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Genetics and Demography in Biological Conservation

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Predicting the extinction of single populations or species requires ecological and evolutionary information. Primary demographic factors affecting population dynamics include social structure, life history variation caused by environmental fluctuation, dispersal in spatially heterogeneous environments, and local extinction and colonization. In small populations, inbreeding can greatly reduce the average individual fitness, and loss of genetic variability from random genetic drift can diminish future adaptability to a changing environment. Theory and empirical examples suggest that demography is usually of more immediate importance than population genetics in determining the minimum viable sizes of wild populations. The practical need in biological conservation for understanding the interaction of demographic and genetic factors in extinction may provide a focus for fundamental advances at the interface of ecology and evolution.

DESTRUCTION AND FRAGMENTATION OF NATURAL AREAS, especially tropical rain forests with their high species diversity, is now causing extinction of species at a rate that is orders of magnitude as high as normal background rates of extinction (1). If there are any paleontologists in the distant future, our “modern age”—the 20th and 21st centuries—will likely be

recorded as a period of one of the greatest mass extinctions of all time, comparable to the event 65 million years ago in which it can be estimated that the majority of species then living on Earth perished (1, 2). In addition to the ethical problem of extirpating life forms that evolved over millions of years, there are practical reasons for conserving wild areas containing species of potential medical, agricultural, recreational, and industrial value (3). Ultimately, sufficient alteration of natural ecosystems may destabilize regional and global climate and biogeochemical cycles, with potentially disastrous effects (4).

Awareness of the benefits of conserving biological diversity is growing rapidly in many countries, but it remains to be seen whether conservation efforts will increase fast enough in relation to the rate of destruction to preserve much of the natural diversity that existed in the last century. As the remaining natural areas become smaller and more fragmented, it is increasingly important to understand the ecological and evolutionary dynamics of small populations in order to effectively manage and preserve them for a time when future restoration of natural areas may allow expansion of their ranges. Propagation of endangered species in captivity, for example, in zoos and arboreta, can contribute significantly to global conservation efforts; this alone, however, is not a viable alternative because limited facilities are available and because inevitable genetic changes from random genetic drift and selection in artificial environments

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may make it difficult for captive strains to be reestablished in the wild (5). Protection and restoration of natural habitats is the best and cheapest method of preserving the biological diversity and stability of the global ecosystem (2).

Most theories of extinction deal with statistical properties of large assemblages of species, ignoring details of the species' ecology and population structure (6) and, therefore, these theories cannot predict the extinction of particular species. With accelerating disturbance of natural ecosystems by habitat alteration and introduction of exotic species, it is important to develop predictive models of extinction that can be used in programs to preserve or to control particular species. Soulé and Simberloff (7) advocate an approach to the design of nature reserves that is based on target or keystone species instead of species diversity itself. Furthermore, much of the legal basis for conservation in the United States (the Endangered Species Act of 1973 and the National Forest Management Act of 1976) is oriented toward particular species rather than habitat types.

The demographic and genetic consequences of population subdivision have been subjects of increasing interest among conservationists, although inbreeding depression and the maintenance of genetic variability, traditional subjects of population genetics, have recently received by far the most attention (8). This has led to relative neglect of basic demography (the description and prediction of population growth and age structure), and conservation plans for some species have been developed primarily on population genetic principles. In this article I argue that demography may usually be of more immediate importance than population genetics in determining the minimum viable sizes of wild populations. First I review the genetics of inbreeding depression and the maintenance of genetic variability within populations. I then consider four demographic factors of fundamental importance for the survival of small populations. Finally I describe two management plans based on population genetics in which demographic principles were neglected with apparently dire consequences for the species involved.

Population Genetics

Inbreeding depression. Historically large, outcrossing populations that suddenly decline to a few individuals usually experience reduced viability and fecundity, known as inbreeding depression. In many species, lines propagated by continued brother-sister mating or self-fertilization tend to become sterile or inviable after several generations. Rapid inbreeding in small populations produces increased homozygosity of (partially) recessive deleterious mutants that are kept rare by selection in large populations, and by chance such mutations may become fixed in a small population despite counteracting selection (9, 10). Detailed genetic analysis of *Drosophila* populations indicates that roughly half the inbreeding depression is due to individually rare, but collectively abundant, nearly recessive lethal and semi-lethal mutations at about 5000 loci; individuals in large outbred populations typically are heterozygous for one or a few recessive lethals (11). The remaining inbreeding depression in *Drosophila* is caused by numerous slightly detrimental mutations that are mildly recessive (12). It is not generally realized that gradual inbreeding or reduction of population size creates relatively little permanent inbreeding depression since selection tends to purge the population of deleterious recessive alleles when they become homozygous (9, 10), although the slightly detrimental, more nearly additive mutations may be difficult (or impossible) to eliminate (12). Many invertebrate and plant species normally reproduce by sib-mating or self-fertilization; these have reduced, but appreciable, inbreeding depression manifested in heterosis or hybrid vigor upon crossing different inbred lines (10, 12).

Managers of captive populations only recently became aware of the importance of avoiding inbreeding depression in propagating small populations (13). Now attempts frequently are made to minimize inbreeding and maximize genetic variability within populations by transporting individuals (or gametes) long distances for breeding purposes (14), sometimes without sufficient attention to social factors or population structure and dispersal ability of the species in nature, or any attempt to gather or evaluate data on inbreeding depression (15). Some workers incorrectly assume that inbreeding depression is proportional to the mean inbreeding coefficient calculated from pedigree information or census data on a population (13, 16) and ignore the operation of selection during slow inbreeding. For species with an initial mean fitness high enough to withstand some inbreeding depression, even the fixation of a deleterious mutation should not preclude continued management of the population; for example, laboratory cultures of *Drosophila* homozygous for major mutations not only can persist but often gradually reevolve the wild phenotype by natural selection of minor genetic modifiers (17).

Genetic variation within populations. In small populations, random fluctuation in gene frequencies (random genetic drift) tends to reduce genetic variation, leading eventually to homozygosity and the loss of evolutionary adaptability to environmental changes. The maintenance of genetic variability in a finite population can be understood through Wright's concept of effective population size. This refers to an ideal population of N individuals with discrete generations reproducing by random union of gametes. The effective size of a population, N_e , is the number of individuals in an ideal population that would give the same rate of random genetic drift as in the actual population. Unequal numbers of males and females, increased variance in family size (greater than the mean), and temporal fluctuations in population size are the main factors causing the effective sizes of natural populations to be substantially less than their actual sizes (18). In the absence of factors acting to maintain genetic variation, such as mutation, immigration, or selection favoring heterozygotes, the expected rate of loss of heterozygosity, or purely additive genetic variance in quantitative characters, is $1/(2N_e)$ per generation.

Only a small fraction of the genetic variation will be lost on average in any one generation, because only rare alleles, which contribute little to heterozygosity or heritable variation in quantitative traits, are likely to be lost in a single generation of random sampling of gametes. However, small population size sustained for several generations can severely deplete genetic variability. Nonadditive gene expression in quantitative characters within and between polymorphic loci (dominance and epistasis) can cause transient increases in genetic variation in small populations (19), as can chance fluctuations in a purely additive genetic system, but this alone will not prevent the loss of most genetic variability within about $2N_e$ generations.

Using evidence that I compiled showing the high mutability of quantitative characters in *Drosophila*, maize, and mice (20), Franklin (21) proposed that a population with an effective size of 500 could maintain typical amounts of heritable variation in selectively neutral quantitative characters. This figure may be roughly correct even for characters under stabilizing natural selection favoring an intermediate optimum phenotype (5), but this does not justify its blanket application to species conservation. Since $N_e = 500$ has been advocated as a general rule that gives the minimum population size for long-term viability from a genetic point of view (8, 21), it has been incorporated in species survival plans for both captive and wild populations (22–24), neglecting other factors, described below, that may require larger numbers for population persistence.

Although quantitative (polygenic) characters are of major impor-

tance in adaptive evolution, other types of genetic variation also should be considered, such as the recessive lethal component of inbreeding depression, selectively neutral polymorphism (that may be adaptive in an altered environment), and single genes of large effect conferring resistance to specific selective agents causing sustained high mortality (such as pesticides or diseases). For example, the maintenance of substantial heterozygosity by mutation at neutral loci may require N_e larger than 10^5 individuals because single loci usually have low mutation rates on the order of 10^{-6} per gamete per generation (5). The relatively high mutability of quantitative traits implies that, following a period of small population size during which most genetic variability has been lost, if the population regains a large size then typical levels of heritable variance can be restored by mutation on a time scale of 10^2 or 10^3 generations, which is much faster than the 10^5 or 10^6 generations for restoration of heterozygosity by mutation at neutral loci (5). Low genetic polymorphism in soluble proteins reported in several species of large mammals (25), therefore, does not necessarily mean that the population is devoid of heritable variance in quantitative characters, or of inbreeding depression. Substantial independence of different types of genetic variation undermines the "genetic uniformitarianism" of Soulé (8), which supposes that levels of all kinds of genetic variation are proportional.

Attempts to establish the minimum size for a viable population on genetic grounds alone are highly questionable for several reasons. The management goal of preserving maximum genetic variability within populations is based on the assumption that the rate of evolution in a changing environment is limited by the amount of genetic variation (7, 8). This assumption has been previously rejected, in favor of ecological opportunity (natural selection), as the primary rate-controlling factor, at least in morphological evolution (26). Recent writings on genetics and conservation also espouse the view that genetic variation is adaptive in and of itself (7, 8).

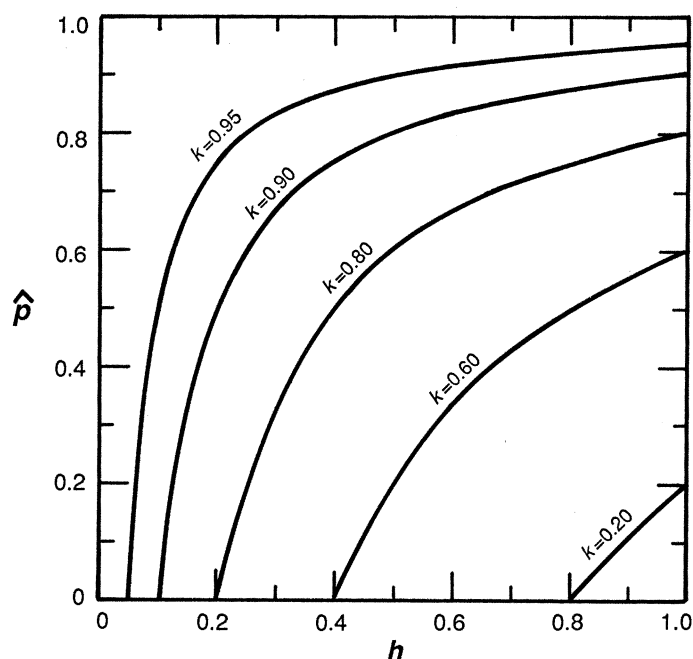


Fig. 1. The proportion of suitable habitat occupied at demographic equilibrium, \hat{p} , for a territorial age-structured population in a patchy environment; h is the proportion of a large region composed of patches of suitable habitat, each the size of individual territories, that are assumed to be randomly or evenly distributed in space. The demographic potential of the population, k , gives the equilibrium occupancy in a completely suitable region, as determined by the life history and dispersal behavior. [Reproduced with permission from (45)]

However, there is little direct evidence that heterozygosity per se increases fitness (that is, that heterozygote advantage at single loci is common), beyond simply avoiding inbreeding depression and allowing adaptation to environmental change (12). For populations tracking a moving optimum phenotype in a fluctuating environment, too much genetic variation can be detrimental since, in any generation, individuals deviating from the optimum phenotype are selected against; the optimal amount of heritable variation in a quantitative character depends on the magnitude and pattern of fluctuations in the optimum phenotype and on the strength of stabilizing selection within generations (27).

Extinction is fundamentally a demographic process, influenced by genetic and environmental factors. If a population becomes extinct for demographic reasons, such as habitat destruction, the amount of genetic variation it has is irrelevant. For example, natural extinctions of small populations of butterflies in California appear to be unrelated to their levels of protein polymorphism (28). Even for closely managed populations in a controlled environment, where genetics plays a leading role, demography cannot be neglected in achieving a stable population size and age distribution (29). For wild populations in natural or seminatural environments, demography is likely to be of more immediate importance than genetics in determining population viability. Below is an outline of demographic factors crucial to the persistence of small populations.

Demography

Allee effect. In many species, individuals in populations declining to low numbers experience diminished viability and reproduction for nongenetic reasons, and there may be a threshold density or number of individuals from below which the population cannot recover. Known as an Allee effect, this can be caused by the organisms physically or chemically modifying their environment by social interaction or by density-dependent mating success. For example, some aquatic microorganisms condition their medium by releasing substances that stimulate growth of conspecifics. Social animals frequently increase individual survival by group defense against predators and competitors. In very sparse populations, social interaction necessary for reproduction may be lacking, or it may be difficult to find a mate (30).

Stochastic demography. Extinction of single populations is influenced by two kinds of random demographic factors. "Demographic stochasticity" arises because, at any time, individuals of a given age or developmental stage have probabilities (or rates) of survival and reproduction, called vital rates. Assuming that these apply independently to each individual, demographic stochasticity produces sampling variances of the vital rates inversely proportional to population size. In contrast, "environmental stochasticity" is represented by temporal changes in the vital rates that affect all individuals of a given age or stage similarly; the sampling variances of the vital rates are then nearly independent of population size. For this reason, and because most populations undergo substantial fluctuations due to changes in weather and the abundances of interacting species, environmental stochasticity is generally considered to dominate demographic stochasticity in populations larger than about 100 individuals (31, 32). This conclusion is supported by observations of birds on islands, which, except for very small populations (initially less than 30 breeding pairs), become extinct at rates far greater than predicted by demographic stochasticity alone (31).

Simple analytical models describing the stochastic dynamics of density-dependent populations without age structure (31, 32), or density-independent populations with age structure (33), yield qualitative insights into the importance of different patterns of

fluctuations in demographic parameters in causing the decline or extinction of a population. In most cases, however, accurate prediction of extinction probabilities for density-dependent age-structured populations requires extensive computer simulation (34).

Edge effects. Two types of edge effects can be distinguished. The first is deterioration of habitat quality near an ecological boundary. Thus, after clearing surrounding areas for pastureland, new patches of tropical rain forest quickly undergo desiccation and vegetational changes up to hundreds of meters from the boundary, which makes the edges unsuitable for many rain forest species (35). The second type of edge effect concerns dispersal of individuals across an ecological boundary into unsuitable regions where they may perish or fail to reproduce. The rate of dispersal of individuals into unsuitable areas determines the minimum size of a patch of suitable habitat on which a population can persist, known as the critical patch size (36).

Kierstead and Slobodkin (37) employed a reaction-diffusion equation to describe population growth and random dispersal of individuals on a patch of suitable habitat surrounded by a region unsuitable for individual survival. They derived a condition for the population to increase when rare, assuming that population growth is density-independent at low densities (no Allee effect) and that individual dispersal movements are randomly oriented (no habitat selection behavior). Their result can be expressed in terms of the variance in dispersal distance per generation, d^2 , and two conventional demographic parameters that apply to individuals within the suitable region (excluding dispersal into unsuitable areas). The intrinsic rate of increase, r , is the exponential rate of population growth per unit time, and the generation time, T , is the average age of mothers of newborn individuals (38), in a population with a stable age distribution. Persistence of a population with a low intrinsic rate of increase per generation ($rT \ll 1$) requires the diameter of a circular patch of suitable habitat to be much larger than d .

The critical patch size model has been extended to include Allee effects, survival (and reproduction) of individuals outside the patch (38), nonrandom dispersal through behavioral habitat selection, and movement of the patch caused by climatic change (39). The second and third of these decrease the critical patch size, whereas the first and last increase it. Of course, if an area with fixed boundaries has been established as a natural preserve containing suitable habitat for some species, long-term climatic trends may induce major evolutionary changes in the population, or render the entire preserve unsuitable (40). This problem is compounded for species that undergo long-distance seasonal migrations and require two or more widely separated patches of suitable habitat (41).

Local extinction and colonization. Many species exist in subdivided populations for social reasons or because suitable habitat has a patchy spatial distribution. Fluctuating environments may make some habitat patches temporarily unsuitable, so that a widely distributed population persists through a balance between local extinction and colonization. For example, some species of plants in tropical forests exist only in light gaps left by fallen trees and rely on rapid growth and efficient dispersal to use a continually shifting mosaic of suitable habitat (42). Such localized sporadic disturbances help maintain species diversity in many natural communities (43). Critical factors affecting the persistence of a subdivided population include the number, size, and spatial distribution of patches of suitable habitat and dispersal rates between them (6).

Levins (44) developed a model of a subdivided population maintained by local extinction and colonization of suitable habitat patches. I modified his model to describe habitat use by territorial species (45). Territorial behavior ranges from the mere occupation of space to active maintenance of interindividual distance or patrolling

and defense of a home range (46). Classical demography can be integrated with habitat occupancy by identifying the individual territory as the spatial unit. Local extinction then corresponds to the death of an individual inhabiting a territory, and colonization corresponds to individual dispersal and settlement on a suitable unoccupied territory. For analytical tractability, I assumed that patches of habitat, each the size of individual territories, are either suitable or unsuitable for survival and reproduction, and suitable territories are randomly or evenly distributed in space. Juveniles disperse prior to reproduction and can search a certain number of potential territories before perishing from predation, starvation, and so on, if they do not find a suitable unoccupied territory.

The proportion of a large region composed of suitable territories is denoted as h , and the proportion of suitable territories that are occupied by adult females is p . The dispersal behavior and life history information are contained in a composite parameter, k , called the demographic potential of the population (45), because it gives the equilibrium occupancy (\hat{p}) in a completely suitable region ($\hat{p} = k$ when $h = 1$). Increasing either the number of territories a dispersing individual can search, or the expected number of offspring produced, increases both the demographic potential of the population and the equilibrium occupancy of suitable habitat. At demographic equilibrium the occupancy of suitable habitat is $\hat{p} = 1 - (1 - k)/h$ if $h > 1 - k$, and $\hat{p} = 0$ if $h \leq 1 - k$ (Fig. 1).

This model demonstrates two important features of populations maintained by local extinction and colonization. First, as the amount of suitable habitat (randomly or evenly distributed) in a region decreases, so does the proportion of the suitable habitat that is occupied. Second, there is an extinction threshold, or minimum proportion of suitable habitat in a region necessary for a population to persist. If the proportion of suitable habitat falls below $1 - k$, the population will become extinct. Extensions of this model show that an Allee effect caused by difficulty in finding a mate, an edge effect due to the finite extent of the region containing suitable habitat, or a fluctuating environment all increase the extinction threshold (45).

Conclusions

The difficulty of incorporating a multiplicity of factors into a realistic model of extinction has prompted conservation biologists to suggest numbers for minimum viable population sizes based on single factors. By whatever criteria, populations with these numbers are supposed to have a high probability of persistence for some specified period of time—for example, a 95% probability of persistence for at least 100 years, or a 99% probability for 1000 years (47). An effective population size of 500 has been suggested as sufficient to maintain genetic variation for adaptation to a changing environment (8, 21), but, as explained above, this number is of dubious validity as a general rule for managing wild populations. To illustrate this point, I give two examples of management plans based primarily on population genetics. These plans threaten the existence of the populations they were designed to protect because basic demographic factors were ignored. Both examples concern bird species inhabiting mature or old forests that now occur mainly on federal lands subject to intensive logging.

The northern spotted owl, *Strix caurina occidentalis*, is a monogamous territorial subspecies that inhabits old-growth conifer forests in the Pacific Northwest. Pairs maintain home ranges of roughly 1 to 3 square miles of conifer forest more than about 250 years old below an elevation of about 4000 feet (48). They usually nest in old hollow trees and require an open understory, characteristic of old-growth forests, for effective hunting of small mammalian prey that compose the bulk of their diet. Adults are long-lived but have low fecundity, and juveniles experience high mortality (49). Recent

estimates put the total population size of the northern spotted owl at 2500 pairs (48). In western Oregon and Washington, the remaining old-growth forest is restricted mainly to 12 national forests that are largely contiguous. To comply with the National Forest Management Act of 1976, which requires that native vertebrate species be maintained well distributed throughout their range on federal land, the U.S. Forest Service developed a plan to preserve the northern spotted owl. Originally, this was based on the supposition that protection from logging of territories for about 500 pairs distributed throughout the region would maintain enough genetic variability for the population to survive (23). However, models of stochastic demography and habitat occupancy indicate that the plan is likely to cause extinction of the owl because suitable habitat in the region will be too sparsely distributed to support a population (49). An independent assessment by the Forest Service also predicts extinction on demographic grounds, but essentially the same management strategy remains in effect (50).

The red-cockaded woodpecker, *Picoides borealis*, ranges across the southeastern United States, inhabiting pine forests more than about 80 years old, most of which currently exist on federal lands. Their preferred habitat has substantial openings, and is maintained by recurring fires that prevent succession to hardwoods. These birds live in colonies, composed of one breeding pair and up to several offspring serving as helpers, that occupy an annual home range averaging about 215 acres in which they forage for insects. Nesting occurs in cavities that may take a year for the birds to hollow out of living, mature longleaf pines (80 to 120 years old) that have had their heartwood destroyed by a fungus. The total size of the breeding population was recently estimated to be 6000 individuals (51). The recovery plan for the red-cockaded woodpecker, based on genetic considerations, has as its goal the establishment of local populations of 250 clans (500 breeding individuals) (24). The species has been listed as federally endangered since the passage of the Endangered Species Act in 1973, but subsequently has declined rapidly throughout its range as a result of fire prevention and logging of suitable, unoccupied habitat, which has severely fragmented the remaining suitable habitat (51). For example, under management by the U.S. Forest Service, populations on national forests in Texas have been declining by about 10% per year (52). Unless management practices are drastically altered, it seems that the red-cockaded woodpecker will soon be extinct.

Scientific advisory panels reviewed the inadequacies of the management plans for the northern spotted owl and the red-cockaded woodpecker and in both cases recommended abandoning simple genetic rules for establishing minimum viable population sizes (48, 51). Management of particular species should incorporate details of the species ecology, especially its life history and demography, which may require larger populations than has been suggested on genetic grounds alone.

Since conservation of the northern spotted owl and the red-cockaded woodpecker involves preserving habitats worth billions of dollars to the lumber and paper industries, in principle there should be no difficulty in funding long-term scientific studies to obtain the information necessary for sound management decisions. Already a great deal is known about both species. Why then does it appear that the conservation plans for these species are unsuccessful? Short-term economic and political interests often dominate scientific considerations in the development and implementation of management plans for threatened or endangered species. Whether economics and politics continue to produce scientifically deficient conservation plans will be decided in many cases only by extended litigation.

Future conservation plans should incorporate both demography and population genetics in assessing the requirements for species survival, recognizing that for wild populations demographic factors

may usually be of more immediate importance than genetic factors. A realistic integration of demography and population genetics, applicable to species in natural environments, is a formidable task that has enticed but largely eluded ecologists and evolutionary biologists. The immediate practical need in biological conservation for understanding the interaction of demographic and genetic factors in the extinction of small populations therefore may provide a focus for fundamental advances at the interface of ecology and evolution.

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Recruitment Dynamics in Complex Life Cycles

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Organisms living in the marine rocky intertidal zone compete for space. This, together with predation, physical disruption, and differing species tolerances to physiological stress, explains the structure of the ecological communities at some sites. At other sites the supply of larvae is limiting, and events in the offshore waters, such as wind-driven upwelling, explain the composition of intertidal communities. Whether the community ecology at a site is governed by adult-adult interactions within the site, or by limitations to the supply of larvae reaching the site, is determined by the regional pattern of circulation in the coastal waters. Models combining larval circulation with adult interactions can potentially forecast population fluctuations. These findings illustrate how processes in different ecological habitats are coupled.

HUMANITY HAS LONG BEEN PERPLEXED BY ERRATIC FLUCTUATIONS in the abundance of commercially exploited marine populations, such as sardines, herring, squid, lobsters, and crabs. One of the first models of theoretical ecology was proposed by Vito Volterra to explain such fluctuations as oscillations resulting from a nonlinear predator-prey interaction (1). Although Volterra's model is still of mathematical interest, fluctuations in marine populations are not regular enough to be considered oscillations (2) and their cause has remained mysterious.

Most biologists assume that marine population fluctuations are somehow caused by events in the offshore waters. The great Danish

marine biologist, Gunnar Thorson, observed that a majority of the marine invertebrate species whose adult phase lives on rocks or burrowed in mud have a two-phase life cycle (3). The conspicuous adult phases of barnacles, starfish, snails, clams, worms, and so forth, are usually preceded by nearly invisible larval phases that live and feed in the coastal waters for a few days to a few months, depending on the species. Most fish also have a two-phase life cycle. The dynamics of a two-phase species can, in principle, be affected at either phase. But Thorson further noted that two-phase species have large fluctuations in abundance when compared to otherwise similar one-phase species. Thus, the larval phase, and not the adult phase, was implicated as the point at which fluctuations affect marine population dynamics. Because most coastal marine populations have

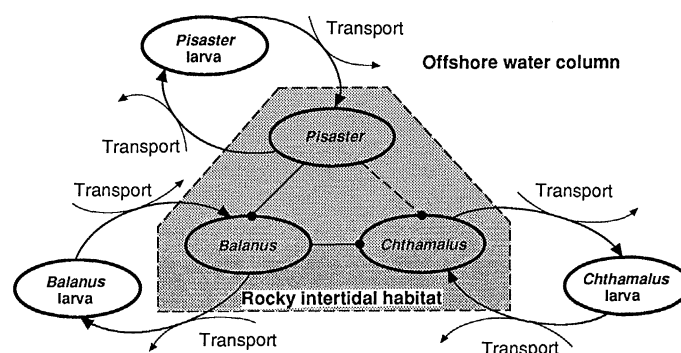


Fig. 1. Schematic of interactions between species in a community of the rocky intertidal zone. Physical contact between adult animals attached to the rocks leads to hierarchical competition for space. As shown with a line terminating in a dot, an individual of *Balanus glandula* overgrows or crushes an individual of *Chthamalus dalli*. Also, mortality from abiotic mechanisms, and from predation by the starfish *Pisaster ochraceus*, affects *B. glandula* more than *C. dalli*. Both species release a larva to the water column that may eventually return to settle on vacant space, as illustrated by the arrow coupling each life cycle to offshore transport mechanisms.

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