6

"... breaking of the mere. To a stranger these terms are somewhat misleading as they appear to suggest a violent agitation of the water, or its bursting through its banks, whereas the phenomenon resembles the breaking of wort in the process of brewing, causing a discolouration of the water rendering it unfit for consumption, and spoiling the fisherman's sport. In its normal condition the water is pure and limpid . . . but when it breaks it becomes turbid from the formation of small dark-green bodies in countless thousands, which not only float as a scum on the surface but abound throughout the whole of the water . . ."
[a population explosion of cyanobacteria].

William Phillips, *The Breaking of the Shropshire Meres,* 1884.

Population Dynamics in Limnology: Population Size Changing with Time

CHANGE IN LIMNOLOGY

As soon as we meet the players in the freshwater ecological theater, we notice that they are not only moving about, but their numbers are changing constantly. Lakes and streams are inhabited by different kinds of organisms at different times of the year. Dramatic changes occur in the abundance of organisms. For example, in a eutrophic lake, cyanobacteria (such as *Aphanizomenon*) can be undetectable in the winter but are present as a 1-cm-deep scum during the late summer. *Daphnia* may seem to totally disappear during the winter or in late spring but are the most abundant crustacean during mid-spring. This chapter explains various ways to describe populations and gives examples from aquatic habitats. However, description is just the beginning. A major reason for studying populations is to be able to predict changes before they happen.

DEFINITION OF POPULATION DYNAMICS

A **population** is a group of individuals of the same species, living in the same place. For example, the *Daphnia pulicaria* in Lake Mendota, Wisconsin form a population, as do the *Anax junius* (large blue and green dragonflies, similar to those shown in figure 4.18d and 4.19f) whose nymphs live in the ponds, streams, and lake littoral zones of the Yahara River (Dane County, Wisconsin) watershed. Populations have the potential to share the same gene pool.

Population **size** is measured as the number of individuals in a defined area (such as a lake or riffle), as a **density** of individuals per unit area or volume, or as **biomass.** Density means the number of individuals per unit area (as in the number of macrophytes per square meter) or per unit volume (as in the number of copepods per liter), and biomass is the dry or wet weight of the organisms of interest per unit area or volume.

Numerical density is often expressed as the average density, based on a number of samples of an environment. However, Carol Folt (1993; Folt and Burns, 1999) pointed out the importance of perceived density, which can be very different from average density. If individuals

are clumped, living in dense clouds or patches, then each individual will perceive a much higher density than predicted by the overall average density. The difference between average density and perceived density can be important for models of population dynamics and interactions among populations (as in predator-prey systems).

Populations change size and structure through time—they are **dynamic.** Many aquatic organisms show marked patterns of seasonal changes. Populations can increase, decrease, or even become locally extinct (extirpation). Predation and competition are two major biological interactions that affect population dynamics. An understanding of population dynamics contributes to our understanding of communities in lakes and streams.

Distribution of a Population

There are two important scales related to the population concept. At the smaller scale, the distribution of an aquatic population is defined by the shores of the lake or stream. For example, the distribution of smallmouth bass nests in Pallette Lake (Vilas County, Wisconsin) (figure 6.1) gives an indication of the size and shape of the population. The number of nests is proportional to the total population size, and the population appears to occupy the whole lake.

Aquatic organisms do not typically occupy an entire lake or stream. (Vertical patterns were discussed in chapter 2.) In the horizontal plane, organisms are often limited to littoral or pelagic, pool or riffle, or other subdivisions of the aquatic habitat. Organisms have specific environmental requirements that produce patchy distributions. For example, aquatic macrophytes are not distributed evenly throughout the lake, but in patches defined by water depth, light conditions, temperature, and wave action factors. Different species of aquatic plants living in the large, shallow Austrian lake Neusiedlersee produce a pattern of patches when seen on a map.

The pattern of distribution of the population within a water body depends on the ecological preferences and life-history stages of the organisms. For example, in the case of zebra mussels (dreissenids) living in Lake Erie, the simplest description of the population distribution is that it occurs in the lake. However, a closer look reveals that, in one sense, the population is restricted to individuals living within 1 meter or so of other zebra mussels. Zebra mussel sperm can probably swim only about 1 meter and still have enough energy to penetrate an egg (David Culver, personal communication). Once the fertilized eggs develop into larvae, however, they can drift great distances throughout the lake, during the 2 weeks
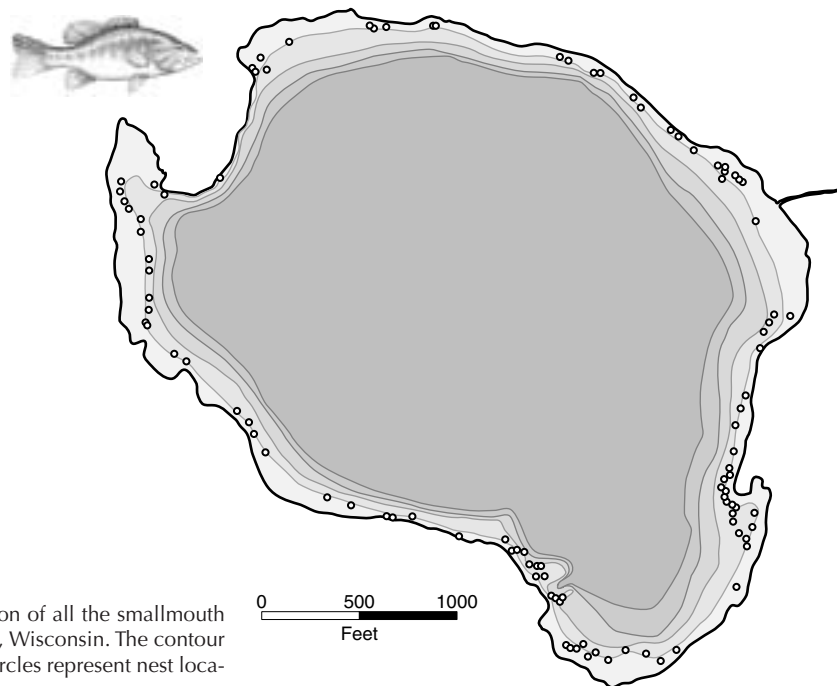

FIGURE 6.1   A map of the location of all the smallmouth bass nests in Pallette Lake, Vilas County, Wisconsin. The contour lines are at 5-foot intervals. The open circles represent nest locations. **Source:** Map data from Jeff Baylis.

or so that they are in the plankton. The larvae then settle and can contribute their specific genotypes to the group of mussels within 1 meter or so of settling.

At a larger scale, the *boundary* of a population might be defined as the collection of all the aquatic sites occupied by individuals of the species. The individual lakes could be considered **metapopulations** that make up the total population. A metapopulation is a *population of populations,* an assemblage of discrete local populations that have their own dynamics, and with migration among the discrete populations (Hanski & Gilpin, 1997). The metapopulation concept makes the most sense for adjacent sites, and is probably less valuable for widely separated sites such as populations of zebra mussels in the Caspian Sea and in North America. A metapopulation can be thought of as the result of a landscape pattern of suitable habitat separated by unsuitable habitat. Dispersal agents such as boats or flowing water could allow enough migration from one site to others, so that if a local population goes extinct, the site can be recolonized from nearby sites. This appears to happen in lake districts because lakes surrounded by many other lakes have a longer species list for zooplankton than do isolated lakes (Dodson, 1992). The term *metapopulation* is most often used by population geneticists and evolutionary biologists—in many cases, ecologists still prefer the simpler term *population.*

Estimating Population Size

In population ecology, there is the question of what to count. If we are interested in a trout population (figure 6.2), it is important to specify if a population size represents all developmental stages (eggs, larvae, juveniles, and adults) or just one stage, such as the adults.

Population sizes can be quite enormous. For example, a lake 1 hectare (ha) in area is a small lake. Imagine this lake has an average depth of 1 meter, so it has a volume of 10,000 cubic meters. Common crustacean zooplankton species occur at abundances of about 10 per liter. Thus, the lake might contain 10 million of each of the common species. The more common phytoplankton species might occur at a level of 10,000 per milliliter, or a total of 10 billion individuals per species in the lake. Because of the huge population sizes of microscopic organisms in lakes and streams, populations are often expressed as numbers per unit volume or area; for example, number of *Daphnia* per liter or number of midge larvae per square meter on the bottom. The actual size of the entire population is often ignored.
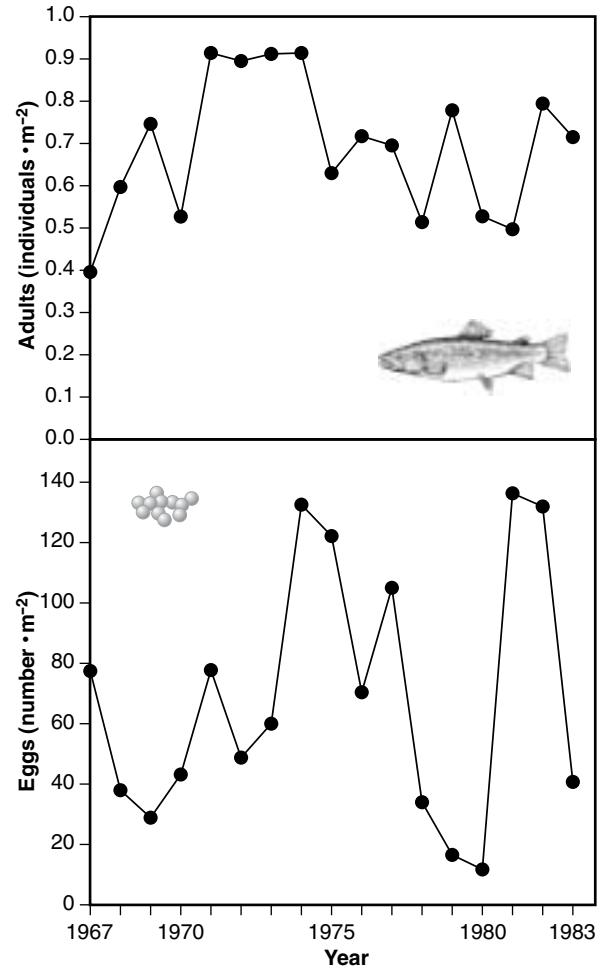

FIGURE 6.2   The density of brown trout eggs and of fish more than 1-year-old, in Black Brows Beck, a tributary of the River Leven in the English Lake District. Note that the scale for the adult trout is much smaller than that for the eggs. **Source:** Data from Elliott, 1984.

Problems may arise with organisms, such as macrophytes, for which the population is not made up of distinct individuals. Macrophytes often have many stems connected by rhizomes lying in the lake or stream sediments. In such cases, it is permissible to use number of stems, or length of stem per square meter, or even weight per square meter, as a surrogate of population size.

Hutchinson (1965) noted that quite large populations of microscopic organisms might be perceived as rare or can even go undetected in a lake. For example, limnologists have difficulty detecting planktonic microorganisms if they are present at a density of less than 1 per cubic meter. This means that, in the previous example, it is quite possible for a population of

10,000 individuals (of, say, *Daphnia*) to exist undetected in a small lake.

There are a number of techniques used to estimate population size, depending on the kind of organism being studied (table 6.1) and the kind of data that is desired. Quantitative samples attempt to give an accurate estimate of the number of organisms per unit area or volume. Qualitative samples are designed to produce a species list. For example, an aquatic dip net can be used for qualitative samples of stream insects, but more sophisticated sampling equipment (such as a grab or sediment corer) is needed to estimated insect densities.

Stability

Stability refers to the tendency of a population to remain at the same size (or density) over time. Calculating the **variance** of population size is one way to estimate temporal stability.

Equation (6.1)

$$\textbf{Variance} = (\text{sum } (x_i - \text{average})^2) / (n - 1)$$

where x_i is the size of the population observed at time i, and n is the total number of observations. The **standard deviation** of the mean is the square root of the variance.

Table 6.1 Examples of the Different Sampling Techniques Used to Study Different Kinds of Organisms

Organism Being Studied	Organism Size Range	Techniques
Bacteria	0.01–1 μm	Collect a few milliliters of water or mud, culture in the laboratory, or analyze for nucleic acid diversity. Count the stained cells under a microscope (smallest cells are invisible). Because most species of bacteria are difficult to culture, this is an imprecise technique, greatly underestimating species diversity.
Phytoplankton	0.1–1000 μm	Collect a few milliliters to a liter or so of water, preserve with gluteraldehyde (health hazard!) or Lugol's solution, allow cells to settle, and count using an inverted microscope.
Protozoa	0.1–1000 μm	Similar to technique for phytoplankton, except protozoa are much more likely to disintegrate upon preservation.
Rotifers	30–3000 μm	Use a fine-mesh plankton net (ca 90 μm) to concentrate animals; preserve with alcohol. Fine mesh is readily clogged with algae, so typically only a few liters are sieved.
Crustacean zooplankton	0.3–5 mm	Use a medium-mesh plankton net (ca. 200 μm to concentrate animals; preserve with alcohol. Typically less than 1 cubic meter is sieved.
Macroinvertebrates	1–20 mm	For a qualitative sample, use a coarse-mesh (ca. 1 mm) dip net to sweep up organisms or to catch them in a water current. For a quantitative sample, sample 1 square meter or so of substrate to a depth of a few centimeters. Take the organisms from the net, put them into a pan of clear water, and individually pick them out of the pan and preserve in alcohol.
Mollusks	1 mm–100 mm	Similar to technique for insect macroinvertebrates, except that more digging may be involved. Wash benthic samples through a 0.5-mesh screen to separate the organisms from the fine sediment.
Fish	5 mm–1000 mm	Use various kinds of large-mesh nets to capture fish that swim into the nets. Fix with formalin (health hazard!), wash, and preserve in alcohol.
Macrophytes	5 mm–2000 mm	Use rakes to gather macrophytes or quadrats (square sampling frames) to sample stems per unit area. Dry representative specimens in a plant press.

The average population size is calculated as:

Equation (6.2)

$$\textbf{Average (or mean)} = \text{sum } x_i / n$$

Note that the mean and standard deviation have the same dimensions (they both have the units of "individuals"). When comparing two populations with different means, it is useful to calculate the **coefficient of variation** (CV), which is the standard deviation divided by the mean, for each population. The CV standardizes variability to a per individual basis. Often, the CV is expressed as a percent, so:

Equation (6.3)

$$CV = (\text{standard deviation}) / (\text{mean})) \times 100\%$$

Populations with low variance have a relatively high stability. For example, consider the population of trout in a stream in the English Lake District (Elliott,

Table 6.2   Densities m^{-2} of Two Developmental Stages of Brown Trout in a Stream in the English Lake District

Statistic	Eggs	Fish Age 1+ (May–June)
Mean	68.7	0.70
Variance	1712.8	0.03
Standard deviation	41.4	0.17
Coefficient of variation	0.60	0.24

Source: Elliott, 1984

1984). This population of brown trout was studied 17 years, from 1967 to 1983. The number of eggs m^{-2} and the number of fishes aged 1 year and older show different levels of temporal stability (table 6.2).

Egg densities were more variable over the 17 years than were the number of adult fish. Notice that the coefficient of variation of the eggs is more than twice as large as that for the adult fish. The key here is that biological processes, such as territoriality and predation, tend to reduce the CV of adult densities, relative to egg densities. Thus, these biological processes are stabilizing.

Stability has a temporal scaling component. For example, copepod populations in Lake Washington (figure 6.3) typically have a high seasonal variance for any single year, with very few copepods present in the winter, a period of exponential population growth in the spring, followed by a population crash in late spring or summer (Edmondson & Litt, 1982). In some years, there is a second peak and crash of the population during the summer or early fall. The within-year variance in copepod abundance is much greater than the variance in the number present at the same time of year, measured over several years, because there is a repeated annual pattern of population growth and crashes.

Populations typically increase and decrease, often with an annual cycle. For organisms like the calanoid copepod Diaptomus ashlandi (Edmondson & Litt, 1982) that have one or more generations per year, the population will typically show short periods of rapid increase and rapid decrease. However, the annual growth rate must average zero if the population is to persist—if the population has long-term stability. Otherwise, populations with a net long-term negative growth rate are headed for extinction, and populations with a net positive growth rate are probably involved in a "population explosion" (or **bloom**) to be followed by a decrease.
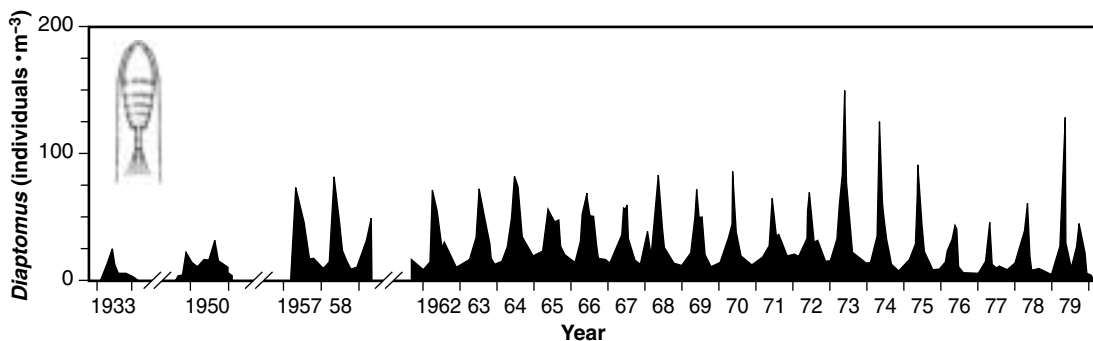

FIGURE 6.3   A graph of number of the calanoid copepod (*Diaptomus ashlandi,* an aquatic population with high variance in numbers over time, with a strong annual component to the variation, Lake Washington. **Source:** Data from Edmondson & Litt, 1982.

Long-lived animals, such as fishes, sometimes appear to have **cycles** in population abundance over several years—cycles are regular oscillations in population size. Cycles in population size are evident in aquatic systems in arctic or temperate climates where extreme annual climate cycles drive biological cycles. Cycles are less obvious or nonexistent in tropical systems with relatively constant climate.

An example of population cycles in a temperate lake is offered by the yellow perch in Crystal Lake, Wisconsin, which exhibited cyclic-like behavior (Sanderson et al., 1999). In this population, a cohort (of one or two **age classes**) dominated the population for about 5 years (figure 6.4). There was a pulse of recruitment about every 5 years, with little or no recruitment in the intervening years. Despite the annual variation in population density, in the long term, the population remained fairly stable, as if it were oscillating around an average value. This stable oscillation is probably the result of predation (cannibalism) of larger perch on perch larvae, so that recruitment is only possible when adult perch are scarce. This is an example of **density-dependent** control of population dynamics.

Models of Population Dynamics

Mathematical models allow prediction of future population sizes (the mathematically inclined may wish to look at papers in Tuljapurkar & Caswell, 1997). The most direct application of population models is to predict future populations sizes, in situations like fish management and aquatic macrophyte control, or in predictions of the spread of invading species. Even when a prediction is not realized, the gap between prediction and observation provides important information about biological processes such as reproduction and mortality. When there is such a gap, limnologists have an opportunity to learn something new about how aquatic communities work.

There are two main models for understanding population dynamics in aquatic organisms: exponential growth and the egg bank.

The **exponential growth model** is used to understand organisms living under near-optimal conditions for fast reproduction and development. Under these conditions, the organisms that leave the most offspring are those that reproduce the most offspring the fastest. Fast and abundant reproduction (leading to fast population growth) can be optimized by asexual reproduction, in which females produce only female offspring.

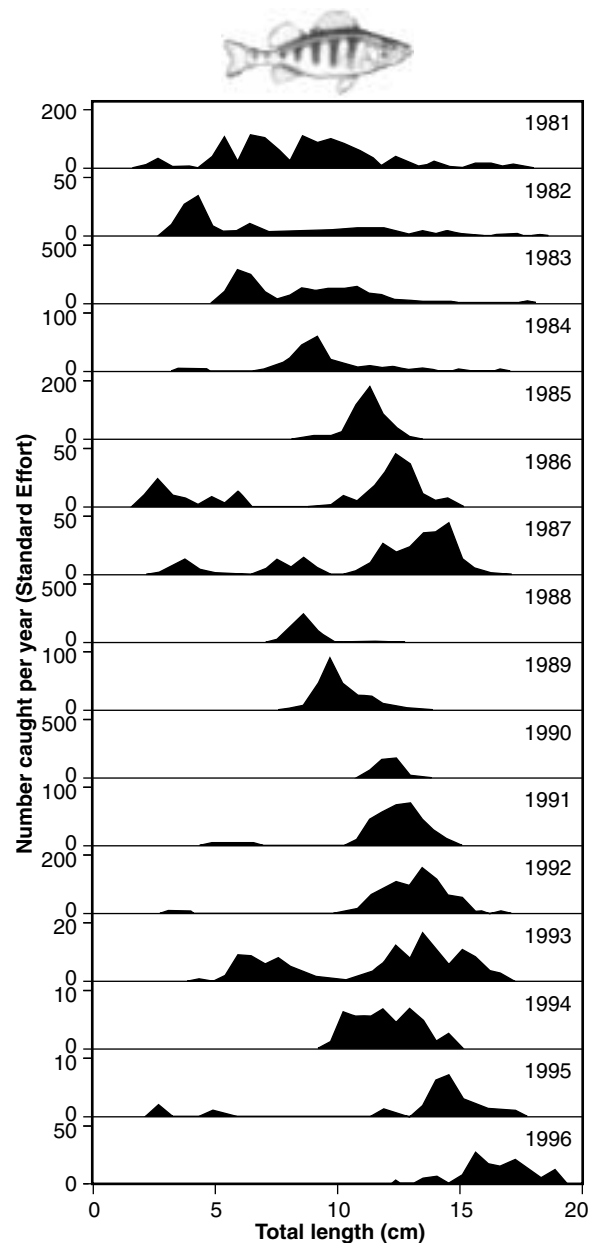The egg (or seed) bank growth model is a conceptual model used to understand population dynam-

FIGURE 6.4 The number of yellow perch in Crystal Lake, Wisconsin showed cyclic population dynamics over a period of 10 years (annual size-frequency distributions). The year is indicated on the right-hand y-axis. The numbers along the left y-axis indicate relative fish abundance for each year. **Source:** data from Sanderson et al., 1999.

ics of organisms with diapause stages—living under environmental conditions for which fast population growth is not often an option. The egg bank model is appropriate for organisms constrained by resources or time (as in growing season), in which the goal is first to produce **propagules** (dispersal stages, such as diapausing resting eggs, spores, or seeds) that can withstand environments that would kill the adults. In some situations (short growing season because of cold climate, or rapid drying-up of ephemeral water), it may be more important to produce resting stages or propagules rather than having the fastest rate of population growth.

Individual-Based Models

Before the advent of accessible computers, about 1990, population models were simple, using only a few variables and using average rates, such as the population growth rate. Now that powerful computers and software are available, models have become more elaborate. Instead of population averages, **individual-based** models use data for large numbers of individuals. The idea with individual-based models is to simulate the lives of a large number of individuals. Each individual can even be assigned a slightly different value for important life-history parameters, such as age-specific **fecundity** (number of offspring produced per female) and **survivorship** (the fraction of the population surviving from one age to the next). This individual variation is used to calculate what are probably more realistic estimates of population parameters such as growth rate and population age structure.

Individual variation is especially important whenever an unusual event occurs. In real populations, the response in population growth rate will probably not depend on the average response, but on the activity of unusual individuals. For example, in fish populations, annual population recruitment depends not on the average fate of individuals (which is death) but on the success or failure of a few individuals that live to reproduce.

THE EXPONENTIAL POPULATION GROWTH MODEL

The exponential population growth rate can be quantified for growth over a short time interval (usually less than a generation) for populations with overlapping generations using the exponential model equation:

Equation (6.4)

$$dN/dt = rN$$

where N is the population size, t is time, and r is the population growth rate coefficient. The term dN/dt is a derivative, implying a rate of change of the population through time. Equation 6.4 says that the rate of change of the population with time is equal to a constant rate (r) times the size of the population. This equation can also be rewritten:

Equation (6.5)

$$(dN/dt)/N = r$$

which says that the rate of change of the population with time, per individual, is constant. The units of r are per unit time, such as per day or per year.

Equation 6.5 can be integrated to give Equation 6:

Equation (6.6)

$$N_T = N_o * e^{rT}$$

In Equation 6.6, N_o is the initial population size and N_T is the size of the population at the end of time interval T. The e is a constant equal to about 2.7183. A graph of Equation 6.6 shows a pattern of exponential growth. The distinctive characteristic of exponential growth is a graph showing an ever-increasing growth rate (figure 6.5). This
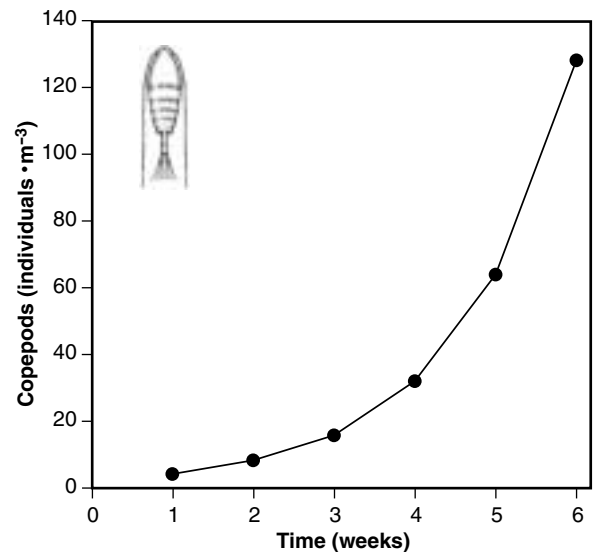

FIGURE 6.5 A model curve for exponential population growth. This simulated population of the calanoid copepod *Diaptomus* is doubling every week. The initial population size is four copepods per m³.

pattern is often seen in aquatic populations over a time interval of days or weeks. For example, the population of *Diaptomus ashlandi* grows exponentially for several weeks each spring (see figure 6.3).

Equation (6.6) has a number of uses for aquatic ecologists. It can be used to estimate the value of the population growth rate coefficient between two sample times. It can also be used to predict the amount of time it will take for a population to double. When the population doubles, N_T is $2 * N_o$, which leads to the equation:

Equation (6.7)

$$T_D = (ln\ 2)/r \text{ or } T_D = 0.69/r$$

where T_D is the time needed for the population to double in size.

Population growth, represented by *r,* is the result of two more basic biological processes:

Recruitment (due to birth or immigration).

Loss (due to mortality and emigration).

In a lake, where migration is minimal, population growth is due to the interaction of birth and death. Each process can be important, and there is often a seasonal component to the relative importance of birth and death.

Understanding population growth means understanding what controls birth and death. The first step is to measure birthrates and death rates. The rates are related to population growth rates:

Equation (6.8)

$$r = (b + d)$$

where *b* is the population birth rate and *d* is the population death rate (a negative number). Both *b* and *d* have the same units as *r.*

Separating the population growth rate into birthrates and death rates allows us to begin to understand what factors control population growth rate and size. For example, the number of eggs produced by a population of smallmouth bass in Nebish Lake (northern Wisconsin; Raffetto et al., 1990) is not correlated with the number of 1-year-old fish found the next spring. Birthrate has no correlation with the number of fish in the lake. What is important is the survivorship of the juveniles in their first year (age-specific survivorship is the fraction of the original cohort—age class—that survives to a specific age). This suggests we need to know more about sources of **mortality,** and that finding out more about egg production could be a lower priority.

Population Data Calculation

W.T. Edmondson (1960) developed an *egg-ratio* technique for estimating rates of population change: *r* (population change), *b* (birth or recruitment), and *d* (mortality) from field samples, plus a little information from the lab. While still an undergraduate student at Michigan State University, Caswell (1972) published an improved mathematical derivation of the technique.

The value of *r* is calculated from field data, which will typically be a sequence of population densities measured at regular time intervals (such as every 2 weeks). The value of *r* can be calculated for each sampling interval. The population is sampled (producing a population size at time zero $= N_0$) and then after some time interval (T) is sampled again (producing a population size at time $T = N_T$). For example, if a population grows from 10 to 12 individuals in 10 days, then the value of *r* (using Equation 6.6) is 0.018 per day.

The value of *r* typically is different for each time interval because the age-specific survivorship and age-specific fecundity patterns are constantly changing in nature. If the population is increasing, *r* is positive. If the population is decreasing, *r* is negative. A static population has an *r* value of zero.

The Edmondson Egg-Ratio equation for estimating *b* requires information from laboratory cultures: the average time it takes an egg to complete its development (at a specific temperature). The developmental time is estimated by separating individual egg-carrying adults into separate jars and recording the time of egg release or hatching. Adults are chosen at random, so at least some of the individuals will have just produced a new batch of eggs. The longest time taken to release offspring (after excluding sick animals) is taken as the developmental time. The value of *b* is calculated from the equation:

Equation (6.9)

$$b = ln\ (1 + E/♀)/D$$

where $E/♀$ is the number of eggs in a sample divided by the total number of individuals in the population (juveniles and adults), and *D* is the average time it takes an egg to complete its development (at a specific temperature). The number of eggs per individual is typically known from lake samples. (Note: If you know *r* and *b,* you can calculate mortality rate *d* as the difference between *b* and *r.*)

This Edmondson Egg Ratio Technique has been applied to rotifers and other members of the plankton, such as *Daphnia,* that hold onto their eggs during development and have overlapping generations. For these species, the

technique provides useful information about the relative importance of food limitation and predation in controlling population size. The "$E/♀$" variable is affected mainly by food supply. The more food, the more offspring are produced. The D variable is affected mainly by temperature. The higher the temperature, the shorter the developmental time and the higher the birth rate.

Don Hall's Surprise

In a ground-breaking study, Don Hall (1964) studied *Daphnia* birthrates and death rates in Base Line Lake, a small lake in central Michigan. His purpose was to use field and laboratory data and a simple (exponential) model to predict the population dynamics of the *Daphnia* population. Base Line Lake has the typical pattern for a mesotrophic, temperate zone lake—algae are scarce during the winter and most dense in the late spring, followed by a dramatic decrease in abundance for the rest of the growing season (figure 6.6). The zooplankton (represented by *Daphnia*) also show a typical pattern of being scarce in the winter and most abundant in the late spring, followed by a dramatic decrease in abundance for the rest of the season (figure 6.6).

Based on previous limnological research, Hall identified two environmental variables—food level and temperature—which were probably important determinants of *Daphnia* population dynamics. He hypothesized that these two factors limited *Daphnia* population growth rate during the summer. He expected to find that the summer *Daphnia* decline was due to low food concentration, which would show up as a decline in reproductive rate, or *b*. During the summer, when the *Daphnia* population is low and not changing (*r* is variable but approximately zero), he expected the birthrates and death rates to be negligible. To test this hypothesis, he compared population predictions based on the laboratory study with actual observations from the lake. Hall's approach was to:

- Measure *Daphnia* and food abundance and temperature over an entire year (1961), sampling approximately twice a month.

- Estimate the population growth rate coefficient, *r,* each time interval, using Equation 6.6 for *Daphnia* abundance data collected during 1961.

- Predict the *Daphnia* birthrate, *b,* in the lake for each time interval, using lake levels of food and temperature and a predictive model developed with laboratory cultures.

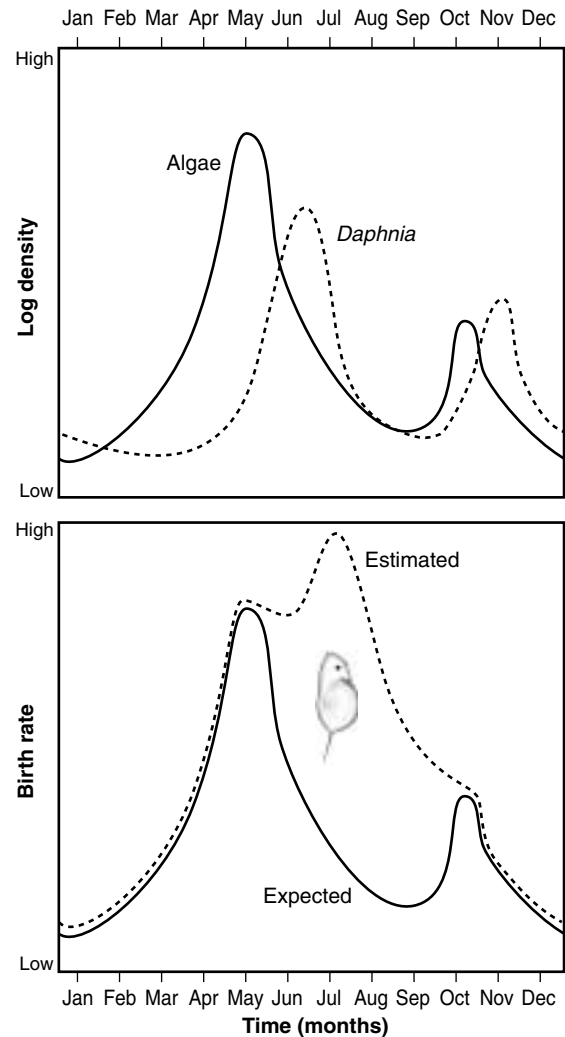- Estimate death rate using Equation 6.8 as the difference between *r* and *b*.

FIGURE 6.6   An idealized interpretation of a *Daphnia* population studied by Hall (1964). The top graph shows the generalized pattern of population dynamics of the algae population and *Daphnia galeata mendotae* in Base Line Lake, Michigan. The lower graph shows the *expected Daphnia* birthrate (the solid line, correlated with algae density in the upper graph) and the actual *observed* rate estimated from the algae and temperature model (dotted line). Hall's surprise was that something besides food appeared to be controlling *Daphnia* birthrate during the summer months.

Earlier research had assumed that food concentration was the main factor that controlled *Daphnia* birthrate. To Hall's surprise, he saw that, based on algal abundance and temperature data from the lake, the estimates of *Daphnia* birthrates remained high during the summer months of June, July, and August (figure 6.6) even when the *Daphnia* population was falling. The

summer conditions of moderate food and high temperature predicted a high birthrate, which should have been expressed as a rapidly growing population. Hall proposed that the *Daphnia* population was static during the summer, not because food was limiting, but because predation was removing *Daphnia* as quickly as they could reproduce. This was such an unexpected result that he had collected no data on predation intensity during the study period. However, the result inspired a large number of studies that did estimate the effect of predation by vertebrates (fishes) and invertebrates (various groups) on *Daphnia* population dynamics. This was one of the first studies with results that suggested predation could be an important factor in controlling the population dynamics of an aquatic species.

Chris Luecke and a group of colleagues (1992b) used the Edmondson technique to estimate the total mortality on a *Daphnia* population in Lake Mendota, Wisconsin (figure 6.7). They could estimate how much of this mortality was due to predation by the four most important fish and invertebrate predators, using their knowledge about predator diet and feeding rate. They concluded that (1) fish predation intensity varies by up to eight-fold from year to year, and (2) during all 3 years, most of the annual total mortality was not due to the four most important predators.

Age-Specific Models

Edmondson, Hall, and Luecke used simple, highly abstract models to study population dynamics of natural populations. **Age-specific models,** which use information about birth and death for each age group of a population, are much more flexible and powerful than the simple models.

However, age-specific data are hard to come by—such data often require years of sampling, collecting data on all developmental stages of the organism in question. In aquatic systems, age-specific data are collected most often for crustacean zooplankton, fishes, and mollusks.

Fish populations have been studied in sufficient detail to allow understanding of how the age-specific birth and death schedules result in the observed pattern of population growth. For example, for smallmouth bass living in small lakes in northern Wisconsin, egg production and recruitment of young fishes is not dependent on the size of the population (Wiegmann et al., 1997). Rather, sources of mortality, perhaps predation by odonate nymphs and by fishes,
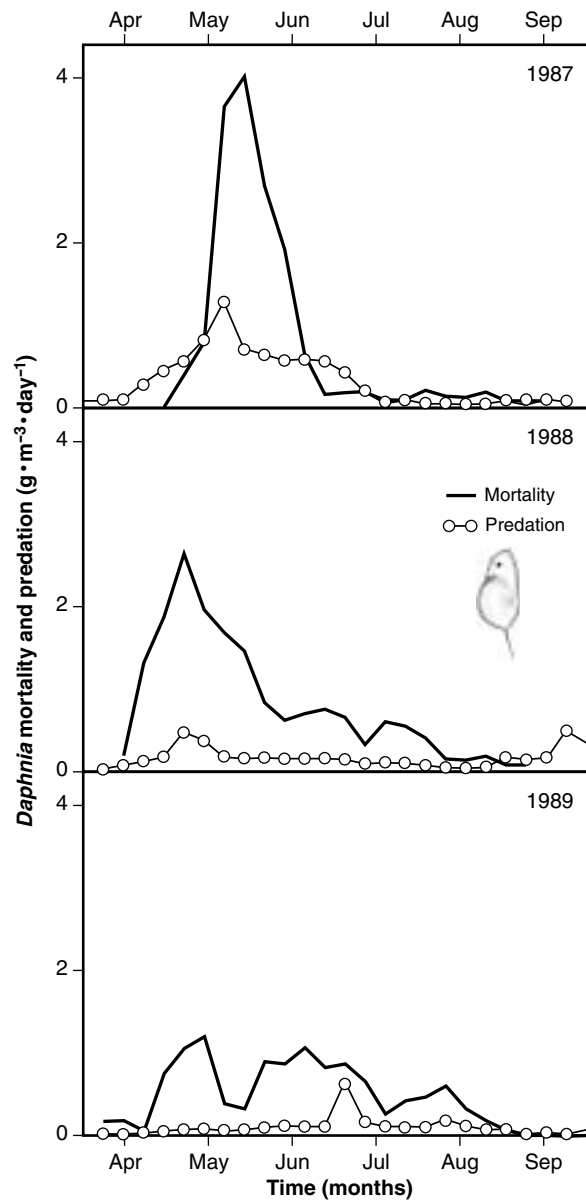
FIGURE 6.7 Two measures of predation in 3 years in Lake Mendota, Wisconsin. The solid line represents total mortality calculated using the Edmondson egg technique, and the line with open circles represents total fish consumption estimated from fish stomach contents. **Source:** Data from Luecke et al., 1992.

are important in determining whether the population grows or declines.

Leptodiaptomus minutus is a small calanoid copepod common in lakes and rivers of central North America. The population dynamics of this copepod

are most strongly influenced by the intensity of predation on the nauplius stages (Confer & Cooley, 1977). Mortality was much less on the larger copepodid stages. This is an example of **size-selective** predation. Because size and developmental stage are closely linked, it is often possible to use age-specific models to understand the influence of size-selective predation on population dynamics.

Age-specific survivorship information can be obtained by following a cohort through time. For example, zooplankton eggs might be produced all during the summer, but often hatch synchronously (within a few days of each other), producing a spring cohort. Fishes often produce young only during a short period of time, producing distinct cohorts that can be followed for years. For example, Lake Mendota, Wisconsin, contains a population of a whitefish, the cisco (Magnuson & Lathrop, 1992). Cisco require cold, oxygenated water. This population crashed during the summer of 1987, when the cold hypolimnion became anoxic. A small population remains in the lake, but has had little success reproducing, probably because the decade of the 1990s was the warmest decade in the century. Eventually, environmental conditions will allow reproduction and a strong age class (year class-cohort) will be produced.

Exponential Population Growth and Invasion

People often create new aquatic habitats by building reservoirs or stock ponds. Zooplankton eventually appear in the new habitat, but with a time lag due to the time needed for a single individual to produce a population large enough to be detected. Maximum crustacean population growth rates are about 0.5 d^{-1}, at 20°C. This rate is associated with a doubling time of about 1.4 days. A small pond of 1 hectare, averaging 1 meter deep, has a volume of 10,000 cubic meters, or 10 million liters. Zooplankton are abundant enough to be noticed at about 0.01 per liter using standard collecting techniques. This means the pond population needs to grow to 100,000 organisms. This increase in population size requires about 16.5 doublings. Therefore, it will take an individual invading organism about 23 days, during the summer, to become common enough to be detected by limnologists. Of course, organisms that have an annual life cycle (some copepods and most vertebrates) will take much longer to become abundant after invasion.

THE EGG (OR SEED) BANK POPULATION GROWTH MODEL

The **egg bank** is made up of the resting stages stored in an aquatic habitat (usually in the sediments or along the edge of a stream, lake, or wetland). There are many situations in which understanding zooplankton population dynamics means knowing how many resting eggs are produced at the end of a growing season. Resting eggs (or spores or seeds) can persist for many years and typically break diapause over several or many years (Hairston et al., 1999). If environmental conditions are distinctly suboptimal, or if a population has a severe time constraint, population growth rate during the season may be less important than the number of resting eggs produced at the end of the season. There may even be a tradeoff between the number of resting eggs and the total number of offspring produced.

For example, *Daphnia* in arctic ponds experience about 30 to 60 days of open water (Dodson, 1984). This is enough time to produce one to two generations of *Daphnia*. When the ice melts, female *Daphnia* hatch from resting eggs, grow to adulthood, and then are faced with a decision about reproductive strategy. The goal is to put as many resting eggs as possible back into the pond before the water freezes.

In years with long seasons, there is enough time for the first females to reproduce once asexually, produce several daughters, and for this generation to grow and produce resting eggs. If the seasons were always long, the best reproductive strategy would be to produce all subitaneous eggs the first generation. These offspring could then produce all resting eggs. This strategy results in the most resting eggs possible.

If, however, the seasons were always short, the best reproductive strategy of the initial females would be to produce only resting eggs and no subitaneous eggs. This strategy produces fewer resting eggs than the two-generation strategy can in a long season, but in short seasons, the two-generation strategy produces no resting eggs at all.

The *Daphnia* solution is to produce some resting eggs and some subitaneous eggs in the first generation. If the subitaneous young survive, they produce even more resting eggs. If the subitaneous young do not survive, at least the first-generation resting eggs are in the bank.

During the shortest seasons, the only way for *Daphnia* to have resting eggs is to produce them asexually. These eggs allow the population to persist but do

not afford the benefit of genetic recombination. Resting eggs produced by sexual reproduction are only possible in the second generation (during years with long seasons) because the males, produced as young in the first generation, need time to mature. *Moina* species are water fleas that live in temporary ponds. The *Moina* solution is resting eggs that can hatch into either a male or a female.

Not all resting eggs (or spores or seeds) hatch (or germinate) the year after they are produced. Some persist in diapause for several years, decades, or even centuries! Of course, the longer a resting stage is in diapause, the more likely it is to die. However, the benefit of being in diapause for a long time is that diapause can be broken before a particularly good growing season. It is particularly important to produce resting stages with variable times of diapause, if the environment is variable from year to year and if there are often years with unsuitable conditions during the growing season.

BIOLOGICAL FITNESS AND POPULATION GROWTH RATE

Biological fitness is measured by the relative number of fertile and viable offspring that a **genotype** contributes to the next generation. A *genotype* is the inheritable material passed from one generation to the next—the biological instructions for producing a living organism. The physical expression of the genotype is the **phenotype,** and the exact form of the phenotype depends on many factors, such as the genotype, the history of development, and environmental conditions. Fitness has an obvious connection to evolution—genotypes that contribute more than their share of offspring to future generations become more common in the population.

In actual practice, it is difficult or impossible to measure biological fitness in real populations. In many situations, the maximum exponential population growth rate (r_{max}) is used as a **surrogate** (substitute) for an actual measurement of biological fitness (Boersma et al., 1999). This substitution makes some sense, especially for populations, such as *Daphnia* during the summer, that are specialized for fast reproduction. In *Daphnia,* the individuals (genotypes) that can reproduce fastest are most likely to survive predation and to produce the largest population by

the time the food supply becomes limiting. However, achieving the fastest population growth rate (by early reproduction) is just one of many possible **life-history strategies** that are common among aquatic organisms.

LIFE-HISTORY STRATEGY

All organisms face a fundamental "general life-history problem" (Stearns, 1992). The problem is how to optimize life-history strategy in order to make the largest contribution to the next generation—or, indeed, any contribution at all to the next generation, in a particular environment.

The success of a particular life-history strategy depends on the environment as well as the genotype. Each set of environmental conditions and each community of interacting organisms **constrains** the range of possible strategies that might be successful. If, as is usually the case, there is a limited resource, life-history strategies are constrained by various **tradeoffs.** The limited resource is often energy (food) or time.

Life-history strategy includes a number of aspects, which will be discussed in general, followed by more specific examples listed in table 6.3.

Seasonal Timing of Life History, Including Reproduction

Timing is everything. Organisms require rather specific environmental conditions for successful completion of each stage of the life cycle (see chapter 8). Natural selection tends to result in organisms that are adapted to a specific seasonal pattern. However, there is typically genetic variation in populations because of climatic variation. A random sequence of warm and cool summers will result in organisms in the population that are adapted to both warm and cool conditions.

Size and Number of Offspring

There is often a tradeoff between number and size of eggs or juveniles—as if there is a set amount of resource (stored energy) that can be used to produce offspring, and this total amount can either be divided up into a few large individuals or many small individuals. Size-selective predation influences the success of this aspect of life-history strategy. For example, fishes eat

Table 6.3   Examples of Different Life-History Strategies and the Environments (Abiotic and Biological) in Which Each Strategy Is Beneficial.

Strategies are for warm (summer or southern) conditions. Fewer generations would be expected under alpine or arctic conditions.

Organism Life History	Life-History Strategy	Optimal Environmental Conditions
Branchiopods such as *Daphnia* in temperate lakes	Reproduce fast and often to keep up with losses to predators; have little ability to escape predators after encounter. Filter large amounts of algae. High mortality balanced by a higher birthrate. Sex ratio is all female.	3–10 generations possible per year, high food abundance
Calanoid copepods in lakes	Reproduce slowly; allocate energy to fast swimming to escape predators; efficiently capture only high-quality food.	1–5 generations per year, low food abundance, cool temperatures
Microcrustaceans in temporary or arctic ponds	Produce resting eggs as soon as possible (population growth rate is low, but persistence from year to year is assured).	Life history constrained by the short time available during the annual climate cycle for growth and development—must reproduce before the water dries or freezes
Macroinvertebrates, macrophytes, and fishes	Reproduce once or twice a year in the temperate zone. In warmer, more constant climates, more generations per year may be possible.	Extreme annual seasonal conditions and timing are very important for organisms that take about 1 year for a life cycle. Summer conditions are typically optimal, when prey are most abundant and temperature is optimal for highest survival of young, and in time for young to grow sufficiently or even mature before the end of the summer season. In tropical climates, the annual rain cycle can also constrain reproduction timing.

large *Daphnia* and copepods eat small *Daphnia* (Zaret, 1980). If mortality due to predation is mainly due to fishes, then producing small young will be a more successful strategy than producing large young. On the other hand, if copepod predation predominates, producing large young will be the more successful strategy.

Age-Specific Energy Allocation Patterns—Reproduction, Growth, and Body Maintenance

Juveniles allocate energy to growth and maintenance. A common strategy for adults is to stop growing and to allocate energy to reproduction and maintenance. If energy is allocated to adult growth, the tradeoff is that initial reproduction may be lower, but after some time,

the larger adults can produce many more offspring than can the small adults.

Rate of Population Growth versus Resting Egg Production

As described in the egg-bank model section, fast reproduction works well when environmental conditions are optimal. The fastest population growth occurs in asexual-reproducing organisms (such as branchiopods, rotifers, and plants), in which all offspring are females and in which energy is allocated to subitaneous egg production rather than resting eggs.

The rate of population growth also depends on the environment—temperature has the ability to either increase or inhibit growth. Typically, there is an optimal temperature for growth. The optimal temperature is not

necessarily the highest temperature (Threlkeld, 1986). This is an environmental constraint on life-history strategy (see chapter 9).

Age of First Reproduction and Size- or Age-Selective Predation

Aquatic organisms often face a tradeoff between reproductive output and survival in the presence of size-selective predators. This tradeoff determines the duration and timing of the juvenile developmental period. Early maturation has the advantage of tending to increase reproductive rate (Cole, 1954). If predation falls most heavily on the largest (oldest) adults, the optimal strategy is to reproduce early at a small size. However, reproducing at a small size also results in smaller and fewer offspring, which can lower birthrate. On the other hand, if size-selective predation is intense on small offspring and small adults, the best strategy may be to delay age of first reproduction in order to produce a few, large offspring (Sommer et al., 2001; Zaret, 1980).

Possible reproductive strategies include reproducing only once to producing many batches of offspring. To some extent, the success of these different strategies depends on the probability of surviving to reproduce more than once, which can depend on the environment or on the timing of predation, as well as on the pattern of size-selective predation.

Life Span

Length of life (**life span**) is an aspect of life-history strategy that is closely related to other factors such as seasonal timing, growth rate, pattern of reproduction, and even locomotion behavior. Mathematical analysis of life-history strategy suggests that there is often little advantage to a long life, in terms of contributions to the next generation. One way to understand this is that offspring of an old adult are produced at the same time as the (naturally more numerous) grandchildren that are being produced by early-reproducing adults. On the other hand, many organisms grow as they age, and old, large adults can sometimes produce many more offspring at a time than can smaller younger adults.

The tradeoff between life span and locomotion behavior (see table 6.3 for an example) was discussed in chapter 4. Branchiopods, such as *Daphnia,* tend to allocate energy toward reproduction and have short lives. Calanoid copepods, such as *Diaptomus,* allocate energy toward escape response, enjoy a longer life than branchiopods, and produce relatively few offspring over their life span.

Life-History Adaptations

All of these life-history factors (and others) are under some degree of genetic control—they can be passed from one generation to the next. If these heritable characters increase reproductive success, relative to the average population rate of reproduction, the characters are considered beneficial **adaptations.** Some genotypes will be successful and some will not. Through time, the interaction between the genotype and the environment will produce a specific life-history strategy. Table 6.3 gives examples of adaptive life-history strategies and their environmental context.

It is important to understand that a specific life-history strategy will work best in a specific environment. A change in climate or a change in predator populations can have a large effect on what is the most successful strategy (Boersma et al., 1999).

Life history of a given genotype depends on environmental conditions or signals (Dodson et al., 1994; Larsson & Dodson, 1993). Conditions such as food concentration and temperature have a strong effect on life-history parameters such as growth rate and amount of reproduction. (Effects of food concentration and temperature will be discussed in chapter 9.) These are environmental parameters that have an immediate and direct effect on life histories of aquatic organisms. Less food often means fewer and smaller offspring that are more susceptible to starvation. Temperatures that are too cool or too hot result in suboptimal population growth.

Signals such as predator smell or **photoperiod** (day length) cause changes in behavior or development that have strong effects on life-history parameters. Chemical signals modify energy allocation, growth rates, and developmental patterns. A change in photoperiod can also modify life history. For example, day length is a major signal determining sex ratio in *Daphnia* (Hobaek & Larsson, 1990).

TRANSITION

The material in this chapter is focused on descriptions of populations and population dynamics. Natural next questions are, "What controls population size and rate of change?" and "How do multiple populations of different species live together?" The next four chapters present material that helps answer these questions. In chapter 7, we take a close look at the ecological inter-actions, especially competition and predation, that constrain the distribution and abundance of aquatic organisms. This is followed by chapter 8, which dis-cuss how communities change over time. Community ecology is followed by two chapters (9 and 10) on ecosystem topics, in which we consider constraints imposed by physics and chemistry on aquatic organisms and their interactions, distribution, and abundance.

Study Guide

Chapter 6	Population Dynamics in Limnology: Population Size Changing with Time

Questions

1. What is *population dynamics?*

2. What is a rare species in an aquatic habitat?

3. How does the coefficient of variation assist interpretation of variability in populations with different size mean values?

4. Can an individual-based model also be age-specific?

5. How can different life-history strategies have the very same average result—contribution by each adult to the next generation of one successful offspring? What are the tradeoffs?

6. The value of *r* has units of "per time." For smaller organisms, this time unit is "per day," and for larger organisms, the time unit is more conveniently "per year." How is the value of *r* related to daily (or annual) percent change of the population?

7. Limnologists studying aquatic populations can easily calculate the rate at which a population is changing, as percent change per unit time. If a *Daphnia* population is growing at a rate of 15% per day, how many days will it take for the population to double in size?

8. What are major differences between the exponential and the egg bank models of population growth?

9. How does the concept of biological fitness relate to the concept of tradeoff in the context of life-history strategy for some groups of common aquatic organisms? Review the example of tradeoffs given in this and earlier chapters: chapter 2—the tradeoff faced by stream insects feeding in a current; chapter 4—the copepod tradeoff between photoprotection and vulnerability to predation.

Words Related to Aquatic Populations and Population Dynamics

adaptation	density	life span	size
age class	density-dependent	loss	size-selective
age-specific model	dynamic	mean	stability
average	egg bank	metapopulation	standard deviation
biological fitness	exponential growth model	mortality	strategy
biomass	fecundity	phenotype	surrogate
bloom	genotype	photoperiod	survivorship
coefficient of variation	individual-based	population	tradeoff
constraint	life-history strategies	propagule	variance
cycle		recruitment	

Major Examples and Species Names to Know

Tommy Edmondson and the egg ratio technique

Don Hall's surprise

Steve Stearns and the general life-history problem

Additional Resources

Further Reading

Gotelli, N. J. 2001. *A primer of ecology.* 3rd ed. Sunderland, MA: Sinauer Press. 265 pages.

Welcome to McGraw-Hill's Website

Location: http://www.mhhe.com/limnology

Mc Graw Hill

Exploring the Internet

simulation model

The *Populus* web site of the University of Minnesota offers several free computer simulation exercises that demonstrate traditional models in population ecology.