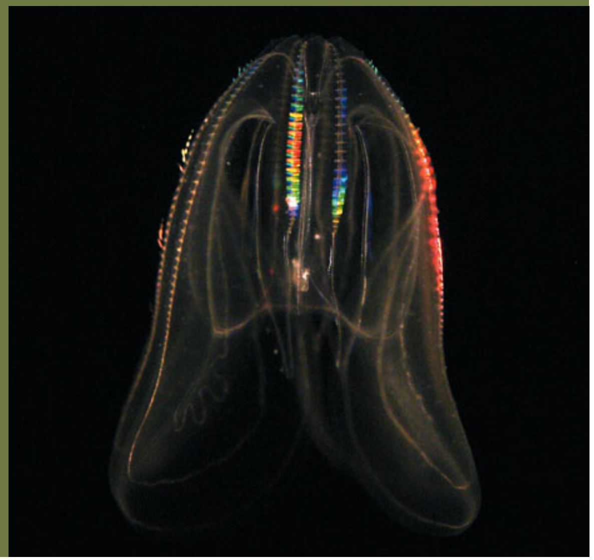
10

Population Dynamics



- *Case Study*: A Sea in Trouble
- Patterns of Population Growth
- Delayed Density Dependence
- Population Extinction
- Metapopulations
- Case Study Revisited
- *Connections in Nature*: From Bottom to Top, and Back Again

The comb jelly *Mnemiopsis leidyi* was introduced accidentally into the Black Sea in the 1980s, most likely by the discharge of ballast water from cargo ships.

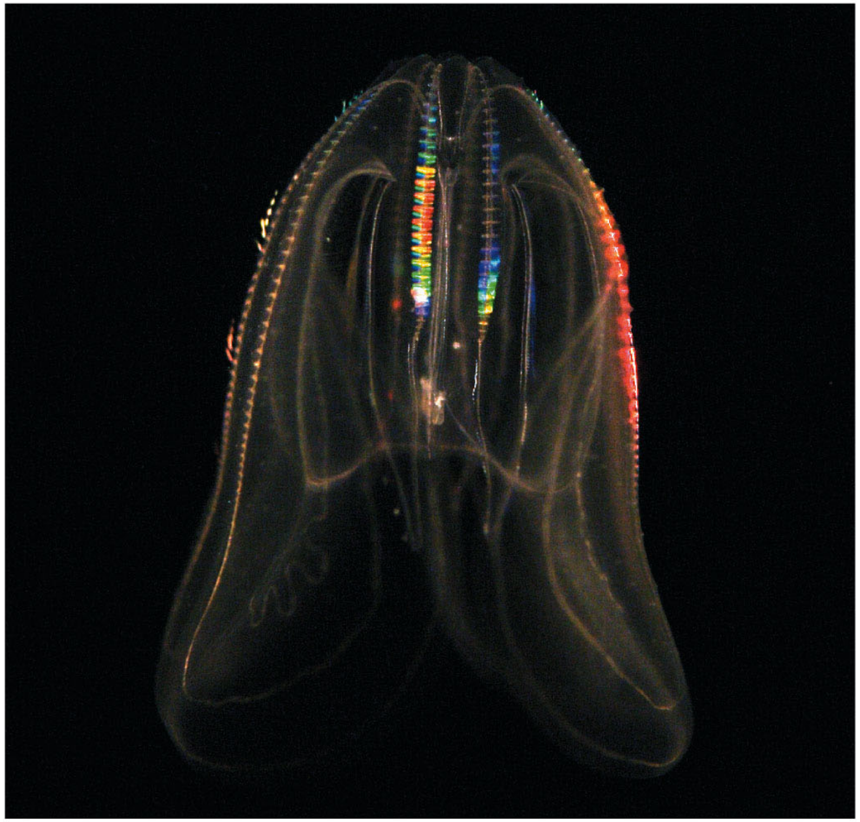


Figure 10.1 A Potent Invader

Case Study: A Sea in Trouble

The Black Sea ecosystem was already in trouble—nutrients inputs had caused eutrophication.

Phytoplankton abundance increased, water clarity decreased, oxygen concentrations dropped, and fish populations experienced massive die-offs.

Mnemiopsis is a voracious predator of zooplankton, fish eggs, and young fish.

It continues to feed even when completely full, causing it to regurgitate large quantities of prey stuck in balls of mucus.

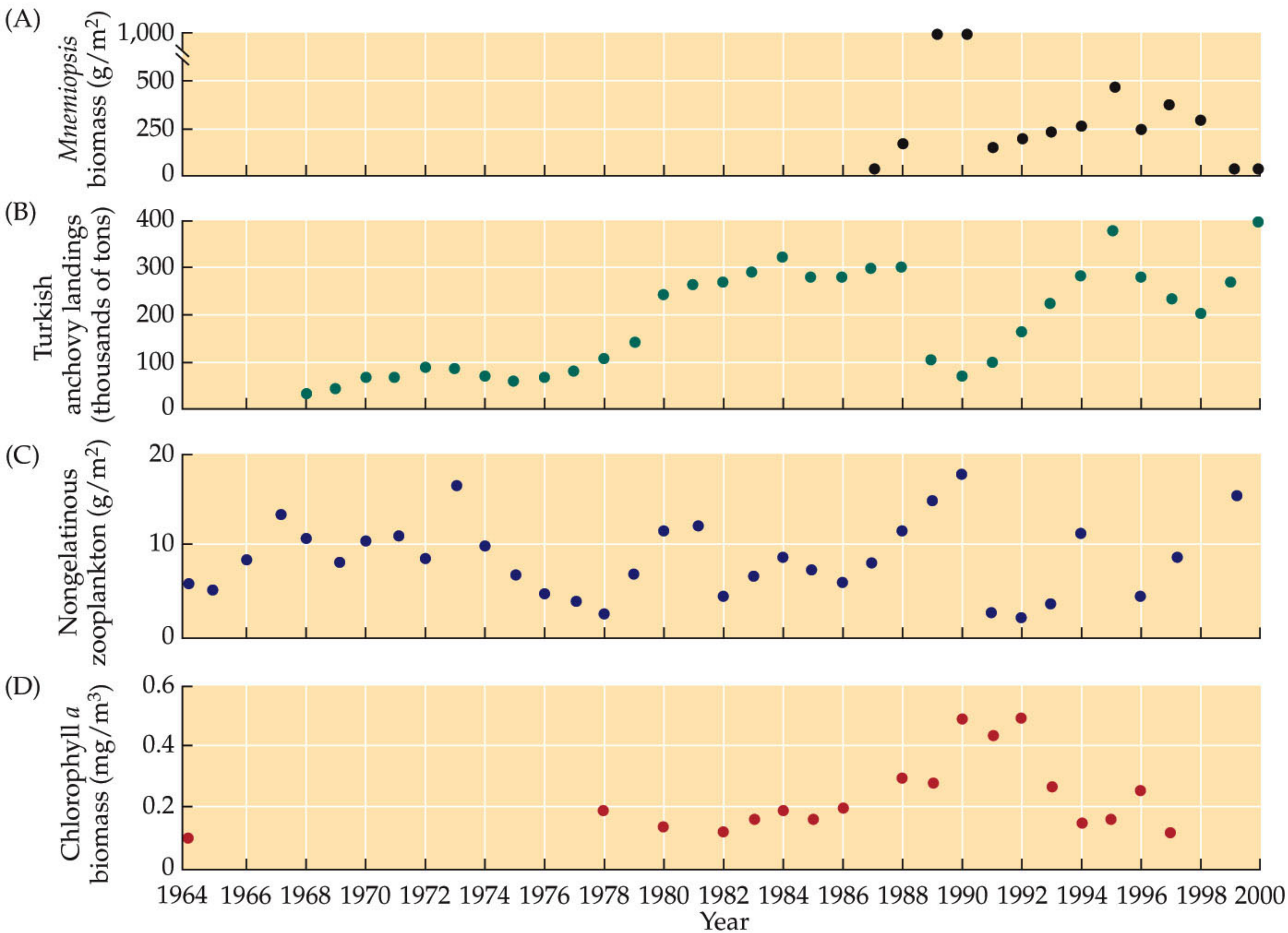
An individual *Mnemiopsis* can produce up to 8,000 offspring just 13 days after its own birth.

Case Study: A Sea in Trouble

In 1989, *Mnemiopsis* populations exploded: The total biomass of *Mnemiopsis* in the Black Sea was estimated at 800 million tons (live weight).

Feeding by *Mnemiopsis* caused zooplankton populations to crash, which caused phytoplankton populations to increase even more.

Figure 10.2 Changes in the Black Sea Ecosystem



***ECOLOGY*, Figure 10.2**

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Case Study: A Sea in Trouble

The large numbers of phytoplankton and *Mnemiopsis* that died provided food for bacterial decomposers, which use oxygen.

As bacterial activity increased, oxygen levels decreased, harming some fish populations.

Mnemiopsis also devoured the food supplies (zooplankton), eggs, and young of important commercial fishes such as anchovies, and led to a rapid decline in fish catches.

Case Study: A Sea in Trouble

Native predators and parasites had failed to regulate *Mnemiopsis* populations.

Today, *Mnemiopsis* populations have decreased, and the Black Sea ecosystem is recovering.

Populations can change in size as a result of four processes: Birth, death, immigration, and emigration.

$$N_{t+1} = N_t + B - D + I - E$$

N_t = Population size at time t

B = Number of births

D = Number of deaths

I = Number of immigrants

E = Number of emigrants

Introduction

Populations are open and dynamic entities.

Individuals can move from one population to another, and population size can change from one time period to the next.

Population dynamics refers to the ways in which populations change in abundance over time.

Concept 10.1: Populations exhibit a wide range of growth patterns, including exponential growth, logistic growth, fluctuations, and regular cycles.

These four patterns of population growth are not mutually exclusive, and a single population can experience each of them at different points in time.

Exponential Growth

A population increases by a constant proportion at each point in time.

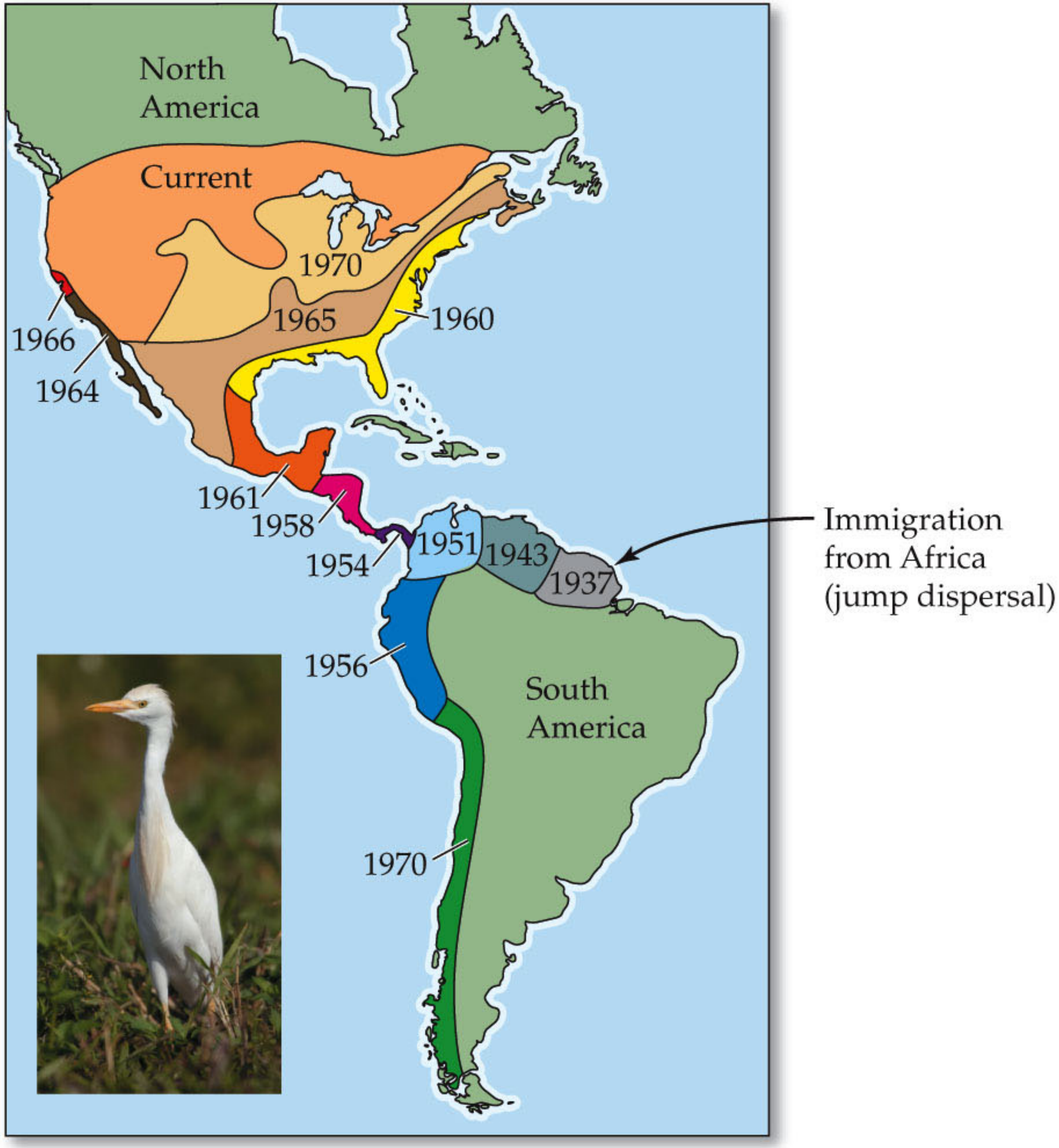
When conditions are favorable, a population can increase exponentially for a limited time.

Patterns of Population Growth

Exponential growth can also occur when a species reaches a new geographic area.

If conditions are favorable in the new area, the population may grow exponentially until density-dependent factors regulate its numbers.

Figure 10.3 Colonizing the New World



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Patterns of Population Growth

Species such as the cattle egret typically colonize new geographic regions by long-distance or **jump dispersal** events.

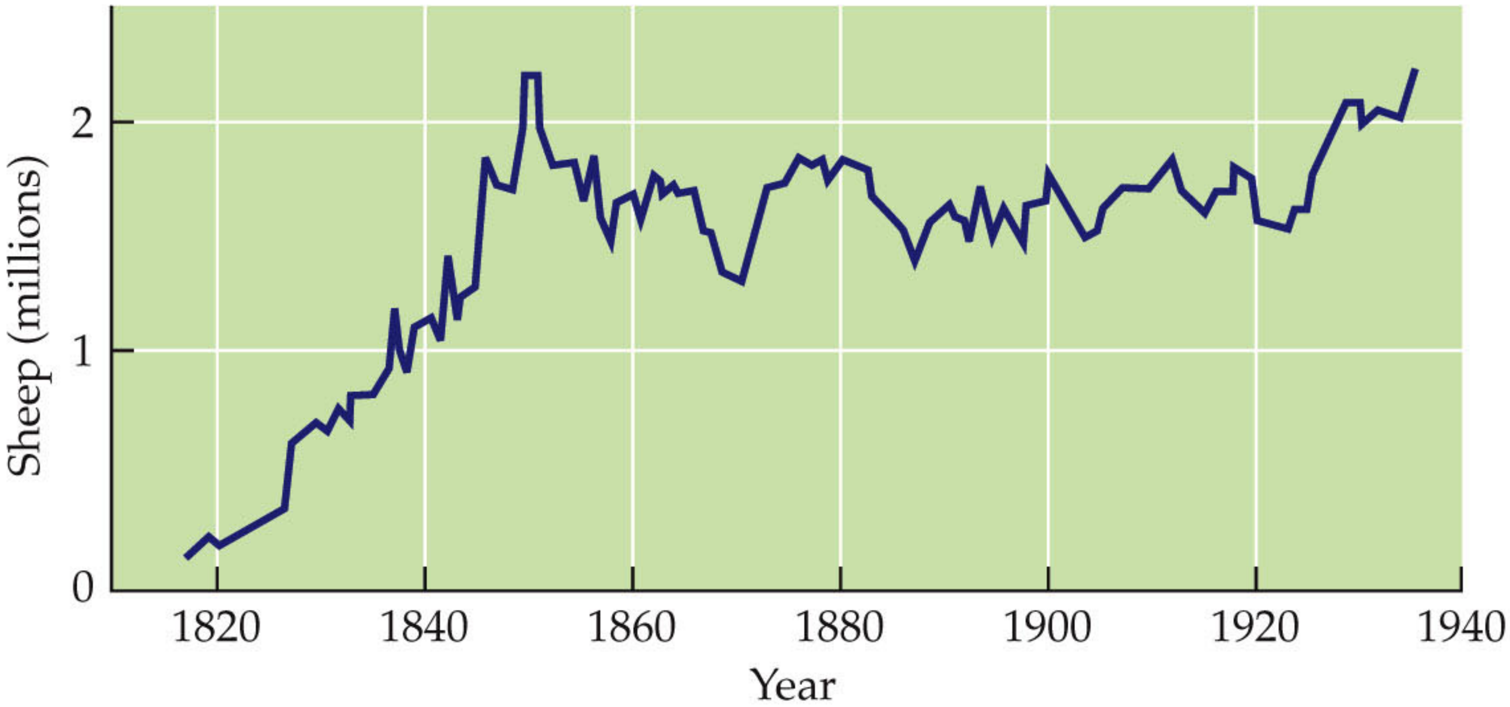
Then, local populations expand by short-distance dispersal events.

Logistic Growth

Some population reach a stable size that changes little over time.

Such populations first increase in size, then fluctuate by a small amount around what appears to be the carrying capacity.

Figure 10.4 Population Growth Can Resemble a Logistic Curve



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Plots of real populations rarely match the logistic curve exactly.

“Logistic growth” is used broadly to indicate any population that increases initially, then levels off at the carrying capacity.

In the logistic equation

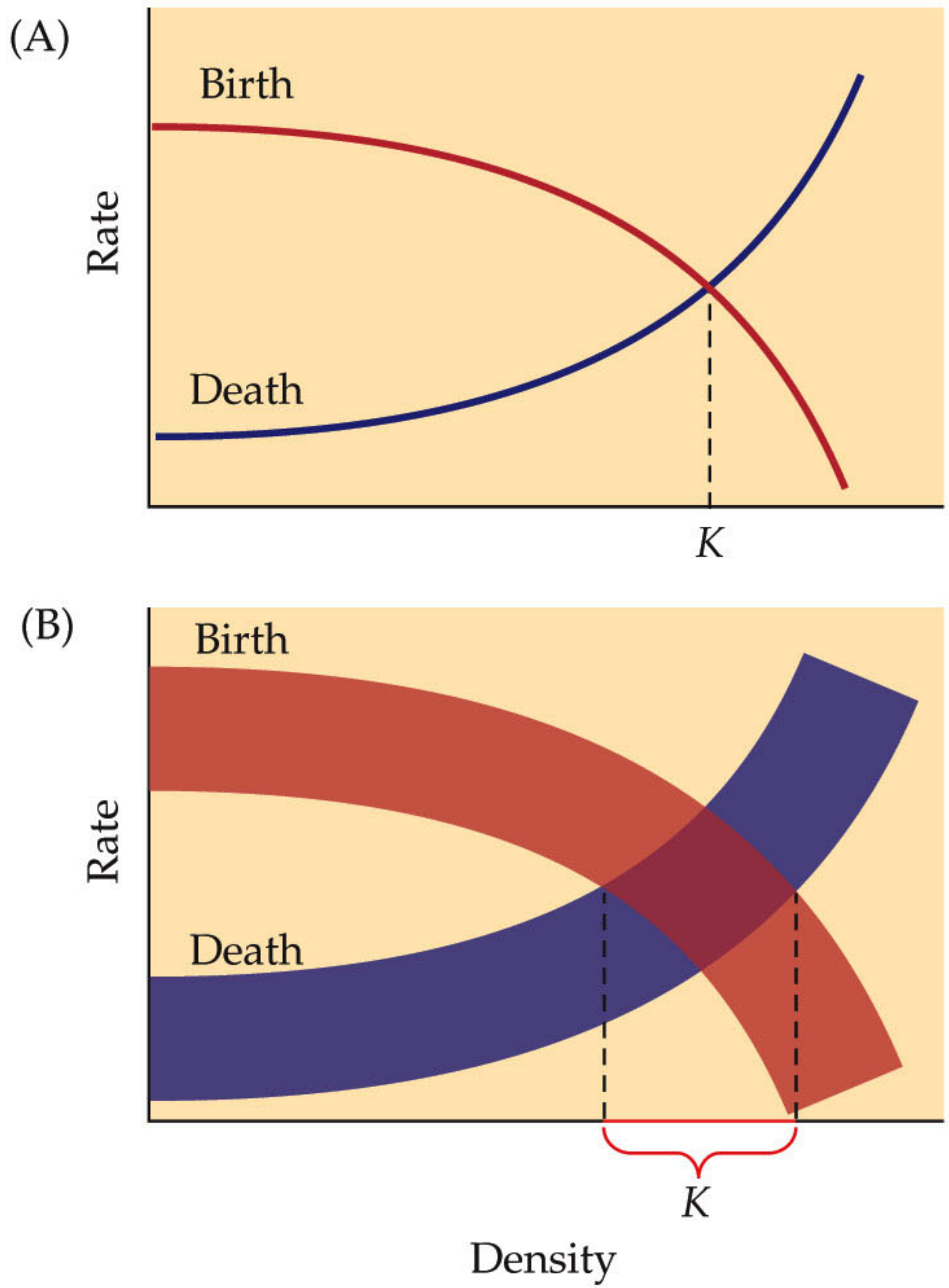
$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

K is assumed to be constant. *K* is the population size for which birth and death rates are equal.

For *K* to be a constant, birth rates and death rates must be constant over time at any given density.

This rarely happens in nature. Birth and death rates do vary over time, thus we expect carrying capacity to fluctuate.

Figure 10.5 Why We Expect Carrying Capacity to Fluctuate



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Population Fluctuation

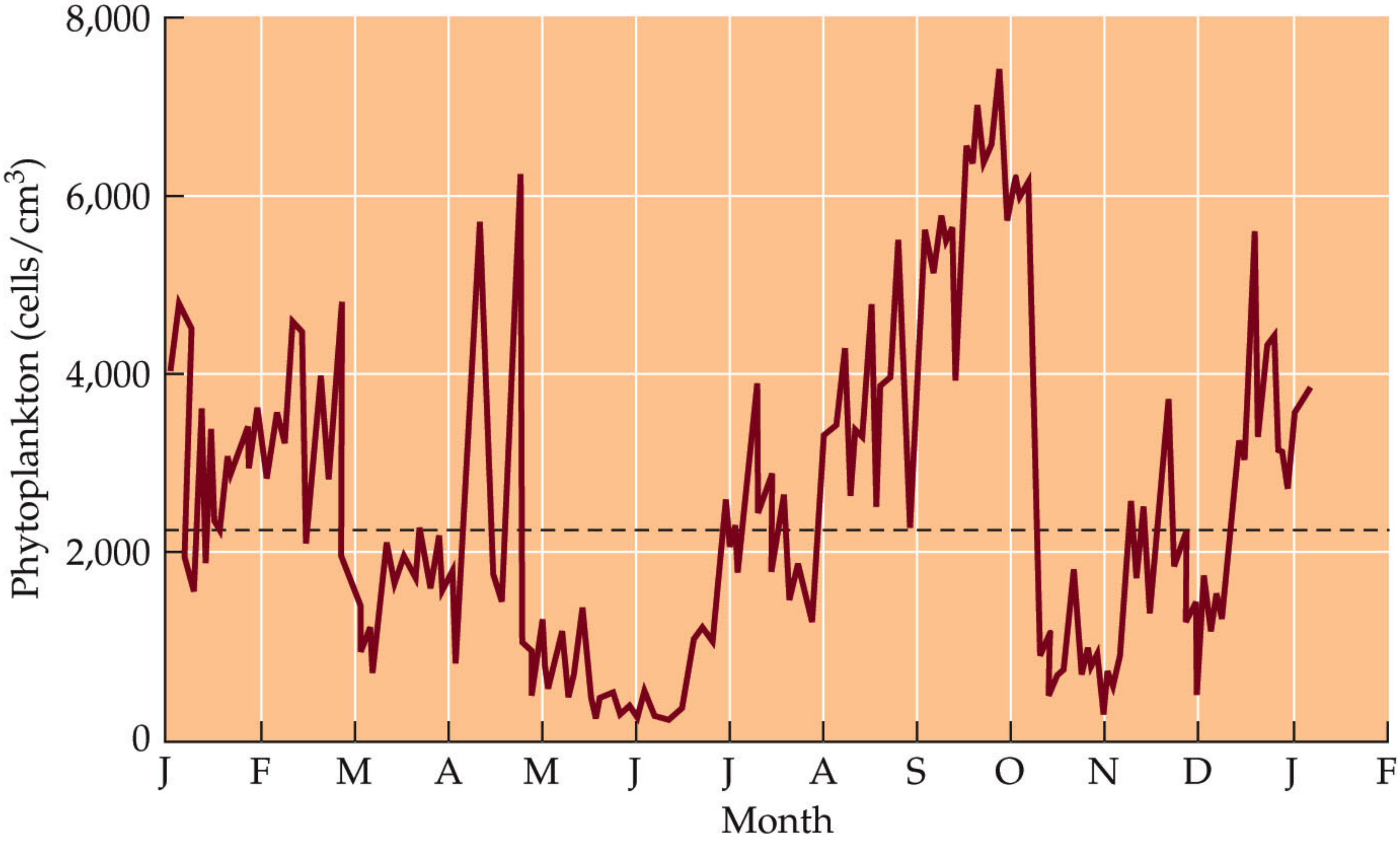
A rise and fall in population size over time.

Fluctuations can occur as deviations from a population growth pattern, such as the Tasmanian sheep population.

In some populations, fluctuations occur as increases or decreases in abundance from an overall mean value.

Changes in phytoplankton abundance in Lake Erie could reflect changes in a wide range of environmental factors, including nutrient supplies, temperature, and predator abundance.

Figure 10.6 Population Fluctuations



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For some populations, fluctuations can be large.

Populations may explode, causing a **population outbreak**.

Biomass of the comb jelly *Mnemiopsis* increased more than a thousandfold during a 2-year outbreak in the Black Sea.

Figure 10.7 Populations Can Explode in Numbers

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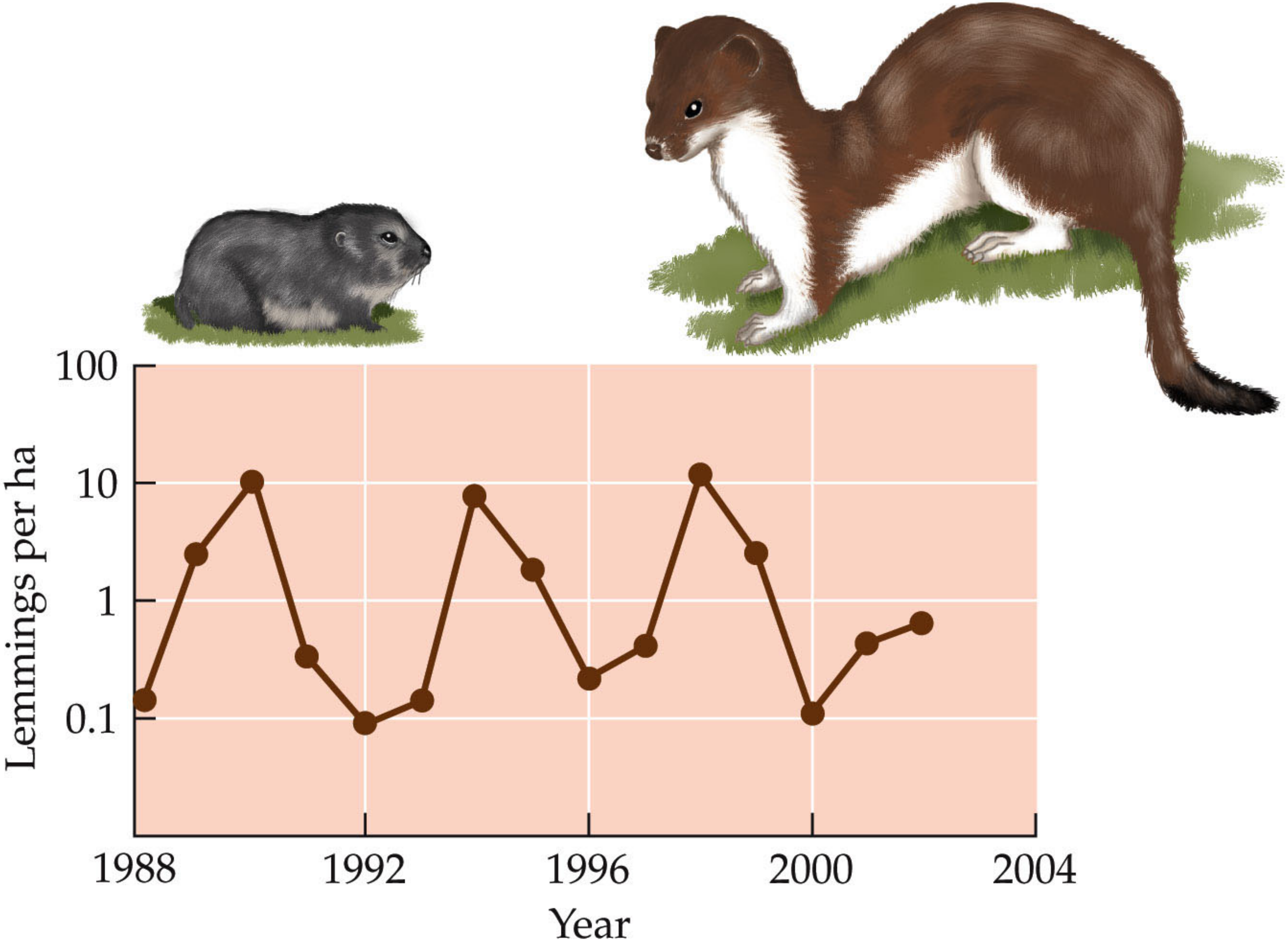
Population Cycles

Some populations have alternating periods of high and low abundance at regular intervals.

Populations of small rodents such as lemmings and voles typically reach a peak every 3–5 years.

Figure 10.8 A Population Cycle



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Patterns of Population Growth

Different factors may drive population cycles in rodents.

For collared lemmings in Greenland, Gilg et al. (2003) used field observations and mathematical models to argue that their 4-year cycle is driven by predators, such as the stoat.

In other studies, predator removal had no effect on population cycles.

Factors that drive population cycles may vary from place to place, and with different species.

Delayed Density Dependence

Concept 10.2: Delayed density dependence can cause populations to fluctuate in size.

The effects of population density often have a lag time or delay.

Commonly, the number of individuals born in a given time period is influenced by population densities that were present several time periods ago.

Delayed density dependence: Delays in the effect that density has on population size.

Delayed density dependence can contribute to population fluctuations.

Delayed Density Dependence

Example: When a predator reproduces more slowly than its prey.

If predator population is small initially, the prey population may increase, and as a result the predator population increases, but with a time lag.

Large numbers of predators may decrease the prey population, then the predator population deceases again.

Delayed Density Dependence

The logistic equation can be modified to include time lags:

$$\frac{dN}{dt} = rN\left[1 - \frac{N(t-\tau)}{K}\right]$$

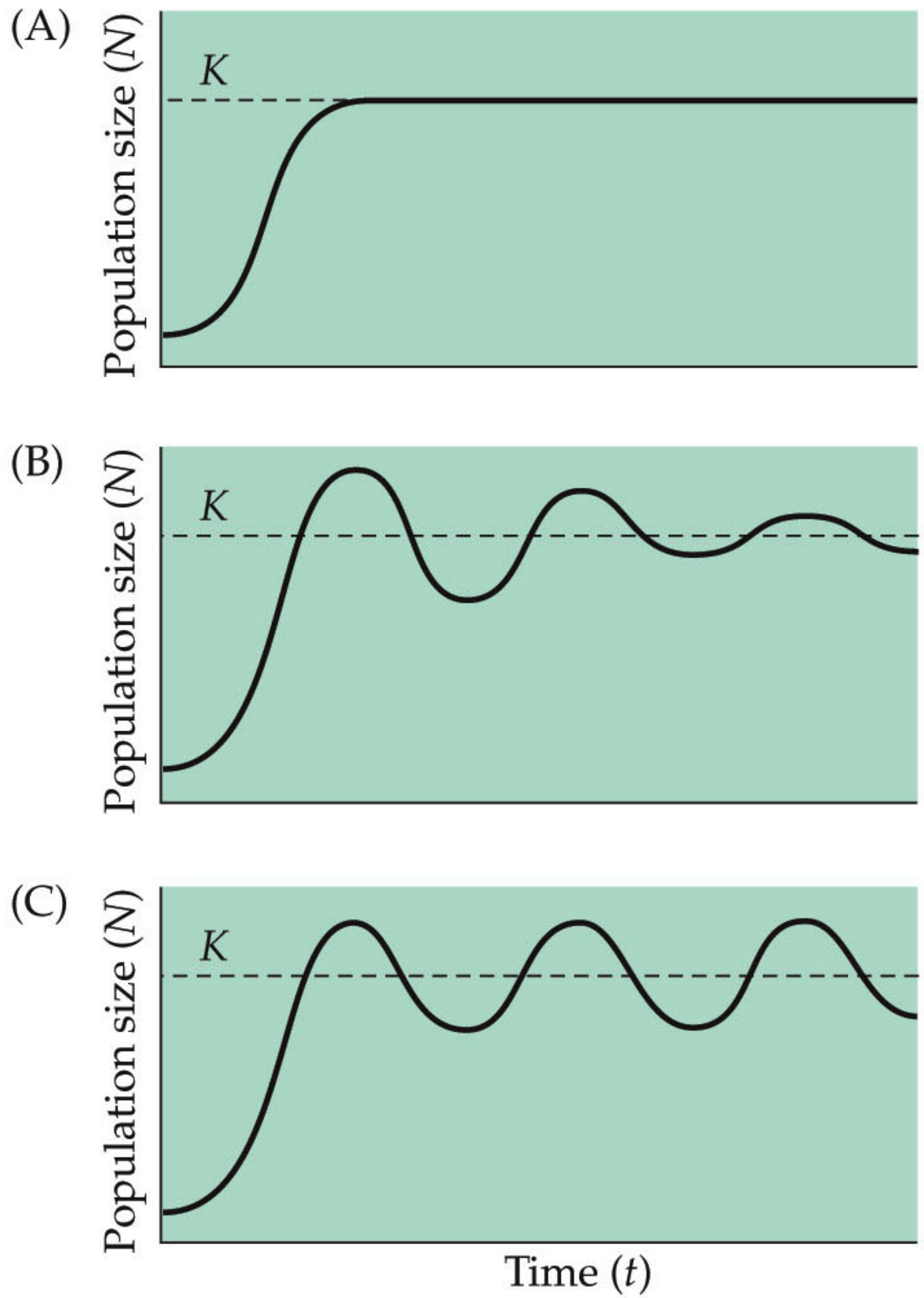
$N_{(t\text{-}\tau)}$ = population size at time t-τ in the past.

The occurrence of fluctuations depends on the values of r and τ.

Robert May (1976) found that when $r\tau$ is small ($0 < r\tau < 0.368$), no fluctuation results.

At intermediate levels, ($0.368 < r\tau < 1.57$), **damped oscillations** result.

Figure 10.9 Logistic Growth Curves with Delayed Density Dependence



ECOLOGY, Figure 10.9

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Delayed Density Dependence

When $r\tau$ is large ($r\tau > 1.57$), the population fluctuates indefinitely about the carrying capacity.

This pattern is called a **stable limit cycle**.

Delayed Density Dependence

A. J. Nicholson studied density dependence in sheep blowflies in laboratory experiments.

In the first experiment, adults were provided with unlimited food, but the larvae were restricted to 50 g liver per day.

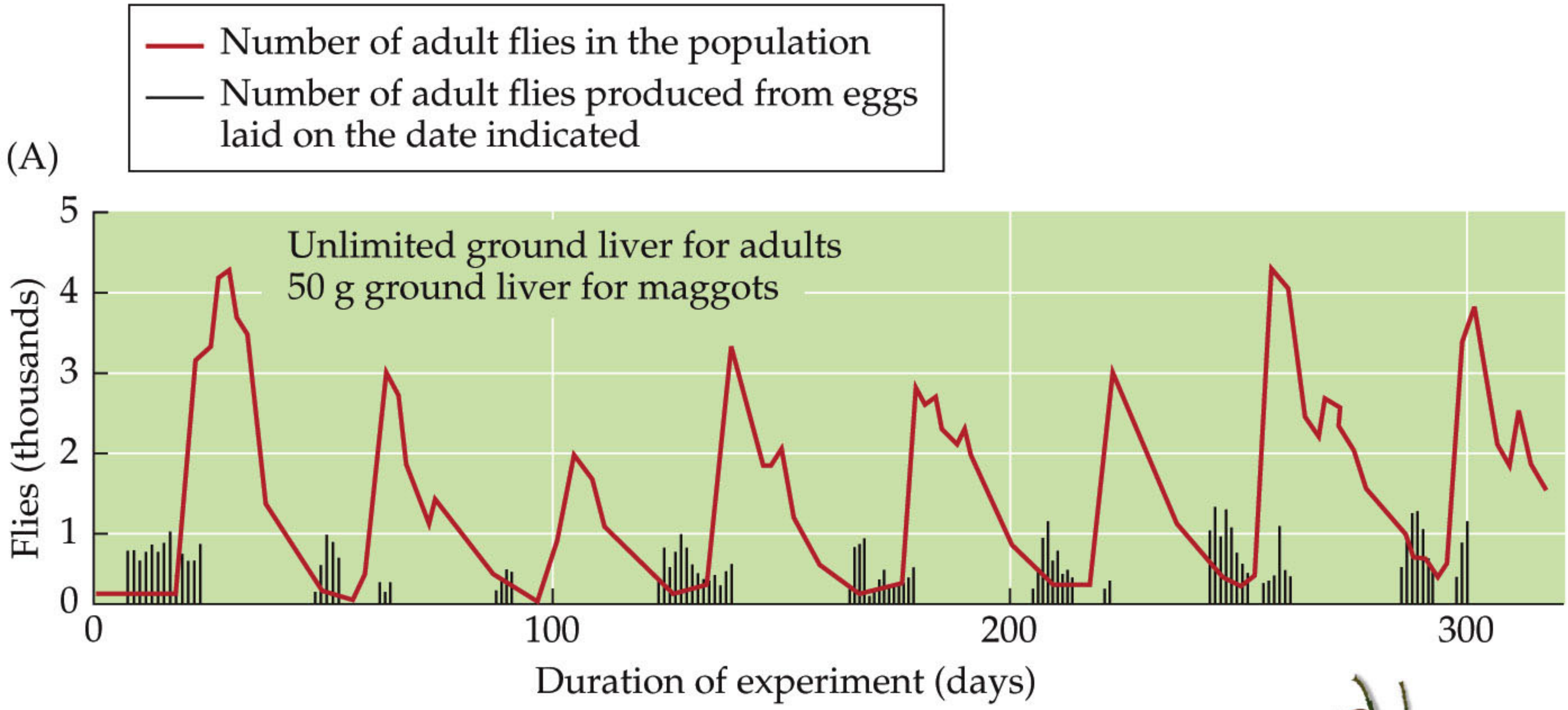
Delayed Density Dependence

Because of abundant food, females were able to lay enormous numbers of eggs.

But when the eggs hatched, most larvae died because of lack of food.

This resulted in an adult population size that fluctuated dramatically.

Figure 10.10 A Nicholson's Blowflies



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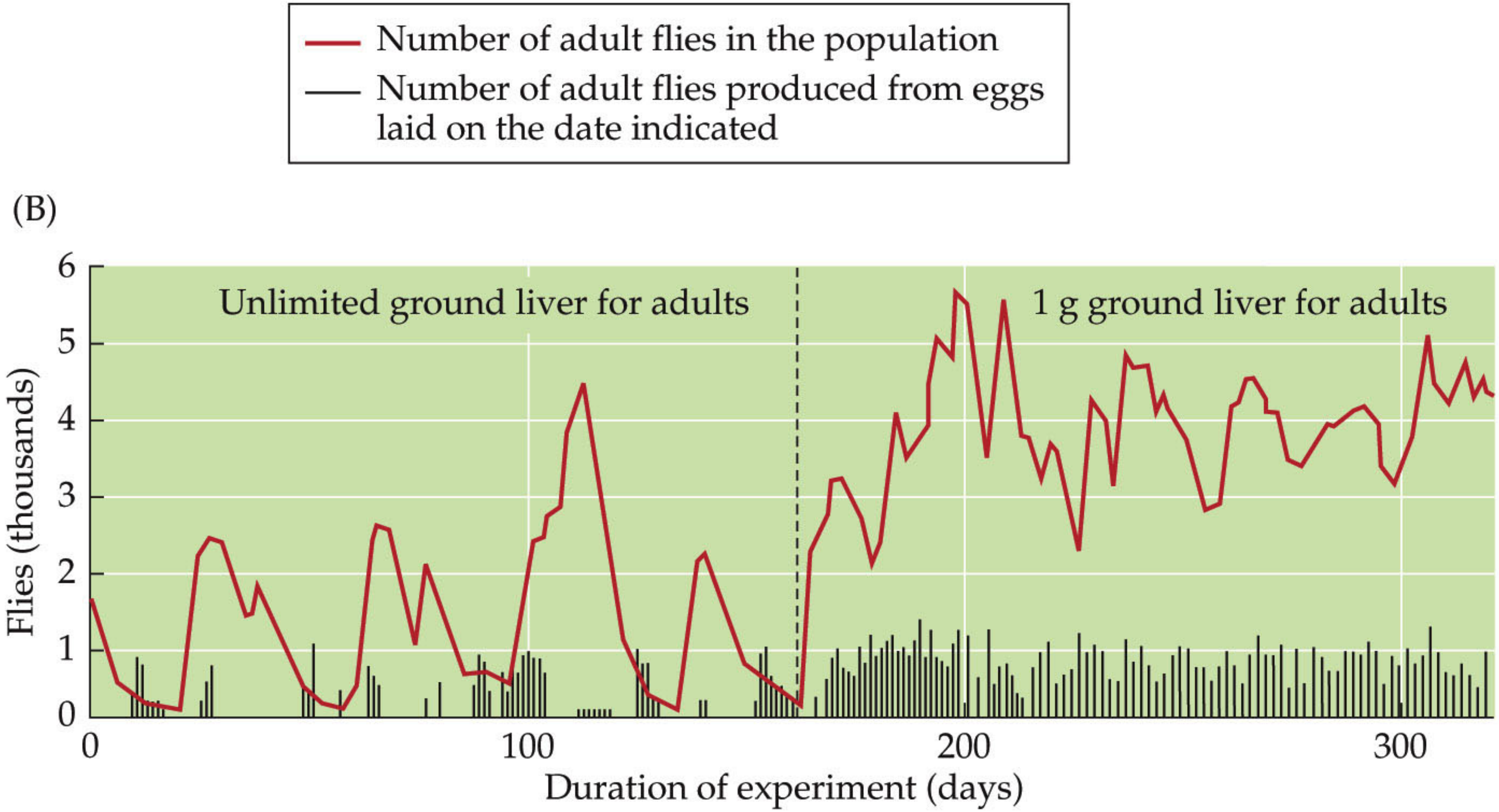
Delayed Density Dependence

In the second experiment, both adults and larvae were provided with unlimited food.

The adult population size no longer showed repeated fluctuations.

Figure 10.10 B Nicholson's Blowflies



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Concept 10.3: The risk of extinction increases greatly in small populations.

Many factors can drive populations to extinction:

Predictable (*deterministic*) factors, as well as fluctuation in population growth rate, population size, and chance events.

Population Extinction

Consider a version of the geometric growth equation that includes random variation in the finite rate of increase, (λ).

If random variation in environmental conditions causes λ to change considerably from year to year, the population will fluctuate in size.

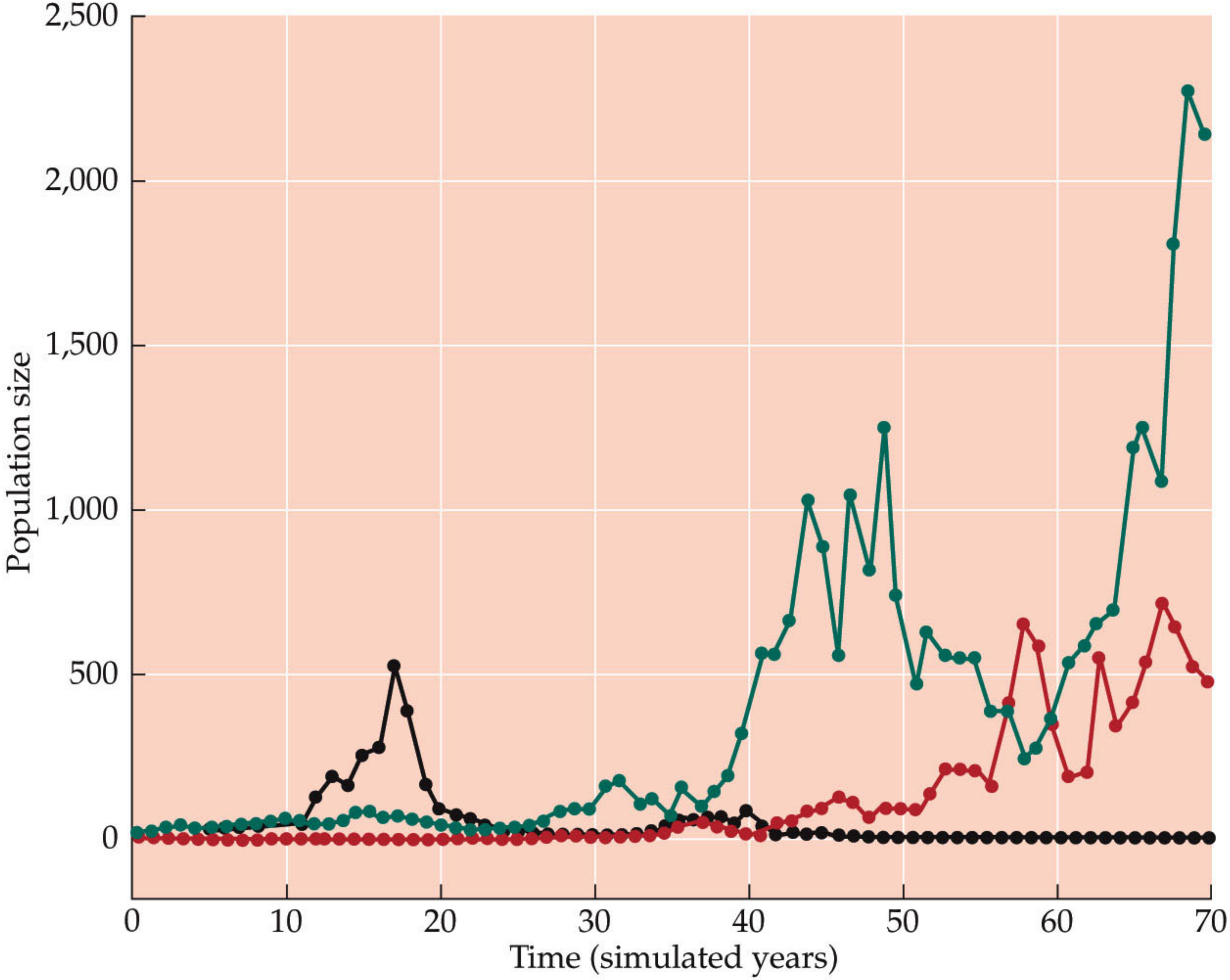
Population Extinction

Computer simulations of geometric growth for three populations allowed λ to fluctuate at random.

Two of the populations recovered from low numbers, but one went extinct.

Fluctuations increase the risk of extinction.

Figure 10.11 Fluctuations Can Drive Small Populations Extinct



ECOLOGY, Figure 10.11

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Population Extinction

Variation in λ in the simulations was determined by the standard deviation (σ) of the growth rate, which was set to 0.4.

Population Extinction

In 10,000 simulations (initial population size = 10), when σ = 0.2, only 0.3% of the populations went extinct in 70 years.

When σ was increased to 0.4, 17% of the populations went extinct in 70 years.

When σ was increased 0.8, 53% of the populations went extinct.

Population Extinction

When variable environmental conditions result in large fluctuations in a population's growth rate, the risk of extinction of the population increases.

Small populations are at greatest risk.

Population Extinction

If the 10,000 simulations are repeated starting with population size = 100, and $\sigma = 0.8$, 29% of populations went extinct in 70 years.

If initial population size is increased to 1,000 or 10,000, populations going extinct drops to 14% and 6%, respectively.

Population Extinction

These patterns have been observed in real populations.

Studies of bird populations on the Channel Islands in California showed that 39% of populations with fewer than 10 breeding pairs went extinct.

No extinctions occurred in populations with over 1,000 breeding pairs (Jones and Diamond 1976).

Figure 10.12 Extinction in Small Populations (Part 1)

***ECOLOGY,* Figure 10.12 (Part 1)**

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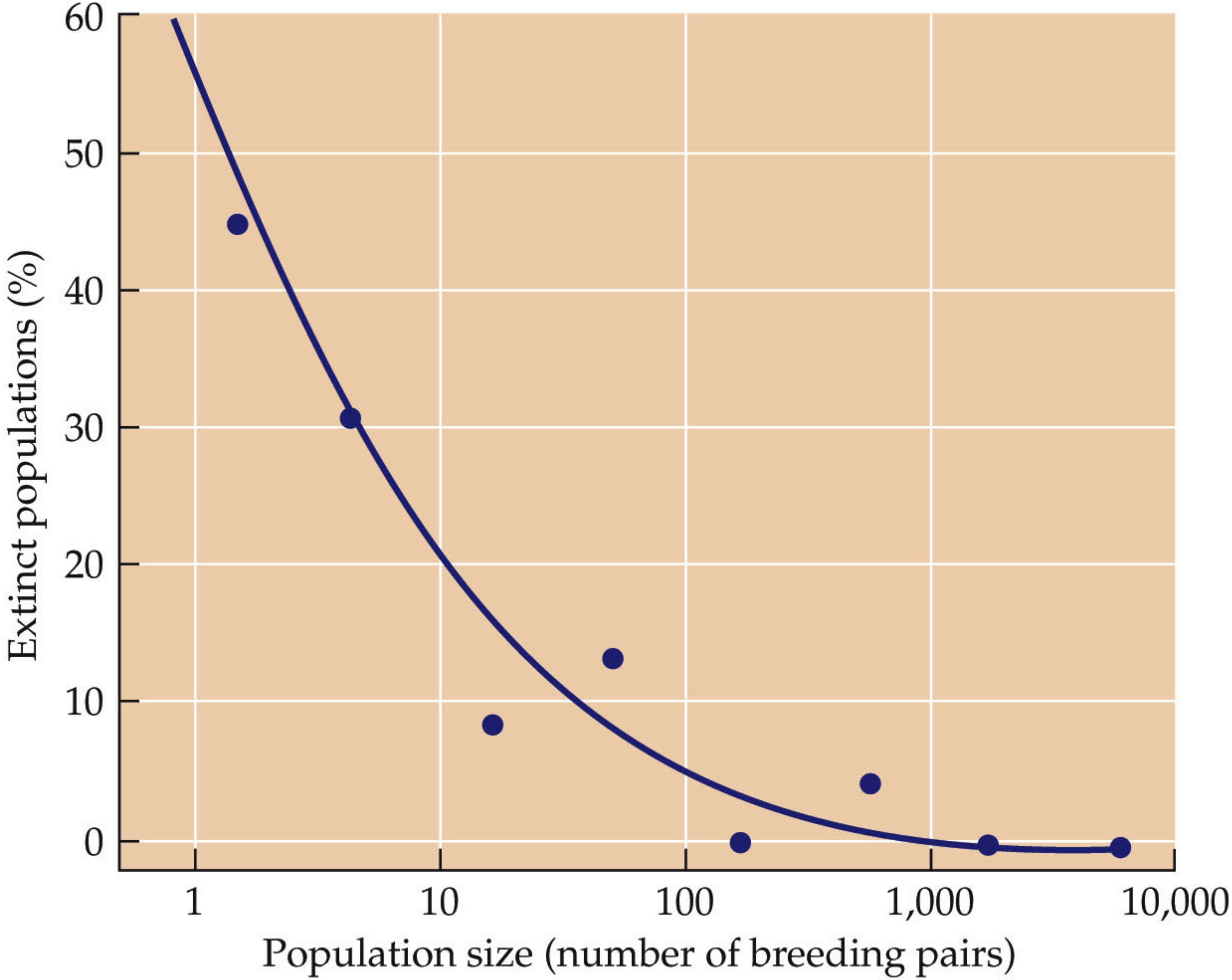
Figure 10.12 Extinction in Small Populations (Part 2)



ECOLOGY, Figure 10.12 (Part 2)

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Population Extinction

Chance events can influence fluctuations in population growth rates over time.

Chance genetic, demographic, and environmental events can play a role in making small populations vulnerable to extinction.

Genetic drift—chance events influence which alleles are passed on to the next generation.

This can cause allele frequencies to change at random from one generation to the next in small populations.

Drift reduces the genetic variation of small populations, but has little effect on large populations.

Population Extinction

Small populations are vulnerable to the effects of genetic drift for three reasons:

1. Loss of genetic variability reduces the ability of a population to respond to future environmental change.

2. Genetic drift can cause harmful alleles to occur at high frequencies.

Population Extinction

3. Small populations show a high frequency of **inbreeding** (mating between related individuals).

Inbreeding tends to increase the frequency of homozygotes, including those that have two copies of a harmful allele, which can lead to reduced reproductive success.

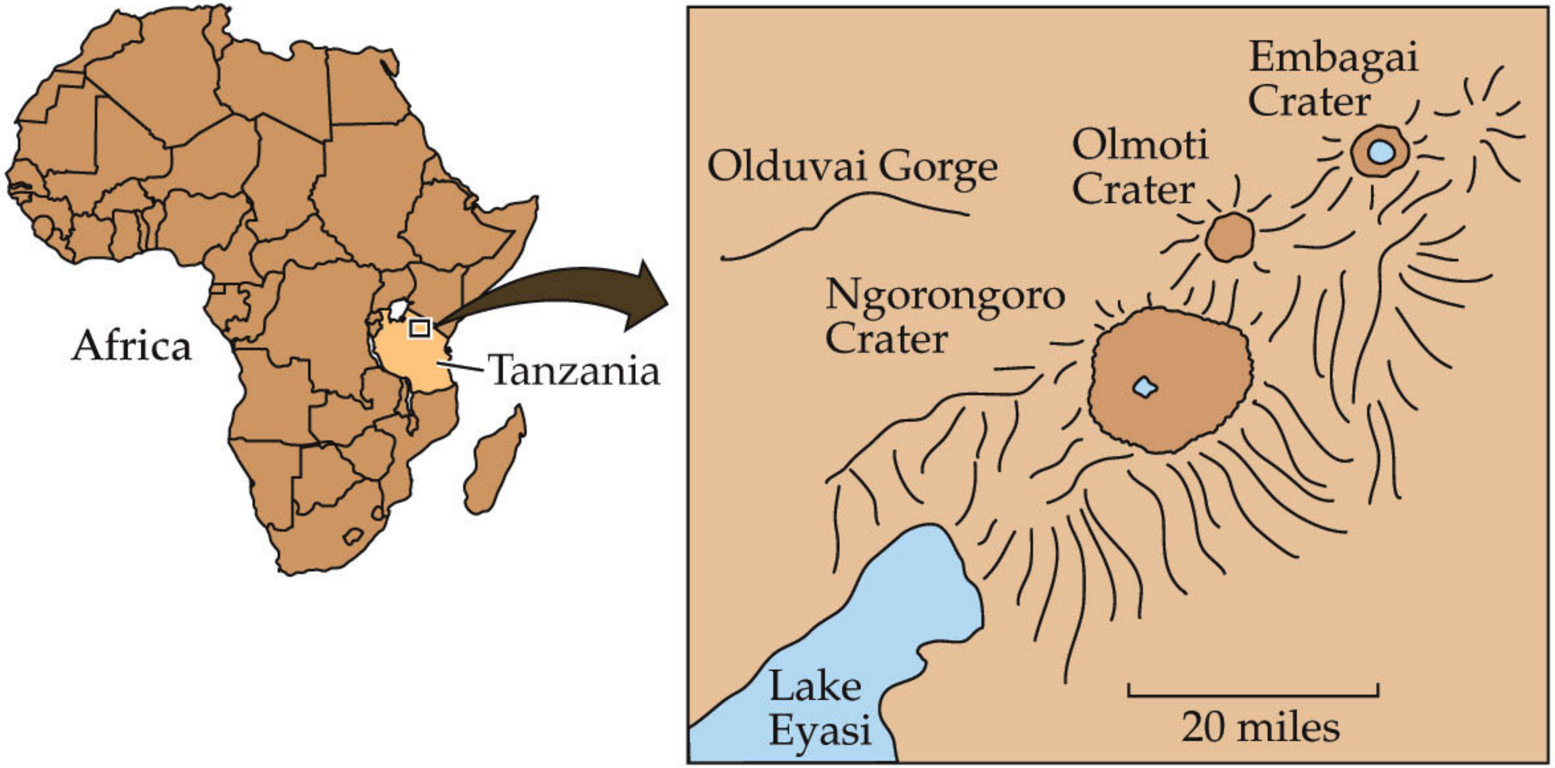
Population Extinction

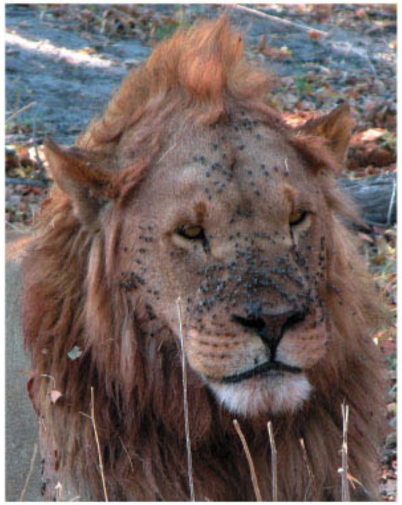
Genetic drift and inbreeding appear to have reduced the fertility of male lions in a crater in Tanzania.

In 1962 the population was reduced to a few males. Population size has since increased, but testing shows all individuals are descended from 15 lions.

The population has a high frequency of sperm abnormalities.

Figure 10.13 A Plague of Flies





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Demographic stochasticity—chance events related to the survival and reproduction of individuals.

For example, in a population of 10 individuals, if a storm wipes out 6, the 40% survival rate may be much lower than the rate predicted on average for that species.

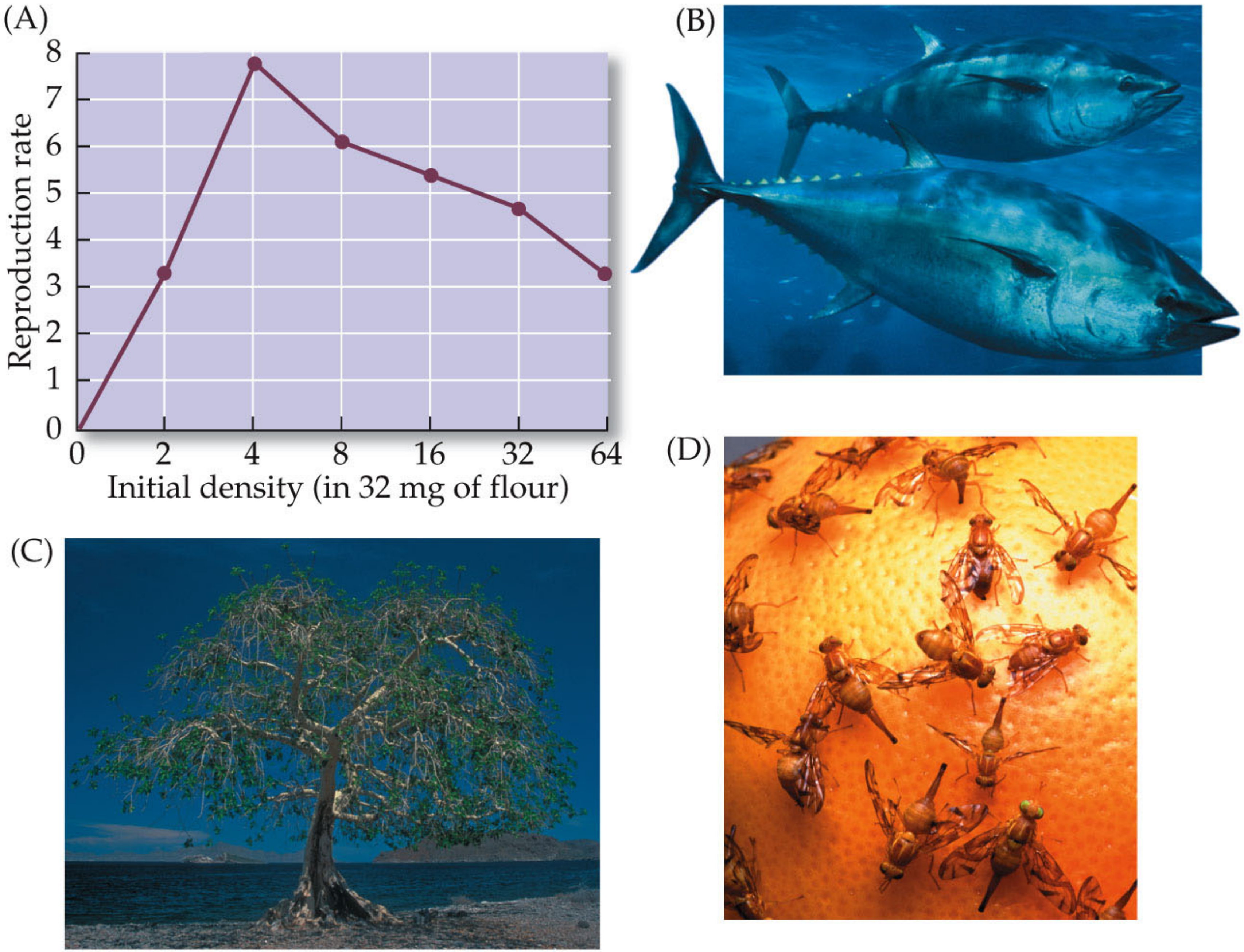
Population Extinction

When the population size is large, there is little risk of extinction from demographic stochasticity because of the laws of probability.

Allee effects—population growth rate decreases as population density decreases; individuals have difficulty finding mates at low population densities.

In small populations, Allee effects can cause the population growth rate to drop, which causes the population size to decrease even further.

Figure 10.14 Allee Effects Can Threaten Small Populations



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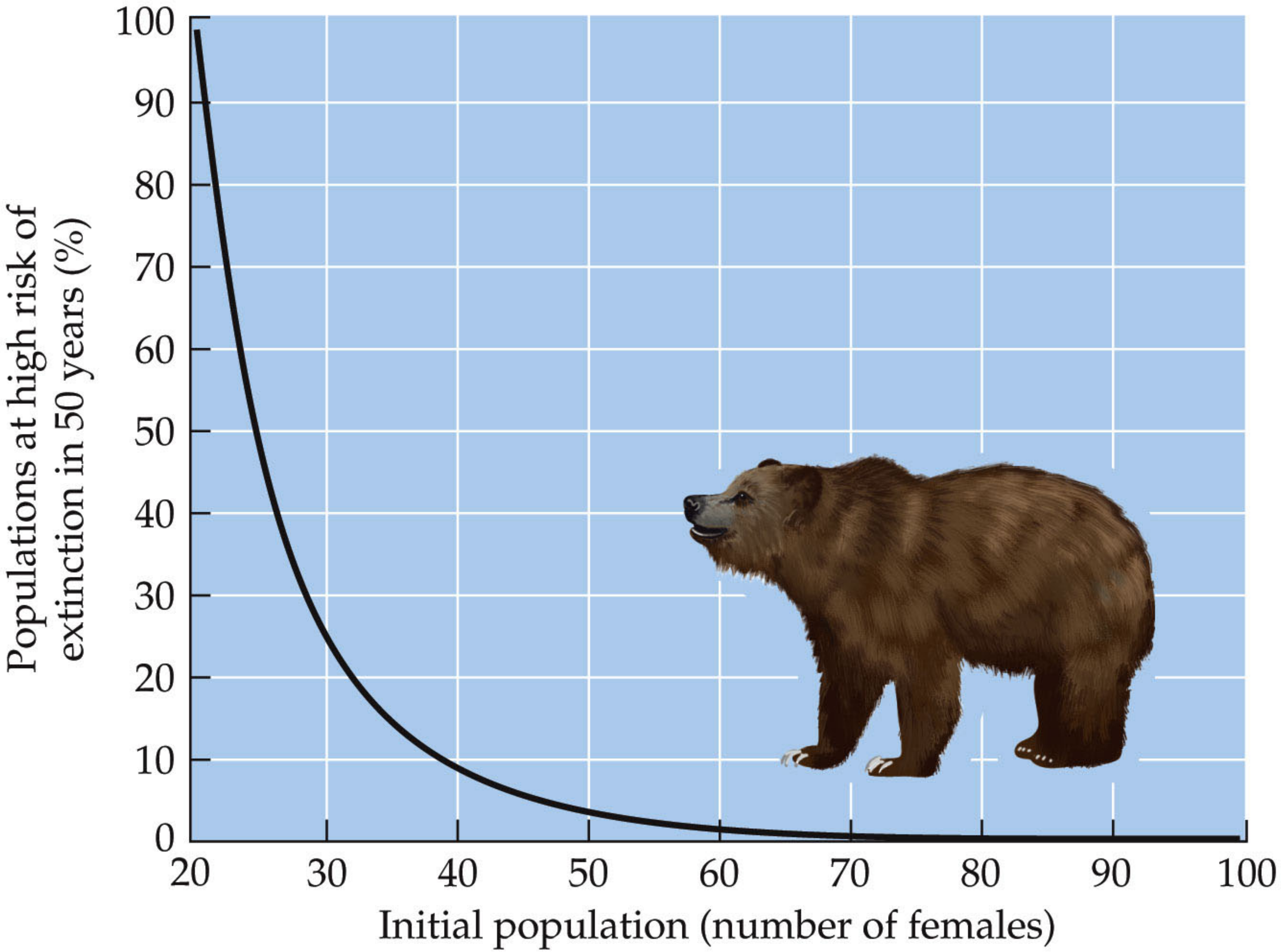
Environmental stochasticity— unpredictable changes in the environment.

Environmental variation that results in population fluctuation is more likely to cause extinction when the population size is small.

Figure 10.15 Environmental Stochasticity and Population Size



ECOLOGY, Figure 10.15

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Population Extinction

Environmental stochasticity—changes in the average birth or death rates that occur from year to year because of random changes in environmental conditions.

Demographic stochasticity—population-level birth and death rates are constant within a given year, but the actual fates of individuals differ.

Population Extinction

Natural catastrophes, such as floods, fires, severe windstorms, or outbreaks of disease or natural enemies can eliminate or greatly reduce populations.

A species can be vulnerable to extinction when all are members of one population.

Population Extinction

Heath hen populations were reduced by hunting and habitat loss to one population of 50 on Martha’s Vineyard, Massachusetts.

A reserve was established, and population size increased, but then a series of bad weather, fires, diseases, and predators decreased the population to extinction.

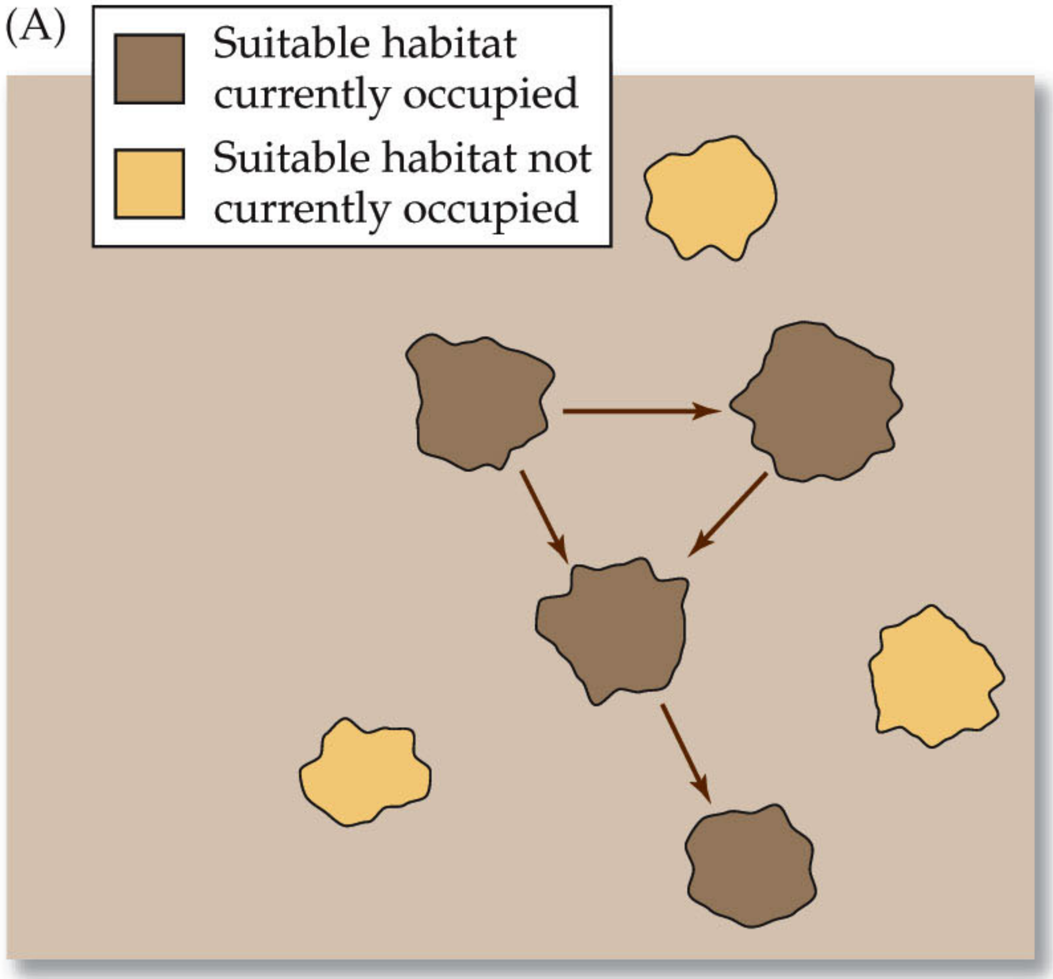
Metapopulations

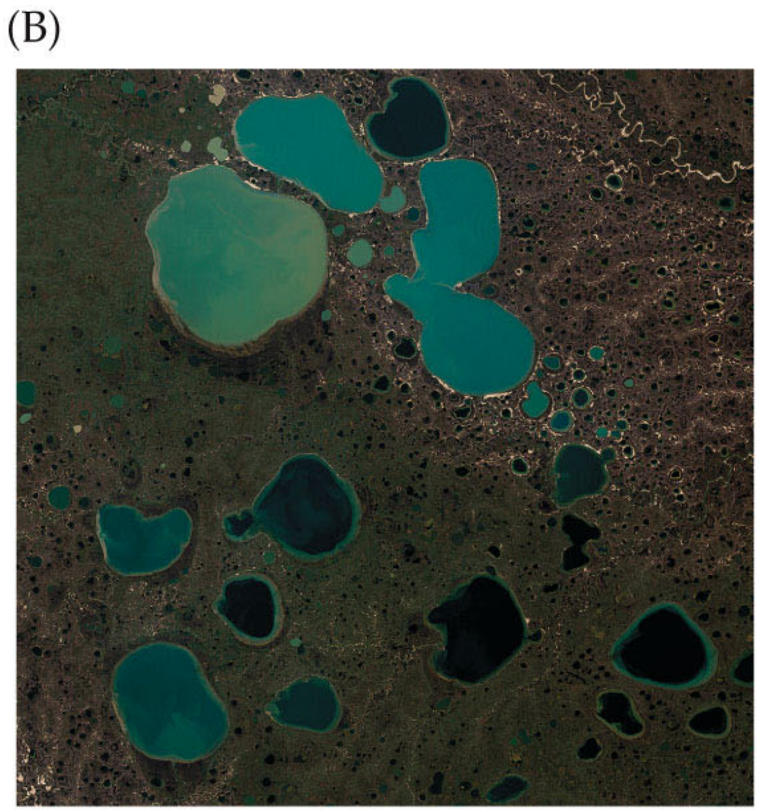
Concept 10.4: Many species have a metapopulation structure in which sets of spatially isolated populations are linked by dispersal.

For many species, areas of suitable habitat exist as a series of favorable sites that are spatially isolated from one another.

Metapopulations—spatially isolated populations that are linked by the dispersal of individuals or gametes.

Metapopulations are characterized by repeated extinctions and colonizations.





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Populations of some species are prone to extinction for two reasons:

1. The landscapes they live in are patchy (making dispersal between populations difficult).

2. Environmental conditions often change in a rapid and unpredictable manner.

Metapopulations

But the species persists because the metapopulation includes populations that are going extinct and new populations established by colonization.

Extinction and colonization of habitat patches can be described by the following equation:

$$\frac{dp}{dt} = cp\left(1 - p\right) - ep$$

p = Proportion of habitat patches that are occupied at time *t*

c = Patch colonization rate

e = Patch extinction rate

The equation was derived by Richard Levins (1969, 1970), who made several assumptions:

1. There is an infinite number of identical habitat patches.

2. All patches have an equal chance of receiving colonists.

3. All patches have an equal chance of extinction.

4. Once a patch is colonized, its population increases to its carrying capacity more rapidly than the rates of colonization and extinction (allows population dynamics within patches to be ignored).

This leads to a fundamental insight: For a metapopulation to persist for a long time, the ratio *e*/*c* must be less than 1.

Some patches will be occupied as long as the colonization rate is greater than the extinction rate; otherwise, the metapopulation will collapse and all populations in it will become extinct.

It led to research on key issues:

- How to estimate factors that influence patch colonization and extinction.
- Importance of the spatial arrangement of suitable patches.
- Extent to which the landscape between habitat patches affects dispersal.
- How to determine whether empty patches are suitable habitat or not.

Habitat fragmentation—large tracts of habitat are converted to spatially isolated habitat fragments by human activities, resulting in a metapopulation structure.

Patches may become ever smaller and more isolated, reducing colonization rate and increasing extinction rate. The *e*/*c* ratio increases.

If too much habitat is removed, e/c may shift to >1, and the metapopulation may go extinct, even if some suitable habitat remains.

Metapopulations

In studies of the northern spotted owl in old-growth forests in the Pacific Northwest, Lande (1988) estimated that the entire metapopulation would collapse if logging were to reduce the fraction of suitable patches to less than 20%.

Figure 10.17 The Northern Spotted Owl

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Real metapopulations often violate the assumptions of the Levins model.

Patches may vary in population size and ease of colonization; extinction and colonization rates can vary greatly among patches.

These rates can also be influenced by nonrandom environmental factors.

Metapopulations

Research on the skipper butterfly in grazed calcareous grasslands in the U.K. highlighted two important features of many metapopulations:

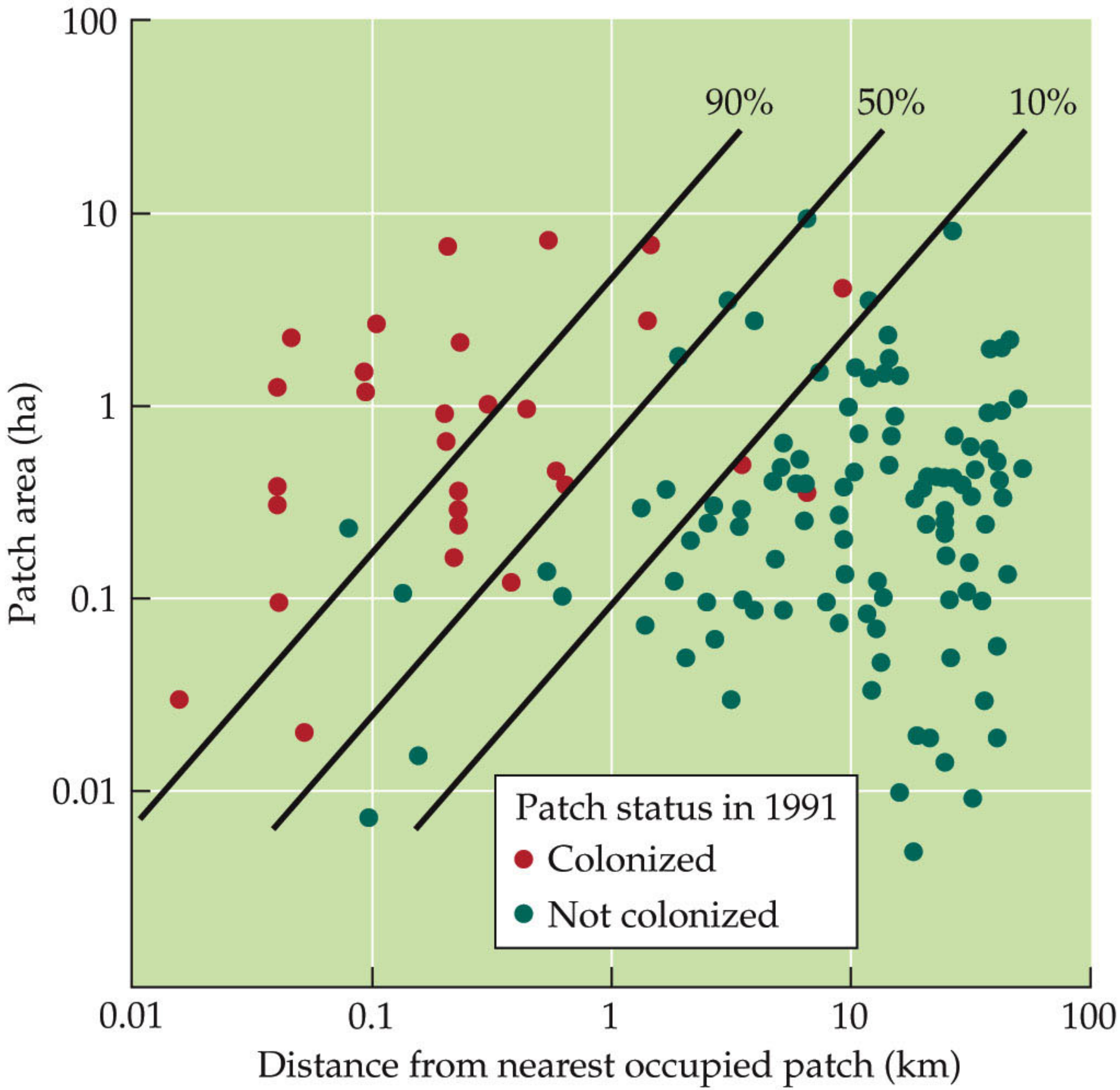
- Isolation by distance.
- The effect of patch area (or population size—small patches tend to have small population sizes).

Metapopulations

Isolation by distance—patches that are located far from occupied patches are less like to be colonized than near patches.

Patch area: Small patches may be harder to find, and also have higher extinction rates.

Figure 10.18 Colonization in a Butterfly Metapopulation



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Isolation by distance can affect chance of extinction—a patch that is near an occupied patch may receive immigrants repeatedly, making extinction less likely.

High rates of immigration to protect a population from extinction is known as the **rescue effect**.

The pool frog is found in about 60 ponds along the Baltic coast in Sweden.

Research to determine why pool frogs are not found in all ponds within its range included measurement of several environmental variables.

Figure 10.19 A Frog Metapopulation (Part 1)

ECOLOGY, Figure 10.19 (Part 1)

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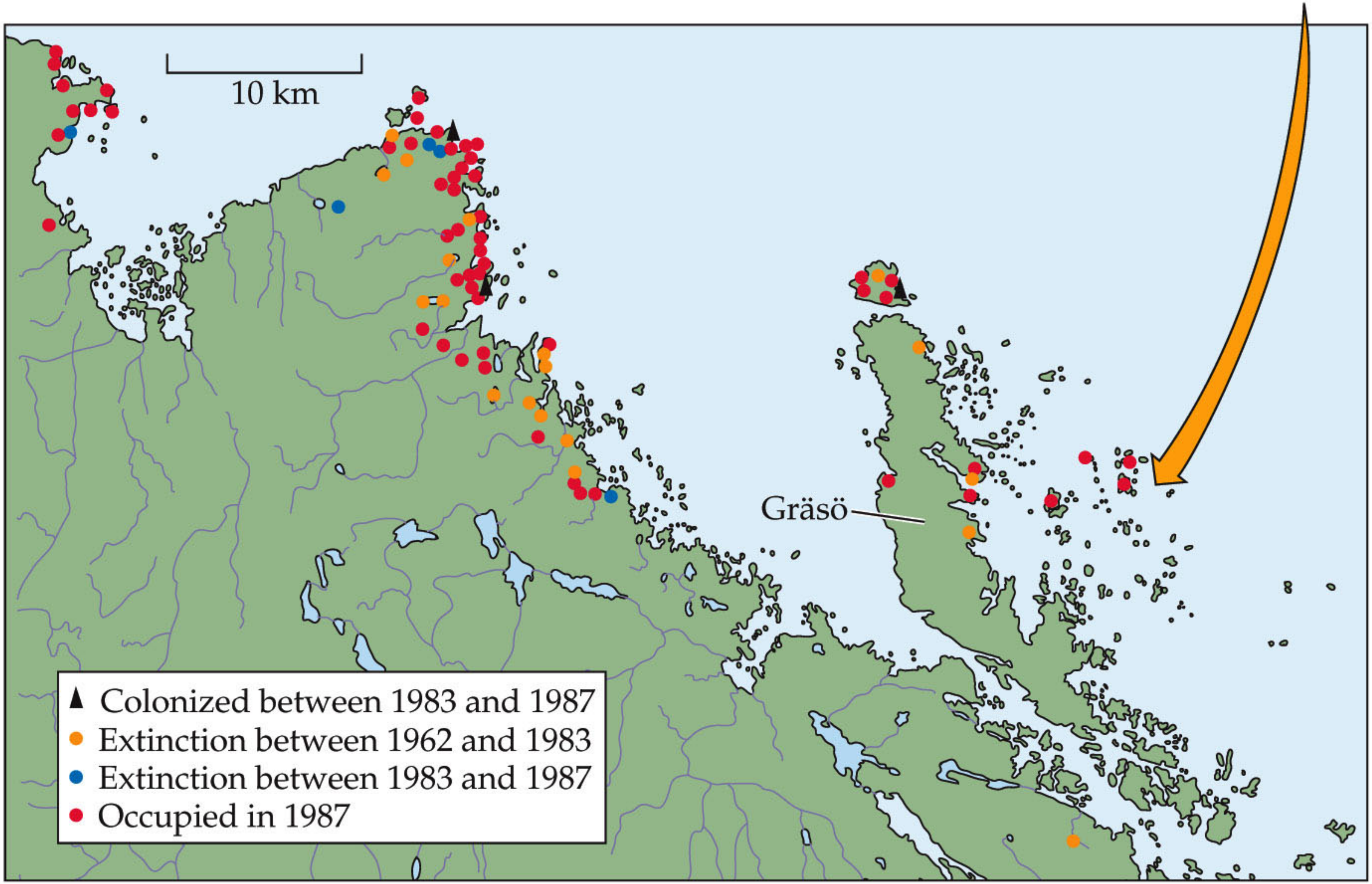
Figure 10.19 A Frog Metapopulation (Part 2)



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Several factors influenced the metapopulation:

- Ponds far away from occupied ponds experienced low colonization rates and high extinction rates.
- Pond temperature—warmer ponds were more likely to be colonized successfully because breeding success was greater in them.

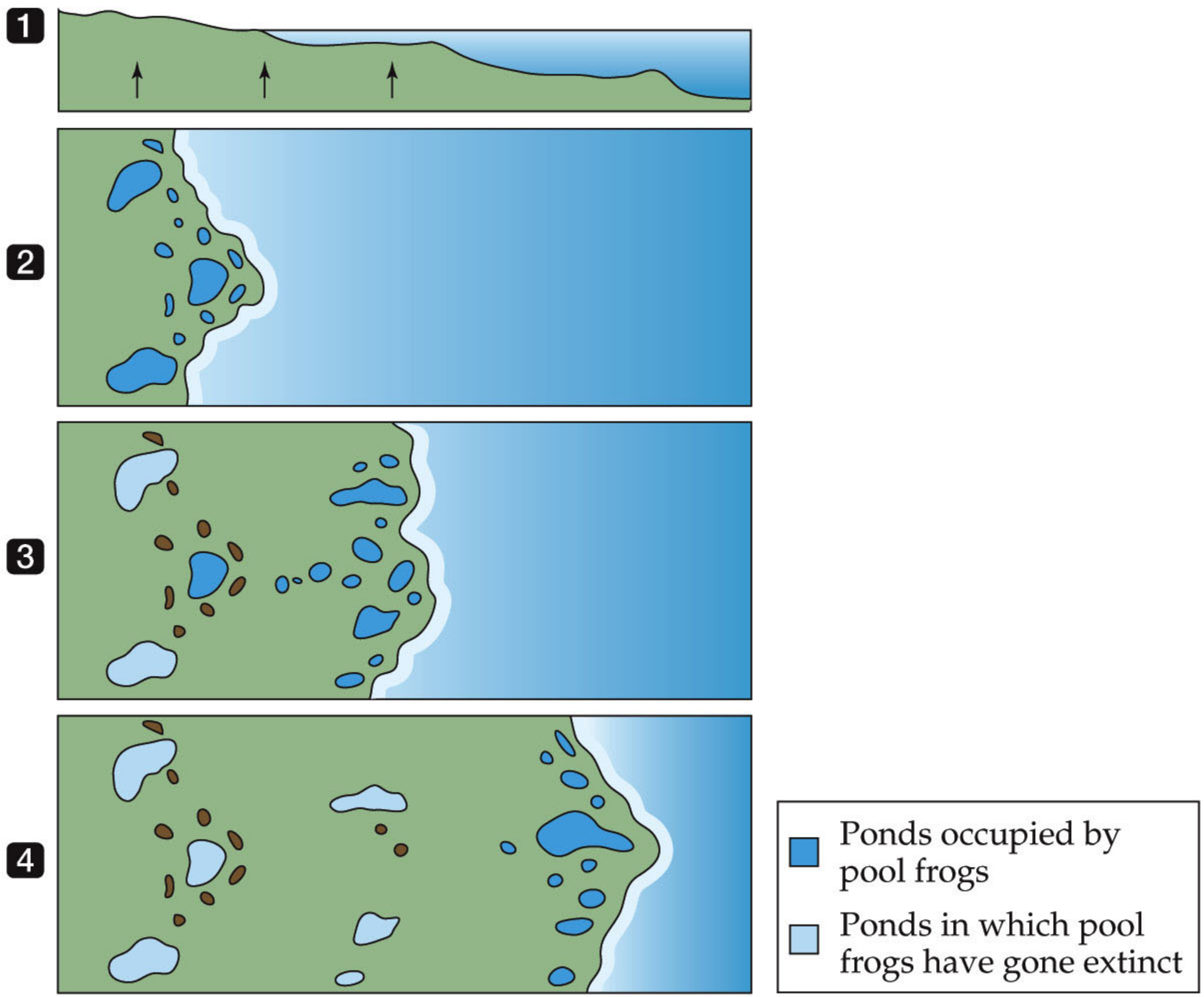
Metapopulations

- Spatial patterns suggested long-term environmental changes are important.

Uplifting of the land surface following deglaciation results in new land areas emerging from the sea, and small bays become ponds.

Over time, the small ponds gradually fill in and disappear.

Figure 10.20 Uplifting Shapes the Pool Frog Metapopulation



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Case Study Revisited: A Sea in Trouble

Recovery of the Black Sea ecosystem was underway by 1999.

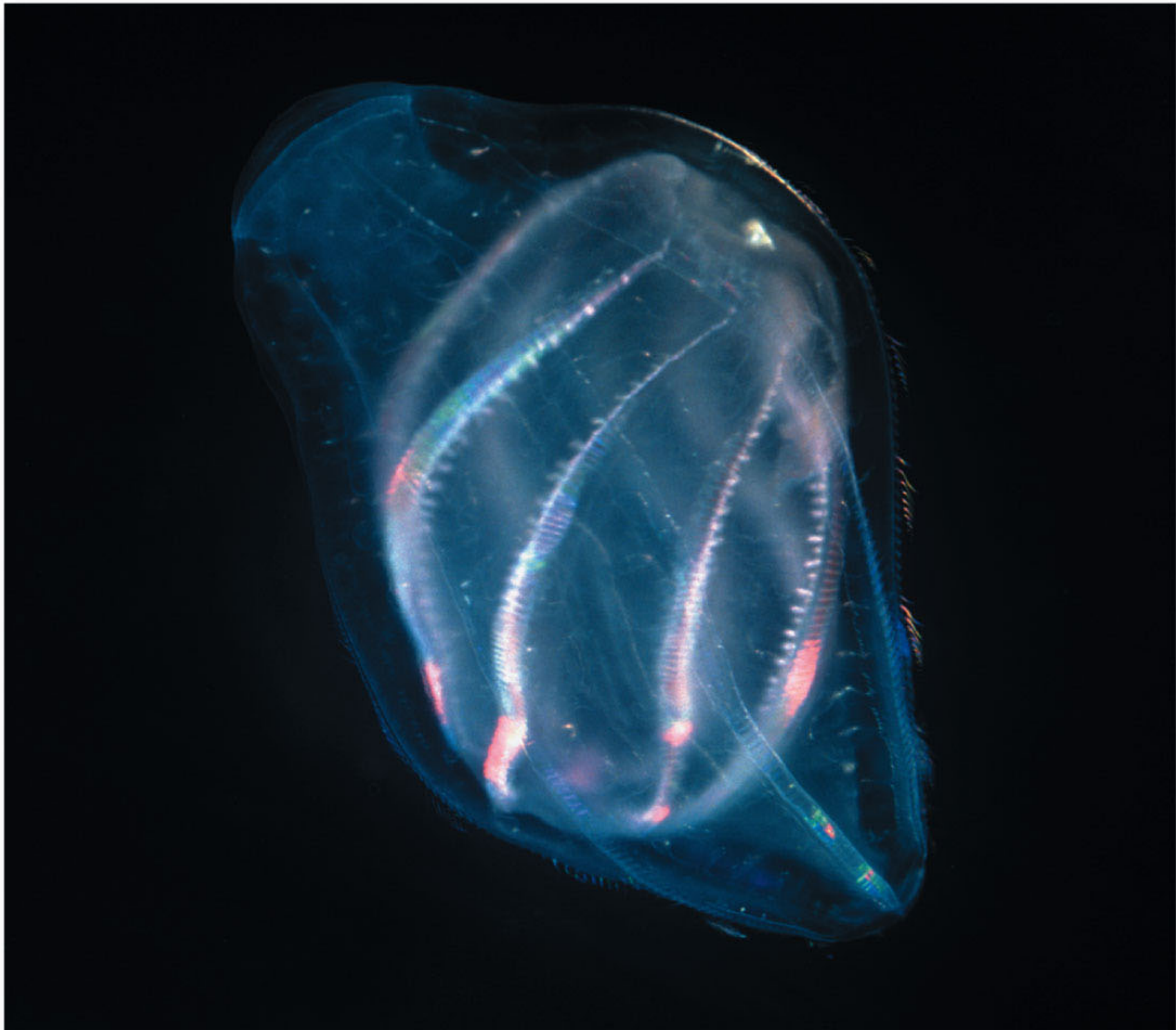
Nutrient inputs were being reduced by national and international efforts: Phosphate concentration decreased, phytoplankton biomass decreased, water clarity increased.

Case Study Revisited: A Sea in Trouble

Mnemiopsis was still a problem, but in 1997 another comb jelly arrived, *Beroe,* which feeds almost exclusively on *Mnemiopsis*.

Within 2 years of *Beroe's* arrival, *Mnemiopsis* numbers plummeted.

Figure 10.21 Invader versus Invader



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Case Study Revisited: A Sea in Trouble

The *Mnemiopsis* decline led to a rebound in zooplankton abundance and increases in the population sizes of several native jellyfish species.

There was also an increase in the anchovy catch and field counts of anchovy egg densities.

The fall and rise of the Black Sea ecosystem illustrates two important types of causation in ecological communities:

- **Bottom-up control**—increased nutrient inputs caused eutrophication and increased phytoplankton biomass, decreased oxygen, fish die-offs, etc.

- **Top-down control**—the top predators *Mnemiopsis* and *Beroe* altered key features of the ecosystem.

In many ecosystems both top-down and bottom-up controls interact to shape how ecosystems work.