complications, because adjacent to a surface viscous forces can have large effects even in high Reynolds number flows. High Reynolds number flows are also subject to turbulence. Nonetheless, neglecting viscous terms in the Navier-Stokes equations results in simplified equations that are much more tractable. These equations are very useful approximations that have been widely used not only in biomechanical analysis of large, fast organisms but also in engineering.

7.10.3 Reversible and irreversible flows

Viscous forces are directly proportional to the velocity gradient. In mathematical terms, they are *linear*. This results in an interesting and important feature of flows that are dominated by viscous forces – that is, for flows in which $\mathcal{R}\rceil \ll 1$: they are *reversible*.

If we think about the sliding plates in our estimates of drag forces, it seems intuitive that moving the plate at a speed v to the left would produce an equal and opposite fluid motion compared to moving it to the right. Furthermore, moving it at half the speed would produce half as much force, but if it acts for twice as long the final positions of the plate and the fluid will be the same.

This is what is meant by reversibility of low $\mathcal{R}\rceil$ flow. A classic video by G. I. Taylor shows a demonstration of reversible flow. In this video, dye is placed in a viscous fluid between rotating cylinders. The cyclinders are rotated until the dye is greatly stretched; then reversed back into their original positions to restore the originam dye blob.

Reversibility has important consequences for microorganism swimming. In particular, waving a fin back and forth is a propulsive motion that works well for many fish and other high Reynolds number swimmers. However, at low Reynolds number, this reciprocating motion would have no net propulsive effect. Instead, microorganisms must propel themselves with motions that are non-reversible. For example, the bacterial flagellum is a helical filament that rotates in a propeller-like way in only one direction.

7.10.4 Final points

A couple additional points to note:

$\mathcal{R}\rceil$ is a non-dimensional number – because the denominator and the numerator both have units of force, the result has no units. So, whichever system of units you use to calculate $\mathcal{R}\rceil$, as long as you use it consistently you will get the same answer.

The Reynolds number also be written using the kinematic viscosity,

$$\mathcal{R}\rceil = \frac{UL}{\nu}. \tag{7.15}$$

This is one of many instances that kinematic viscosity, ν, appears in biomechanics and fluid dynamics applications, which is why it is often tabulated in addition to dynamic viscosity, μ.

7.11 "Look-up tables" for drag forces on moving particles

A key benefit of the Reynolds number is that it dramatically shrinks the number of experimental observations or numerical computations we need to characterize particle movement in fluids. That is because it enables us to make and interpret scale models. If we observe or compute one example of drag forces on an organism moving in fluid, the Reynolds number tells us how to translate that result to any geometrically similar organism in any fluid, as long as it has the same Reynolds number.

As an example, let's consider the general problem of drag forces on spherical organisms moving through a variety of fluids (air, water of different salinities, blood, mucus, etc.). As with many biomechanics models, assuming an organism is spherical applies to a few organisms exactly, but to a great many organsims approximately. Our goal is to create a lookup table that tabulates the drag forces on these organisms, to understandhow fast they rise or sink, as biomechanical consequences of size, habitat etc.

To cover relevant biological applications, we have at least four parameters to vary:

- organism *size*, L
- organism *velocity*, U
- fluid *viscosity* μ
- fluid *density*, ρ

If we need 20 values of each parameter to fully characterize the parameter space for our lookup table, we need to make $20^4 = 160000$ observations. Furthermore, some of these observations are difficult or impossible, such as measuring the forces on bacterium-sized organisms.

The Reynolds number rescues us from this difficult situation. We know that all geometrically similar organisms with the same $\mathcal{R}\rceil$ are scale models of each other (that is, they are *dynamically similar*). This means we need only make one observation for each value of $\mathcal{R}\rceil$; from this observation, we can calculate all the specific instances of organisms, fluids etc. with the same Reynolds number.

For example, we can choose one convenient organism size (L), and a convenient fluid (with a given visosity, μ, and density, ρ). We can then measure drag forces across a range of velocity, U, giving us the complete range of $\mathcal{R}\rceil$ we need to span the biologically interesting applications. This gives us a lookup table that covers the whole range of organisms by measuring only 20 different values of $\mathcal{R}\rceil$!

To use this concise approach, we need a formula for converting the drag forces on one organism to another organism that is dynamically similar. That formula has been provided by engineers and fluid mechanicists, and is called the Coefficient of Drag[10], C_d (also called the ***Drag Coefficient***). The formula for C_d is

$$C_d = \frac{F}{\frac{1}{2}\rho L^2 U^2} \tag{7.16}$$

The Coefficient of Drag has been measured or calculated for many shapes, as for example for spheres.

[10] Also called the *Drag Coefficient*.

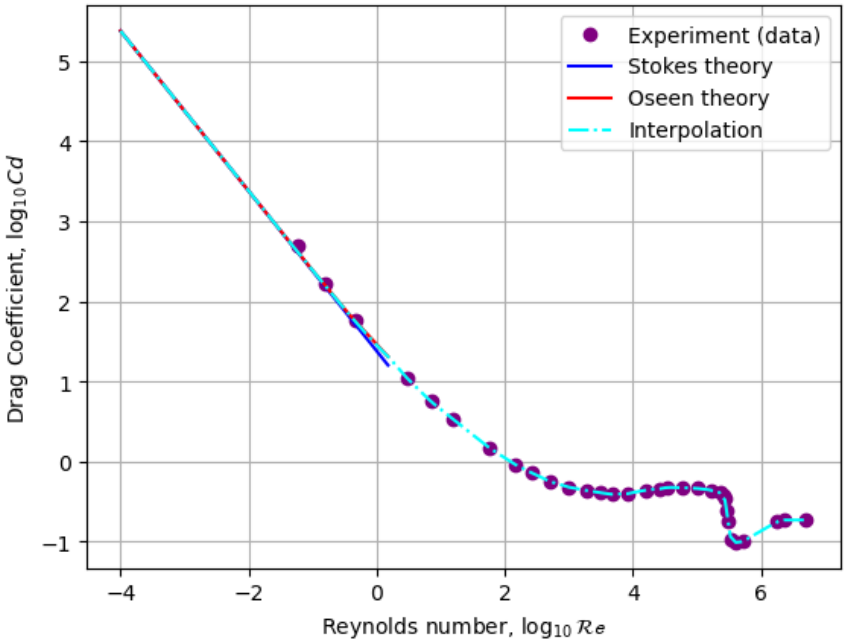
7.12 The Coefficient of Drag

As described in the previous page, the resistance force F on an immersed organism moving in a fluid is commonly expressed in a ratio known as the Coefficient of Drag:

$$C_d = \frac{F}{\frac{1}{2}\rho L^2 U^2} \tag{7.17}$$

The Coefficient of Drag is the formula used to calculate the drag forces on an organism from an observation made on a dynamically similar scale model (that is, a model that is geometrically similar and has the same Reynolds number, $\mathcal{R}\rceil$).

The power of this approach is illustrated by the plot below, which shows the drag force on *any* size spherical organism moving at *any* velocity in fluid of *any* viscosity and density.



In this plot, note that the scales are logarithmic base 10 for both axes. Note also that there are several types of data used to define the curve:

- cyan line (and purple dots) for experimental observations
- blue and red lines for analytical model calculations.

The dash-dot cyan line interpolates between these data in a sensible way, providing a consistent function across many orders of magnitude of Reynolds number. The interpolation shown by the cyan line is the form in which C_d would typically be calculated in a biomechanical investigation.

7.12.1 How to calculate drag forces on organisms

To obtain the drag force on a spherical organism, use the following steps:

1. Use the organism's size (L) and velocity (U), and the fluid's viscosity (μ) and density (ρ) to calculate its Reynolds number,

$$\mathcal{R}\rceil = \frac{\rho U L}{\mu} \tag{7.18}$$

2. Take the logarithm, base 10, of the Reynolds number

3. Find the position on the horizontal axis corresponding to that $\log_{10} \mathcal{R}\rceil$

4. Move vertically to the cyan curve; this is the $\log_{10} C_d$.
5. Calculate the coefficient of drag, $C_d = 10^{\log_{10} C_d}$
6. Calculate the drag force,

$$F_{drag} = \frac{1}{2}\rho L^2 U^2 \tag{7.19}$$

Some tools to make these calculations easier and more precise are provided in this worksheet.

7.12.2 Trends in the C_d curve

Several features of the C_d curve are worth pointing out.

- The denominator in this expression is very similar in form and rationale to our estimate of the wake momentum. The rationale is that, in cases where the drag forces are dominated by increases in wake momentum, the numerator will change in a roughly similar way as the denominator. By the logic in the scaling of fluid forces, wake momentum is dominant when $\mathcal{R}\rceil \gg 1$. Therefore, we predict that C_d will change relatively slowly at high Reynolds number.
- In contrast, at low Reynolds number, we expect the drag from vicous forces to be much higher than from wake momentum. Therefore, we predict that C_d will be large and (increase with decreasing Reynolds number) when $\mathcal{R}\rceil \ll 1$.
- In the range $10^4 < \mathcal{R}\rceil < 10^6$, the coefficient of drag has some surprising "wiggles". This is due to the onset of turbulence.

7.13 Calculations for spheres moving through fluids

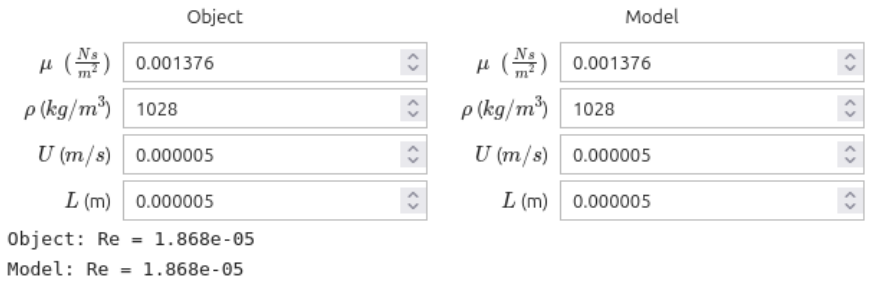
This worksheet provides some computational tools to help you understand and use the ideas of scale models and dynamic similarity, as implemented using the Reynolds number, $\mathcal{R}\rceil$, and the Coefficient of Drag, C_d. The rationale for why these nondimensional indices are useful and concise tools for quantifying

7.13.1 Matching Reynolds numbers for dynamic similarity

This part of the worksheet enables you to calculate the parameters to make a dynamically similar scale model of an organism moving in a fluid. The input panel below has two columns. In the left column, you can enter the characteristics of the object of interest, and the fluid in which it is immersed. In the right column, you can enter the characteristics of the model organism and the fluid in which it is immersed. The worksheet uses the formula,

$$\mathcal{R}\rceil = \frac{\rho U L}{\mu}, \tag{7.20}$$

to calculate the Reynolds numbers of both objects for you. If they match, the model is dynamically similar to the object.



7.13.2 Calculating force on a spherical particle moving at known velocity, U

Force calculator

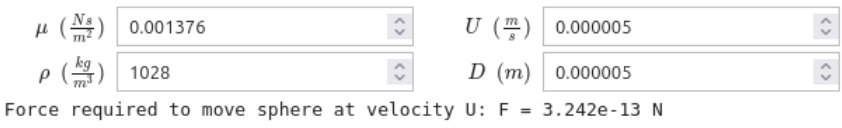
This part of the worksheet enables you to calculate the force required to propel an organism of given size through a fluid with known viscosity and density. The rationale is as follows:

1. Use the organism's diameter, D and velocity, U, and the fluid density (ρ) and viscosity (μ), to calculate $\mathcal{R}\rceil$.
2. Use $\mathcal{R}\rceil$ to calculate the Coefficient of Drag, C_d,

$$C_d = \frac{F}{\frac{1}{2}\rho L^2 U^2} \tag{7.21}$$

3. Use C_d, the organism's size and velocity, and the fluid density, to calculate the drag force F. To do this, we need to algebraically rearrange the formula for C_d to solve for F.

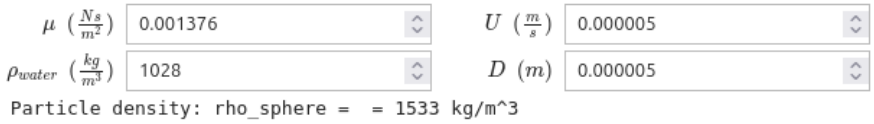
The input panel below has text boxes for the particle size and velocity and the fluid density and viscosity as inputs, and the force required to maintain the particle's velocity as output:



Density calculator

This calculator addresses the situation when we have observed a particle's sinking rate, and we would like to infer its density. This is closely related to the situation above:

Having calculated the force F, we then need to do an additional calculation to find the density of the sphere required to produce that force on the immersed particle. In this calculator, the inputs are the same as above, and the output is the density required to move the particle at the specified velocity.



7.13.3 Calculating velocity of a spherical particle propelled by known force, F

Velocity calculator #1

As noted, the $\mathcal{R}\rceil - C_d$ curve describes the movement of all spheres at all speeds in all Newtonian fluids like air and water. This is sufficient to determine the velocity of a sphere if we know its size, the force exerted on it, and the fluid characteristics.

There is however a slight complication: Both Re and C_d are functions of particle velocity, U, (see the equations above). However, because we don't in general have a convenient formula for C_d, we can't write down an analytical formula to obtain the U that satisfies both these equations simulataneously.

To get past this hurdle, we'll use a time-honored mathematical technique: We'll guess.

Guessing, or more precisely developing an intelligent sequence of trial-and-error iterations, is a great way to solve many computational problems. In fact, this type of iteration is essentially what a lot of computer algorithms for solving many hard problems are doing. Below, I've made a calculator that does this iteration for you.

Before trusting in the software, however, it's important that you gain some first-hand experience with this iterative process. This part of the worksheet enables you to efficiently perform a sequence of iterations to determine the velocity of a particle with known force. The rationale is as follows:

1. Guess a velocity, U_{est}.
2. Use the rationale in Section 3 to calculate the force, F_{est}, required to propel the particle at U_{est}.
3. Compare F_{est} to the required force, and use the error to adjust the next guess of velocity up or down as needed.

Repeat until the necessary accuracy has been achieved. With a little practice, you will be able to calculate velocity to within a percent or less error in a few iterations.

The input panel below has text boxes for the particle size, the actual force on the particle, and the fluid density and viscosity – and your guess at the velocity – as inputs. Its output is the force required to move the particle at the velocity you guessed.

Velocity calculator #2

This calculator is an extension of Velocity Calculator #1. This calculator automatically does the iteration to find the U which simultaneously satisfies the equations for $\mathcal{R}\rceil$ and C_d. It also incorporates the calculation in the density calculator above, so that the input is not force directly but particle density. The input panel below has text boxes for the particle size and density, and the fluid density and viscosity. Its output is the velocity of the corresponding particle.

μ $(\frac{Ns}{m^2})$	0.001376	ρ $(\frac{kg}{m^3})$	1028
F (N)	1e-11	D (m)	0.000005
U_{guess} $(\frac{m}{s})$	0.001		

```
Using guessed velocity, U_est = 0.001
Reynolds number: Re = 0.003735

Force required to move sphere at velocity U_est:
F_est = 6.489e-11

F_est-F_actual = 5.489e-11

Relative error is 548.9 %
```

μ $(\frac{Ns}{m^2})$	0.001376	ρ_{sphere} $(\frac{kg}{m^3})$	1105
ρ $(\frac{kg}{m^3})$	1028	D (m)	0.000005

```
Volume = 6.545e-17
Excess mass = -5.04e-15
Gravity/buoyancy force = -4.944e-14
Reynolds number: Re = 2.848e-06
U = -7.624e-07
```

7.14 Transport of organisms by currents and turbulence

Most environmental fluids – masses of air in weather systems, or the water in lakes, rivers, estuaries, and the open ocean – are moving at velocities that can vary from almost undetectable to extremely rapid. We experience these as winds, river flows, tidal fluctuations and large scale ocean currents, among other ways. Here, we begin to consider the effects of these environmental flows on the movement and distribution of organisms.

7.14.1 Examples of transport in environmental flows

To get a concrete sense of the relevant phenomena, let's begin with a couple examples:

Reproductive biology

Most benthic marine invertebrates are free spawning, meaning that they release their gametes into the water. Sperm must encounter eggs for fertilization to happen, but this is more challenging than it might seem. That's because the surrounding water is almost always moving, due to waves, currents and tides. Movement of the water into which gametes are released means that in a very short time – possibly within a few seconds – these gametes have been moved far from the adults that released them. Though sperm are motile, their swimming abilities do not enable them to find and fertilize eggs that have been transported over long distances.

This has important consequences for the life histories of many species. Marine invertebrates typically accumulate metabolic resources to produce gametes for months or even years before spawning. Once spawning begins, however, it's essential that multiple individuals precisely synchronize the timing of spawning. If an individual is early or late, its eggs will not encounter sperm to fertilize it, or its sperm will not encounter eggs to fertilize. This risk of reproductive failure leads to behavioral strategies such as formation of large colonies or reproductive aggregations; use of environmental cues such as moon phases; and chemical communication among reproductive adults.

Given synchronized spawning, successful reproduction then depends on maximizing encounters of eggs with approriate concentrations of sperm, sufficient to make fertilization successful but not so dense as to make polyspermy likely. The encounter rate of eggs with sperm – and hence, reproductive success – is determined in large part by how fast these gametes sink, rise or swim, along with the rates at which they are transported, mixed and diluted by environmental flows.

Agriculture

Suppose a rice farmer uses a crop-dusting airplane to apply pesticide to a rice paddy under no-wind conditions. The crop-duster has nozzles that emit droplets of known size. If we know the density of the pesticide mixture, we can calculate the sinking velocity of the liquid pesticide droplets using the calculators in this worksheet. If we know the height at which pesticide particles were released, we can use the sinking rate to estimate how long it takes pesticide particles to arrive at ground level.

Under no-wind conditions, a long descent time means only a delay in arrival at the rice paddy. However, suppose rather than no-wind conditions there is a moderate breeze. In this scenario, as particles sink vertically they are carried horizontally from the release point by the wind. If you have walked downwind of a sprinkler or fountain in a stiff wind you are familiar with this phenomenon.

In the windy scenario, sinking time has a consequence that is potentially much more important than a delayed arrival time at the paddy: a long delay and strong wind might mean the pesticide arrives at ground level far downwind. It may even miss the rice paddy entirely, landing instead on a different area which may be occupied by people, grazed by livestock or have other sensitive uses.

The ways in which sprayed pesticides, pollen, dust and a great many other anthropogenic and natural particles are transported and ultimately deposited are determined by their settlement rates, and by the environmental flows that transport and spread them.

7.14.2 Transport by advection

Transport of organisms and other immersed objects or substances by moving fluid is called advection[11]. Environmental flows often *advect* organisms, particles and solutes much faster and in different directions than they would otherwise move. For example, many organisms move vertically – they sink or rise under the influence of gravity and buoyancy. In contrast, the principal direction of wind, currents and many other environmental flows is often horizontal. In such cases, advection causes movement in directions those organisms would not otherwise move.

Even when an organism has some horizontal movement, horizontal advective transport can be orders of magnitude faster than swimming movements. For example, in many aquatic environments, characteristics such as light, temperature and nutrient availability change over a few meters in the vertical direction but are relatively constant over many kilometers in the horizontal direction. The slow swimming of organisms such as plankton is often considered fast enough to regulate their access to light, warmth and nutrients by moving up or down in the water column. However, horizontal swimming at the same rate can have negligble effects, because their environment varies so slowly in the horizontal direction. In these cases, only long-range advection by currents can move plankton sufficiently in the horizontal direction to significantly affect ambient conditions.

7.14.3 Mixing by turbulence

Most environmental flows also have some level of turbulence. If you have been aboard an airplane flying through turbulent air, you have felt first-hand that turbulence is composed of eddies and other small-scale but energetic fluctuations of fluid velocity. Turbulence is also a very effective mechanism for mixing; this is frequently called turbulent diffusion, because it in some ways mimics the effects of molecular diffusion but is much faster.

When you stir your coffee to mix cream or sugar, you can see how effective turbulent diffusion is. Sometime, when you have a lot of time on your hands, add cream or sugar to coffee and wait for the mixing to occur without stirring. This will give you a sense for how much turbulence has sped up the mixing process[12]. Turbulent diffusion has similar effects in environmental flows, greatly enhancing the spread and mixing of organisms and other particles.

7.14.4 Distributions of organisms in environmental flows

We now have three components of velocity to consider when thinking quantitatively about the movement of particles such as microorganisms, pollen or dust immersed in environmental flows:

1. The particles' own velocity relative to the fluid in which they are immersed, such as sinking or rising under the influence of gravity, buoyancy and drag forces.

2. Advection by the directional velocity of the fluid, such as wind or current, often primarily in horizonatal directions.

3. Turbulent eddies, that cause small-scale random movements of individual particles while mixing and spreading a population of particles.

To understand the combined effects of vertical movements with advection and turbulence, it's important to keep in mind the different effects on *population distributions* of advection by currents *vs.* mixing by turbulence.

- Starting with a group of organisms or a blob of solute, *advection* (with no turbulence) moves the overall average position (in engineering jargon, the center of mass) of that group or blob, such that it moves with the current over time.

[11] The phenomenon of population, mass, momentum, energy or any other *conserved quantity* being carried by moving fluid is called *advection* or *convection*. Different fields in the natural sciences and engineering use these terms slightly differently, but in all cases they imply that moving fluid transports a conserved quantity.

[12] Even this is an overestimate of mixing without turbulence, because temperature differences as the coffee cools cause some mixing currents!

- Starting with a group of organisms or a blob of solute, *turbulent diffusion* (with no advection) spreads out the group or blob in a similar way to molecular diffusion or random swimming, but much faster except at very small length scales (much smaller than a millimeter).

Keeping in mind that advection and turbulence are distinct forms of transport by fluids, we can anticipate environmental situations in which we have high adection and low turbulence; low advection and high turbulence, high advection and high turbulence, etc. The next worksheet gives us tools for quantitatively assessing the consequences of these different scenarios for different types of particles.

7.15 Models of particle transport by advection and turbulence

A simple but useful approach for estimating the transport of particles in environmental flows is called a **Gaussian plume model**.

To explain the key assumptions of this model, we'll use a terrestrial example of wind-borne seed dispersal. Useful references are a journal article, Okubo and Levin (1989), and a book by the same authors, Okubo and Levin (2001).

The question we will address is: If a plant or tree releases seeds with sinking velocity U above the ground at a height h, how widely do its seeds disperse? You can think of many examples of pollutant particles, carbon-containing particles in the ocean, aeolian dust particles, etc, whose distribution patterns are exactly analogous. In the Gaussian Plume Model of seed dispersal, we'll assume that there is constant wind velocity, W. In reality, the wind would likely vary over time and at different heights in intensity and direction; we will neglect this variation.

We'll also assume that turbulent intensity, as summarized by the turbulent diffusion coefficient K, is also equal at all times and places. In reality, turbulence would also vary in time and space, but we will again neglect this complication.

We'll assume that, once they hit the gound, seeds stick to it and are not dispersed into the air again.

Finally, we'll assume that at large scales the advective transport is much faster than the turbulent mixing. That is, we assume that turbulent mixing is significant in the vertical direction but can be ignored in the horizontal directions, because advective transport by the wind is much greater. This is mostly a technical detail, because it is almost always true for most parts of environmental flows, but this assumption can have consequences in specific parts of the environment (very near the source, very near the ground, etc.).

If we accept these assumptions, we can calculate formulas for the concentration of seeds in different parts of the atmosphere surrounding the seed source, and for the rate at which seeds are deposited on the ground at various downstream distances. These formulas are calculated for you in the Gaussian Plume calculator below.

7.15.1 Model rationale

The rationale of the Gaussian plume model is that it breaks the three components of movement:

1. the *advection* due to wind velocity, W
2. the spreading in the vertical direction by *turbulence*, K
3. the sinking velocity, U

into sequential, additive steps.

Separating the movement mechanisms makes it easy to approximate the resutling distributions and deposition patterns, in the following ways:

1. Seeds (or other particles of interest) are transported horizontally downwind at a steady velocity, W.
2. As they move downwind, the vertical distribution of seeds is spreading due to the turbulent diffusion, to take the shape of a Gaussian distribution with a variance that increases over time at a rate proportional to K.
3. The vertical position of the mean of the Gaussian distribution of seeds is descending over time, due to the sinking velocity U.

Following these steps, a formula can be written for the spatial distribution of seeds and their deposition rate.

Model Inputs:

In the default settings (to reproduce these, just restart the kernel in the menu at the top left):

- the seed source is set to $h = 10m$;
- the seed's sinking speed is $U = 0.5\frac{m}{s}$;
- the rate at which seeds are released is one per second: $n = 1s^{-1}$;
- the default wind speed is $W = 1\frac{m}{s}$; and,
- the default turbulent mixing intensity is $K = 0.5\frac{m^2}{s}$.

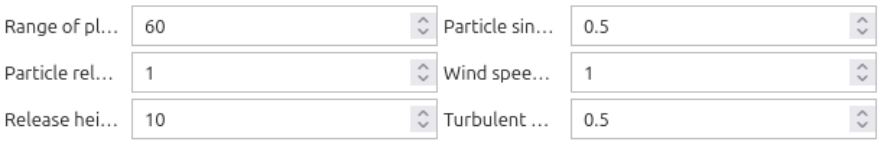
You can modify these as needed to apply to a specific problem, by entering a new value in a textbox and hitting *enter*.

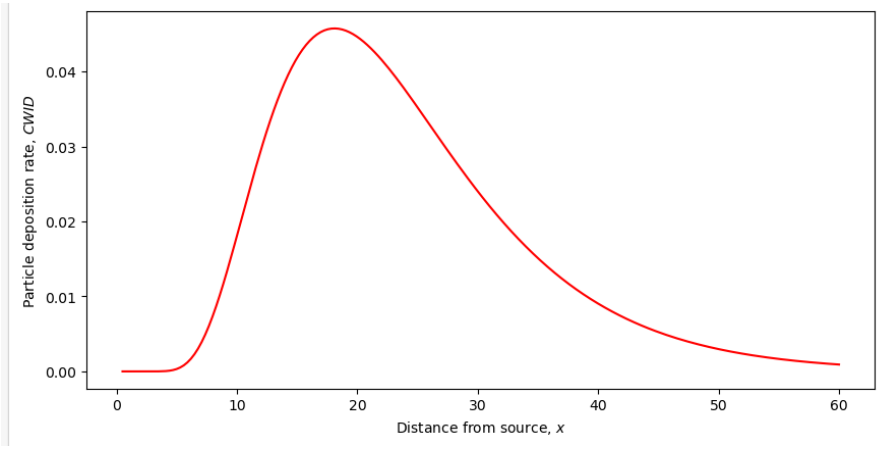
For example, in calculating the distribution pattern of marine invertebrate eggs, or pesticide droplets from aerial spraying, you might calculate the sinking speed of these particle using this worksheet, and use the calculator below to explore the consequences of various release heights, wind or current speeds, turbulence intensities, etc.

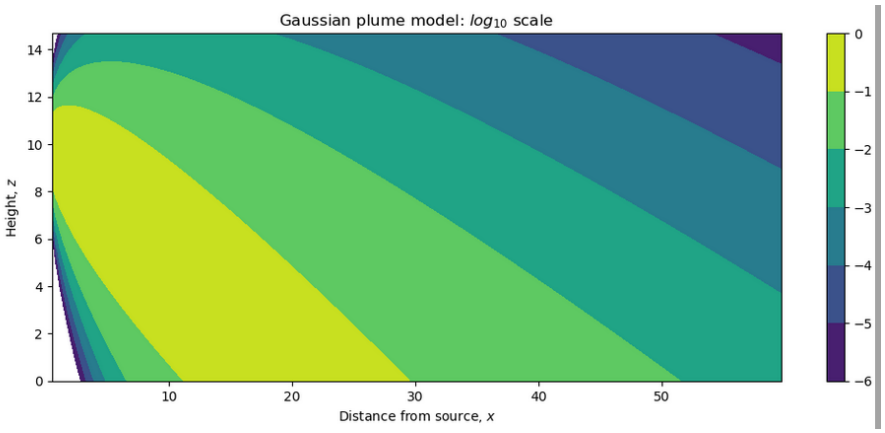
Model outputs:

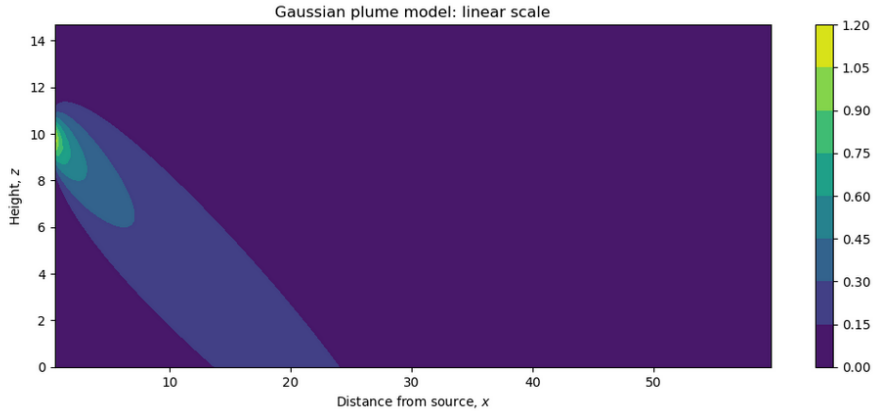
The model output is in the form of three plots.

- The top graph is the total rate of deposition as a function of downstream distance from the source. This is called the *Cross-Wind Integrated Deposition*, or *CWID*.
  This term means simply that we are not primarily concerned with the relatively small spread of seeds, pesticide or other particles in the cross-stream direction. We are instead mainly interested in the much larger dispersal of those particles in the downstream direction.
  The CWID integrates across all cross-stream positions, so it is straightforward to see the downstream transport. In this plot, the horizontal axis is distance downstream from the source, x. You can specify the extent of ground plotted by adjusting the plotting parameter x_{max}.
- The bottom two plots show the distribution of seeds in the air (or other particles in other fluids, as the case may be).
  In these plots, the horizontal axis is x, and the vertical axis is height above the ground, z. The color contours represent particle concentration. The first of these two plots shows this concentration on a $\log_{10}$ scale, as indicated by the scale bar at right. The bottom plot shows the same concentration, but on a linear scale.
  The two plots show the same distribution; it is often easier to get an overall sense for the plume pattern on the linear scale plot, but easier to see dilute parts of the particle distribution using the log scale plot.




Particle deposition rate, CWID
0.04
0.03
0.02
0.01
0.00
0
10
20
30
40
50
60
Distance from source, x


Gaussian plume model: log10 scale
Height, z
14
12
10
8
6
4
2
0
10
20
30
40
50
Distance from source, x
0
−1
−2
−3
−4
−5
−6


Gaussian plume model: linear scale
Height, z
14
12
10
8
6
4
2
0
10
20
30
40
50
Distance from source, x
1.20
1.05
0.90
0.75
0.60
0.45
0.30
0.15
0.00

7.16 Mass flux in and out of moving organisms

We are all familiar with the phenomenon of "wind chill" – we get colder on a chilly, windy day than on a day that is equally cold but has no wind. Similarly, if you pour sugar crystals into your tea and let them sit on the bottom of your cup, they will take some time to dissolve. If you stir your tea so that there is flow over the crystals they dissolve almost immediately. In general, except at microscopic scales, molecular transport mechanisms are usually greatly enhanced by flow.

Just as we used a scale model approach to estimate how fast particles move in fluids, we can use this approach to estimate how molecular transport mechanisms like diffusion are enhanced by particle movement. The most convenient way to perform this calculation is with another *dimensionless ratio*. Recall that the Reynolds number is dimensionless, because it is the quotient of a force divided by another force – the units of force in the numerator and denominator cancel). The new dimensionless ratio is called the Sherwood number, $\mathcal{S}\langle$, and is defined as

$$\mathcal{S}\langle = \frac{\textit{mass flux with diffusion and flow}}{\textit{mass flux with diffusion alone}} \tag{7.22}$$

For example, suppose we consider a phytoplankton cell that is absorbing nutrients as it slowly sinks in the water column. $\mathcal{S}\langle$ is the actual mass transport of nutrients into the cell, divided by the mass of nutrients that would be transported if the cell were not sinking but were stationary in the water. If the cell were stationary, mass transport would occur by diffusion alone. If the cell is moving, the wind chill and stirred tea examples suggest that nutrient transport might be much higher. If so, then actual transport is higher than transport by diffusion alone, and $\mathcal{S}\langle 1$.

Three points are important here:

1. $\mathcal{S}\langle$ is a function of velocity (in this case, the sinking speed).

Possible values range from $\mathcal{S}\langle = 1$, for a particle that is moving very slowly or not at all (that is, no enhancement of transport due to movement) to very large values (e.g. $\mathcal{S}\langle 100$) for some rapidly moving particles. That means mass transport has been increased by a factor of more than 100. As you can imagine, this could make quite a difference to nutrient uptake by cells, and in many other analogous situations

Because Sh depends on velocity, it is effectively summarized as a function of $\mathcal{R}\rceil$ (just as was the coefficient of drag, C_d). Here, $\mathcal{R}\rceil$ summarizes how fluid flows around the particle.

2. $\mathcal{S}\langle$ is a function of the diffusion rate. Because diffusion is involved, we need a way to express the diffusion rate of the nutrient (or other solute, as the case may be).

The convenient way to express this is as yet another dimensionless ratio, the Schmidt number, $\mathcal{S}\rfloor$. $\mathcal{S}\rfloor$ has a simple definition:

$$\mathcal{S}\rfloor = \frac{\mu}{D \times \rho} \tag{7.23}$$

Here, μ is the fluid dynamic viscosity, ρ is the fluid density, and D is the diffusion coefficient of the solute in the fluid. Note that $\mathcal{S}\rfloor$ can also be written in terms of the kinematic viscosity, ν:

$$\mathcal{S}\rfloor = \frac{\nu}{D} \tag{7.24}$$

This simple expression shows that $\mathcal{S}\rfloor$ is actually the ratio of the momentum diffusivity, ν, to the mass diffusivity, D.

3. For many simple shapes, we have a formula for the mass tranport due to diffusion alone.

For example, for a spherical particle, the mass transport of solute into the particle due to diffusion alone is

$$Q_{\textit{diff}} = 2\pi D \times d \times (C_w - C_s). \tag{7.25}$$

In this formula,

- d is the particle diameter;
- C_w is the solute concentration in the fluid far from the particle; and,

- C_s is the concentration at the surface of the particle.

For example, if the particle is extremely effective at absorbing the solute (as might be approximately true for a phytoplankton cell absorbing nutrients) the $C_s \approx 0$. If we have a formula for Q_{diff}, then all we need to know is $\mathcal{S}\langle$. Then, we can calculate the actual mass flux (including diffusion *and* advection) into a moving particle, Q_{adv}.

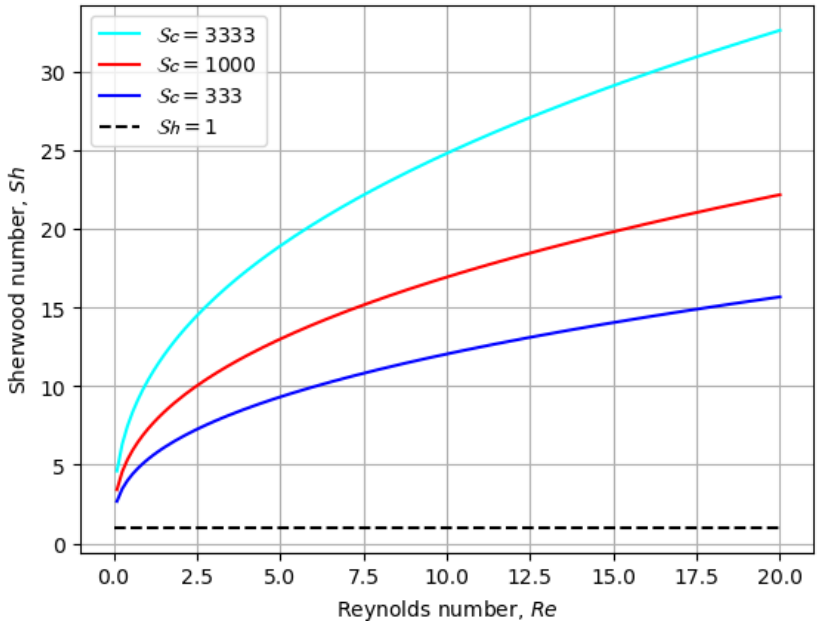
A worksheet that makes it easy to use Sherwood numbers to calculate the fluxes in and out of spherical organisms or other particles is here.

7.17 Effects of flow on molecular transport mechanisms

A very useful set of formulas approximating $\mathcal{S}\langle$ relevant to many environmental particles is given by Kiorboe et al. (2001). Here is a plot of $\mathcal{S}\langle$ as a function of $\mathcal{R}\rceil$ and $\mathcal{S}\rfloor$ for spherical particles:

In this plot, the cyan, red and blue lines represent the Sherwood number, $\mathcal{S}\langle$, for different Schmidt numbers, $\mathcal{S}\rfloor$. $\mathcal{S}\rfloor$is the ratio of the fluid kinematic viscosity to the solute's diffusion coefficient. That is, higher $\mathcal{S}\rfloor$ implies more viscous fluids or less diffusive solutes. Conversely, lower $\mathcal{S}\rfloor$ implies less viscous fluids or more diffusive solutes.

The dashed black line represents $\mathcal{S}\langle = 1$; that is, the case when flow has no effect on mass flux.



7.17.1 Sherwood number calculator

As you can see in the plot above, under some conditions mass transport is greatly increased by fluid flow. But, under other conditions, the increase is minimal. Which applies to a given situation?

The text panel below enables you to enter the particle size, density and surface solute concentration, and the fluid viscosity, density and solute concentration. The worksheet will then calculate for you the corresponding $\mathcal{R}\rceil$, $\mathcal{S}\langle$ and mass transport rates.

In many environmental problems, important issues involve the amount of mass transport per unit mass of particle. For example, a pollution problem may involve knowing whether a given mass of pollutant divided into many small particles has a different environmental effect than the same mass in a few larger particles. In the example of nutrient uptake by phytoplankton, an ecological question might revolve around whether a given biomass of small cells is more effective at competing for nutrients than an equal biomass of large cells. The calculator enables you to address those questions by calculating the mass transport per unit mass of particle.

$\mu\ (\frac{Ns}{m^2})$	0.001376	$\rho_{sphere}\ (\frac{kg}{m^3})$	1105
$\rho\ (\frac{kg}{m^3})$	1028	$D\ (m)$	0.000005
C_w	1	C_s	0

```
Volume = 6.545e-17
Excess mass = -5.04e-15
Gravity/buoyancy force = -4.944e-14
Reynolds number: Re = 2.848e-06
U = -7.624e-07

Sherwood number: Sh = 1.0002738698215627
Diffusive transport: Q_diff = 3.141592653589794e-08
Advective transport: Q_adv = 3.142453041009255e-08

Advective transport per unit mass: Q_adv/Excess mass = 6235473.474212339
```

Part III

Demography

7.18 Cloning in marine invertebrate larvae

In "normal" development (without cloning), a cohort of marine invertebrate larvae always decreases in population due to mortality. This is because there is no mechanism for adding new larvae to the cohort. Assuming there is always a non-zero amount of mortality, the larval population must decrease.

The term *competence* is used by Larval Biologists to refer to a larva that has developed to a stage and size that makes them capable of metamorphosisis. The term larval duration refers to the time required for larvae to reach competence. The ultimate recruitment – that is, the fraction of larvae surviving to successfully metamorphose and join the post-larval population – is then determined by the impacts of the larval mortality rate, acting over the larval duration.

Recently, it has become clear that the larvae of a number of marine invertebrates can clone, either intrinsically or in response to environmental cues such as chemical stressors or predators.[13] In a cloning species, one larva can divide into two or more genetically identical "daughter" larvae. This means that, in cloning larvae, the number of larvae in a cohort can either increase or decrease at any given time during development.

While cloning produces two larvae out of one, it does not provide any additional tissue or nutritional resources to those larvae. This means a larva that clones produces two daughter larvae which are smaller. In most cases it is not known what the metabolic losses of cloning are, as the daughter larvae divide resources from the original larva. If cloning itself is not too metabolically costly, then a reasonable baseline approximation is that the resources of two daughters produced by cloning add up approximately to the resources of the original larva.

While cloning has an obvious benefit in terms of larval numbers, it also has costs. Those costs may include disruptions to key larval functions such as swimming or feeding, as a clone redevelops a complete larval morphology. For example, if either or both clones are initially formed without a functional stomach, feeding is impossible until one is developed. Smaller larvae may experience higher mortality rates, *e.g.*, due to predation (though lower mortality rates are also possible). Many larvae also feed and grow in proportion to their body mass. This means two small larvae feed and grow less than a single large one with equal total body mass.

Other costs may stem from delays to metamorphosis. Clones likely have a longer larval duration than the original larva, because they are smaller and may have disrupted development. During this extended larval duration, larvae face predators, pathogens, transport away from favorable habitats, and other risks.

Because there are relatively few quantitative observations of cloning in marine invertebrate larvae, especially under natural conditions, there is currently little empirical evidence whether or not cloning has important demographic effects on marine invertebrate populations, and if so whether the benefits of cloning outweigh the costs.

[13] Some larvae may also shed parts of their bodies, which are not subsequently capable of developing into adults. This is a form of tissue loss, as distinct from the types of cloning that we consider here.

7.18.1 Modes of cloning

Across species, cloning occurs in different forms. In echinoderms, which represent many of the reported observations of cloning, there are at least two distinct modes of cloning:

1. *The echinoid mode of cloning* In the cloning mode most commonly observed in echinoids sea urchins, larvae bifurcate during development, partway into their larval duration and prior to reaching competence. Each of these clones can either redifferentiate into a complete, smaller larva, or resume growth to reform the lost body parts. Whether it redifferentiates or regrows lost parts, each clone has to grow back to a size and developmental stage at which it is competent.

The model can simulate characteristics of two distinct modes of cloning, exemplified by cloning typically found in Echinoids and Ophiuroids:

- In the **Echinoid mode** of cloning, larvae grow and develop to a threshold size smaller than the size at metamorphosis. At this threshold size, some fraction of individuals clone to form two smaller daughters. These clones resume growth, and have one of three outcomes:
    1. They can remain as larvae until fully grown, and then proceed to metamorphosis.
    2. They proceed to metamorphosis before being fully grown, becoming smaller juveniles.
    3. They can remain as larvae, and clone again when they reach a threshold size.
- In the **Ophiuroid mode** of cloning, larvae grow past the point of competence. These larger larvae then divide into two clones, one of which retains the size and stage needed for competence. This clone metamorphoses immediately. The other, smaller clone then resumes development, repeating growth and either metamorphosing directly or cloning again to form a metamorph and yet another small clone.

The `clone_modelND` model is a simulation of these two cloning stratagies, implemented as a Jupyter notebook.

7.18.2 Modeling the demographic implications of cloning in marine invertebrate larvae

This is a graphical interface for using the `clone_modelND` (for Non-Dimensional) model of cloning in marine invertebrate larvae. The `clone_modelND` model calculates the size distribution of a cohort of marine invertebrate larvae over time. This cohort represents a group of larvae beginning development at the same time and at the same size. For example, the cohort could represent larvae from the eggs of a single mother, or larvae from the eggs of a local population of mothers that spawn synchronously at a given time and place.

Like most larval life history models in the literature, **size is assumed in the `clone_modelND` model to be a *proxy* for developmental state**. This means that the model does not represent developmental state directly. Instead, it assumes that developmental state is closely coupled to size. For example, a larva is assumed to be competent to settle when it reaches a specific size. This approach means that the model does not exactly describe many details of morphology and life history associated with any given species. However, the more general results of this modeling approach may approximately describe a great many different species.

The model implemented through this notebook can simulate characteristics of two distinct modes of cloning, exemplified by cloning typically found in Echinoids and Ophiuroids In addition, the `clone_modelND` model is capable of modeling many scenarios, such as fluctuating environments or multiple potential cloning or metamorphosis sizes, that are not implemented through this Jupyter NoteBook interface. These can be accessed by running the model directly from Python.

Model structure and parameters

The `clone_modelND` model has two independent variables: larval size, s, and time, t. It has one dependent variable: $p(s,t)$, the population of larvae of size s at time t.

The model tracks how $p(s,t)$ evolves as a function of time, under the influence of four mechanisms:

- **Larval growth and development**
  - g_0 determines the basal growth rate.
- **Larval mortality**
  - m_0 determines the basal mortality rate.
  - α determines the *size-dependence* of mortality, e.g. due to predators that preferentially prey on early or late stage larvae ($\alpha < 0$ means mortality is higher for early stages; $\alpha > 0$ means mortality is higher for late stages; $\alpha = 0$ means mortality is the same for all stages). *Note:* These parameters interact so changing $\alpha = 0$ also affects the impact of m_0.
- **Sizes for developmental milestones**
  - s_{egg} determines egg size (starting size for a developing larva)
  - s_0 determines the size at cloning
  - s_1 determines the size of one clone (must have $s_1 < s_0$). The other clone has size $s_0 - s_1$.
  - s_2 is the size at metamorphosis
  - s_{max} determines the upper limit of the population size structure plot. It has no effect on the simulation itself.
- **Probabilities for developmental milestones**
  - c_0 is the probability a larva will clone when it reaches size s_1. $c_0 = 0$ means larvae never clone. $c_0 = 0.5$ means 50% of larvae clone, etc.
  - f_2 is the probability of metamorphosis at size s_2. $f_2 = 1$ means larvae always metamorphose when they reach size at metamorphosis. $f_2 = 0.5$ means 50% of larvae metamorphose when they reach size at metamorphosis.

The *initial condition* – the size distribution at the beginning of a simulation – is that all larvae are initially of size s_0. Because there are only a fixed amount of maternal resources to put into eggs, making larger eggs means there are initially fewer, larger larvae. Conversely, making smaller eggs means there are initially more, smaller larvae.

Meaningful parameter choices

The "ND" in the name of the `clone_modelND` model indicates that the model is **Non-Dimensional**. This means key quantities have been scaled by some parameters, to remove redundant axes of variation.

- The population of larvae have been normalized by the total amount of maternal resources. If N is the initial number of larvae, $N \times S_0 = 1$.
- The sizes of larvae have been normalized by the size at metamorphosis. This means that you should keep $s_2 = 1$.
- The timescale has been scaled so that $g_0 = 1$. This means, essentially, that if larvae take approximately a week to develop, we count time in weeks. If larvae take a month to develop, we count time in months, etc.

The mortality parameters m_0 and α reflect the size and time scales described above. For example, a well developed late stage larva has scaled size approaching $s = 1$, while a very early stage larva is close to $s = 0$. Also, the mortality rate is relative to the time scale of growth. That is, if growth takes approximately a week to develop, the mortality rate is per week, etc.

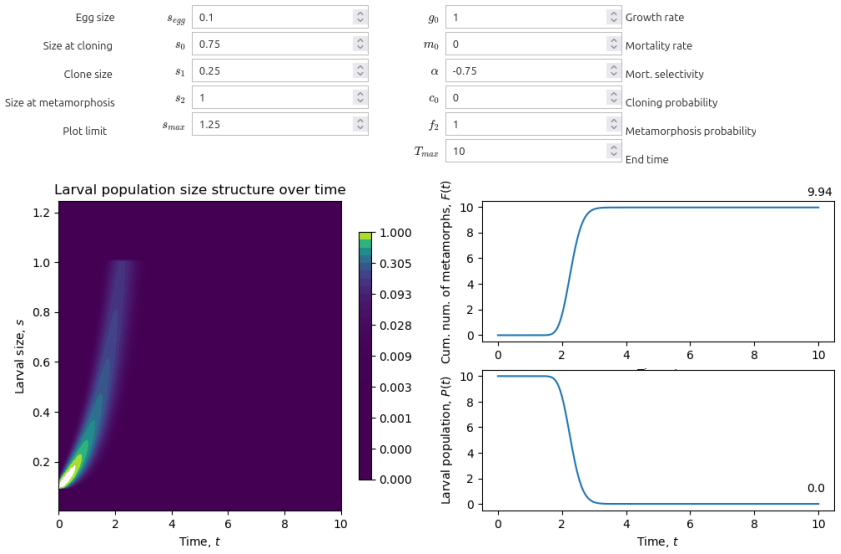
Modes of cloning

- To simulate the **Echinoid mode** of cloning, set:
  $f_2 = 1$
  $s_1 < s_2$
  $0 \leq c_0 < 1$
- To simulate the **Ophiuroid mode** of cloning:
  $f_2 < 1$
  $s_1 > s_2$
  $c_0 = 1$

Understanding model output

The output of this graphical interface for the `clone_modelND` model comprises three plots.

- The plot at the left is a **heat map of size distribution of larvae, $p(s,t)$, over larval size (s) and time (t)**. A vertical line represents the size distribution at one point in simulated time. A horizontal line represents the abundance of larvae of a given size across time.
- The plot at the upper right shows the cumulative number of metamorphs, $F(t)$, across time. The cumulative number of metamorphs at the end of the simulation is given just above the end of this line.
- The plot at the lower right shows the total number of developing larvae of all sizes, $P(t)$, across time. The total number of larvae still developing at the end of the simulation is given just above the end of this line.


Egg size
s_{egg}
0.1
Size at cloning
s_0
0.75
Clone size
s_1
0.25
Size at metamorphosis
s_2
1
Plot limit
s_{max}
1.25
g_0
1
Growth rate
m_0
0
Mortality rate
α
-0.75
Mort. selectivity
c_0
0
Cloning probability
f_2
1
Metamorphosis probability
T_{max}
10
End time
Larval population size structure over time
Larval size, s
Time, t
1.000
0.305
0.093
0.028
0.009
0.003
0.001
0.000
0.000
Cum. num. of metamorphs, $F(t)$
9.94
Larval population, $P(t)$
0.0
Time, t

7.19 Why are diatoms larger in marine than freshwater habitats?

Allometry is the study of how organismal traits vary with organism size. Among aquatic[14] organisms, size is associated with variations in numerous other traits and processes, across all of the organizational scales relevant to Organismal Biology. Examples include physiological traits such as respiration and nutrient uptake rates, organism-level traits such as intrinsic rate of growth and fecundity, behavioral traits such as locomotion and sensing, population-level traits such as reproduction and mortality rates, and ecological traits such as trophic interactions and carbon sequestration. Allometry is a useful tool for understanding linkages between these and many other characteristics of aquatic organisms.

Diatoms are a large group of single-celled algae inhabiting aquatic environments world-wide. Diatoms are diverse, with about 12,000 known species[15]. Across this diversity, diatoms encompass a wide range of sizes ($2 - 2000\mu m$), and morphologies with numerous beautiful and interesting features. Many of these features, such as pores and spines, likely serve functional roles in nutrient acquisition, predator defence and depth regulation.

Diatoms are abundant, and are estimated to produce 20-50% of new oxygen generated worldwide each year. Diatoms are major contributors to primary production, are important consumers of dissolved nutrients and have strong trophic interactions with zooplankton grazers, heterotrophic protists and aquatic pathogens.

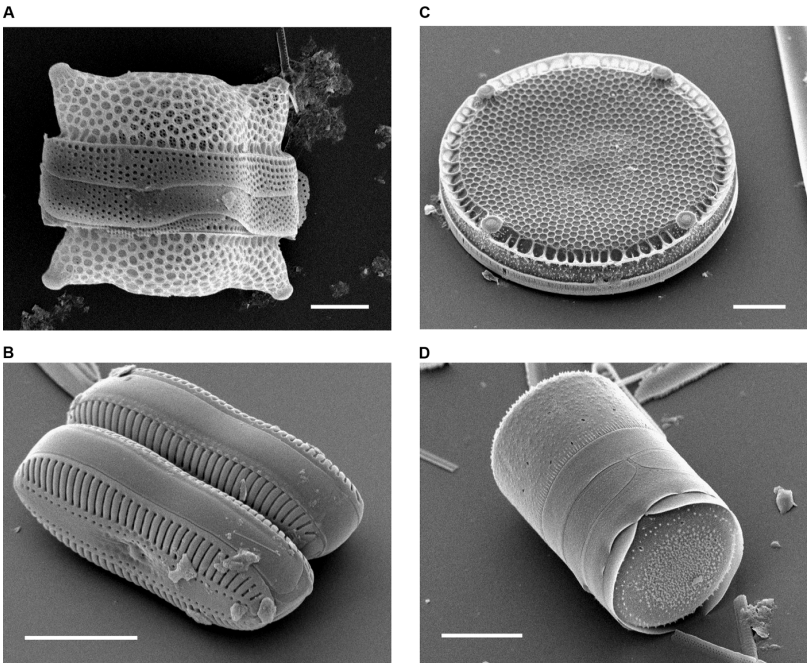


Figure 7.5: Images from Wikipedia of frustules from four species of diatoms (scale bar = 10 micrometres in a, c and d and 20 micrometres in b).

Diatoms are encased in hard silica shells called frustules (Figure 7.5). Due in part to the weigh of these frustules, diatom cells can sink relatively rapidly. This makes diatoms significant contributors to sequestration into deep water of carbon fixed by photosynthesis in surface layers.

In 2009, **?** published a survey of diatom size distributions across a number of marine and freshwater habitats. They found that, though there is a large diversity of sizes in all habitats, the diatom size distribution in marine habitats is consistently larger than the size distribution in freshwater habitats. Litchman *et al.* asked,

> Why does a disparity in size distributions exist between marine and freshwater habitats?

[14] In Organismal Biology, the term *aquatic* is usually interpreted as referring to a water habitat that may be either marine (saltwater) or freshwater.

[15] Estimates of the number of species ranging from 20,000 to as high as 200,000.

Litchman *et al.* noted that diatoms follow the usual allometries for nutrient uptake and growth: Smaller cells have, relative to metabolic demands, faster uptake of nutrients such as nitrogen and phosphorus. Smaller cells also have better ability to absorb very dilute nutrients. Furthermore, smaller cells have faster reproductive rates when replete with nutrients than larger cells. Each of these factors favor smaller cells, raising an even more fundamental question,

> Why do large diatoms exist, when small ones have advantages in both nutrient uptake and maximum growth rate?

A hypothezed factor frequently cited as favoring large cells is size-specific predation: the idea that smaller cells have a higher risk of predation, or of infection by pathogens, than larger cells. Larger cells would then be maintained not because they can grow faster but because they suffer lower predator- or pathogen-induced mortality rates than small cells. This type of regulation of a population by higher trophic levels is called top-down control.

Litchman *et al.* hypothesized that additional answers to both of these questions are found in bottom-up control, modulated by the phenomena in oceans and lakes called Mixed layers.

7.19.1 Diatoms and mixed layers

Most aquatic environments are *vertically stratified* some or all of the time, meaning that there is vertical variation in water properties such as temperature and salinity. Typically, surface waters tend (at least seasonally) to be higher temperature (e.g., because they are warmed by the sun or warm air). In marine environments, surface layers also often have lower salinity than deeper waters (in coastal regions, this can result from river inflows). This variation, in which water in surface layers is less dense than water in deeper layers, is known as *stable stratification*.

In the absence of a mechanism to energetically stir water in a stably stratified water column, lighter near-surface water will remain near-surface indefinitely, and denser deep water will stay deep. The primary stirring mechanism in many oceanic and lake environments is wind, which causes waves, currents and tubulence in surface waters. Stirring from wind typically overcomes stratification near the surface. However, it usually penetrates only partway into a water column.

Within this near-surface zone of penetration, wind-induced turbulence mixes water so that temperature and salinity are relatively uniform. This zone is called the mixed layer. Within the mixed layer, stratification has been lost, so that cells or nutrients at one level within the mixed layer can easily be transported by turbulence to another level within the mixed layer.

However, there remains a density difference between water in the mixed layer and deeper water. That means it takes substantial extra energy to mix lighter mixed layer water with denser water from below the mixed layer. This extra energy is supplied only episodically, by events such as storms and internal waves.

Like phytoplankton in general, diatoms typically inhabit the mixed layer within aquatic environments, where there is sunlight to fuel photosynthesis. Because they are in low-density surface water, they may be moved within the mixed layer but are rarely carried below it into deep, unlit water.

As these cells grow and reproduce, they consume the nutrients in the mixed layer. Once nutrients are depleted, they can be replaced only by mixing events, such as storms, that replace some of the nutrient-depleted surface water with nutrient-rich deep water.

Concurrently, some near-surface water is moved deeper, below the mixed layer. Diatoms and other phytoplankton cells in that water are then typically lost into deep water, where they are unable to photosynthesize and eventually die or are eaten.

The net effect of a mixing event, then, is a partial loss of the diatom population (namely, those cells in the mixed layer water that is lost to deep water) and, simultaneously, a partial replenishment of nutrients in the mixed mixed layer that can support new growth (contained in the formerly nutrient-rich deep water now part of the mixed layer).

7.19.2 Allometry of growth, nutrient acquisition and storage in diatoms

Litchman *et al.* (2009) asked whether the characteristics of mixed layers could explain the diversity and success of large diatoms, and their greater presence in marine habitats relative to freshwater habitats such as lakes. They noted that the differences between typical marine and freshwater habitats are:

1. Mixed layers in marine habitats tend to be deeper than mixed layers in lakes.
2. Nitrogen (nitrate) is more often limiting for diatom growth in marine systems, while phosphorus is more often limiting for diatom growth in freshwater systems.

The significance of the first point is that losses due to cells sinking out of the mixed layer due to their own sinking velocities are lower when mixed layers are deeper. Cell losses due to sinking may be higher for larger diatom cells than for smaller cells[16]. If so, higher losses from shallow mixed layers might favor small, rarely lost cells over larger, more frequently lost cells. Because mixed layers tend to be shallower in lakes, this could impact freshwater diatoms more than marine diatoms.

The significance of the second point hinges on nutrient storage in cells. Diatom cells can store key nutrients, such as nitrogen and phosphorus. However, because they are stored within different parts of cells, diatoms' storage capacities have different allometries for nitrogen than for phosphorus.

Larger diatoms have disproportionately higher storage capacity (relative to requirements for growth) for nitrogen than smaller cells. However, storage capacity (relative to requirements for growth) for phosphorus are more nearly proportional in large and small diatom cells. If so, potential advantages from greater storage capacity are more likely to favor larger cells in nitrogen-limited marine habitats than in phosphorus limited freshwater habitats.

With this in mind, Litchman et al. then asked,

> Do characteristics of some mixed layers confer advantages to cells with higher storage capacities, and if so are those characteristics more prevalent in marine than freshwater habitats?

The intuition behind Litchman *et al.*'s study was that episodic mixing could create conditions in which small cells had exhausted their stored nutrients, but large cells still retained enough nutrient storage to maintain growth. If so, growth of large diatoms in the intervals between mixing events, when small diatoms cannot grow, could explain the persistence of large cells despite the uptake and growth rateadvantages of small cells.

Litchman *et al.* constructed a model to investigate under which conditions this might happen, and whether those conditions occur more frequently in marine than freshwater habitats. Their modeling approach was based on an idea from evolutionary game theory called an Evolutionarily Stable State, and on their analysis of diatom allometry.

[16] This is likely dependent on the condition of the diatom: healthy cells may be able to regulate their densities to prevent sinking, while starved cells may not.

7.19.3 Evolutionarily Stable States: Predicting the outcomes of natural selection

An Evolutionarily Stable State, commonly abbreviated as an **ESS**, is description of the outcome of competition among a set of variants with different traits. ESS's are related to the idea of competitive exclusion, the hypothesis that if two species compete for the same limiting resource, one will be a better competitor and the other will die off[17]. An ESS describes the scenario in which, if one variant (or combination of variants) is initially dominant, no other variants introduced in small numbers can grow. That is, once established, an initial ESS population of variants can exclude "invasion" by a small number of individuals from any other variant.

For example, suppose a set of diatoms varying in size are competing for a limiting nutrient, and that smaller diatoms have a faster growth rate at low nutrient concentrations than larger diatoms. If the initial variant is a middle-sized diatom, it will draw the nutrients to the lowest concentration that allows it to grow. If a few larger cells are then introduced, those cells cannot grow because their nutrient uptake is even worse at the nutrient level set by the established middle-sized cells. However, if a few small cells are introduced, those cells can grow at the nutrient level established by the middle-sized cells. As they grow, the small cells drive the nutrient levels even lower, until the middle-sized cells cannot grow and eventually die off. In this case, a population of middle-sized cells is not an ESS, because a population of middle-sized cells can be invaded by smaller cells.

In contrast, if the initial variant population is small, then the initial nutrient level is so low that neither middle-size nor large cells can invade. In this case, the initial population of small cells is an ESS.

ESS populations are usually, but not always, the same as the outcome of competition among a small, mixed population of variants. Differences can arise due to the key assumption that *the initially dominant population creates the conditions into which other variants must invade.*

Because of this, different outcomes are possible. For example, scenarios are possible in which two or more variants together form an ESS, excluding all other variants. Scenarios are also possible in which multiple ESS's exist, for example variant A when established can exclude all other variants (including variant B), but variant B when established can also exclude all other variants (including variant A).

[17]Note that "better" in this context is defined as the successful competitor. For example, it could be that species A has faster uptake of high-concentration nutrients but species B has faster uptake of low-concentratin nutrients. If the nutrient is limiting, it will be driven down to low concentrations, so species B is "better" in competitive terms, even though under other circumstances species B might have higher growth. For example, under predation, both populations might be reduced so that nutrients are not limiting, and species B might predominate.

7.19.4 Allometry and size-selection in diatoms

To gain a quantitative perspective on the effects of mixed layer dynamics on diatoms, Litchman *et al.* (2009) assumed that many diatom characteristics have allometries of the form of power laws,

$$log_{10}X = log_{10}\ a + (b \times s) \tag{7.26}$$

where X is the trait of interest, and a and b are allometric constants for that trait. The metric of size is

$$s = \log_{10}(\text{cell volume}), \tag{7.27}$$

where cell volume is in μm^3.

Taking the power of 10 of both sides gives the value of the trait for each s,

$$X = a \times 10^{b \times s} \tag{7.28}$$

Litchman et al. analyzed data from the literature to obtain values of the allometric constants a and b for traits involved in growth, mortality and uptake and storage of nitrogen and phosphorus. They separately analyzed diatoms from marine and freshwater environments. Their results are summarized in their **?**.

Model formulation

Litchman *et al.* formulated a model that tracks the increase and decrease of diatom populations in a mixed layer. At intervals, a mixing event such as a storm occurs. A mixing event replaces a fraction of the water in the mixed layer with an equal amount of water from below the mixed layer. The diatoms in the displaced mixed layer water are lost, decreasing the cell populations in the mixed layer. However, the deep water entering the mixed layer brings new nutrient, which can fuel enhanced diatom growth.

Between mixing events, diatoms grow while competing for the diminishing amount of nutrient. If nutrient concentrations get too low, some or all of the diatoms may be unable to grow, and these populations decrease due to mortality. Causes of mortality include "background" mortality, which may be due to predators, pathogens, UV damage or other causes, and losses due to sinking out of the mixed layer.

Litchman *et al.*'s model computed the population trajectories of a series of diatom variants, ranging from small to large cells. For each diatom population, the model acounts for both the **number of cells** and the **nutrient quota**. The quota is the amount of nutrient cells have in storage, compared to their minimum requirement to sustain growth, and to their maximum storage capacity. Cells with a large quota can grow at or near their maximum rates, because they are not limited by nutrients. Cells with a small quota grow slowly or not at all, and may be physiologically stressed, because they are severely nutrient-limited.

A key feature of this model is that growth is determined by stored nutrients, not by the amount of nutrient in the water. Therefore, when a mixing event provides an instantaneous increase in nutrients, cells must first take up nutrients into storage before they can grow. According to Litchman *et al.*'s analysis (and consistent with many other observations), small cells take up nutrients faster and can grow at lower quotas, so they have a faster growth response to new nutrients provided by mixing events.

Conversely, Litchman *et al.* concluded that larger diatom cells have disproportionately higher nutrient storage capacity compared to smaller diatom cells. This means that scenarios potentially exist in which large diatoms utilize stored nutrients to maintain growth when smaller cells have used up their quotas and stopped growing.

Allometric power laws in diatoms

The allometric constants that Litchman *et al.* reported for nitrogen-limited diatoms are shown in Table 7.1.

Table 7.1: **Allometric constants for nutrient uptake and growth in diatoms.** The constants a and b are substituted into Equation (7.28) to obtain the statistically derived allometry for the corresponding variable.

Variable	a	b	Description
$V_{max.i}^{hi}$	-7.8	0.67	Maximum nutrient uptake rate
K_N	-0.49	0.17	Half-saturation constant for nutrient uptake
Q_{min}	-8.59	0.56	Minimum quota for growth
Q_{max}	-8.39	0.81	Maximum quota (full storage)
μ_∞	0.74	-0.14	Maximum growth rate (unlimited nutrient)

In Table 7.1, $b < 0$ means that the quantity is decreasing with larger cell size, s. $b > 0$ means that the quantity is increasing with larger cell size.

Some key points about these allometric relationships are:

1. Because b is negative, the maximum growth rate, μ_∞, is slower for larger diatoms than for smaller diatoms
2. The minimum quota to support growth, Q_{min}, is larger for larger cells ($b = 0.56$).
3. The maximum nutrient uptake rate, $V_{max.i}^{hi}$, increases with diatom size ($b = 0.67$) but the amount of nutrient required to attain maximum quota increases even faster ($b = 0.81$).
4. Both the minimum quota, Q_{min}, and the maximum quota, Q_{max}, increase with diatom size. However, Q_{max} grows faster ($b = 0.81$) with cell size than Q_{min} ($b = 0.56$).

Point 1 means that, with abundant nutrients, small cells can out-grow large cells. Point 2 means that small cells can continue growth at low quotas when large cells cannot. Point 3 means that larger cells take longer to fill their quotas than smaller cells. All these points suggest advantages for small diatom cells.

However, Point 4 means that nutrient storage capacity, which is the difference between the minimum and maximum quotas, is larger in larger cells.

Litchman *et al.*'s hypothesis is that the pulsed nature of nutrients in mixed layers – episodic injections of nutrients duriing mixing events such as storms, followed by long intervals of depleted nutrients – amplify the storage advantages of large diatoms and enable them to compete successfully with small diatoms.

The model they devised to test their hypothesis about the effects of storage allometry and mixed layer dynamics is implemented in this notebook. Explanation of the formulation of this model is in this context page.

7.19.5 Size-selection of diatoms in fluctuating environments

This notebook implements (with some modifications) the **diatom population dynamics model** presented in **?**.

This model uses allometric trends in growth rates and storage capacities to calculate the population dynamics of different-sized diatom variants. The variants compete for a nutrient (nitrogen in the form of nitrate) within a mixed layer. Nutrient is depleted in the mixed layer due to uptake by diatoms.

Mixing events (*e.g.* storms) occur periodically, that replace a fraction of the water in the mixed layer with deep water. This has two effects: It transports some of the diatom cells into deep water, where they ultimately die; and, it injects nutrient (contained in deep water) into the mixed layer. Therefore, a mixing event both lowers the diatom population and provides nutrients to enhance its growth.

Litchman *et al.*'s model is a so-called **quota model**. "Quota" refers to cells' storage of nutrients, increasing as cells take up nutrient from the water and decreasing as that nutrient is consumed during growth. The mode tracks the changes over time in:

1. The number of cells of each diatom variant
2. The quota (amount of stored nutrients) in cells of each diatom variant
3. The amount of nutrient in the water

The key question asked by Litchman *et al.* was,

> **Do variations in the frequency and intensity of mixing events, combined with allometries of nutrient storage and use, explain the size distributions of diatoms in different habitats?**

The rationale and key parameters are explained in this discussion of diatom allometry and this discussion of Litchman *et al.*'s data analysis. Explanation of the formulation of this model is in this context page (and in the original paper).

How to use this notebook

To use the model, start by selecting ***Run All Cells*** under the ***Run*** menu at the top left of this page.

The parameters used in simulating diatom population dynamics are presented in three sets of textboxes and execution buttons, which you will use in sequence to:

1. Set up the number and size range of diatom variants, and the characteristics of the mixed layer they inhabit.
2. Seed the mixed layer with one or more of the diatom variants.
3. Set the interval between mixing events and how many days to simulate the population.
4. Run the simulation and look at the output.
5. Optionally, reseed the population with new cells, and restart the simulation to see how the new set of variants interact.

From the initial conditions you specify, the model runs through many mixing intervals and the diatom populations approach a repeated pattern.

Graphical output The model produces two sets of graphical output:

1. Plots of the population (expressed as biovolume) and quota of each variant, and the nutrient concentration, through the last simulated mixing interval.

   These "period" plots are good indicators of how effectively each variant stores nutrients when it is available, and uses that storage to fuel growth.

2. Plots of the averages over each mixing interval of the population and quota of each variant, and the nutrient concentration, over the entire simulation.

   The averaged plots are good indicators of the outcomes of competition between variants, because they show positive or negative population trends over long timespans.

Biovolume is the number of cells times the volume of each cell, for each of the size variants. If cell densities are approximately constant, then the biovolume of each variant is approximately proportional to the total biomass of that variant.

These plots are automatically saved at the end of each simulation as images, so you can copy and paste them into a document or presentation to record your results. The png format images are *period.png* and *averagred.png*; the svg format images are *period.svg* and *averaged.svg*.

Tabular output

The model also produces two tables of period-averaged results for the final mixing period:

1. A table of **standing stock**, averaged through the last mixing period.

   This table shows, for each size class:

   - class number (i)
   - size metric (s_i)
   - size (10^{s_i})
   - number cells per liter (N_i)
   - relative quota ($\frac{Q_i}{Q_{i,min}}$)
   - biovolume ($BV_i = N_i \times 10^{s_i}$
   - nutrient concentration, R

   Note that R reflects the entire mixed layer, and does not vary by diatom size – it is included in each row only to make a complete table for import into a spreadsheet.

2. A table of **diatom population losses** (in units of biovolume per day), averaged through the last mixing period.

   This table shows, for each size class:

   - class number (i)
   - size metric (s_i)
   - size (10^{s_i})
   - losses due "background" mortality, M
   - losses due to sinking out of the mixed layer, S
   - losses transport to deep water by mixing events (L)

Setting up diatom variants and mixed layer characteristics

This part of the notebook lets you set up the "scenario" of diatom variants and mixed layer characteristics.

The parameters are:

- N_{sizes}, the number of diatom variants
- S_{min} and S_{max}, the minumum and maximum sizes of the variants (variants will be distributed across this range)

- m, the mortality rate due to predation, pathogens, *etc.*, affecting all variants equally
- z_m, the depth of the mixed layer; a shallower layer means more loss due to sinking, which disproportionately affects larger cells.
- a, the fraction (between 0 and 1) of the mixed layer that is replaced in each mixing events. Larger a means more cells are lost, but more nutrients are gained.
- R_{deep}, the nutrient concentration in deep water.

It is a good strategy to start with these default values, to see their results, then modify one of more to see the effects of those changes.

When you have the parameters you want, click the **Set up population** button below to set up the mixed layer.

Seeding the mixed layer with diatom variants

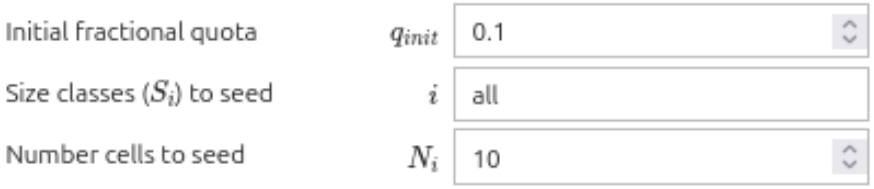
This part of the notebook lets you "seed" diatoms by adding cells into the scenario, as a starting point for simulating population dynamics. When you set up the mixed layer, the populations of all variants were set to zero. Using these textboxes, you can introduce a starting population of diatoms, either all variants simultaneously or only variants you specify.

The parameters are:

- q_{init}, the initial quota in new diatom cells at the start of the simulation
- S_i, the size classes of the variants with which to seed the mixed layer.
  - If this entry is "all", then all variants will be seeded
  - If this entry is one or more numbers, *e.g.* "1" or "2,6" then only those size classes will be seeded
- N_i, the number of cells to seed into each selected size class.

It is a good strategy to start with these default values, to see their results, then modify one of more to see the effects of those changes.

When you have the parameters you want, click the **Seed cell population** button below to set up the scenario.



Setting mixing event intervals, and running the simulation

This part of the notebook lets you specify the interval between mixing events, to see what the effects different intervals have on competition between diatom variants.

Important: These parameters run the simulation using the existing diatom populations. If you want to start with a "blank slate", go back and click the **Set up population** and **Seed cell population** buttons.

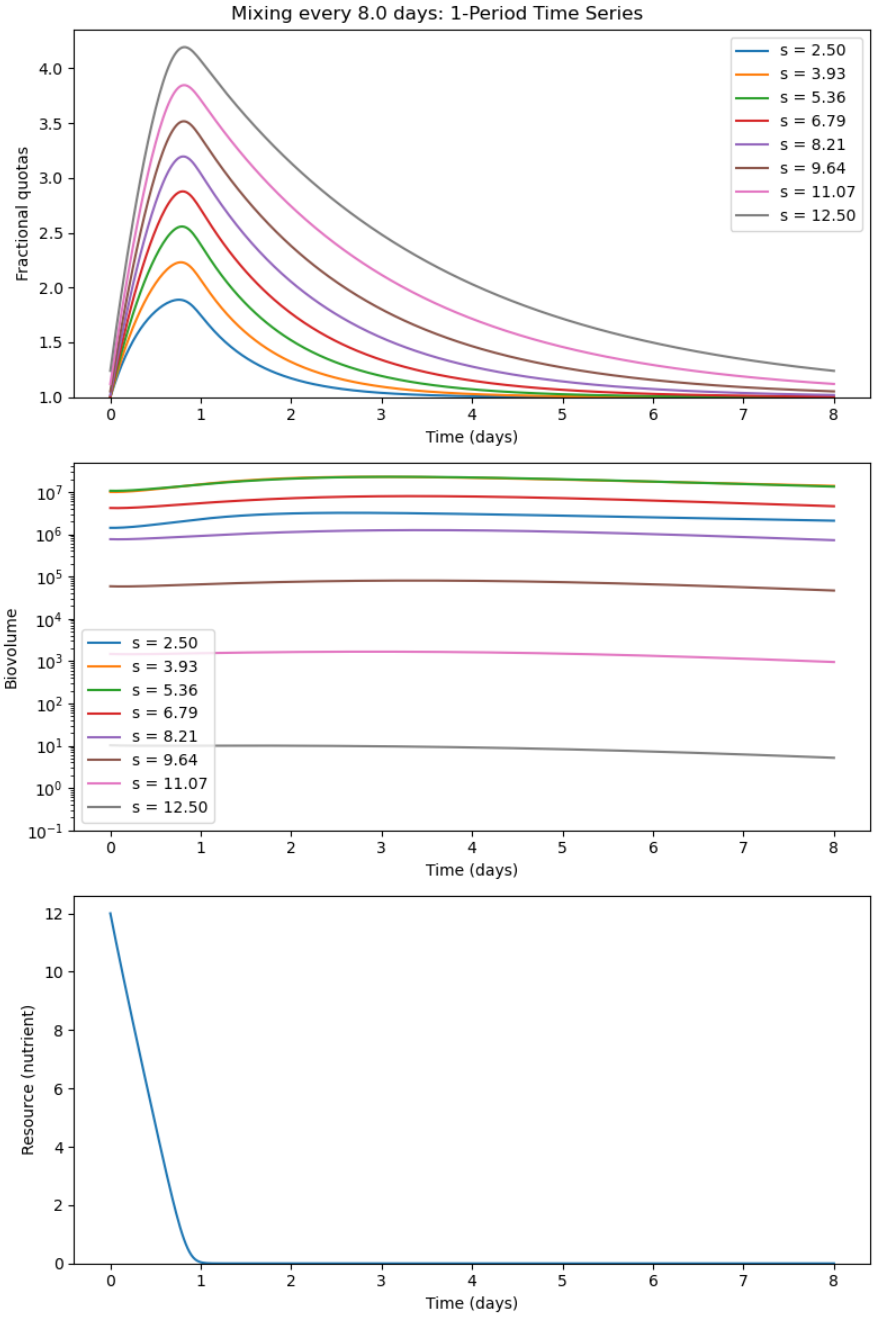
The parameters are:

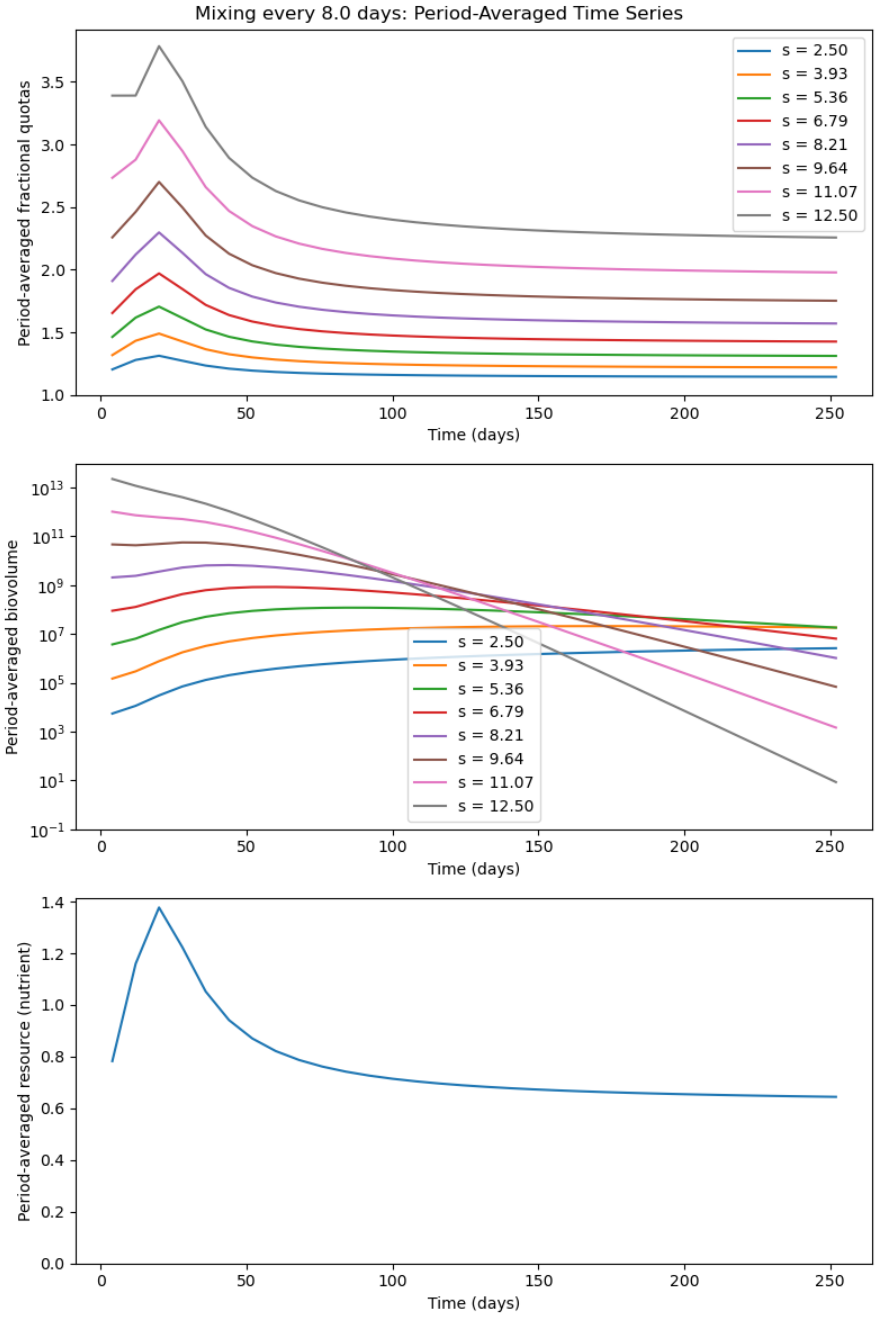
- t_{mix}, the number of days between mixing events
- n_{pers}, the number of mixing periods to simulate
- n_{record}, the number of data points to record during each period. If the period plots look unsmooth, try increasing this parameter.

It is a good strategy to start with these default values, to see their results, then modify one of more to see the effects of those changes.

When you have the parameters you want, click the **Run simulation** button below to simulate the population and plot the results.

```
Running simulation...

***Period-averaged statistics: standing stocks (also in standingstocks.txt)***

  i      s        10^s          N    Q/Qmin        BV      R
---  -----  ----------  ---------  --------  --------  -----
  0   2.5   316          8.23e+03      1.15  2.6e+06   0.644
  1   3.93    8.48e+03   2.14e+03      1.22  1.81e+07  0.644
  2   5.36    2.28e+05  79.7           1.31  1.81e+07  0.644
  3   6.79    6.11e+06   1.05          1.43  6.41e+06  0.644
  4   8.21    1.64e+08   0.0063        1.57  1.03e+06  0.644
  5   9.64    4.39e+09   1.56e-05      1.75  6.83e+04  0.644
  6  11.1     1.18e+11   1.24e-08      1.98  1.46e+03  0.644
  7  12.5     3.16e+12   2.7e-12       2.26  8.53      0.644


***Period-averaged statistics: biovolume losses per day to mortality (M), sinking (S) and mixing
(L) (also in losses.txt)***

  i      s        10^s           M           S          L
---  -----  ----------  ----------  ----------  ---------
  0   2.5   316           2.08e+05    3.18e+04   7.82e+04
  1   3.93    8.48e+03    1.45e+06    6.67e+05   5.21e+05
  2   5.36    2.28e+05    1.45e+06    1.11e+06   5.01e+05
  3   6.79    6.11e+06    5.13e+05    5.51e+05   1.72e+05
  4   8.21    1.64e+08    8.26e+04    1.14e+05   2.71e+04
  5   9.64    4.39e+09    5.47e+03    9.23e+03   1.75e+03
  6  11.1     1.18e+11  117         233         35.7
  7  12.5     3.16e+12    0.682       1.57       0.194

Plotting...
...done.
```


Mixing every 8.0 days: 1-Period Time Series
Fractional quotas
Time (days)
s = 2.50
s = 3.93
s = 5.36
s = 6.79
s = 8.21
s = 9.64
s = 11.07
s = 12.50
Biovolume
Time (days)
Resource (nutrient)
Time (days)


Mixing every 8.0 days: Period-Averaged Time Series
Period-averaged fractional quotas
Time (days)
s = 2.50
s = 3.93
s = 5.36
s = 6.79
s = 8.21
s = 9.64
s = 11.07
s = 12.50
Period-averaged biovolume
Time (days)
Period-averaged resource (nutrient)
Time (days)

7.19.6 Size-dependence of diatom biomass in mixed layers

The point of this activity is to assess the average standing stock of diatoms, across different variants (or combinations of variants), mixing fractions and mixing intervals.

If we assume that the constant mortality rate m represents grazing or pathogens, then m times the standing stock represents the strength of that trophic interaction.

Run is long enough when top line is flat and others are decreasing, and results look the same when simulation is restarted.

This activity explores how cell size affects populations of diatoms in mixed layers. **?** (2009) analyzed the size distributions of diatoms in multiple marine and freshwater habitats. They concluded that, within a wide range of diversity in all habitats, diatom size distributions were larger in marine than in freshwater habitats.

In looking for explanations for this difference, noted that smaller diatoms have some advantages over larger diatoms in growth and nutrient uptake rates. Conversely, larger diatoms have some advantages in nutrient storage over smaller diatoms. Litchman et al.* hypothesized that the different characteristics of mixed layers in marine *cs.* freshwater habitats accentuate the relative advantages of large and small diatoms, causing the differences in size distributions.

To understand the implications of the model Litchman *et al.* devised to explore this hypothesis, this activity leads you through

For comparability, we will use a standard set of diatom sizes for the basic model experiments (feel free to explore additional sizes if you want to): [s=[2.5, 3.55, 5.0, 6.25, 7.5, 8.75, 10.0, 11.25]] and on four mixing intervals, [T=[3,14,35,40]] For these parameter combinations:

Biomass of single variants

Make sure only one variant is present (i.e., with Number of Phytoplankton Size Classes set to 1 at the top of the worksheet). Use different values of s and T to determine:

- \textbf{what are the consequences for total biomass if diatom cells are of small or large sizes?}
- \textbf{What are the consequences of long vs. short mixing intervals for biovolumes of different-sized diatoms?}

In your answers, use the information in the time series of quotas and nutrients to help interpret the patterns you observe in biovolume. \textit{Note that different dynamics are best visualized using different Plotting Intervals. For example, Plotting Interval [0,8] might best show initial transients well, [0,100] might best show longer transients, and [98,100] might best show details of long-term population cycles.}

7.19.7 Evolutionarily Stable States for diatoms in mixed layers

For comparability, we will use a standard set of diatom sizes for the basic model experiments (feel free to explore additional sizes if you want to): [s=[2.5, 3.55, 5.0, 6.25, 7.5, 8.75, 10.0, 11.25]] and on four mixing intervals, [T=[3,14,35,40]] For these parameter combinations:

For 3 different mixing intervals, run simulation to find most successful. That is the candidate ESS variant.

Restart with only that variant, then seed with all and restart the simulation to see if any other variants can invade.

\textbf{Evolutionary stable strategies:} A key idea in evolutionary analysis is the Evolutionary Stable Strategy (a.k.a. Evolutionar\underline{ily} Stable Strategy), or \textit{ESS}. An \textit{ESS} among a range of variants (in this case, diatoms of different sizes), is a variant that once established cannot be invaded by any other variant. For example, suppose a population of variant s_1 is established in the mixed layer. Variant s_1 is an \textit{ESS} if an initially small population of any other size variant s_2 would decrease (due to competition from s_1 diatoms). If at least one variant s_2 can increase from an initially small population, then s_1 is not an \textit{ESS}.

There may or may not be an \textit{ESS} in any particular trait-based model. In some cases, no single variant is an \textit{ESS} but a combination of two variants might jointly form an \textit{ESS}. That is, s_1 and s_2 form a joint \textit{ESS} if established coexisting populations of s_1 and s_2 variants can exclude any distinct s_3 variant (more preciesely, if an initially small population of s_3 variants decreases over time).

To investigate competition, coexistence and \textit{ESS}'s across a range of diatom sizes, we will look at dynamics when multiple variants are present simultaneously. \textbf{Set the Number of Phytoplankton Size Classes at the top of the worksheet to 8 (remember to re-execute the evaluation group!).} The worksheet will create a default range of variants in s. Examine the outcome of 8-way competition for each of the focal mixing intervals T. What sized diatoms appear to be the best competitors under different mixing intervals? Is there an indication of ESS diatom sizes under the assumed fluctuating resources and allometric uptake and storage relationships? Are variants that maximize biomass the same as variants that form \textit{ESS}'s (and if not, which would you expect to see in the plankton)?

7.19.8 Implications of allometry for diatom aquaculture and carbon sequestration

For diatoms competing for nutrients in mixed layers,

Aquaculture

The point of this activity is to assess biomass extraction in an aquaculture setting, analogous to a mixing event.

The metric is biovolume removed in a mixing event, plus biovolume lost by sinking

Need to move *a* textbox to simulation parameters

Need a way to record mixing event losses and sinking losses (or to turn off mixing losses)

Actually mixing losses are proportional to average standing stock, with constant of proportionality $\frac{v_i}{z_m}$. So we have that.

Motivating questions:

- What variants, mixing fraction and mixing intervals maximize biovolume extraction?

Will this always be the smallest cells, most frequent extractions, and whatever interval maximizes extraction? Is there allometry in the payoff per biovolume (and can it be easily implemented)?

The tasks:

Maximize mixing and sinking losses across variation in size, mixing fraction and mixing interval

3 sizes (individually and together –>4 scenarios) x 3 intervals x 3 fractions

\textbf{ Aquaculture:} If you were to use diatoms in a biofuels or aquaculture setting\footnote{In reality, other phytoplankton types would probably be preferable, but the design criteria and rationale might be very similar across taxa.}, you might design a chemostat or closed pond system that functions much like the mixed layer in Litchman et al.'s model: periodically you might extract water containing phytoplankton and replace it with nutrient-enriched water. Based on your answer above, \textbf{which combinations of diatom size and mixing interval would you choose to make maximize productivity?}

Carbon export from the mixed layer

This is related to carbon export to deep water through mixing events and sinking

For comparability, we will use a standard set of diatom sizes for the basic model experiments (feel free to explore additional sizes if you want to): [s=[2.5, 3.55, 5.0, 6.25, 7.5, 8.75, 10.0, 11.25]] and on four mixing intervals, [T=[3,14,35,40]] For these parameter combinations:

7.19.9 A "quota" model of diatom demography

Litchman *et al.*'s model of competing diatom variants uses the idea of nutrient "quotas" to understand the allometric differences between large and small diatoms in traits such as growth and nutrient consumption[18]. In this context, "growth" refers to cell division – that is, *growth of the cell population* rather than increase in a given cell's size. In their model, quotas represent nutrient storage within cells. When cell take up nutrients, they are placed directly into storage, increasing the cell's quota. When the cell grows or divides, it consumes nutrients from its storage, decreasing its quota.

Storage of nutrients has a consequence that is central to Litchman *et al.*'s hypothesis about the larger diatoms present in marine compared to freshwater habitats:

> Cell growth is determined not by the current nutrient concentration in the water, but by the nutrient quota that reflects past nutrient concentrations.

They hypothesized that differences in quotas, quantified by the observed allometries in nutrient storage capacity and uptake rates, interact with the fluctuating conditions within mixed layers to favor larger diatoms in marine habitats and smaller diatoms in freshwater habitats. Specifically, they hypothesized that, large diatoms with disproportionately large storage can continue growing under some conditions, when small diatoms have exhausted their quotas and ceased to grow.

Model rationale

The rationale for Litchman *et al.*'s model is based on accounting for nutrient concentration in the mixed layer, the numbers of cells of different diatom variants, and those cells' nutrient quotas. These variants differ in size, and because of allometry also in nutrient storage and uptake rates, growth rates, sinking velocity and many other traits.

The rate at which the number of cells of a given diatom variant changes between mixing events can be summarized as:

$$\text{change in cell number} = \text{growth} - \text{mortality} - \text{loss from sinking} \tag{7.29}$$

Stored nutrients, accounted for in the diatom cells' quotas, are increased by uptake and decrease when nutrients are withdrawn to fuel growth:

$$\text{change in quota} = \text{nutrient uptake rate} - \text{consumption for growth} \tag{7.30}$$

Finally, the nutrient concentration within the mixed layer is reduced, between mixing events, when nutrients are taken up by diatoms:

$$\text{change in nutrient concentration} = -\text{consumption by cells} \tag{7.31}$$

In the model, mixing events are assumed to happen instantaneously. That is, the model assumes there is an interval of diatom population dynamics as described in Equations (7.29), (7.30) and (7.31). Then a mixing event happens, during which no growth, mortality or nutrient uptake occurs. Then there is another interval of diatom population dynamics as described in Equations (7.29), (7.30) and (7.31), and another mixing event, and so on in a repeating cycle.

At mixing events, water is exchanged between the mixed layer and deep water. Mixed layer water contains diatoms, which are lost when water containing them is moved out of the mixed layer. Deep water contains high nutrient concentration, which is added to the mixed layer when deep water moves into the mixed layer.

[18] Litchman *et al.* modeled both nitrogen (nitrate) limitation and phosphorus limitation, but here we focus only on nitrogen.

Quantifying rates

The development of Litchman *et al.*'s model is the process of devising mathematical expressions for each of the terms in Equations (7.29), (7.30) and (7.31). The key logical steps in obtaining these terms are:

- The metric of size is $s = \log_{10}(\text{Cell Volume})$ where Cell Volume is in μm^3.
- A cell's quota, Q_i, increases due to nutrient uptake and decreases when nutrient is used for growth.
- The rate at which nutrient uptake depends on nutrient concentration, R, is a Michaelis-Menton function,

$$\text{nutrient uptake rate} = C_1 \frac{R}{R + K_i} \tag{7.32}$$

- In Equation (7.32), the coefficient of proportionality C_1 for a cell of size s_i is a linear function of the quota, Q_i, expressed relative to the cell's minimum quota, $Q_{min,i}$ and maximum quota, $Q_{max,i}$:

$$C_1 = C_2 - C_3 \frac{Q_i - Q_{min,i}}{Q_{max,i} - Q_{min,i}} \tag{7.33}$$

- In Equation (7.33), the coefficients C_2 and C_3 are constants,

$$C_2 = V^{hi}_{max.i} C_3 = \left(V^{hi}_{max.i} - V^{lo}_{max.i}\right) \tag{7.34}$$

- In Equation (7.34), C_2 is the maximum rate of nutrient uptake, which occurs when the quota is low. C_3 is the rate at which nutrient uptake decreases at higher quotas. Because $C_2 = C_3$ when the cell quota is $Q_i = Q_{max,i}$, the cell's nutrient uptake rate approaches zero as its quota approach its maximimum capacity, $Q_{max,i}$.
- Decrease in a cell's quota due to growth is determined by its maximum growth rate, μ_i, and its quota Q_i relative to its minimum quota, $Q_{min,i}$:

$$\text{consumption for growth} = \mu_i \left(1 - \frac{Q_{min,i}}{Q_i}\right) \tag{7.35}$$

- Mixing events replace a fraction a of mixed layer water with deep water. That implies that, after the mixing events, the diatom population of each variant i is decreased, while the nutrient level R is increased:

$$N_{i,\text{after mixing}} = (1-a)\ N_{i,\text{before mixing}} R_{\text{after mixing}} = (1-a) R_{\text{before mixing}} + a\ R_{\text{deep}} \tag{7.36}$$

These expressions are substituted into Equations (7.29), (7.30) and (7.31) to formulate a mathematical model that can be simulated on a computer.

Model formulation

The model that results is in the form of a ordinary differential equations, or *ODEs*, which means that it tracks diatom populations, cell quotas and nutrient concentration as they vary continuously over time between mixing events. The familiar Lotka-Volterra and logistic population models are also ODE models.

After substituting each of the mathematical expressions in (7.32)-(7.35), the quantitative expression of Equations (7.29), (7.30) and (7.31) for diatom populatin dynamics between mixing events is:

$$\frac{dQ_i}{dt} = \left(V^{hi}_{max.i} - \left(V^{hi}_{max.i} - V^{lo}_{max.i}\right) \frac{Q_i - Q_{min,i}}{Q_{max,i} - Q_{min,i}}\right) \frac{R}{R + K_i} - \mu_i \left(1 - \frac{Q_{min,i}}{Q_i}\right) \tag{7.37}$$

$$\frac{dN_i}{dt} = \mu_i \left(1 - \frac{Q_{min,i}}{Q_i}\right) N_i - m N_i - \frac{v_i}{z_m} N_i \tag{7.38}$$

$$\frac{dR}{dt} = -\sum_i \left(V^{hi}_{max.i} - \left(V^{hi}_{max.i} - V^{lo}_{max.i}\right) \frac{Q_i - Q_{min,i}}{Q_{max,i} - Q_{min,i}}\right) \frac{R}{R + K_i} N_i \tag{7.39}$$

Equation (7.36) quantifies the effects of a mixing event.

Part IV

Spatial Dynamics

Part V

Experimental Methods

Part VI

Appendix

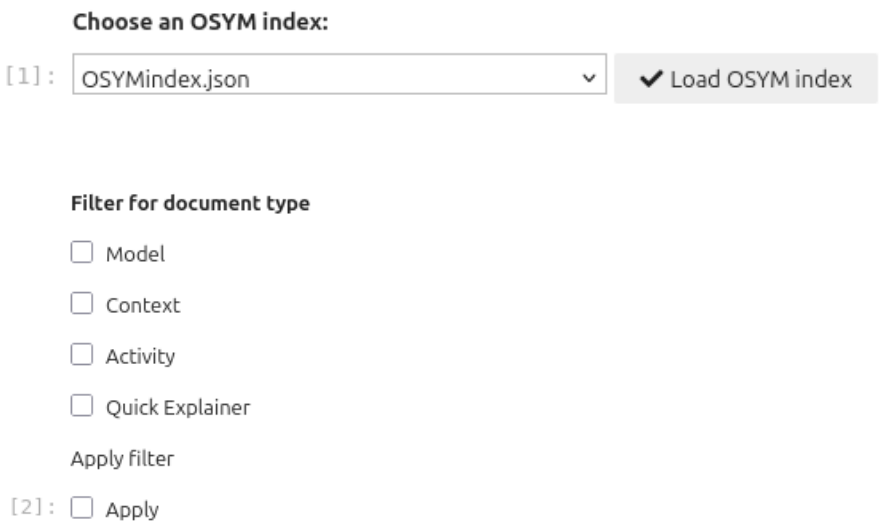
Chapter 8

Searching the OSYM library for Models, Context, Activities and Quick Explainers

This is a utility to facilitate finding resources within the OSYM library. To use the utility, open this notebook within a Jupyter Lab environment. Clicking on this binder button is an easy way to do this:

When the page has loaded, pull down the **Run** menu and select **Run All Cells**. Then, scroll down until you find a set of criteria describing the entries you would like to see. For example, if you want to see all the entries within the topic areas "Biomechanics" and "Demography":

- Scroll down to the set of checkboxes labeled **Filter for Topics**
- Select the boxes labeled "Biomechanics" and "Demography"
- Select the box labeled "Apply filter"
- Scroll down and click the button under the heading **Display selected entries** You can apply as many or as few filters as you want. Un-selecting the "Apply filter" button means that set of criteria will not be used, so you don't have to uncheck the specific entries.



Filter for Topics

- [ ] Overview
- [ ] Biomechanics
- [ ] Demography
- [ ] Spatial Dynamics
- [ ] Experimental Methods

Apply filter

[3]: [ ] Apply

Filter for Organizational Level Transition

- [ ] Sub-Cell
- [ ] Cell
- [ ] Morphology
- [ ] Physiology
- [ ] Organism
- [ ] Habitat Choice/Utilization
- [ ] Community Interactions
- [ ] Ecosystems

Apply filter

[4]: [ ] Apply

Filter for Key Mechanisms

- [ ] Developmental
- [ ] Demographic
- [ ] Biomechanical
- [ ] Genetic
- [ ] Spatial
- [ ] Behavioral

Apply filter

[5]: [ ] Apply

Display selected entries

[7]: ✔ Show filter results