Dynamic Geography of Marine Fish Populations

Alec D. MacCall

BOOKS IN RECRUITMENT FISHERY
OCEANOGRAPHY

Washington Sea Grant Program
Distributed by University of Washington Press
Seattle and London

Publication of this book is supported by grant NA86AA-D-SG-44 from the National Oceanic and Atmospheric Administration to the Washington Sea Grant Program, projects E/FO-2 and A/PC-5. The U.S. Government is authorized to produce and distribute reprints for governmental purposes notwithstanding any copyright notation that may appear hereon.

Cover design (paperback) by Victoria Loe

Library of Congress Cataloging-in-Publication Data

MacCall, Alec D.
Dynamic geography of marine fish populations / Alec D. MacCall.
p. cm. —(Books in recruitment fishery oceanography)
Bibliography: p.
Includes index.
ISBN 0-295-96911-3 (University of Washington Press). —ISBN 0-295-96912-1 (University of Washington Press: pbk.)
1. Marine fishes—Geographical distribution. 2. Fish populations—Geographical distribution. I. Title. II. Series.
QL620.M33 1990
597.092—dc20 89-16509
CIP

DEDICATION

This book is dedicated to the memory of Reuben Lasker, whose unfailing support for the California Cooperative Oceanic Fisheries Investigations made this work possible.

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FOREWORD

The Washington Sea Grant monograph series, Books in Recruitment Fishery Oceanography, was established in 1988 with publication of Michael Sinclair's *Marine Populations: An Essay on Population Regulation and Speciation*. The series, of which this is the second volume, is intended to communicate current thinking and findings in the field and to accelerate the synthesis of ideas.

Recruitment fishery oceanography is concerned with the effects of environmental variability on recruitment in populations of marine organisms, especially those of commercial importance. Such studies deal with the factors that determine the continuing productivity of living resources under environmental and fishing stress. They revolve around the intriguing scientific question of how population size in marine organisms is controlled.

The interactions of the control processes are complex but are slowly being disentangled. A short-term goal of this series is to improve the predictions of the level of catch that fish populations can sustain, so that fisheries can be managed beneficially. In the longer run, these studies also will lead to a better understanding of the consequences that natural or man-induced changes in climate have for marine organisms and their human predators.

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BOOKS IN RECRUITMENT FISHERY OCEANOGRAPHY

PREFACE

The field of ecology is particularly concerned with understanding the distribution of organisms in space and time. Theoretical ecology has often addressed how organisms *should be* distributed, based on abstract principles, while field ecology (here defined as observation- or data-oriented study) has generally addressed the issue of how organisms *are* distributed. Applied ecology is more concerned with predicting the consequences of perturbations (such as harvesting) on distribution and abundance. Unfortunately, there has been too little communication and interaction among these areas of ecology (Fretwell 1972, preface; Pielou 1981). In this study I address an interconnecting set of problems that bridges these three areas of theoretical, field, and applied ecology.

As Sinclair (1988) observes, fishery research was near the mainstream of ecology through the 1920s, but the two disciplines have since separated, with very little interchange of ideas or data in recent years. Ecologists are nowadays justifiably hesitant to research the fishery literature, which is voluminous, full of jargon, often trivial, and very "gray" by academic standards. Yet population ecologists rarely have access to studies on the extensive time and space scales typical of fishery research. In turn, fishery biologists are faced with Fretwell's (1972, p. xiii) dilemma: their field requires multidisciplinary specialization such that they must become "jack of all trades, master of none" and perhaps suffer a low prestige among their more specialized counterparts in academia.

One solution is to bring ecologists and fishery biologists together occasionally in a workshop environment wherein both groups can gain a better understanding of the problems and opportunities offered by the respective disciplines. One such workshop (May 1984) was rather successful in this regard.

Another solution, which I attempt here, is to borrow an established concept from academic ecology and apply it to a major problem in fisheries. This approach has the advantage not only of demonstrating to the academic ecologist the strength and value of the large fishery data bases but also, at the same time, of suggesting to the fishery biologist the benefits that can arise from knowledge of mainstream field and theoretical ecology.

Unexpectedly, the theory of density-dependent habitat selection, which I have borrowed from academic ecology, is being returned with some modifications or at least interpretations that should be of considerable interest to the lenders. The "basin model," which I developed initially for the purpose of understanding the dynamics of exploited populations, provides a synthesis that should be useful to field ecologists as well as to theoretical ecologists. It presents a holistic view of the population dynamics determining abundance, productivity, movement, and distribution as a function of habitat or environment, and casts the model in a way that allows easy geographic visualization of entire populations. Realizing that this is a lot to promise, I can only invite ecologists to consider this "basin model" of dynamic biogeography and judge whether that promise is fulfilled.

As a fishery biologist, I feel more secure in promising my own field a new and useful tool. Indeed, the potential utility of a tool should be easier to assess in a field that is concerned primarily with application. Yet, even in the well-developed applied science of fishery ecology and management science, the utility of research is often not well understood.

WHY DO FISHERY RESEARCH?

The question "Why do fishery research?" is a reasonable one. It is seldom asked seriously, however, and serious answers are even rarer. Perhaps the main reason is that the answer seems to be obvious: Fishery research provides knowledge that enables resources to be used to greater societal benefit through increased yield or value, or perhaps for a predictive capability which decreases risk. Unfortunately, this answer is not fully consistent with actual practice (MacCall 1986).

It is a reasonable assumption that more knowledge or information should allow a closer approach to optimum utilization of a resource. Still, the resource itself has limits to the benefits it can provide. Thus, the value of relevant information is also limited and must conform to the rule of diminishing returns. Initial information on a resource is valuable in establishing reasonable expectations by management, whereas additional information serves mainly to refine the approach to optimum utilization.

It is arguable whether there is a limit to information in the way that there is a limit to the benefits or value of a fishery. Certainly, there is a limit to information on future environmental conditions that may determine major resource fluctuations. In any case, accumulation of useful information also conforms to the rule of diminishing returns as a function of cost.

The relationship between the cost of information and its benefit in an ideal fishery is instructive (Figure P.1). The net value of a fishery is benefit less cost. Optimality consists of maximizing that value when benefit and cost are appropriately measured. Because of the rule of diminishing returns described above, the maximum net value achievable from a fishery must occur at relatively low levels of information. Such a management regime would be characterized as low-expectation, low-cost, and robust or self-limiting (low risk). For example, the fleet would be limited to a size that is able to harvest a quantity well short of the estimated maximum sustainable yield. Costs associated with quota determinations, monitoring, and enforcement would be avoided.

Ideal management is somewhat of a fiction but serves mainly to contrast with actual management (Figure P.1). Performance of actual management has been variable, but most often fishery value has been dissipated by excess fleet capacity (so-called overcapitalization) and excess fishing pressure, placing the fishery on the descending limb of the production curve (i.e., increased fishing intensity leads to decreased average yield). Importantly, this dissipation occurs in spite of substantial knowledge about its causes and cures.

Information costs can be evaluated in terms of fishery economics: research is in effect a form of capital investment, and monitoring incurs an operating cost. From this viewpoint, actual management tends to overinvest (or overcapitalize) in information, and this habit has been a further source of dissipation of total fishery value.

It is easy to see the forces that cause this problem. Managers, researchers, and the various interest groups that vie for allocations of the resource all agree on the need for more information to support their individual interests or arguments. The cost of the research is seldom a consideration; usually it is not borne directly by the fishery or by the interest group requesting or benefiting from it, but rather by government agencies. Private interest groups may add to this total expenditure by hiring consultants to arm them with new information. Furthermore, such expenditures are often matched by the cost of government or opposing interest groups' responses to such efforts.

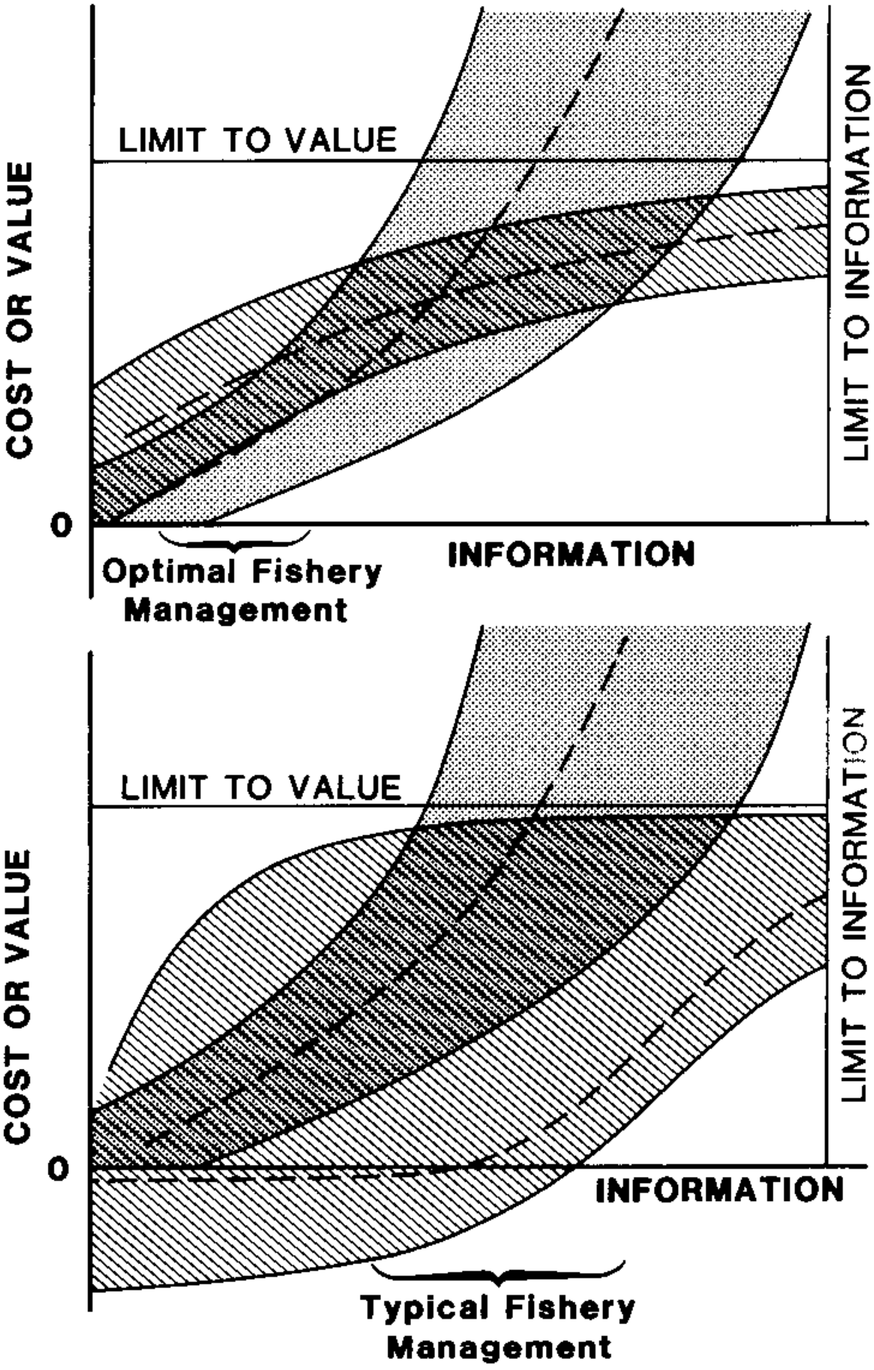

Figure P.1 Probable cost of information (stippled region) relative to its probable benefit to a fishery (hatched region): *upper*, "ideal" management; *lower*, "typical" management. Dashed line represents the most likely outcome. From MacCall (1986).

WHAT SHOULD WE DO?

Contrary to first impressions, the solution is not simply to spend less on monitoring and research. Present fishery management institutions have locked themselves into policies and operating procedures that require intensive research and monitoring efforts. For example, in the United States most implementations of the Magnuson Fishery Management and Conservation Act have required annual setting of harvest limits, quotas, or allocations. These determinations require timely information on the status of the resource, harvests, and concerns of relevant interest groups. Given the existing management frameworks, substantial reduction of investment in information would incur a high risk of further declines in fishery value due to subsequent misinformed or uninformed management decisions.

The model in Figure P.1 suggests that there are two courses of action that promise to improve the cost-effectiveness of research, monitoring, and management. The first, and less likely of the two, is to change management toward a "low-information" system. The potential value realizable from low-information management is critically dependent on establishing the appropriate management expectations and institutions. Such institutions would be substantially different from those governing most fisheries in the United States and elsewhere, and most likely they would be perceived to be nondemocratic, or at least nonegalitarian, requiring severe limitation on the freedom of new participants to enter the fishery. Unless it were enforced by property rights, this closure would be politically fragile because the fishery would be very profitable to those participants who are able to gain access.

The second course of action seeks to change the shape or position of the cost and benefit curves in Figure P.1. Good management requires that routine fishery monitoring and research be conducted efficiently, or cost-effectively. Although there usually is room for improvement, I will assume that the cost of information has already been made as low as possible. This leaves the problem of shifting the benefit curve while remaining under the constraint of existing management institutions, tools, and policies. The opportunity to open up new management possibilities within the existing management philosophy occurs rarely. Here I introduce one such opportunity, based on principles of biogeography, and I invite the fishery biologist to explore and consider those possibilities.

ACKNOWLEDGMENT

I am indebted to the many people who have worked on and supported the California Cooperative Oceanic Fisheries Investigations (CalCOFI) Program since 1950, including scientists, technicians, ships' personnel, and the commercial fishermen whose self-imposed tax initially generated the CalCOFI Program. During the development of this work, I have had the good fortune to be associated closely with all three of the primary institutions participating in CalCOFI: the California Department of Fish and Game, the Southwest Fisheries Center of the National Marine Fisheries Service, NOAA, and the Scripps Institution of Oceanography of the University of California at San Diego.

As with any research involving the development of concepts, many people have contributed to this effort, generating new ideas and suggestions, and critically examining others. The informal nature of most of these developmental discussions makes it difficult to recognize everyone who should be acknowledged, but at a minimum I must thank John Hunter, Daniel Goodman, Richard Methot, Roger Hewitt, Gary Stauffer, and the late John Radovich. I thank Gary Sharp for the discussions and circumstances (a workshop he convened) that provided the germinal idea leading to these studies. I am grateful to Richard Charter and James Power for invaluable technical assistance. Timothy Ragen, Wayne Getz, and an anonymous reviewer provided valuable suggestions for clarifying and improving the manuscript. I am indebted to Roy Allen for his skill and patience in drafting many of the figures.

Finally, I must thank Warren Wooster and the University of Washington for inviting me to present the series of lectures leading to this book. It was a pleasure working with Washington Sea Grant, and especially with Patricia Peyton and Alma Johnson, who are the kind of editors every author wishes for.

1

POPULATION THEORY OF DENSITY-DEPENDENT HABITAT SELECTION

Considerable ecological literature, both observational and theoretical, has treated the subject of habitat selection and habitat distribution. Most of the observational literature examines how individuals apportion their time among habitats, or would be expected to apportion it, or how apparently sympatric species are differentially distributed among local habitats.

1.1 BACKGROUND

Perhaps due to the short-term nature of most field studies, little observational work has been done regarding the influence of intraspecific population density on habitat selection. In those studies where abundance has varied sufficiently, it is common to observe differential utilization of habitats depending on overall population size. The term ''density-dependent habitat selection'' (DDHS) refers to this special category of habitat selection, in which population size and local density are important factors influencing choice of habitat and hence relative distribution of the population among habitats.

There also is a large body of theoretical literature that generically has been called population dynamic models in heterogeneous environments (reviewed by Levin 1976, 1986). These models and simulations include interacting elements of habitat variability in space and time, population growth, habitat selection, movement, and diffusion, many of which bear some tangential relationship to the present study. I refer to this literature at various places in the following discussions but will not attempt a coherent review. Rosenzweig's (1985) review focuses on habitat selection and is quite useful in the present context, particularly as it relates to DDHS and larger-scale population behavior.

1.1.1 Historical Development

The theory of DDHS has developed along two separate lines. The first is biogeographic, documenting relationships among habitat distribution, local density, and overall population abundance. Much of the early work was done by European ornithologists, e.g., Svardson (1949), Kluyver and Tinbergen (1954), and Glas (1960), who observed differential relationships between changes in local densities and changes in population abundance. One of the most commonly observed phenomena associated with DDHS is expansion and contraction of population range or differential utilization of marginal habitat with changes in population abundance (Table 1.1). This line of investigation is now being rejuvenated by modern biogeographers such as Brown (1984).

TABLE 1.1 Examples of species showing differential utilization of habitats or expansion-contraction of range with changes in abundance.

CATEGORY	EXAMPLE	REFERENCE
Fish	Anchovy	Kramer and Ahlstrom (1968)
	Sardine	Kondo (1980), Murphy (1977)
	Minnow	Fraser and Sise (1980)
Birds	Canary	Mayr (1926)
	Duck, gull	Svardson (1949)
	Titmouse	Kluyver and Tinbergen (1954)
	Chaffinch	Glas (1960)
	Blackbird	Lenington (1980)
Insects	Aphid	Whitham (1980)
	Bee	Thomson (1978)
Reptiles	*Anolis* lizard	Schoener and Schoener (1980)
Small mammals	Lemming (2 spp)	Pitelka (1973)
	Snowshoe hare	Wolff (1980)
Large mammals	Baleen whale	Allen (1972)
	Elephant seal	Bodkin et al. (1985)
	Man	Knight (1924), Gordon (1954)

The second line of investigation seeks to explore or explain DDHS by behavioral models, often accompanied by mathematical or graphical representations of the governing principles. These behavioral theories of DDHS have developed as numerous independent treatments in ecology, most of which address very localized geographic scales. One of the earliest was Morisita's (1952, 1971) theory of "environmental density." Morisita's treatment did not gain wide acceptance, perhaps due to an apparent, though not substantive, lack of generality. The Fretwell-Lucas theory (e.g., Fretwell and Lucas 1970, Fretwell 1972, Whitham 1980, Rosenzweig 1981, Morris 1987) is the most general treatment. The Verner-Orians theory (e.g., Verner 1964, Orians 1969, Downhower and Armitage 1971, Lenington 1980) is more fully developed in terms of evolutionary theory. Although this theory has been rather narrowly restricted to polygynous mating systems, in many ways it can be considered to be a special case of the Fretwell-Lucas theory.

Beckmann (1957) developed a similar economic-geographic model of human demography based on analogies to physical principles such as energy potential and fluid dynamics. It is the most mathematically complete treatment, and the only one that has attempted to describe phenomena at the population level. Again, Beckmann's model failed to gain significant recognition in ecological circles, perhaps because social and economic concepts used in human demography did not at the time have immediately obvious equivalents in population ecology.

It seems appropriate to note the independent development of concepts akin to DDHS in the field of economics, extending back to the work of David Ricardo, who pioneered the concepts of diminishing returns and economic rents in the early nineteenth century. Knight (1924), exploring these ideas in relation to social welfare, treated the "marginal value theorem," which was independently discovered in the biological context of optimal foraging some forty years later by Charnov (1976). Again, Gordon's (1953, 1954) analysis of fishermen's choices among alternative fishing grounds produced habitat utilization diagrams nearly identical to those of Fretwell.

Cross references among the various treatments of DDHS are exceedingly rare, even in review articles such as those by Davies (1978), Partridge (1978), and Garson et al. (1981) (but see Parker [1984] and Vehrencamp and Bradbury [1984] for possible exceptions). This lack is especially surprising, given that the Fretwell-Lucas and Verner-Orians theories both first appeared and are well known in ornithological contexts. These reviewers, and hence many ecologists, may not have recognized fully the unifying principles of DDHS underlying the various models.

1.1.2 Fretwell-Lucas Theory of DDHS

The Fretwell-Lucas theory postulates multiple discrete habitats that may be ordered in terms of a basic "suitability" (a vaguely defined term which will be treated later). As the density of individuals increases in a habitat, realized suitability decreases from the basic level (defined as the suitability at zero density), due to density-dependent effects (Figure 1.1). In the "ideal free distribution" all individuals are capable of choosing the most suitable habitat, and are free to occupy that habitat regardless of prior occupants. Initially individuals occupy habitats with the highest basic suitability, but as realized suitability of these habitats declines due to increasing population density, other previously less suitable unoccupied habitats become equally attractive and are colonized. As a consequence of this process, the ideal free distribution is characterized by equal realized suitability in all occupied habitats: no individual has a better habitat to which it can go.

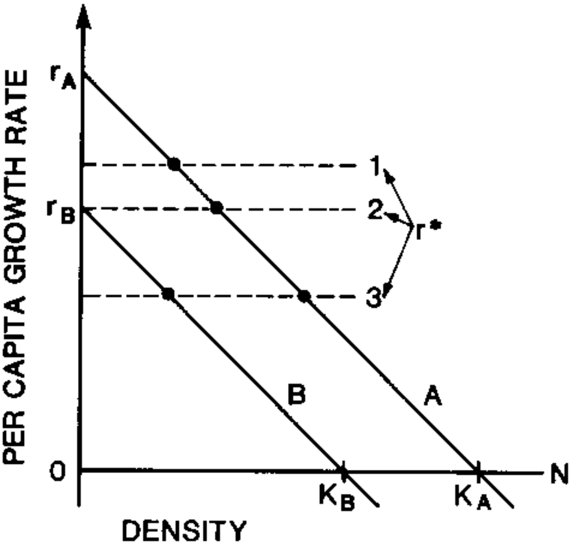

Figure 1.1 Habitat suitability, as realized per capita growth rate (r^*) versus local population density (N), based on the "constant slope" logistic model. A and B are two example habitat types with respective basic suitability r and carrying capacity K; 1, 2, and 3 are realized per capita growth rates at respectively larger total population sizes; solid dots indicate habitat population densities according to the ideal free distribution. Modified from Fretwell (1972, Fig. 31).

This population behavior can also be described by the game theory of the evolutionarily stable strategy (ESS) pioneered by Maynard Smith (1982). Pulliam and Caraco (1984) point out that when no individual in an *n*-person game can increase its fitness by moving, we have a "Nash equilibrium." If all individuals possess equal fitness as a result, we have the ideal free distribution, which is also an ESS.

Many interesting variants of the ideal free distribution arise when complications are added. For example, territoriality may prevent an individual from occupying the most suitable habitat because it is already occupied. In this case, the individual is forced to occupy a less suitable habitat, resulting in Fretwell's (1972) "ideal despotic distribution."

Few attempts have been made to investigate population growth dynamics associated specifically with DDHS. As mentioned previously, Beckmann's (1957) model, which did treat the subject, was not widely familiar to ecologists. Brown (1969) recognized that differential occupation of good and poor reproductive habitats should influence population productivity curves. He graphically examined productivity of various distributions of birds between two habitats but had no criterion for assuming a particular distribution, as was subsequently developed by Fretwell and Lucas (1970) and Orians (1969). Prior to Brown's model, population productivity had been assumed to decrease if territoriality forced some individuals to reproduce in poor habitat. Brown correctly concluded that this behavior could actually increase total productivity over the case in which all individuals were allowed to crowd into the best habitat with consequent decreased per capita reproductive success in that habitat.

1.1.3 Habitat Suitability

The concept of "suitability" is not well defined in previous development of the theory of density-dependent habitat selection. Fretwell (1972) equated habitat "goodness" with habitat suitability, and proceeded to say that "the goodness of each occupied habitat is related to the average potential contribution from that habitat to the gene pool of succeeding generations of the species." Suitability is the measure of that goodness, being "thought of as the average success rate in the context of evolution (and/or 'adaptedness') of adults resident in the habitat." Fretwell's wording suggests an intuitive concept akin to Fisher's (1958) more formally developed "reproductive value," which offers a basis for a more rigorous definition of habitat suitability.

Many recent interpretations of Fretwell's theory substitute "fitness" for the original concept of suitability, often with no reference to the original term. In a recent review of theoretical aspects of habitat selection, Rosenzweig (1985) assumes that "individual organisms select particular habitats because they thereby enhance their fitness." In reviews of the Fretwell and Lucas model, Pulliam and Caraco (1984) and Łomnicki (1987) use the term "fitness" exclusively, without any reference to the original concept of "suitability." In "fitness" we again have a vaguely defined term that is akin to reproductive value. As there has been a heated and not clearly resolved debate over the relationship between reproductive value and fitness (for an entry, see Stenseth 1984), I am reluctant to enter into the controversy.

Goodman (1982) has shown that an optimal life history is equivalent, under specific constraints, to maximization of reproductive value at all ages. Habitat selection adds another level of complexity to this already difficult problem: Beyond optimizing the choice of life table schedules within a demographically or environmentally imposed fitness set (Levins 1968), the individual organism must choose among alternative fitness sets corresponding to available habitats and population densities. Until recently the Fretwell and Lucas model was cast implicitly in terms of identical individuals, but Harper (1982) and Łomnicki (1987) have extended the concept of the ideal free distribution to include differences in fitness among individuals.

Thus, in principle, true habitat suitabilities should be closely related, if not equivalent, to marginal changes in Fisher's reproductive value due to habitat and the population density therein. Moreover, if large numbers of organisms (whether or not they differ individually) select habitats according to similar rules, these marginal changes in reproductive value should be manifested as marginal changes in the intrinsic rate of increase of the local population.

From a practical viewpoint, habitat selection often involves little more than selecting one of the better immediately available habitats. When viewed as a process, rather than in terms of the ultimate distribution of individuals (a state), optimality does not have to be considered explicitly. The process of iteratively selecting better available habitats will "track" optimality without necessarily ever achieving that ephemeral state (cf. Roughgarden 1974). Of course, as Fretwell noted, "the stimuli directly influencing the choice of habitat may be no more than correlated with habitat goodness." Insofar as behavioral responses to such stimuli tend to optimize an organism's life history, natural selection should favor those responses however indirect the actual stimuli may be. The result may be a very imprecise, but nonetheless beneficial, set of behaviors regarding choice of habitat.

The remainder of this discussion will mostly treat an idealized organism with the simple population dynamics represented by the logistic growth model. This model has the convenient properties that age structure is immaterial and that degradation of habitat suitability is linear with local density. Importantly, habitat suitability is instantaneously manifested as a per capita growth rate, providing a convenient analog for reproductive value. After exploring the case of the locally logistic growth model, I extend this habitat selection model to include some alternative and perhaps more realistic nonlinear growth models.

1.2 POPULATION MODEL OF HABITAT SELECTION

Most previous models of density-dependent habitat selection have been confined to portrayal of discrete habitats (e.g., Fretwell and Lucas 1970, Rosenzweig 1981). A discrete formulation is often appropriate to terrestrial organisms, and is useful in simulation models such as those in Chapter 2. But as Levin (1986) points out, a continuous formulation is more amenable to analytic treatment, and on biological grounds may be preferable for modeling aquatic systems. Thus, extension of the DDHS model to a formulation of continuous habitat lays the groundwork for considering the dynamics and geographic behavior of entire fish populations.

This extension consists of three steps. First, I describe local population growth rates as functions of local basic habitat suitability and population density under the equal-suitability constraint of an ideal free distribution. Second, I portray habitat suitabilities as a continuum over the potential geographic range of the population. Finally, I add the dynamics of movement among habitats, thereby providing a mechanism by which the ideal free distribution can be approached.

1.2.1 Local Dynamics

The logistic model describes the local population growth rate in habitat *h* by the differential equation

$$\frac{dN_h}{dt} = r_h N_h \left(1 - b_h N_h\right) , \tag{1.1}$$

where r_h is the basic habitat suitability, and b_h is a coefficient of the density-dependent decrement in per capita growth rate. For the present discussion, I assume unit area, so that density and abundance (N_h) are locally equivalent. Thus, the realized per capita growth rate, denoted r^*, is determined by basic habitat suitability and declines linearly with local population density (Figure 1.1),

$$r^*(N,h) = \frac{1}{N_h} \frac{dN_h}{dt} . \tag{1.2}$$

While the coefficient of density dependence may well vary among habitats, this complexity prevents easy visualization of the geographic model being developed. I consider a simpler model for the remainder of the immediate discussion: *b* is taken as constant among all habitats, leading to a family of parallel per capita growth curves as shown in Figure 1.1(see Appendix).

According to the ideal free distribution, individuals distribute themselves among available habitats so that all individuals experience the same realized suitability (viz. marginal reproductive value); r^* is constant for all occupied habitats but varies with total population size. Thus, if the ideal free distribution holds, the geographic pattern of population density will follow and in effect will ''map'' the geographic pattern of basic habitat suitability. This map is scaled according to the coefficient of density dependence, *b*, which relates population density to the difference between basic suitability for the location and the uniform realized suitability for the entire population. Areas of high basic habitat suitability will exhibit a correspondingly high local density of individuals, whereas areas of lower basic habitat suitability exhibit a lower density of individuals. In this context, it is apparent that Morisita's concept of "environmental density" is virtually identical to Fretwell's "suitability," except that they are expressed in different units. Also note that if *b* varies among habitats, population densities would provide a distorted map of basic suitabilities.

1.2.2 Continuous Habitat

A long tradition of plant biogeography has developed an extensive knowledge of plant distributions. In a review of 135 species' distributions, Austin (1972) found that 95 percent of them showed densities that were higher toward the center than toward the edges of the distribution and 73 percent were unimodal. The distributions of animals have not been reviewed as extensively, but Brown (1984) concurs that animal densities commonly follow a similar geographic pattern. The plant ecologists have tended to hypothesize a Gaussian normal physiological response to gradients of controlling environmental factors. However, Westman (1980) found that of 40 factors examined in a Gaussian factor analysis of a community of 40 species of coastal sage scrub, no single factor was able to explain more than about 30 percent of the variance of the best fitting 25 species. He concluded that distributions of abundances must have a multifactor basis.

Brown (1984) further argues that the abundance and distribution of a species is determined by many physical and biotic variables, and that many of these variables are serially correlated in space and time. The statistical properties of these additive random variables creates a continuous habitat that supports an approximately Gaussian spatial distribution of abundance. Brown seems satisfied to conclude that abundances will be higher where conditions are more favorable, but avoids discussion of mechanisms that determine abundance as a function of habitat suitability; he does not address the possible role of density dependence in this hypothesis, except to imply that it is potentially one of the factors.

In the present model, where density-dependent reduction of habitat suitability plays an active role, the multifactor Gaussian habitat model works well. The basic suitability of habitats may be determined by combinations of density-independent factors, as well as by physiological response curves, and the most favorable combinations of these factors occurs near the center of the species' range. Importantly, the factors determining suitability may be quite different at opposite ends of the species' range, but the net suitabilities themselves may nonetheless be similar.

In recent years the idea of density dependence has become controversial in ecological circles, and indeed, there are many possible alternative mechanisms that may determine population abundance and distribution. However, the sustainability of fishery harvests gives support to the existence of strong compensatory mechanisms in fish; and very few mechanisms other than direct density-dependent influences on growth, fecundity, and survivorship can provide this amount of compensation. Also, density-dependent compensatory mechanisms have been fairly well identified for many harvested fish populations. These mechanisms, such as cannibalism (also see Chapter 3) and population size or density-dependent growth and fecundity, have been reviewed by Garrod and Knights (1979) and by Goodyear (1980).

1.2.3 Basin Model

If habitat suitability or per capita growth rate is depicted graphically as *increasing downward,* habitats can be described as a continuous geographic suitability topography having the appearance of an irregular basin (Figure 1.2), whose shape may also vary over time. According to the ideal free distribution, the population will fill this basin as if it were a liquid under the influence of gravity (this analogy is equivalent to Beckmann's "potential").

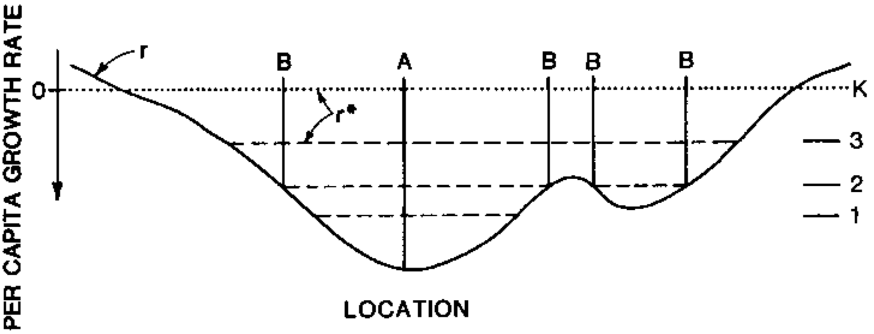

Figure 1.2 Transect through a continuous geographic fitness topography. A and B are the habitat types, and 1, 2, and 3 correspond to the total population sizes in Figure 1.1. Realized suitability (per capita population growth rate), shown by the dashed line, is equal in all occupied habitats due to the ideal free distribution. A population size of carrying capacity (K) is reached when growth rate becomes zero.

- The free surface of the liquid will be approximately level, corresponding to the uniform realized suitability, r^*, resulting from the ideal free distribution.
- The "shoreline" corresponds to habitats whose basic suitability is exactly equal to r^*, establishing the range of the population.
- The depth of the liquid at any location is proportional to the density-dependent reduction in realized suitability at that location, and is proportional to local density.
- The total volume of liquid in the basin is thereby functionally related to total population size.

Insofar as densities tend to be highest toward the center of an organism's range, the deepest area of the basin (i.e., greatest basic suitability) will be central, and the topography will become progressively shallower toward the periphery. Parsons (1982) warns that ecologically marginal habitat tends to be correlated with geographically peripheral habitat but may occur in more central areas as well. Interior marginal habitat appears as peaks or ridges within the basin topography.

In this model "carrying capacity" (K) corresponds to the population size that fills the basin to a level producing zero growth rate of the population ($r^* = 0$). As in the usual logistic model, overall abundance is limited by density dependence. However, here the carrying capacity is determined by the integrated total quantity of habitat at all levels of suitability better than the margin at population size K (i.e., $r_{h(K)} = 0$, where $h(K)$ denotes marginal habitat at carrying capacity). As the population grows or declines toward K, the limitation is more gradual than in the corresponding logistic population model, and is related to the slope of the sides of the basin in the vicinity of $h(K)$. Indeed, a logistic population model would result from the special case of a constant-slope local logistic model and a habitat suitability basin that is flat bottomed with vertical walls.

This "basin model" of biogeography is consistent with Mayr (1963, 1970), who observes that the influence of density-dependent factors logically should be the greatest at the center of a population. Both Mayr and Levins (1968) agree that density-independent factors accordingly should prevail at the edges of the population. This property is shown by the basin model, but the location of the edges for a given population can now be seen to be determined in part by the interaction of habitat selection and density dependence in other areas: the range of the population will necessarily expand and contract with changes in overall abundance (recall Table 1.1). The ideal free distribution and constant rate of density dependence in this basin model produce the somewhat surprising prediction that a single additional individual would have the same effect wherever it is added to the population, i.e., despite the local relative importance of density-dependent versus density-independent factors.

1.2.4 Movement

While the previous section describes the ideal spatial distribution at equilibrium, a complete model should include the dynamics leading to that equilibrium. Previous models of DDHS have assumed that individuals are highly mobile, are able to assess the suitabilities of all potential habitats, and simply make the best selection from among them. While this assumption is perhaps reasonable at the community level, especially for birds, it is insufficient to describe the community dynamics of less mobile species, or population-level dynamics of most species.

The following dynamics require that habitat be sufficiently fine-grained that individuals are able to respond to large-scale gradients of habitat suitability that tend to be detectable at the scale of their short-term ambits. There are a multitude of possible models that portray these dynamics, and this has been an active area of theoretical ecology, as can be seen in the extensive review by Okubo (1980). Nearly all of the components of the following model have appeared in the literature. The treatment offered here differs from previous migration and diffusion models in that the equilibrium spatial distribution of abundance must approach an ideal free distribution. This distribution arises from movements of individual organisms in response to gradients in realized habitat suitability (described by the model given in the previous section), and/or from differential population growth among habitats.

The movement model treated here is relatively continuous in its behavior. An important class of alternative models would be those that are nonlinear or perhaps discontinuous, where movement is minimal below a threshold level of density or suitability but very active above that threshold. This type of "irruptive" movement was envisioned by Brown (1957) in his theory of "centrifugal speciation" and has been discussed in the context of small mammals by Lidicker (1962, 1975). Some mathematical models of this type of movement may be found in Okubo (1980) but are not pursued here.

Change in abundance (ΔN) at a particular location is given by the general model

$$\Delta N = G - H + D + (I - E) \;, \tag{1.3}$$

where G is the in situ population growth (births less natural deaths), H is harvest, D is diffusion into or out of the location, and I and E are immigration and emigration. The partitioning of movement into diffusion and immigration-emigration corresponds to a vectorial partitioning of individual movement into variance and mean directional movement terms, respectively. Immigration and emigration are oriented to gradients in qualities of local habitat. Diffusion arises from random movements, and resultant net movement is oriented only to gradients of population density, independent of habitat suitability.

In theoretical models, Equation (1.3) is often expressed as a partial differential equation. Here the equation will relate to a one-dimensional continuous habitat, with the understanding that similar equations can be written which simultaneously describe dynamics including a second or third orthogonal spatial dimension. The components of Equation (1.3) are discussed separately.

Population growth (G) is given by the "constant slope" logistic model described previously (Equations 1.1 and 1.2). Harvest (H) is represented by a per capita death rate (F), giving

$$\frac{\partial N}{\partial t} = r^*N - FN \,. \tag{1.4}$$

(In the following equations, the habitat subscript (h) is omitted for simplicity.)

Diffusion, immigration, and emigration are often modeled by analogy to the molecular advection-diffusion equation

$$\frac{\partial S}{\partial t} = \mathscr{K}\frac{\partial^2 S}{\partial x^2} - u\frac{\partial S}{\partial x}\,, \tag{1.5}$$

where x denotes location along a continuum, S is the concentration of a substance, $\mathscr{K}$ is a coefficient of diffusivity, and u is an advective velocity. As Okubo (1980) warns, "the direct importation of a diffusion equation that applies strictly to such microscopic phenomena as the diffusion of molecular solutes to problems involving macroscopic diffusions, especially animal diffusion, is dangerous." However, equations similar to the form of (1.5) have been developed from plausible biological assumptions by Gurney and Nisbet (1975, 1976), Okubo (1980), Shigesada et al. (1979), and Skellam (1951).

The form of equation required by the present abstract model is arbitrary: simplicity and clarity are the main requirements. By assuming that the rate of migratory flow (u) is proportional to the gradient in realized habitat suitability ($\partial r^*/\partial x$), I obtain the equation

$$\frac{\partial N}{\partial t} = \mathscr{K}\frac{\partial^2 N}{\partial x^2} - V^{-1}\frac{\partial r^*}{\partial x}\frac{\partial N}{\partial x} \tag{1.6}$$

where V is a constant determining the rate of population flow per unit gradient in realized habitat suitability, and is a biological analog of viscosity; i.e., the higher the viscosity, the lower the rate of flow in response to gradients in realized habitat suitability. Note that this use of the term "viscosity" is different from some recent ecological usages (e.g., Pollock 1983) in which viscosity and diffusivity are nearly synonymous. Here it is worthwhile distinguishing between rate of movement oriented to gradients in habitat suitability (viscosity) and rate of movement oriented to gradients in population density (diffusivity).

The complete model is obtained by combining Equations (1.4) and (1.6):

$$\frac{\partial N}{\partial t} = r^*N - FN + \mathcal{K}\,\frac{\partial^2 N}{\partial x^2} - V^{-1}\,\frac{\partial r^*}{\partial x}\,\frac{\partial N}{\partial x} \tag{1.7}$$

where $r^* = r(1 - bN)$. Note that r^* influences both the rate of population growth and migratory flow. This is a theoretically desirable property of such a model, as the evolutionarily appropriate reward for responding to a habitat suitability gradient should be increased reproductive value.

Equation (1.7) is a convenient abstract summary of the forces in the basin model. Importantly, the basin model can be implemented in many other ways, including more realistic dynamics and processes. Some alternative forms, including nonlinear growth models and territoriality will be considered later in this chapter. Simulations more closely resembling fish life histories with a diffusive meroplanktonic larval phase will be considered in Chapter 2.

1.3 BEHAVIOR OF THE POPULATION MODEL

This model is capable of rather complicated behavior, especially with regard to transients and spatial-temporal variability in the topography of basic habitat suitability (r_h). Its primary purpose is to combine the dynamics of population growth with geographic considerations of habitat and population distribution or movement. For example, a major climatic change such as the eastern Pacific oceanic warming called El Niño is associated with species displacements as well as severely impacted reproductive rates (Caviedes 1975). The basin model might portray such a change as a shifted and raised basin (Figure 1.3), where the population moves to the most suitable habitat under the changed environment, and at the same time shifts from a condition of population growth to one of decline. Again, rapid temporal or intense spatial variability in the habitat basin topography may be realistic for some populations. The basin model remains a potentially useful tool for describing these cases, but its behavior becomes difficult to generalize. This discussion will examine some of the most straightforward properties of the model, focusing on equilibrium and near-equilibrium behavior.

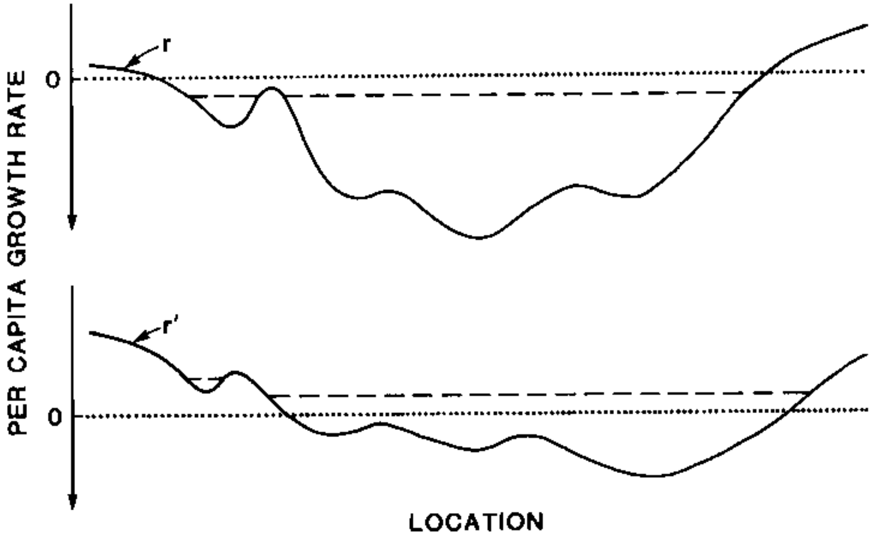

Figure 1.3 Idealized population response to a climatic shift. The preshift habitat suitability basin (r) is more favorable than the postshift (r') basin. The population moves in response to the shift, maintaining an ideal free distribution, but changes from a condition of growth to one of decline. The peripherally isolated segment of the habitat basin at the left is viable under preshift conditions, but it is not viable after the shift and could experience local extinction or catastrophic selection.

1.3.1 Expansion and Contraction

One of the most important features of the basin model is its ability to account for changes in the range of the population as a function of overall abundance and large-scale changes in density-independent factors. As described previously, the range or location of the "shoreline" is determined by the basin topography and the volume of "liquid" that corresponds to the total population abundance.

It is the expansion and contraction of this shoreline, with residual outlying pools in peripheral depressions of the basin topography (Figure 1.3), that Brown (1957) envisioned as providing the conditions for "centrifugal speciation." This theory envisioned speciation in isolated pockets of abundance left after population cycles of geographic expansion and contraction which are "the sequelae of inevitable density fluctuations affecting all or part of the species at one time." Brown lamented the lack of formal or theoretical explanations for these expansions and contractions but felt secure with the strong empirical evidence for their existence.

Lewis (1962), carrying the idea somewhat further, postulated that peripheral isolated segments of the population may undergo "catastrophic selection" whereby adverse conditions eliminate all individuals except for a very few with rare deviant phenotypes which may act as founders of new species. This basin model accommodates this mechanism quite naturally: Conditions leading to an overall decline in population abundance and isolated peripheral segments are also likely to produce submarginal conditions ($r_h < 0$) in some of those peripheral locations, so that the occupying population segments tend toward extinction (Figure 1.3) and experience catastrophic selection. Moreover, this basin model suggests that individuals in these peripheral habitats are likely to have been subject to forces toward centrifugal speciation prior to the catastrophe, so that there may well have been preselection toward those deviant phenotypes that survive the catastrophe.

Bearing in mind that the local density-dependent decline in realized habitat suitability formally is the product of the local density and the coefficient of density dependence (b in the above equations), this model also predicts expansion and contraction of the range if there were changes in the assumed uniform coefficient of density dependence. The volume of "liquid" is the integral of the product bN over the population; that volume is proportional not only to N but to b as well. Again, if b were to change among local habitats, distortion would result.

A simple simulation of expansion and contraction due to change in b is shown in Figure 1.4. The simulated population has access to four habitats, which it occupies according to the ideal free distribution. At the normal rate of density dependence, three of the habitats are occupied. However, if the rate of density dependence is doubled, all four habitats become occupied. Similarly, a reduction in the rate of density dependence leads to contraction into the two best habitats. As expected, the carrying capacity or population size at equilibrium is also affected by these changes, so that the expanded population will tend to decline and the contracted population will tend to grow. Surprisingly, the *relative* equilibrium (i.e., at $r^* = 0$) distribution of abundances among the four habitats is the same; the population tends toward this distribution independently of the mean rate of density dependence.

1.3.2 Effects of Diffusion

Local equilibrium is described by $\partial N/\partial t = 0$. If we assume that the population exhibits an ideal free distribution, the advection (immigration, emigration) term must equal zero since r^* is the same everywhere. Also assuming that the population is at carrying capacity (i.e., growth

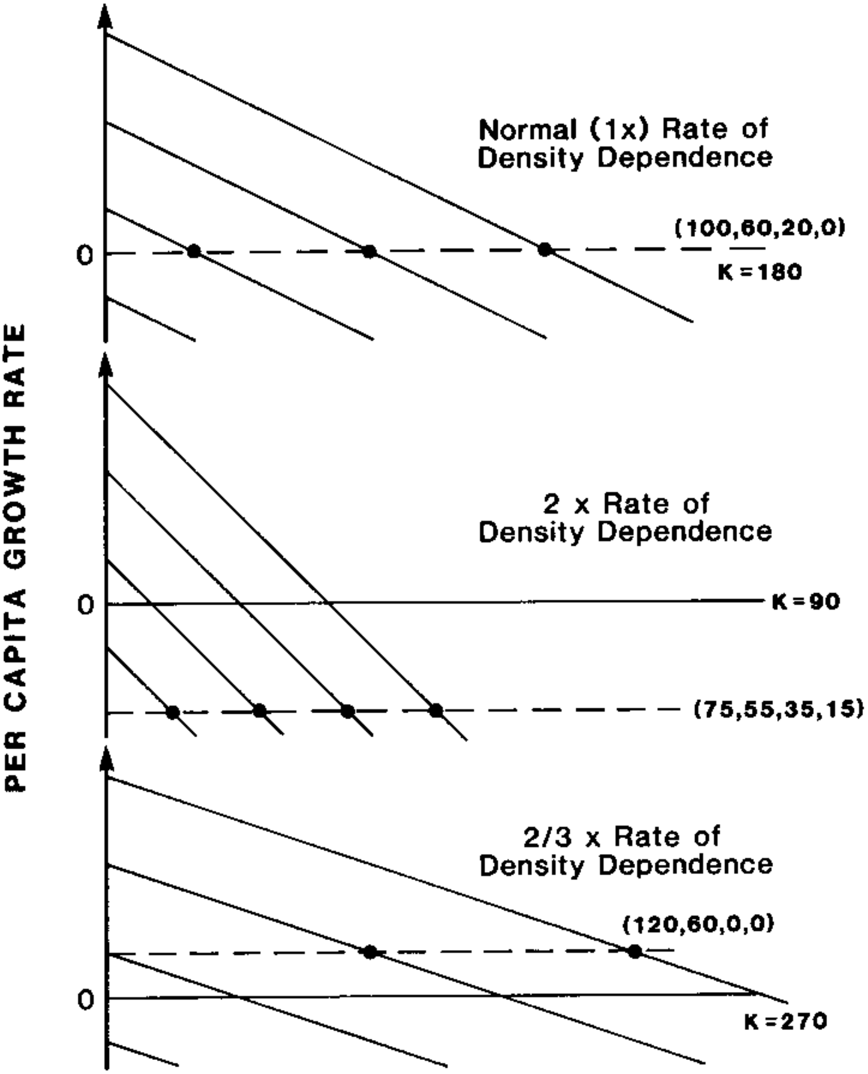

Figure 1.4 Expansion and contraction of the range due to a change in the rate of density dependence. The population is distributed among four habitats. The ideal free distribution is shown by the dots (abundances are given in parentheses, sum is 180). *K* indicates total abundance at equilibrium (carrying capacity).

equilibrium), r^* equals zero, and therefore population growth must be zero everywhere. However, the diffusion term cannot equal zero everywhere, since population density is not uniform (the departure from uniformity is dictated by the habitat basin topography). Thus, diffusion is incompatible with assumption of an ideal free distribution. Of course, an ideal free distribution can be approached closely if either the coefficient of diffusivity or the viscosity is relatively small; in either of these cases, tendencies for movement oriented to the gradient in realized suitability are much stronger than simple diffusive forces.

A general stable solution requires that overall population abundance be at equilibrium; excess growth in some areas must be balanced by deficits in other areas. Diffusion results in a component of movement toward a more uniform distribution of population density. Therefore, diffusion will result in a tendency for individuals to flow from the central areas of high density toward the periphery or other marginal habitat where density is low. For the geographic distribution to be at equilibrium ($\partial N/\partial t = 0$ everywhere), there must be a counterbalancing inward-directed tendency resulting from oriented response to the suitability gradient, so that the diffusion and migration terms approximately balance (any difference is accounted for by in situ population growth, positive or negative).

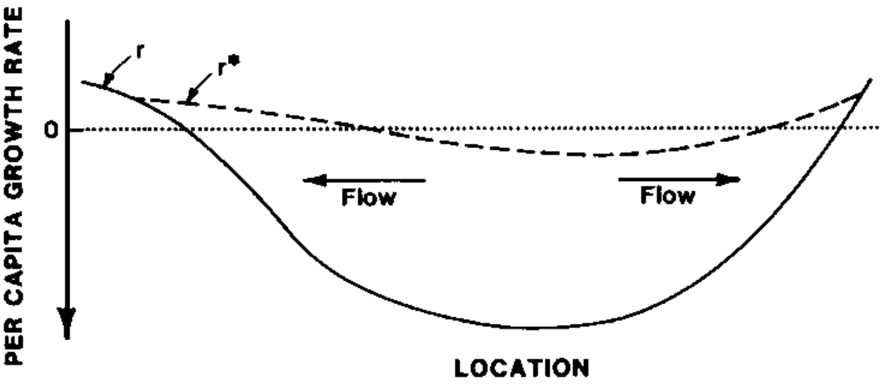

Figure 1.5 Transect through a simple habitat topography demonstrating the effect of diffusion on distribution and realized per capita growth rate at equilibrium.

Thus, the equilibrium surface of the "liquid" filling the habitat basin is depressed near the center and raised toward the edges (Figure 1.5). This distribution requires that $r^* > 0$ in areas of high abundance and $r^* < 0$ in areas of marginal habitat. Accordingly, there will tend to be excess productivity near the center and net loss near the edges; this condition is maintained by an equilibrium flow of individuals from areas of high population density toward the edges and other marginal habitat. The flow will be maximal at the boundaries between areas of productivity and areas of loss, where $r^* = 0$ (the difference between net production and net loss on respective sides is maximal at this point). Pulliam (1988) explores this phenomenon of "sources and sinks" in a more general context.

The phenomenon of a peripherally directed gene flow was described by Mayr (1963, 1970), who felt it produced conditions allowing speciation at the periphery. Interestingly, Mayr does not use the term "centrifugal speciation," and he apparently does not recognize Brown's (1957) paper. Mayr's gene flow hypothesis does not require as large an environmental perturbation as does Brown's mechanism of expansion and contraction. However, Mayr does not describe a clear mechanism by which this gene flow is produced. Gadgil's (1971) simulations indicated that dispersal could play a role in generating such a flow, but his use of a constant r-variable K logistic model prevented examination of the important marginal ($r_h \approx 0$) and submarginal ($r_h < 0$) habitats that occur at the periphery (see Appendix).

This basin model supplements Gadgil's analysis in this regard: it presents a mechanism by which a peripheral flow of individuals or genes is generated, it represents the marginal nature of peripheral habitat, and it shows how peripheral segments of the population can become connected or disconnected as a function of population abundance and spatial and temporal changes in the geographic suitability topography. Significantly, it provides a description of population dynamics that simultaneously accommodates the alternative mechanisms of centrifugal speciation proposed by Brown and Mayr, as well as the concept of catastrophic selection proposed by Lewis.

From the standpoint of evolution, the equilibrium flow arising from diffusive forces causes individuals to move toward areas of lower realized growth rate or reproductive value (r^*), indicating that random dispersal may be maladaptive. But oriented and random movements (i.e., mean directed movement and variance components) may be inseparable at the behavioral level of the individual organism. Also, dispersal may have benefits not included in this model. For example, Hamilton and May (1977) showed that dispersal may allow opportunistic colonization of unpredictable habitats. The advantage of this strategy is related to the frequency of such opportunities, and it may be selected for despite otherwise maladaptive consequences. Hamilton and May's unpredictable habitats could be portrayed in this basin model as a highly irregular suitability topography with local depressions (i.e., favorable habitat) forming unpredictably. High diffusivity would speed (or, in the case of intervening ridges where $r_h < r_{h(K)}$, even enable) colonization of these ephemeral habitats. However, the benefit of diffusivity would be realized mainly in peripheral or marginal habitats where densities are low and these habitats would otherwise not be reached.

Presence of an equilibrium internal flow of individuals toward marginal habitats, especially toward the periphery, suggests that gene flow may not be isotropic. The spread of traits arising near the center of population abundance will be aided by this flow, whereas the spread of traits arising in marginal habitats will be hindered; the latter will tend to be confined to the marginal habitats. An extreme case might consist of a population separated into two habitat basins, thinly connected across an intervening permanent ridge of poor habitat (Figure 1.6). The two population segments would appear to be connected, but the net flow of individuals toward the ridge from both sides could intensify the genetic isolation of the two basins by impeding flow of genes from the ridge toward the opposite centers. Also, the individuals near the ridge experience net reproductive deficits, further reducing the probability of genes crossing the intervening ridge.

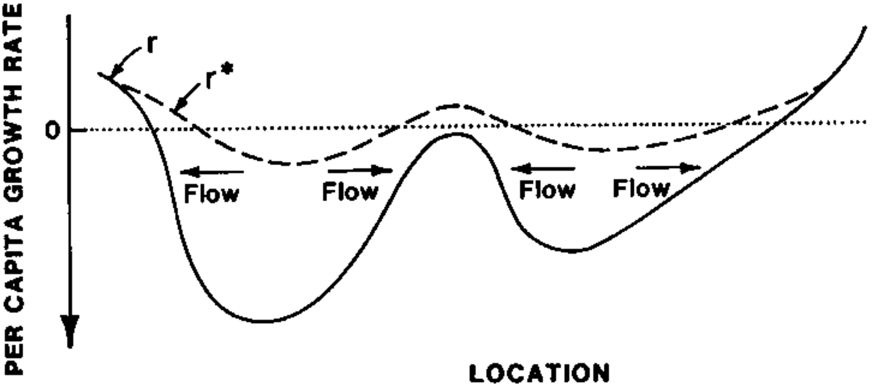

Figure 1.6 Transect through a two-basin habitat topography showing increased potential for genetic isolation due to equilibrium internal flow of individuals arising from diffusion.

1.3.3 Effects of Viscosity

Viscosity is inversely related to the rate of population flow toward more suitable habitat in the presence of a suitability gradient. Low-viscosity and high-viscosity populations exhibit very different responses to changes in the shape and level of the geographic suitability basin. The former "track" changes in suitability mainly through relatively rapid population movement, whereas the latter respond more through differential in situ rates of population growth or decline. Recognizing that most populations will be intermediate, the behavior of the model is easiest to examine at the extremes of viscosity. Diffusivity will be assumed to be negligible for the remainder of this discussion of viscosity effects.

Low viscosity results in maintenance of the ideal free distribution, where r^* is the same everywhere. The geographic distribution of abundance is determined by the current habitat suitability topography and by the total population size. The latter can be described as a function of r^*. The logistic model of local dynamics (Equations 1.3 and 1.4) gives

$$r^* = r - bN . \tag{1.8}$$

Here it is desirable to express population growth rate as a function of density, so that the quantity of habitat h, (A_h), is explicit:

$$r_h^* = r_h - \frac{bN_h}{A_h} , \tag{1.9}$$

where coefficient b has been redefined appropriately. The total abundance in habitat h is obtained by solving for N_h,

$$\begin{aligned} N_h &= A_h\left(r_h - r^*\right)/\,b \quad \text{if } r_h > r^* \\ N_h &= 0 \text{ otherwise,} \end{aligned} \tag{1.10}$$

and total population abundance (N_{tot}) is obtained by integrating local abundance over all habitats occupied at realized suitability level $r^*(N_{\text{tot}})$:

$$N_{\text{tot}}(r^*) = \int_{l_1}^{l_2} \left[A_h\left(r_h - r^*\right)/\,b\right] dh . \tag{1.11}$$

All habitats are assumed to be accessible. The quantity of habitat corresponding to each value of basic suitability can be described in functional form by

$$A_h = g\left(r_h\right) , \tag{1.12}$$

which provides a convenient summary of the distribution of habitat. This relationship, or alternatively the cumulative amount of habitat more suitable than r_h, can be termed a *hypsogram* by analogy to its use in geodesy, where it summarizes the distribution of altitudes or depths for a physical topography. The shape of the hypsogram depends on the shape of the basin topography. Because the area of extensive marginal habitat increases approximately with the square of the radial distance, the quantity or area of marginal habitat often will increase as basic habitat suitability declines from the most favorable level. An analytic solution to the integral in Equation (1.11) can be obtained if the hypsogram is in the form of a power function:

$$A_h = c\left(r_0 - r_h\right)^p , \tag{1.13}$$

where $p > 0$, c is a constant of proportionality, and r_0 denotes the basic suitability of the very best habitat. As a mathematical convenience, Equation (1.13) can be expressed as a pair of parametric equations where y is a parameter that relates to the order of habitats from best (central) to worst (peripheral):

$$r(y) = r_0 - r_1 y^m \qquad m > 0\,; \tag{1.14}$$

$$A(y) = ay^n \qquad n > 0\,, \tag{1.15}$$

where $p = n/m$, $c = ar_1^{-p}$, and the set of all habitats, h, is described by a corresponding set of values of y. Note that Equation (1.15) has a convenient geometric interpretation, in that the area of habitat increases as a power function of the distance from the center. As we proceed toward more peripheral habitats, suitabilities may decline at an accelerating ($m > 1$) or at a decelerating ($m < 1$) pace. Equation (1.11) can now be rewritten as an integral over y,

$$N_{\text{tot}}(r^*) = \int_{l_1}^{l_2} \{A(y)\,|\,r(y) - r^*\,|/b\}\,dy \tag{1.16}$$

or

$$N_{\text{tot}}(r^*) = \int_{l_1}^{l_2} \left[ay^n\left(r_0 - r_1 y^m - r^*\right)/b\right] dy \tag{1.17}$$

The lower limit of integration, l_1, corresponds to the best habitat, r_0, which is given by $y = 0$; hence $l_1 = 0$. The upper limit of integration, l_2, corresponds to the value of y at the extensive margin of the population. From Equation (1.14) and the assumption of an ideal free distribution, $r(l_2) = r^*$, or

$$r^* = r_0 - r_1 l_2^m \tag{1.18}$$

which has the solution

$$l_2 = \left[\frac{r_0 - r^*}{r_1}\right]^{1/m} \tag{1.19}$$

Since functions $A(y)$ and $r(y)$ are power functions, Equation (1.17) is easily integrated. First, separating the function into two integrals,

$$N_{\text{tot}}(r^*) = \frac{a}{b}\left[\left(r_0 - r^*\right)\int_{l_1}^{l_2} y^n\,dy - r_1 \int_{l_1}^{l_2} y^{m+n}\,dy\right], \tag{1.20}$$

performing the integrations,

$$N_{\text{tot}}(r^*) = \frac{a}{b}\left[\frac{\left(r_0 - r^*\right)}{(n+1)} \Big|_0^{l_2} y^{n+1} - \frac{r_1}{(m+n+1)} \Big|_0^{l_2} y^{m+n+1}\right],$$

and letting $\phi = (n + 1)/m$, I obtain

$$N_{\text{tot}}(r^*) = \frac{a}{b}\left(\frac{1}{n+1} - \frac{1}{m+n+1}\right) r_1^{-\phi}\left(r_0 - r^*\right)^{1+\phi}. \tag{1.21}$$

This equation also allows carrying capacity (K) to be calculated by substitution of $r^* = 0$:

$$K = \frac{ar_1}{b}\left(\frac{1}{n+1} - \frac{1}{m+n+1}\right)\left(\frac{r_0}{r_1}\right)^{1+\phi}. \tag{1.22}$$

Moreover, Equation (1.21) can be solved for r^* as a function of N_{tot}, giving

$$r^*\left(N_{\text{tot}}\right) = r_0 - \left[\frac{br_1^{1/\phi} N_{\text{tot}}}{a\left(\frac{1}{n+1} - \frac{1}{m+n+1}\right)}\right]^{1+\phi}. \tag{1.23}$$

Equation (1.23) is similar in form to Equation (1.8), which described the local per capita growth rate, except that in Equation (1.23) abundance is raised to a power. Thus, Equation (1.23) can be rewritten in condensed form as

$$r^*\left(N_{\text{tot}}\right) = r_0 - b'N_{\text{tot}}^{\theta} \qquad 0 < \theta < 1 \tag{1.24}$$

where b' is a new constant defined in terms of the old constants a, b, r_1, m, and n, and $\theta = 1 + \phi = m/(m + n + 1)$. Note that the constraints of $m > 0$ and $n > 0$ (see Equations 1.14 and 1.15) require that $0 < \theta < 1$.

Equation (1.24) is a generalization of the logistic model that has been investigated extensively by Gilpin et al. (1976), Pella and Tomlinson (1969), and Richards (1959), among others. The shapes of population growth curves corresponding to various values of θ are shown in Figure 1.7. As shown in the previous literature on the generalized logistic model, maximum population growth rate occurs at a total population size (N_{opt}) which is

$$N_{\text{opt}} = K(1+\theta)^{-1/\theta} \tag{1.25}$$

At the maximum value of $\theta = 1$, overall population growth remains logistic, and maximum population growth rate (or equivalently, maximum equilibrium yield) occurs at $N_{\text{opt}} = 0.5K$. This value of θ would be approached only as m approaches infinity. Examination of Equations (1.14) and (1.15) shows that for the constant slope local logis-

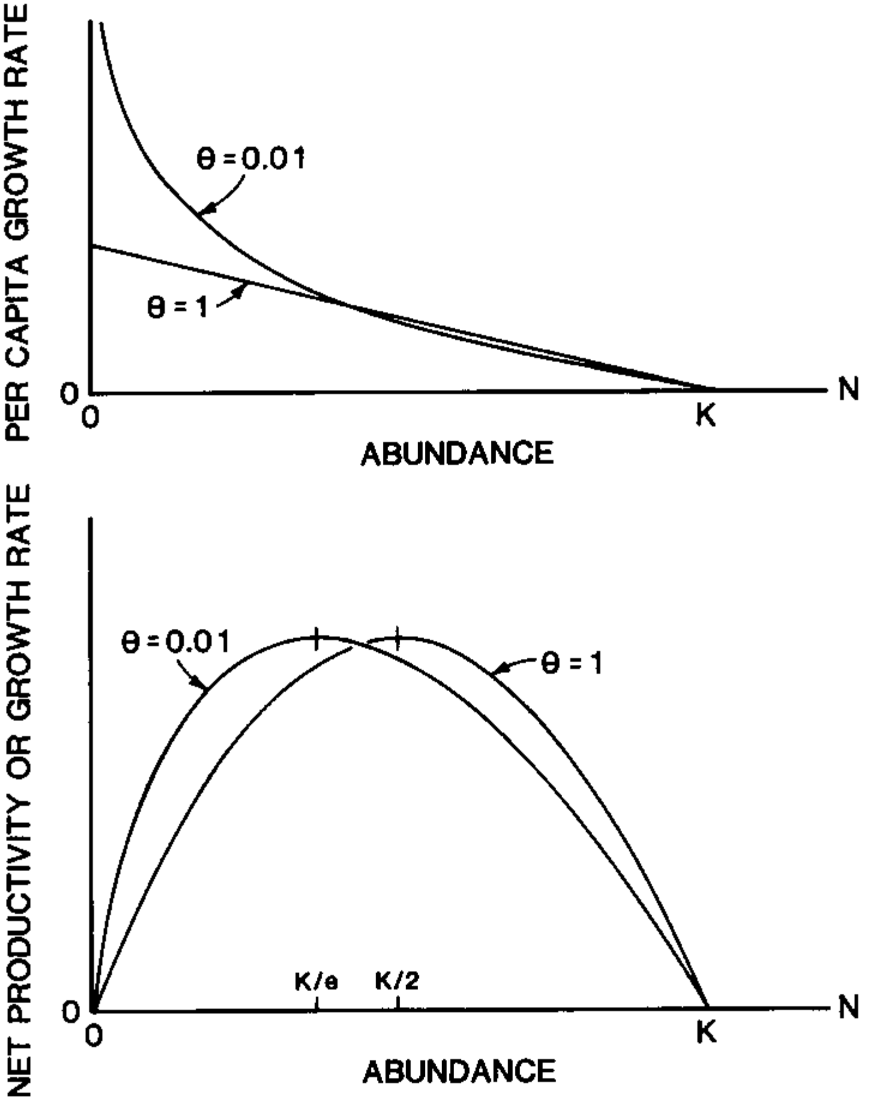

Figure 1.7 Comparison of productivity curves for limiting values of θ in the generalized logistic growth model (Equation 1.23). For comparison, maximum net productivity is the same for both curves.

tic model, the limiting case of $m \rightarrow \infty$ would correspond to a flat-bottomed, vertical-sided habitat basin topography. Such a case might correspond to a small island or lake with relatively uniform internal habitat characteristics sharply bounded by extremely unfavorable external habitat.

In most cases a substantial range of basic habitat suitabilities will be available for occupation, in which case DDHS will shift peak population growth to a population size less than $0.5K$, despite the fact that local maximum productivity occurs at one-half the local saturation density everywhere in the range. In this model, population size giving maximum population growth rate cannot fall below K/e, where e is the base of the natural logarithm (this limit corresponds to $\theta = 0$, see Gilpin et al. 1976). As Gilpin notes, "The case of $\theta < 1$ could correspond to a situation of resource heterogeneity in which the first individuals [viz. low population size] exhaust the quality resources." This corresponds to the present model behavior but also demonstrates that a population growth curve is not determined solely by the nature of local density dependence experienced by the individual organisms. If a population exhibits DDHS, the topography of habitat suitability may strongly influence the shape of its population growth curve.

As defined previously, *high viscosity* refers to the case in which changes in abundance due to oriented movement are small compared with those due to local reproduction and mortality. Viscosity becomes particularly important when there is a change in abundance relative to local carrying capacity, perhaps due to a change in the habitat basin level or shape (i.e., a change in the environment), or perhaps due to removal of individuals by predators or by harvesters. Because r_h and local carrying capacity are proportional in this constant-slope logistic model, variability in r_h is equivalent to variability in local carrying capacity. As is discussed later, viscosity also is an important consideration in harvested populations.

If we ignore movement, local dynamics of the constant slope model should be consistent with the simple model studied by May (1973). When the local carrying capacity, K, is subject to random variability, May found that both the mode and the mean population size were below the mean carrying capacity of a habitat wherein a population grows according to a constant-slope logistic model with stochastic variability in r_h. This suggests that the mean surface of the viscous population "liquid" inhabiting the habitat basin again will be slightly depressed in the center. However, this is an average distribution rather than an equilibrium distribution; in contrast to the diffusive case, there would not necessarily be an accompanying production of excess individuals near the center nor an extension into submarginal habitat, and a strong peripheral flow would not be generated.

If the temporal variability in habitat suitability were very strong but relatively local, the basin topography might appear as very irregular, with bumps and depressions continuously appearing and disappearing.

Population movements in response to continual changes in suitability gradients would tend to be indistinguishable from diffusive movement. Many real populations may be faced with this problem of coarse spatial and temporal grain, and such populations would be continually approaching but would never attain an ideal free distribution wherein abundance accurately maps the geography of habitat suitabilities.

The presence of viscous population movement also suggests that productivity curves of dN_{tot}/dt versus N_{tot} should exhibit hysteresis: population productivity curves exibited by growing populations would not be retraced by declining populations. Growing populations would tend to be centrally distributed, and the surface of the "liquid" would be domed near the center. In contrast, declining populations would show a depressed surface near the center, and at the same levels of abundance the population would be more peripherally distributed as the range contracts. To the extent that the habitat distribution of a viscous population tends to remain the same, the overall shape of the productivity curve would not be modified as much as in the low-viscosity case examined previously.

1.4 EXTENSIONS OF THE MODEL

The basin model provides ample room for modifications and extensions. For example, one possibly more realistic representation of population dynamics will be examined in Chapter 2, which treats optimal harvesting strategies for an organism (e.g., fish) with diffusive meroplanktonic larvae. Extension to age-structured populations and complicated life histories is feasible but is beyond the scope of this presentation. In the present class of models, the most useful and revealing modifications involve alternative local population growth models. Maintaining the analogy of realized per capita growth rate and reproductive value, alternative growth models are equivalent to alternative relationships between density and changes in habitat suitability.

1.4.1 Other Growth Models

A major theoretical and conceptual benefit of the constant-slope logistic model used above is the graphical equivalence among the density-dependent decrease in realized suitability, density itself, and the depth of the "liquid" in the basin. Other linear and nonlinear growth models lack this graphic convenience, but their behaviors can be visualized with respect to the constant-slope logistic case.

There are two general requirements of variable-habitat growth models used in the present context. The first requirement is that the model must be able to portray realistic dynamics in submarginal habitats, in which $r_h < 0$, and $r^* < 0$ even at very low densities. The second requirement is that for any habitat, including submarginal habitat, realized suitability must decline monotonically with increasing density (i.e., $dr^*/dN < 0$). The latter requirement rules out behavioral effects that might reduce per capita growth rates at low densities, such as have been suggested by Allee et al. (1949), and which were shown by Fretwell (1972) to produce seemingly erratic changes in habitat distributions.

Two of the most popular variable-habitat *logistic* models have been the "fixed r-variable K_h" and "fixed K-variable r_h" families (see Appendix, Figure A.1). They have severe shortcomings in the context of DDHS; these problems are reviewed in detail in the Appendix and are summarized here. Because both families fail to meet the requirements regarding submarginal habitats, they are of little use in the present context.

Moreover, even within the realm of $r > 0$, these two models produce questionable patterns of habitat selection. The popular "fixed r-variable K_h" family does not generate differential occupation of habitat: relative habitat distribution remains the same at all population sizes, and all habitats are equally suitable at low population size or density; the population behaves logistically, as do the local habitats. The "fixed K-variable r_h" family allows reasonable variation in habitat suitability at low population size, but differential selection of habitats disappears as density approaches K, and apparent order of habitat suitabilities is inverted if K is exceeded (densities in habitats with low r_h exceed densities in habitats with high r_h). While the latter model has been used mainly to describe temporal variability and has been justified only by its mathematical convenience, it nonetheless appears to have potential use for approximating growth of some territorial species such as Morisita's (1952, 1971) ant lions.

Two families of logistic models that potentially are useful are those that pass through a fixed point in either of the quadrants ($r < 0, N > 0$) or ($r > 0$, $N < 0$), respectively termed the SQFP (second quadrant fixed point) and FQFP (fourth quadrant fixed point) models, as shown in the Appendix, Figure A.2. These models require some restriction on the range of basic habitat suitabilities in order to preserve the required negative slope, but within these restrictions submarginal habitats can be portrayed. Notably, Schoener's (1973) time- and energy-based logistic model corresponds to the SQFP family. The SQFP model also seems to provide a fair approximation to Whitham's (1980) fitness curves for aphids on leaves of various sizes. Historical changes in distribution of anchovy spawning off southern California are consistent with assuming that reproductive success follows the FQFP model (Chapter 3).

There are substantial differences between the ideal free distributions resulting from the SQFP and FQFP logistic models (given the same suitability basin topography). The FQFP model produces relatively little range expansion as population size increases, with most of the increased abundance being accounted for by nearly proportional increases in already-occupied habitats (the intensive margin). The SQFP model produces the opposite behavior: much of the increase in abundance is accounted for by range expansion (the extensive margin), and densities approach similar levels over broad regions of central habitat as carrying capacity is approached.

Because the factors determining basic habitat suitability in different parts of the range are likely to be different, the per capita rate of decline in habitat suitability, b, may also vary. Up to this point, I have tried to avoid this complication. However, unless the nature of local variability in b can be described and modeled, little can be done to examine the consequences. Brown's (1984) hypothesis that factors are serially correlated in space would require that the rate of density dependence be similar in extended contiguous portions of the range. This restriction seems to be sufficient to maintain an orderly population response in the context of the basin model; ideally, distortion should be very coarse grained, allowing most of the properties of the model to be retained, at least qualitatively.

As with variable-habitat logistic models, there is an even greater variety of possible variable-habitat *nonlinear* growth models. Fortunately, they fall into two broad categories, each with characteristic behavior. The per capita growth rate may be *convex* with respect to density, as is often the case for birds and large mammals which show most of their compensatory capacity at abundance levels near carrying capacity (Fowler 1981, Murray 1979). Alternatively, the relationship may be *concave*, as is the case with many smaller organisms such as insects and fishes which exhibit most of their compensatory capacity at low levels of abundance (Cushing 1971, 1973, Fowler 1981, Garrod and Knights 1979, Stubbs 1977). One possible family of nonlinear growth curves is that in which each habitat is characterized by a basic suitability, r_h, and the slope of the per capita growth rate curve is a nonlinear function only of density (Figure 1.8):

$$r^* = r_h - f(N_h/A_h) . \tag{1.26}$$

This model is analogous to the linear constant-slope logistic model (top of Figure 1.8) in that all habitats have the same dr^*/dN for a given density.

The concave growth rate curves typical of small organisms such

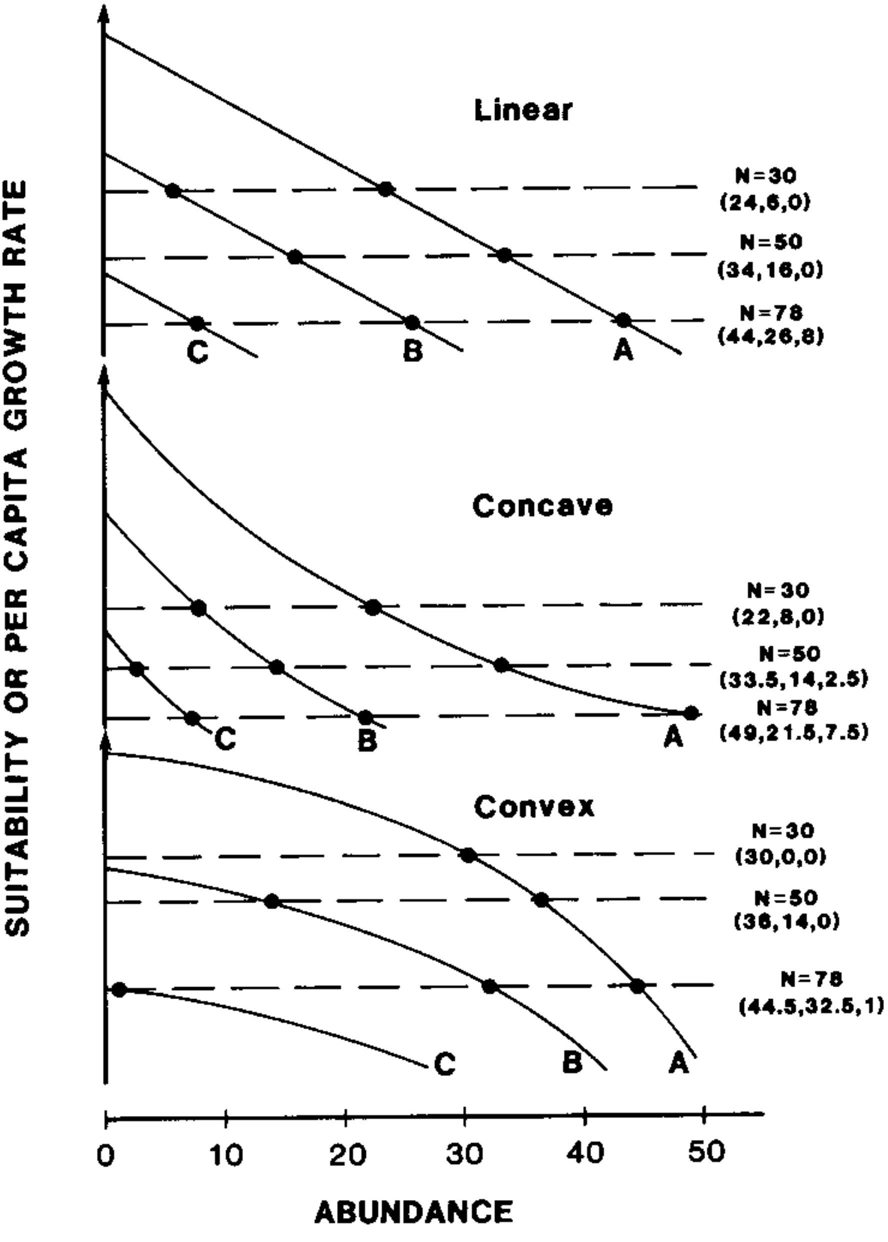

Figure 1.8 Families of linear and nonlinear "constant slope" habitat suitability curves. Solid dots indicate habitat population densities according to the ideal free distribution: *top*, linear family; *middle*, concave family typical of small animals; *bottom*, convex family, typical of large animals.

as insects and fishes are shown in the middle of Figure 1.8. While changing range to some extent, these populations would show relatively large changes in density in habitats that are already occupied (the intensive margin). Because species with concave curves favor changes mainly in the intensive margin, where the bulk of the population resides, the population productivity curve will be approximately congruent with the local productivity curve.

The convex growth rate curves typical of large organisms is shown at the bottom of Figure 1.8. For these types of animals, changes in total population size are expected to be associated with changes in range (the extensive margin), while densities in already-occupied habitats would change relatively little. As these species favor large changes in the extensive margin, their population productivity curves are skewed relative to the productivity curves characteristic of local habitats. While a sensitive response allows these populations to regulate their abundance at a level near carrying capacity (Fowler 1981), differential occupation of habitats provides a potential resilience to severe depletion that is not apparent from traditional single population growth curves.

Note that the ideal free distributions associated with this family of nonlinear models are nearly indistinguishable from those associated with the SQFP and FQFP logistic models for convex and concave nonlinear models, respectively (Figure 1.9). While DDHS theory suggests the possibility of inferring the shape of the local suitability (or population growth) curves as a function of density (e.g., Whitham 1980), in most cases it may not be feasible to do more than discriminate between converging (convex) versus diverging (concave) families of curves (also see Morris 1987).

Changes in the shape of population growth curves due to density-dependent habitat selection can be important to resource management. Pella and Tomlinson (1969) examined some of the consequences of skewed growth curves on sustainable fishery harvests. An example of direct application involves management of marine mammals in the United States under the Marine Mammal Protection Act, which specifies that marine mammals must be managed for *optimum sustainable population* (OSP).

The term *optimum sustainable population* has been defined operationally to be a population size falling between the level of maximum net productivity (MNPL) and maximum population size, or carrying capacity, *K* (Gehringer 1976). Consequently, much research has been directed toward understanding the relationship between MNPL and *K* for these organisms (see Fowler 1981).

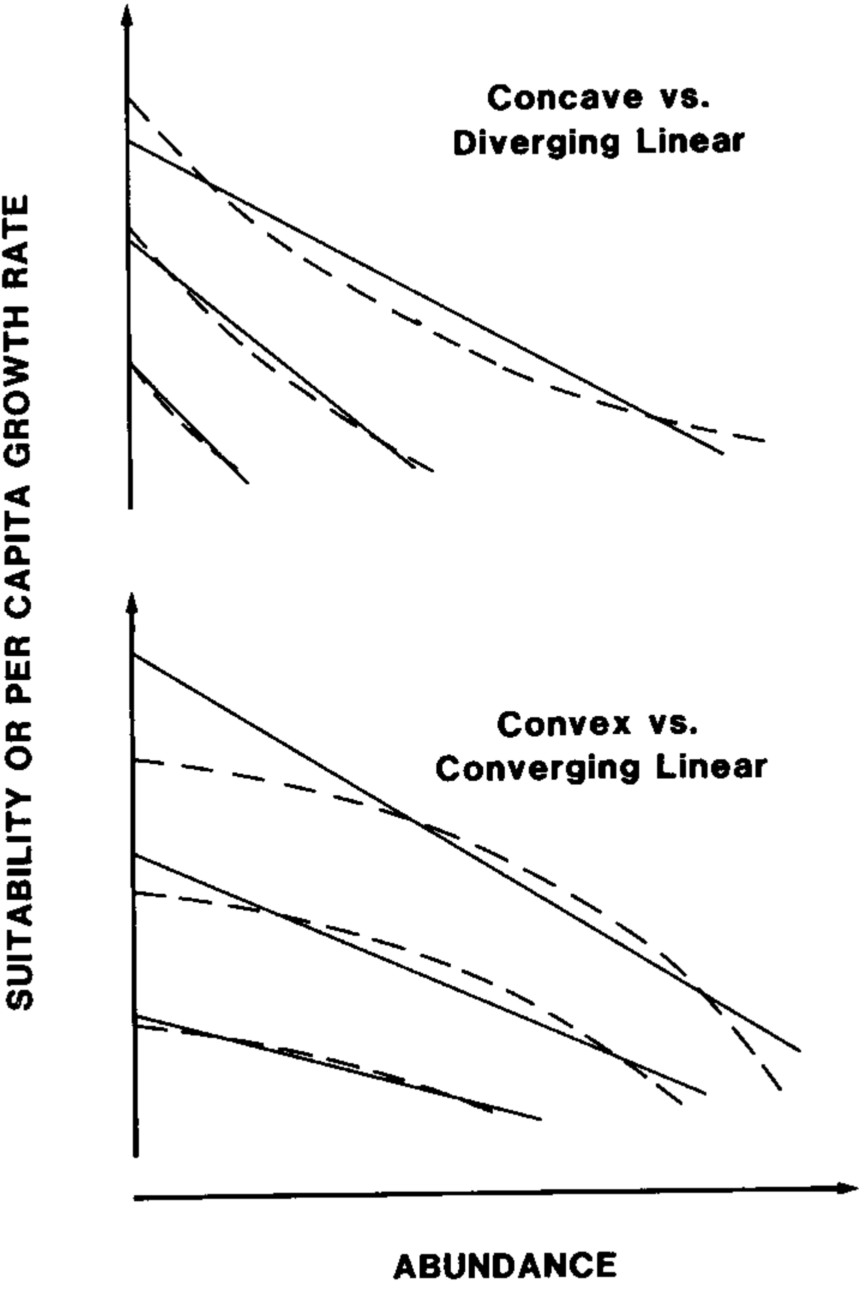

Figure 1.9 Comparison of nonlinear and nearly equivalent linear families of habitat suitability curves. See Appendix for explanation of FQFP and SQFP models.

Nearly all of the previously considered mechanisms influencing the shape of marine mammal growth curves have indicated that MNPL should occur at a relatively high abundance, approaching K, and well above the logistic MNPL of $0.5K$. The convexity of these per capita population growth curves suggests that DDHS may be a mechanism that can produce estimates of MNPL that are lower than those arising from usual homogeneous population models. The extent of this change cannot be assessed without extensive historical information, especially on changes in historical geographic ranges or distributions.

Fretwell (1972) discusses the relation of his DDHS model to several types of *territoriality*. One possible consequence of territoriality is simply to produce convex suitability curves (bottom of Figure 1.8). In this case suitability declines rapidly at high densities, but an ideal free distribution is possible.

A more interesting effect of territoriality is the case in which behavior prevents attainment of an ideal free distribution, so that occupiers of good territories (high r_h) are able to maintain $r^* > 0$ at all population sizes. Fretwell examined the effect of this "ideal despotic distribution" in relation to several hypotheses about the nature of territoriality. O'Connor (1985) compares predictions from Brown's (1969) rigid territoriality with those of Fretwell and Lucas (1970) or Fretwell (1972), where territorial compression is possible.

In the context of the basin model, rigid territoriality might be represented as a limit to the number of individuals that can occupy a given habitat (the dashed line in Figure 1.10). Within that limit, individuals are free to occupy the best available habitats. The amount of decline in realized suitability is accordingly limited, so the good habitats continue to produce more offspring than are needed for replacement ($r^* > 0$). A population that fills the basin to the level $r^* = 0$ (which is experienced only at the margins) will be producing offspring in excess of replacement, so the population will still be growing. These excess individuals must choose either to occupy submarginal habitat or to forgo reproduction.

Presumably this choice will be based ultimately on comparative reproductive value. Thus, submarginal habitats would be utilized either to the point where excess production in the good habitats is balanced by insufficient reproduction in the poor habitats or to the point where being a "floater" confers a higher reproductive value, whichever solution occurs at the lower level of abundance. The ideal free (or despotic) distribution requires that the reproductive value of a floater be equivalent to the reproductive value conferred by possessing the poorest occupied habitat. As in other cases of convex per capita growth curves (this is an extreme), the

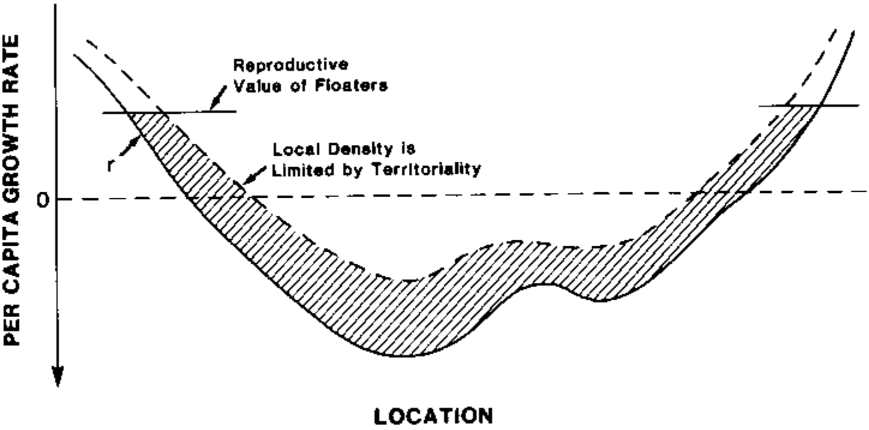

Figure 1.10 Basin model applied to a territorial species. The dashed line indicates the limiting density due to territoriality and approximately follows the basin topography. The shaded region is the maximum occupied habitat at carrying capacity (no net population growth), with production of floaters.

severe limit on utilization of the intensive margin requires that population growth be accommodated almost entirely by utilization of the extensive margin, i.e., expansion of the range.

1.4.2 Fish Stock-Recruitment Models

Fish stock-recruitment models attempt to describe the quantity of offspring (recruitment) that is produced by various levels of parental (stock) abundance. The two stock-recruitment models that appear most frequently in fishery studies are the Ricker (1954) model and the Beverton and Holt (1957) model. Some comparisons of the two models are given by Cushing (1973) and Ricker (1975).

As a simplification, suitability of spawning habitat can be measured by the expected number of recruits produced per spawner. By focusing only on immediate reproductive success, this assumes that there are no trade-offs between spawning and survival or future fecundity. An ideal free distribution therefore is the geographic distribution of spawners that results in all spawners expecting to achieve the same reproductive success. Thus stock recruitment models can be examined in terms of the Fretwell-Lucas model and the basin model.

The *Ricker model* is often written in the form

$$R = aS\exp(-bS) , \tag{1.27}$$

where R is recruitment and S is parental spawning stock. If, according to the ideal free distribution, the quantity (R/S) is equal among all occupied habitats, then the quantity Ln(R/S) also must be equal. Equation (1.27) is equivalent to

$$\mathrm{Ln}(R/S) = \mathrm{Ln}(a) - bS\ , \tag{1.28}$$

where density-independent factors such as environmental effects on spawner fecundity and density-independent sources of offspring mortality are included in Ln(a), and density-dependent sources of mortality and reduced fecundity are included in the term bS. If density-dependent effects on fecundity are ignored and spawner abundance is measured in terms of eggs released, the two terms correspond to exponential coefficients of density-independent and density-dependent mortality, with Ln(R/S) being the coefficient of total mortality. This gives the simple distribution rule,

$$\begin{aligned} Z^* &= Z_h + bS_h \qquad && \text{if } Z_h < Z^*\,, \\ S_h &= 0 && \text{otherwise,} \end{aligned} \tag{1.29}$$

where Z^* and Z_h represent total and density-independent coefficients of mortality, respectively (Figure 1.11).

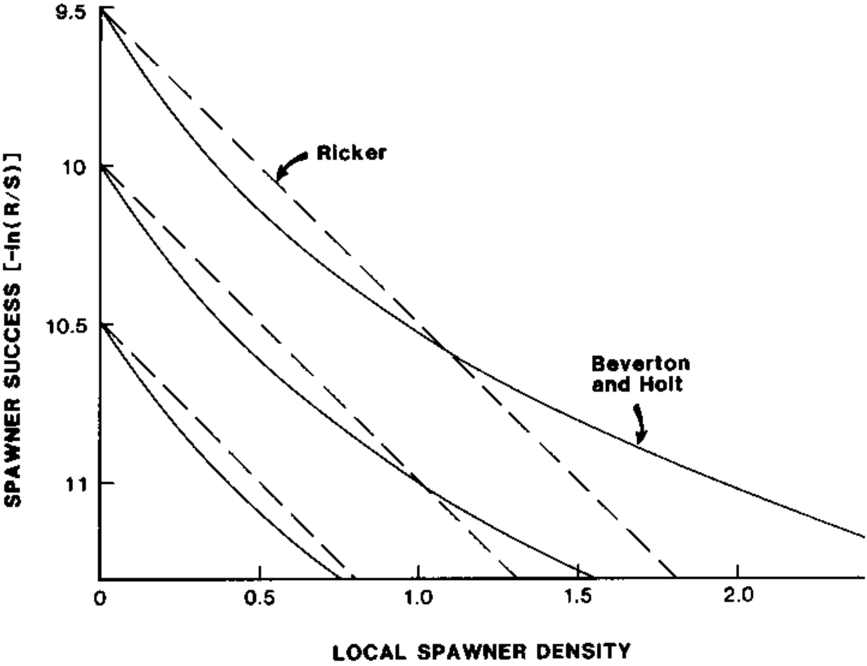

Figure 1.11 Comparison of habitat suitability curves for the Ricker and Beverton-Holt stock-recruitment relationships. Density dependence is scaled so that spawning success is the same for the two models at a density of 1.0 in the middle habitat.

Assuming that the value of b is independent of habitat, the Ricker stock-recruitment model is equivalent to the constant-slope logistic model described previously, and variability in b would produce similar distortions. In any case, we would expect to see substantial expansion and contraction of range with changes in spawner abundance. Murphy (1977) noted that this population behavior is characteristic of clupeoid fishes (anchovies, sardines, and herring), contributing to their susceptibility to overfishing (cf. Figures 1.12–1.16).

The basin model predicts that such populations will tend to contract toward the most favorable habitat as they are fished down. Moreover, catch per nominal fishing effort, which is potentially an index of abundance in the fished area (i.e., the depth of the "liquid" at the center of the population), will not decline as fast as the total abundance, which is the volume of the "liquid" in the basin. Thus, the basin model accounts for one mechanism leading to the most pernicious fishery problem, that of a stock-dependent rather than a constant catchability coefficient (the probability that a unit of fishing effort will capture an arbitrary single fish in the stock, increases as the stock becomes smaller).

Pelagic fishes, such as the clupeoids, exhibit very high mobility and hence low viscosity. Because of the similar linear properties of the Ricker model, the relationship between the local stock-recruitment relationship and the population stock-recruitment relationship can be derived by analogy to the logistic case in Equations (1.8) through (1.24). The result is the population stock-recruitment model,

$$R = aS\exp\left(-bS^{\theta}\right) \tag{1.30}$$

the quantity θ being defined as it was in Equation (1.24). The population stock-recruitment relationship is altered by habitat selection, so that the descending limb characteristic of the Ricker model tends to be eliminated (Figure 1.17); at high abundances, productivity at the center of the resource may be on the descending limb of the local stock-recruitment curve, but increasing productivity from marginal habitats tends to offset that decline. In the presence of random year-to-year variability in stock and recruitment data, the modified stock-recruitment relationship might be indistinguishable from the asymptotic Beverton-Holt relationship (see below).

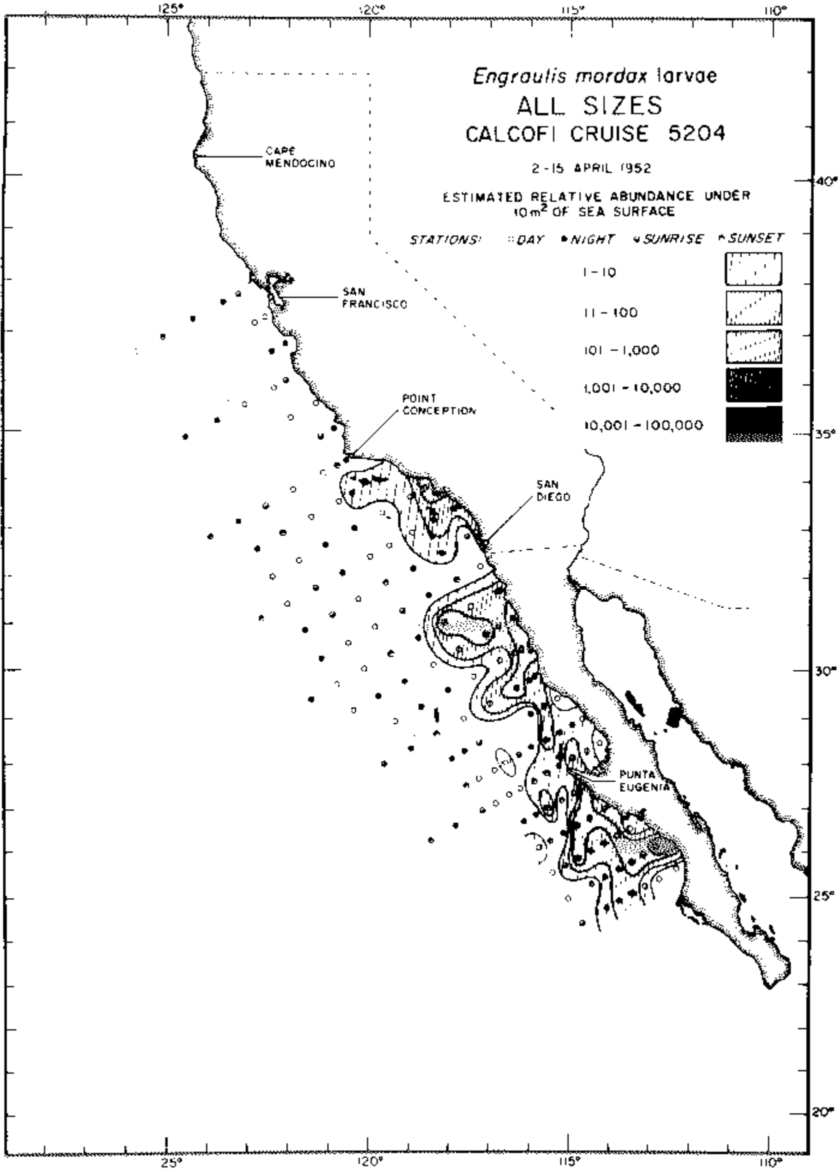

Figure 1.12 Geographic distribution of northern anchovy *(Engraulis mordax)* larvae at low population size. Abundance of central subpopulation (California and northern Baja California) was ca. 20,000 tons in 1952. Units are numbers per 10 m^2, and shading scale is logarithmic. From Kramer and Ahlstrom (1968).

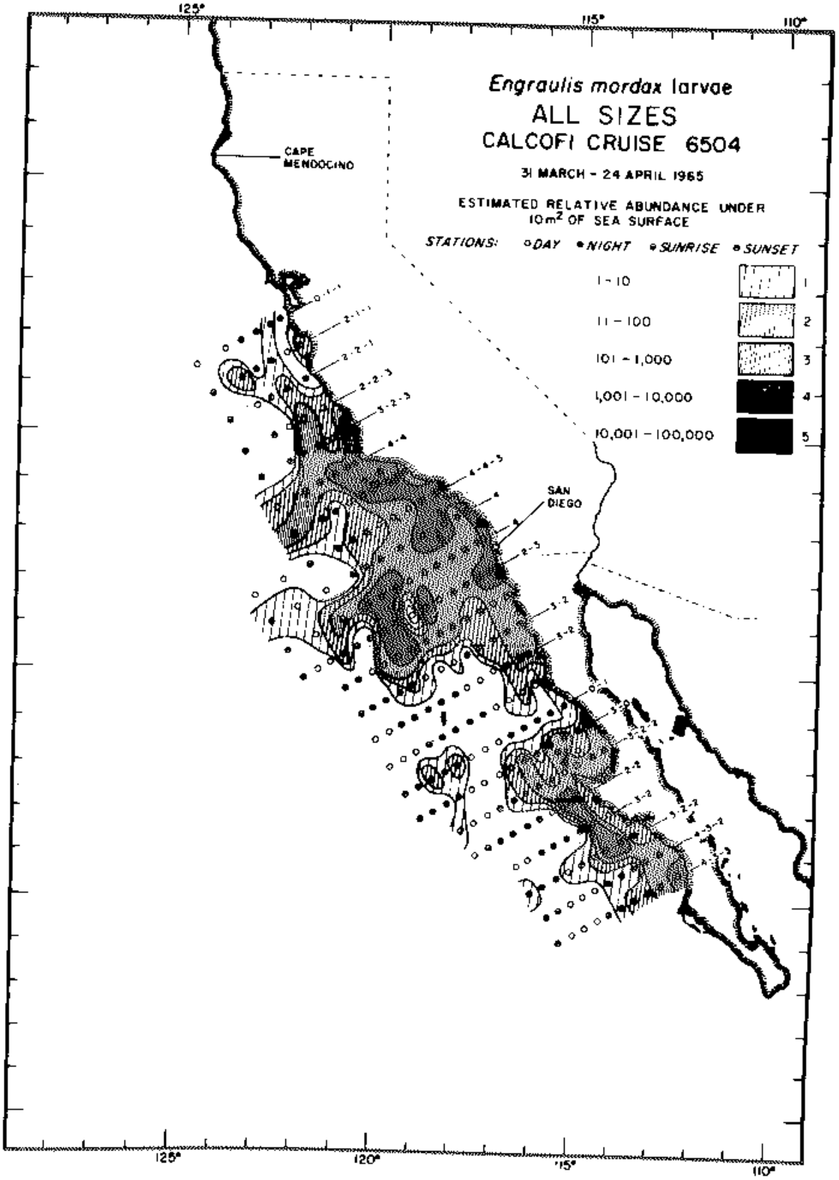

Figure 1.13 Geographic distribution of northern anchovy *(Engraulis mordax)* larvae at high population size. Abundance of central subpopulation (California and northern Baja California) was ca. 700,000 tons in 1965. Units are numbers per 10 m², and shading scale is logarithmic. From Kramer and Ahlstrom (1968).

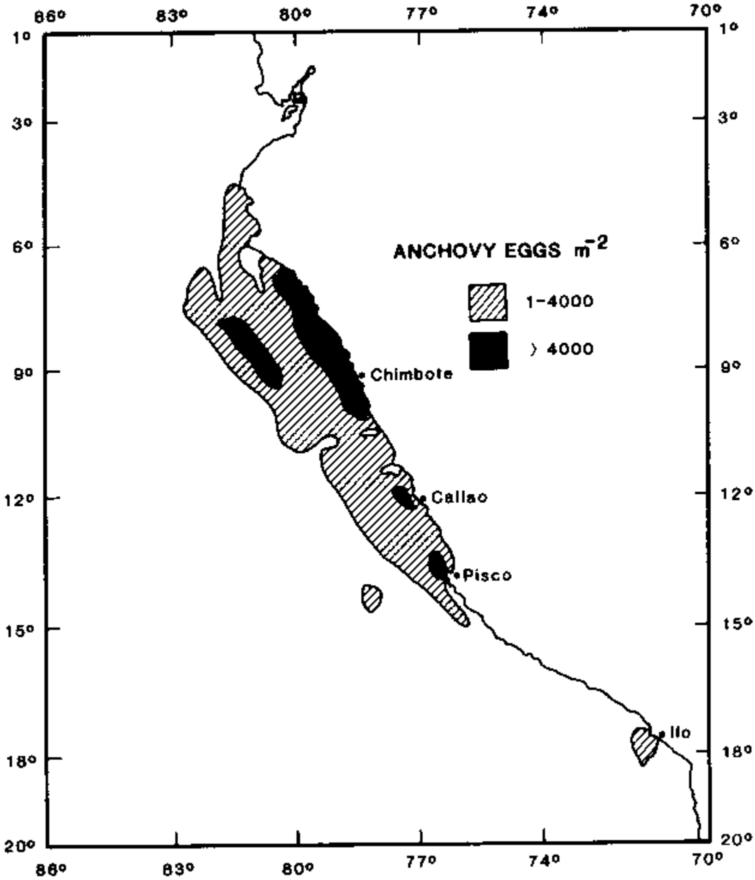

Figure 1.14 Geographic distribution of Peruvian anchoveta *(Engraulis ringens)* eggs at high population size (abundances are from IMARPE cruise 6708, September 1967). Modified from Santander et al. (1982).

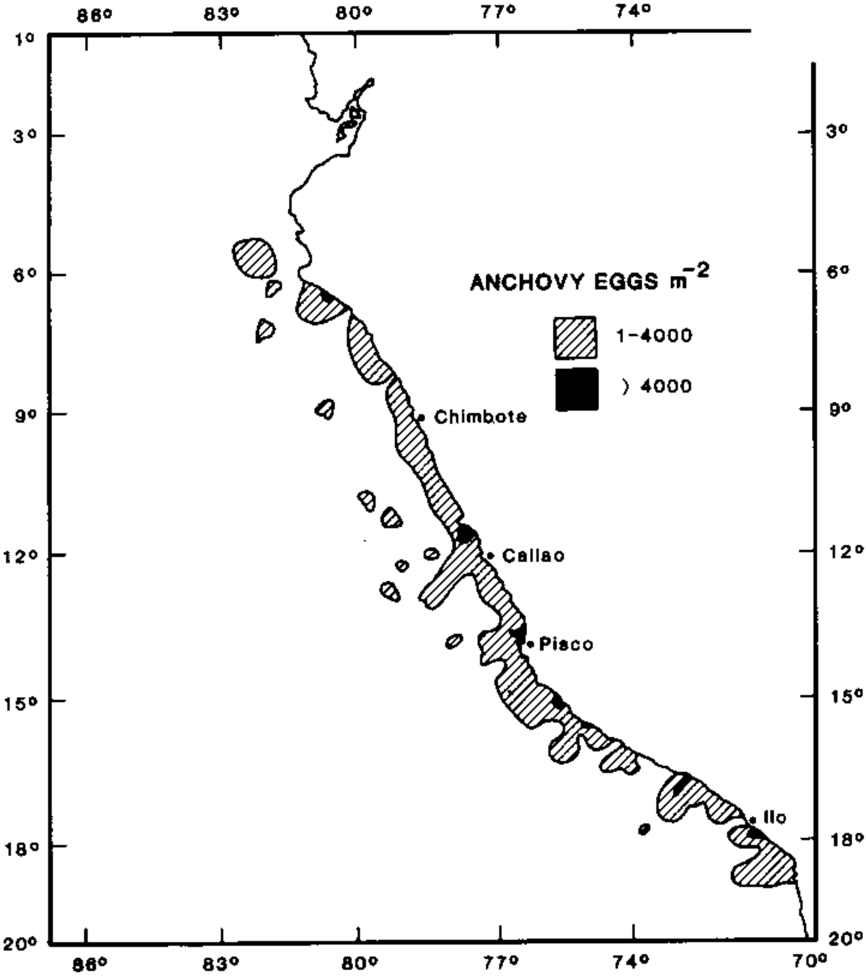

Figure 1.15 Geographic distribution of Peruvian anchoveta *(Engraulis ringens)* eggs at low population size (abundances are from IMARPE Eureka cruise 42, September 1979). Modified from Santander et al. (1982).

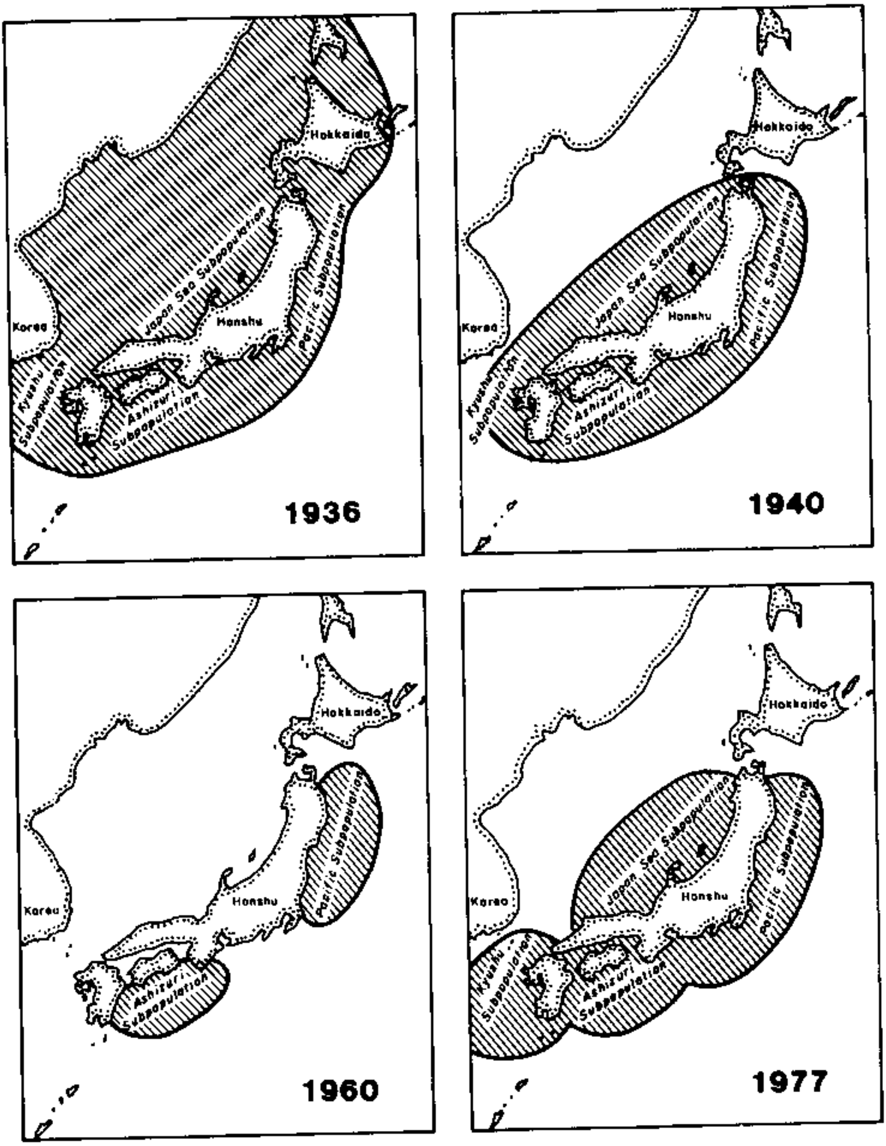

Figure 1.16 Geographic distribution of Japanese sardine *(Sardinops melanosticta)* catches at high and low population sizes. Catches were 2.7 million tons in 1936, 1.8 million tons in 1940, less than 0.1 million tons in 1960, and 1.4 million tons in 1977. Redrawn from Sharp (1980).

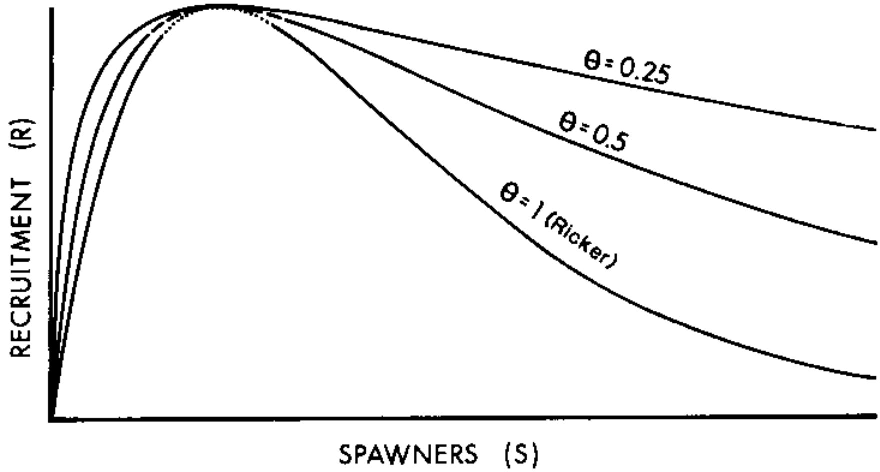

Figure 1.17 Population stock-recruitment relationships arising from local Ricker dynamics and density-dependent habitat selection.

The power function bS^θ in Equation (1.30) describes the relationship between the depth (density dependence) and volume (stock size) in a basin model based on a Ricker stock-recruitment relationship. Assuming that most of the fishing occurs in the area of highest density, the relationship between the catch per unit of nominal fishing effort (CPUE) and the stock abundance should follow approximately the same power function. MacCall (1976) estimated such a power function for the relationship between overall CPUE and abundance in the Pacific sardine fishery off California, and obtained θ values of 0.3–0.4, which are consistent with but not proof of this geographical theory.

Csirke (1980) developed an unusual form of the Ricker model for the Peruvian anchoveta, in which the abundance in the density-independent term (S) is based on virtual population analysis, while CPUE is substituted for abundance in the density-dependent term. His rationale is that the total production of eggs is best represented by the total spawning population size, while the intensity of density-dependent effects is best measured by CPUE, which reflects the relative crowding of the fish. Csirke's model,

$$r = aS\exp(-bU) , \tag{1.31}$$

where U, a catch-per-unit-effort index of density, is entirely consistent with the basin model. Not only is Csirke's model much less demanding in information than the basin model, but the use of CPUE potentially is more responsive to short-term variability in population distribution.

The *Beverton-Holt model* often appears in the form

$$R = \frac{S}{aS+b}, \tag{1.32}$$

which describes a hyperbola with an asymptote of $R \rightarrow 1/a$ as S becomes large. Unfortunately, this parametrization does not allow clear separation of density-dependent and density-independent influences. A more useful form is an equation developed by Beverton and Holt (1957, p.48) as an intermediate step in solving the differential equation

$$\frac{dN}{dt} = -N(Z+bN), \tag{1.33}$$

where Z is the density-independent mortality rate. The solution of this differential equation leads to Equation (1.32) and describes the rate of decline of a cohort of larvae (with abundance N) where the individuals interact adversely. I have reparametrized this intermediate equation (see Beverton and Holt for its derivation):

$$R = \frac{fS_h}{\frac{fS_h b}{Z_h}\left[\exp\left(Z_h t\right)-1\right] + \exp\left(Z_h t\right)}. \tag{1.34}$$

where f is fecundity per unit of spawner abundance (S_h), Z_h is the density-independent mortality rate in habitat h, and t is the duration over which density-dependent mortality acts. The rate of density dependence, b, describes the mortality rate of larvae per unit of larval density, showing why fecundity must be be considered explicitly. Equation (1.34) is difficult to work with, but the quantity $Z_h t$ is usually enough greater than 1 (in light of typical larval mortality rates) to allow the approximation $\exp(Z_h t) - 1 \approx \exp(Z_h t)$. This allows an approximate solution of Equation (1.34) in terms of recruits (R) per spawned egg (fS), which is the quantity that should be equal among habitats according to the ideal free distribution. Equation (1.34) is easier to solve in terms of fS/R, which is the reciprocal of spawning success,

$$\frac{fS_h}{R} \approx \exp\left(Z_h t\right)\left[\frac{fS_h b}{Z_h} + 1\right], \tag{1.35}$$

which must be equal among habitats giving the distribution rule

$$Z^* = Z_h t + \text{Ln}\left[\frac{fS_h b}{Z_h} + 1\right]. \tag{1.36}$$

Thus, the Beverton-Holt model assumes that habitat suitability declines approximately as the logarithm of spawner abundance (Figure 1.11). This approximate solution is in the family of concave nonlinear "constant slope" suitability curves described by Equation (1.26). Accordingly, the habitat distribution of spawners would follow the pattern of relatively little expansion and contraction of range but rather large changes in density of spawners in the best habitats. The shape of the Beverton-Holt curve will not be affected strongly by habitat selection because changes in abundance would be associated primarily with changes in intensive rather than extensive marginal use of habitats.

The existence of well-defined spawning seasons for many species of fish (Cushing 1969) suggests that temporal changes in suitability of spawning habitat would conform to a lowering of the suitability basin, followed by a raising. Peak spawning presumably would be near the period when the basin reaches its lowest (most favorable) level. In the case of multiple-batch sequential spawners such as the anchovy (Hunter and Goldberg 1980, Hunter and Leong 1981), active spawning may span the favorable period. But for single-batch spawners, optimal timing of spawning would require a careful match to the time of maximum habitat suitability.

The problem of optimal timing of single-batch spawning becomes much more interesting as complications are added. What is the optimal strategy if the optimum time cannot be anticipated accurately? How is the optimum strategy altered if larger, early-spawned larvae have a competitive advantage over (or even cannibalize) younger larvae? Or, in the case of salmon and herring, what if the later-spawning individuals suffer less risk of their eggs being rendered inviable by the activity of subsequent spawners? And particularly, how do these strategies and their interactions with demographic effects of exploitation affect the stock-recruitment relationship? Parker (1985) and Parker and Courtney (1983) have examined some aspects of this problem from the sociobiological standpoint of "evolutionarily stable strategies" (Maynard Smith 1982). Their work suggests that the temporal evolutionarily stable strategy, or ESS, for larval competition and risk aversion appears to be to reproduce earlier than the anticipated time of best environmental conditions.

Density dependence complicates the problem of temporal optimization (Williams and Nichols 1984), and this aspect of the problem is especially open to investigation. However, it seems reasonable to conjecture that the optimal "lead time" may be density dependent, being larger at higher population densities. In the present geographic model, an ESS might be for spawning to be earlier in the central densely occupied habitats and to be somewhat closer to the time of maximum environmental suitability in peripheral habitats. However, if the greater lead time in the central habitat causes the effective suitability of that habitat to be less, the ideal free distribution would require further redistribution of spawners toward the peripheral habitats.

In the case of salmon and herring, an appropriate density-dependent "lag time" would be expected, once again with a peripheral redistribution of spawners. Because fisheries often exploit particular temporal and geographic subsets of fish populations (e.g., early spawners and central spawning areas), stock-recruitment curves could be distorted further by differential exploitation patterns.

As a final technical note, these timing problems are not likely to be solved by a "pure ESS" that dictates a single optimal time of spawning: there would probably be another time at which a small number of spawners could be more succesful; i.e., this strategy could be invaded by a rare alternative strategy (Maynard Smith 1982). The solutions are more likely to take the form of a "mixed ESS" that is a distribution of spawning times and locations, each with a specified probability. As Parker (1984) notes, at equilibrium under a mixed ESS, each component strategy must do equally well, which once again is consistent with the principles of habitat selection under an ideal free distribution.

1.5 DISCUSSION

The basin model might be termed "ambitious" in that it attempts to include a wide variety of phenomena in a single framework. This quality incurs two particular dangers. The first is that few actual populations may fit such a generalized model. However, the model should not be dismissed unless some attempt has been made to recognize and incorporate the peculiarities of individual cases; the model provides ample room for modification. An example of such a modification, involving a diffusive meroplanktonic larval stage, is developed in Chapter 2. The second, and more difficult problem is the danger of circular reasoning, which accompanies all models utilizing optimality as a governing principle in attempting to describe real phenomena.

The assumptions of the basin model are exceedingly difficult to validate (see Chapter 3). This is especially the case when we allow that the idealized population and habitat behavior in the model may not be reflected by the "imperfect" behavior of real populations. As the logistic model has been a seriously oversimplified but nonetheless useful description of some aspects of population dynamics (Kingsland 1982), the basin model may similarly prove useful. The question may not be whether but how well the basin model describes population behavior, and then whether the description is good enough to be useful. Of course, the criteria for ''good enough'' depend on the application. An alternative to direct validation of the assumptions may be to test predictions (viz. hypotheses) made by the model about population behavior, especially under novel conditions. Fortunately, the model is rich in this respect.

2

GEOGRAPHICALLY OPTIMAL HARVESTING

Although geographic controls on harvesting are among the oldest forms of resource management, the problem of geographically optimum strategies has seldom been addressed. In the past, geographic controls often have been the result of social or economic considerations, with or without a biological rationalization; examples range from private ownership of habitat to prohibition of harvesting in polluted areas. Instances where geographic controls have been biologically motivated have tended toward establishment of protected areas or refuges, especially during vulnerable stages in the life histories of intensely exploited or overexploited species. For example, salmon usually are protected from commercial harvest while in their spawning streams.

Here I attempt to apply the preceding geographical population model to the classical exploitation problem of maximizing sustainable harvest. So-called maximum sustainable yield, or MSY, is a simple and convenient objective in theoretical investigations, but good management will seldom wish to choose such a narrow objective. More complicated definitions of optimality will want to consider the amount harvested and the fishing effort required to obtain it. Rather than simply open or close areas to exploitation, managers may consider a variety of options that arise from controlling the geographic deployment of fishing effort. How much harvesting pressure should be allowed in various portions of the range of the resource? And more generally, does geographic control of harvesting produce unique benefits? What are the relationships between resource and habitat characteristics and optimal geographic patterns of harvesting?

The basin model also allows consideration of a further set of conservation and management issues that arise from geographic considerations. Environmental impact analyses often attempt to evaluate the consequences of habitat changes at a specific location. Existing ecological theory has provided little help, in part because of the lack of appropriate geographical population models. On the other hand, managers occasionally consider or attempt habitat improvements such as artificial reefs, in some cases as a mitigative measure for anticipated habitat damages in another location. More traditionally, managers also may create refuges, as described above. Yet there have been few guidelines for evaluating or optimizing the siting of such habitat impacts or improvements.

Many of these issues are addressed easily by the basin model developed in the preceding chapter. However, the simple population dynamics portrayed by the logistic model may not form a satisfactory basis for generalizations. In order to address a more realistic life history, I subsequently explore simulations incorporating basin model concepts along with traditional fishery modeling components.

2.1 THE BASIN MODEL REVISITED

The key issue in sustainability as well as optimal geography of harvests is the mechanism by which harvested removals are replaced by the population. At low viscosity, movement of individuals is rapid with respect to growth and harvesting rates, so that harvests have a roughly equivalent effect on the population wherever they are taken. Immediate replacement is by immigration, and the lost biomass is replaced by productivity wherever it occurs in the population.

High-viscosity logistic populations are assumed to replace losses due to harvesting mainly by in situ population growth, with immigration proceeding at a negligible rate. Thus, there is little interaction among harvests in various locations. Accordingly, in the case of high viscosity, maximum sustainable yield is obtained by maximizing local sustainable yields at every location. Since this model assumes locally logistic growth, optimal harvesting must hold the abundance at one-half its carrying capacity or saturation level (i.e., at $0.5K_h$) at every location (Figures 2.1 and 2.2). Coincidentally, optimum total population size is one-half the total carrying capacity. For each location, the optimum rate of harvest (F_h) is equal to one-half the rate of increase corresponding to the local value of basic suitability (r_h), and the central, most productive areas are therefore harvested more intensely than the marginal or peripheral areas. But because optimum abundance (N_h) is highest in habitats with the highest realized rate of increase (r_h*), productivity is effectively proportional to the square of abundance, and the amount of harvest taken from these most productive central areas is disproportionately large. Also, note that any slight suitability-oriented population movement will slowly erode the edges of the distribution, relative to the optimum in Figure 2.2, as individuals move toward better habitat and abandon peripheral margins.

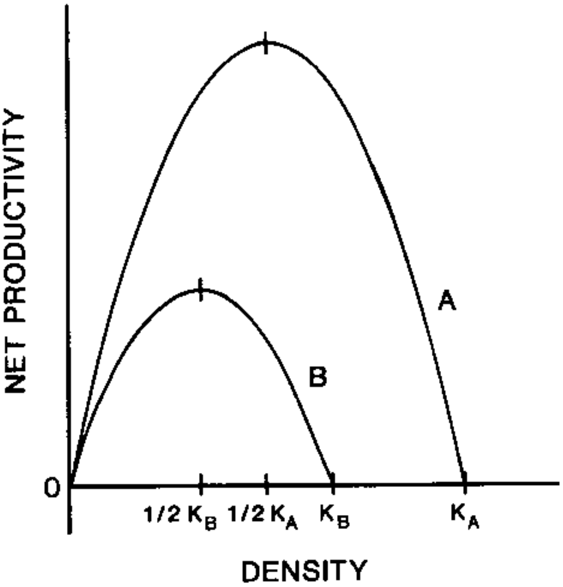

Figure 2.1 Local logistic population productivity curves for the example habitats shown in Figures 1.1 and 1.2.

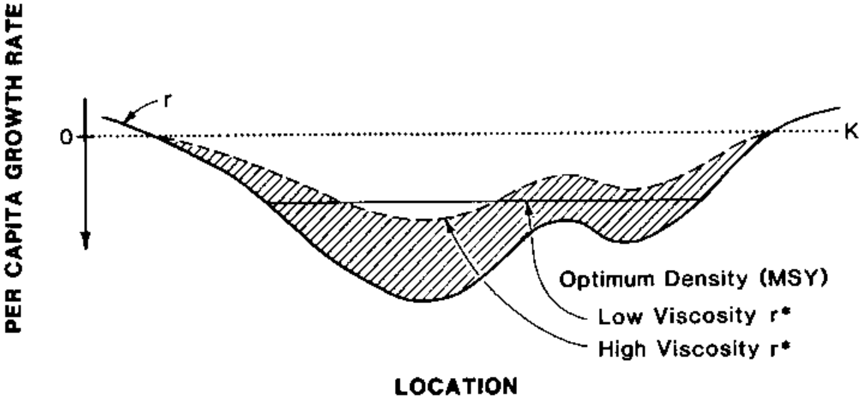

Figure 2.2 Comparison of geographic density distributions maximizing total productivity for low-viscosity and high-viscosity logistic populations.

For the same habitat topography and local density dependence, maximum harvest from a highly viscous population would greatly exceed that from a nonviscous population. This can be seen from the comparison of optimal density distributions for high-viscosity and low-viscosity populations in Figure 2.2. In this figure, the high-viscosity optimum density coincides with the low-viscosity optimum density in only two locations. At all other locations, local productivity of the low-viscosity population is less than the local potential maximum. In the high-viscosity case, optimal harvesting produced maximal harvests at every location.

Practical examples of high-viscosity resources might include plant species such as timber forests where replacement is dependent on natural propagation. Also, benthic invertebrates such as crabs or clams would fall in this category. Many territorial animal species tend to exhibit high viscosity but do not necessarily conform to the ideal free distribution. Optimal harvesting from an ideal despotic distribution may require quite different harvesting strategies due to differences in relative utilization of intensive and extensive marginal habitat. Also, the mechanism by which harvests are replaced may be important to the strategy of optimal harvesting. For example, replacement by nonterritorial "floaters," which have been produced elsewhere (low viscosity, short delay), produces different harvesting properties than does replacement by in situ reproduction by territory holders (high viscosity, long delay).

2.2 A SIMULATED RESOURCE

The rest of this chapter treats simulated populations that are variations of a standard fishery model. The model is driven by a deterministic stock-recruitment relationship and includes a dispersive larval phase, so that recruitment is not restricted to the site of parental spawning (this is a major difference from the logistic model in Chapter 1). The simulations allow comparisons of alternative behaviors, on the part of both the fish and the fishermen.

2.2.1 Life History

The simulated annual life cycle consists of five phases:

1. *Spawning,* which obeys a constant-slope Ricker model (see Chapters 1 and 3).
2. *Recruitment,* after dispersion from the site of spawning, to the adult population.
3. *Natural mortality,* which is a constant fraction independent of age or location.
4. *Harvesting,* as a location-specific instantaneous removal of individuals.
5. *Adult movement,* which may be oriented to the suitability of adjacent habitats.

The movement phase completes the annual cycle, and the simulation begins the next year with spawning. The order of events in the cycle is arbitrary, and experimentation has shown that alternative orders of events (e.g., movement after recruitment but before harvesting) do not produce substantially different population behaviors or results. Also, some of the components could be combined to produce a somewhat more realistic model. For example, natural mortality and harvesting could be represented as a continuous process involving simultaneously competing risks of death, as is standard in fishery models that use the Baranov catch equation. However, such a representation requires iterative solutions to the equations, slowing the computations, and yet produces results that are nearly indistinguishable from the simpler model.

Many previous models and simulations of habitat selection have successfully used a discrete formulation of simple two-habitat models (e.g., Rosenzweig 1981), and Bryant (1973) went so far as to conclude that two-habitat models are sufficient for most generalizations. However, models with larger numbers of discrete habitats may possess important emergent properties (e.g., Hamilton and May 1977, Hassell 1980, Starfield et al. 1981), and certainly provide a more recognizable link to habitat or population geography in the real world. Yet, use of too many habitats incurs a severe computational burden while returning little additional insight.

The geography of these simulated populations and their habitats is one-dimensional, consisting of a series of 19 contiguous sites, or "cells." I chose this formulation because it provided a recognizable habitat distribution, it could accommodate a variety of movement dynamics, and computation was feasible. In keeping with the basin model, the most favorable habitats are at the center of the series. Each cell has attributes such as abundance, harvesting rate, and habitat suitability. I implemented the model on a 16-bit personal computer, using the vector-oriented language APL. Details of the individual components of the simulation model are discussed in greater detail below.

2.2.2 Spawning and the Habitat Basin

The stock-recruitment relationship is modeled as a set of habitat-specific Ricker curves (Equation 1.27). The density-dependent parameter (b) is constant for all habitats, while the density-independent parameter (a_h) is habitat-specific. Habitat suitability is measured in terms of reproductive success, i.e., as $\mathrm{Ln}(R/S)$, which declines linearly with local abundance (Equation 1.28), allowing graphical representation similar to that developed in Chapter 1. The habitat basin is shown in Figure 2.3, where density-independent habitat suitability, $\mathrm{Ln}(a_h)$, ranges from -2.5 at the edges (cells 1 and 19) to 1.5 in the three center cells (9, 10, and 11). The basin is symmetrical and has a very smooth topography. The stock-recruitment relationships for each cell are shown in Figure 2.4. Spawners in the central cells are much more productive than those in the peripheral cells for comparable local abundances. Note that only cells 6 through 14 potentially produce offspring in excess of the amount needed to replace the annual loss of parents due to natural mortality (see below). The realized suitability corresponding to replacement is shown in Figure 2.3 as a horizontal line intersecting the basin between cells 5 and 6 and between cells 14 and 15.

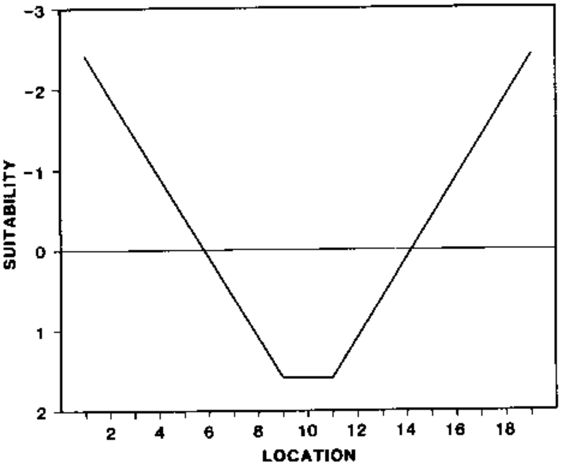

Figure 2.3 Habitat basin used in the simulations. Below the horizontal line, density-independent conditions allow recruitment to equal or exceed replacement levels.

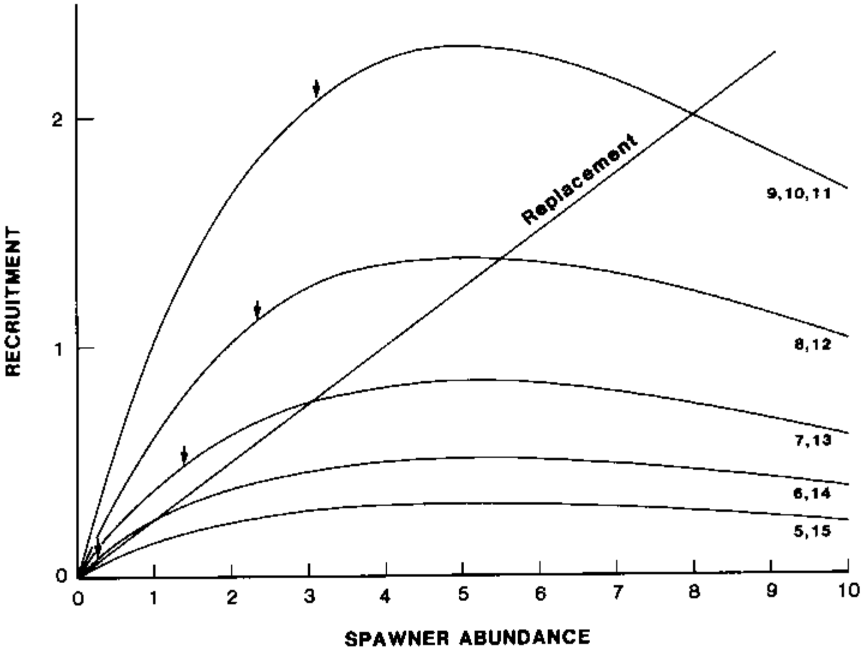

Figure 2.4 Stock-recruitment curves corresponding to the habitats in the simulated suitability basin. Arrows indicate location of maximum surplus recruitment.

2.2.3 Larval Dispersal, Recruitment, and Natural Mortality

After spawning, eggs and larvae disperse before settling in the various cells as recruitment. Two patterns of dispersion are considered here (Figure 2.5). The first pattern has no mean drift or advection, so that larvae settle symmetrically around the source to a maximum distance of four cells on each side. The second pattern includes a two-cell mean drift, so that the same relative dispersion pattern occurs but the entire pattern is advected two cells to the right. Importantly, larvae that drift outside the 19-cell range are lost. If habitat suitability were measured on the basis of larvae that eventually settle rather than simply those that are produced, the basin in Figure 2.3 would show increasing slopes toward the edges and would be asymmetrical in the case of two-cell mean drift.

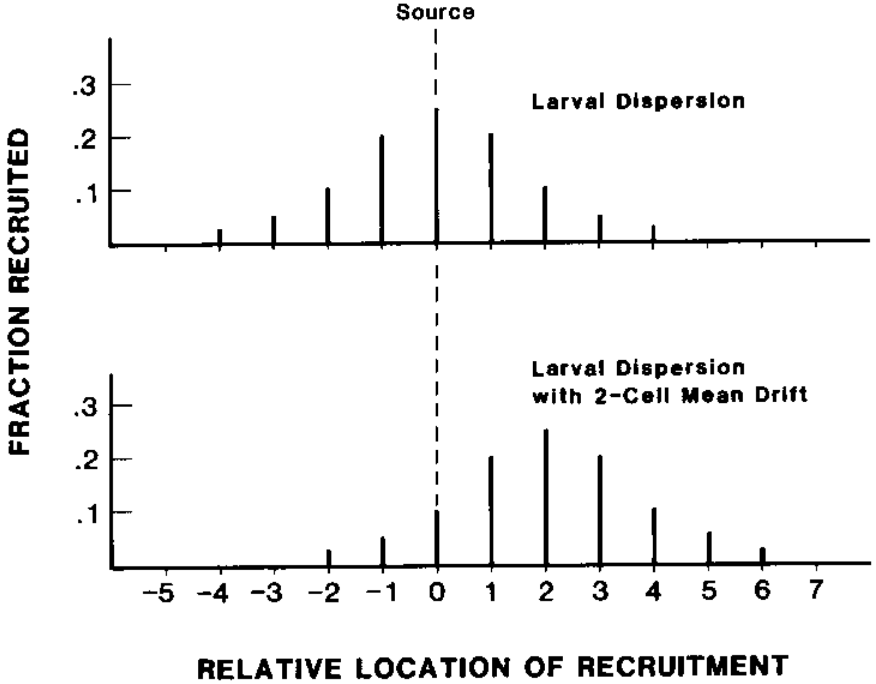

Figure 2.5 Patterns of meroplanktonic dispersal. Upper pattern is diffusive with no net drift. Lower pattern is identical except for a two-cell advective (drift) component.

After dispersal, the arriving offspring (recruitment) are added to each cell's abundance and contribute to the parental abundance in the next spawning. Abundances in all cells are then reduced by a natural mortality of 25 percent. Thus, the replacement line in Figure 2.4 has a slope of 0.25 recruits/spawner. Note that there is no age structure, but the mean life span of a recruit would be four "years" in the absence of fishing.

2.2.4 Harvesting

Harvest consists of subtracting a fraction (H_h, not to exceed unity) of a cell's abundance; the actual fractions depend on the harvesting rule being investigated. Fishing intensity in cell h (F_h) is defined as

$$F_h = -\text{Ln}\left(1 - H_h\right) . \tag{2.1}$$

Thus, F is analogous to an instantaneous fishing mortality rate (Ricker 1975), and individuals are subject to competing risk of capture by independent sources of fishing mortality. For the purposes of these simulations, F is referred to as "fishing effort," and represents a quantity of fishing activity that can be moved from cell to cell in the way individual vessels in a fleet distribute themselves in time and area. Fishing intensity or effort is cell-specific, allowing various geographic harvesting strategies to be investigated. In each simulation, the total amount of fishing effort is held fixed and is allocated among the cells according to the harvesting strategy.

Two particular harvesting strategies are investigated here. The first is a free distribution of fishing effort, representing the distribution of fishing activity in the absence of geographic restrictions. Fishermen are assumed to seek out the locations producing the highest catch rates, hence the locations with the highest abundances. However, their fishing activity reduces the abundance in those locations in the following year, abundance being the sum of the survivors and new recruits. Thus, unregulated fishing is assumed to result in an ideal free distribution of fishing effort whereby abundance or catch per effort (immediately prior to the harvest, when fishermen choose fishing locations) is the same in all exploited cells and is lower in any unexploited cells (Gordon 1953; cf. discussion of DDHS in Chapter 1).

In contrast, optimal harvesting strategies dictate the geographic distribution of the fishing effort in order to maximize the total quantity of harvest. Many other definitions of optimality could be considered, but maximum sustainable yield from a fixed total quantity of effort provides the clearest comparisons for these simulations. In most cases the optimal geographic distribution of effort cannot be determined analytically; it requires a numerical search. Unfortunately, a change in the effort assigned to any one cell generates changes in the harvest taken from many cells, because the fixed total amount of effort requires offsetting changes in effort elsewhere, and because the recruitment arriving in adjacent cells also is altered. For each distribution of fishing effort, the model was allowed to run for 60 simulated years to insure that a steady state had been reached; damped oscillations often lasted for 40 or more simulated years.

2.2.5 Movement

Two contrasting cases are examined. The first is an immobile population, such as clams, whose adults are incapable of movement once the larvae settle out of the water column as recruitment. The second case exhibits viscous movement with habitat selection. Viscous movement is generated by an algorithm called DDHS, which simulates density-dependent habitat selection (Table 2.1). Movement is oriented to the difference in realized suitabilities between adjacent cells, and the quantity moved is proportional to that difference, except that not more than half a cell's abundance is allowed to move in a particular direction in a single iteration. Movement with reduced viscosities is simulated by sequentially applying the DDHS movement algorithm several times.

TABLE 2.1 Movement algorithm DDHS, simulating density-dependent habitat selection. The example basin topography is flat with suitability of 1.0, density dependence is $-0.4/N$, and viscosity scaling factor is 1.25.

			CELL		
	1	**2**	**3**	**4**	**5**
Abundance (N_i)	0.5	1.5	2.5	0.5	1.0
Suitability ($S_i = 1-0.4N_i$)	0.8	0.4	0.0	0.8	0.6
Difference or gradient in suitability[a] ($D_{i,i+1} = S_{i+1}-S_i$)	-0.4	-0.4	0.8	-0.2	
Determine total flux across cell boundaries ($Mtot_{i,i+1}$), based on suitability gradient and arbitrary constant scaling factor related to viscosity[b] ($Mtot = 1.25D$)	-0.5	-0.5	1.0	-0.25	
Flux across left boundary of cell i[c] ($ML_i = \max(Mtot_{i-1,i}, -0.5N_i)$).	0.0	-0.5	-0.5	1.0	-0.25
Flux across right boundary of cell i[c] ($MR_i = \min(Mtot_{i,i+1}, 0.5N_i)$)	-0.5	-0.5	1.0	-0.25	0.0
Net change in abundance in cell i ($ML_i - MR_i$)	$+0.5$	0.0	-1.5	$+1.25$	-0.25
Abundances (N_i) after this single application of the DDHS algorithm	1.0	1.5	1.0	1.75	0.75
Eventual equilibrium abundances	1.2	1.2	1.2	1.2	1.2

NOTES

a. Negative means more suitable to the left, positive means more suitable to the right.

b. Negative means move to the left, positive means move to the right.

c. Limit flux in any direction to one-half of originating cell contents.

2.3 IMMOBILE ORGANISMS

It is often revealing to examine behavior of extreme cases of a model. Because the extreme of viscosity is the case of immobility, I first consider an organism that is incapable of movement in the adult (reproductive) life stage. Most species of plants would be included in this case. Fishery examples might include molluscs such as clams, some crustaceans, and some reef fishes. The planktonic larval stage disperses recruitment among the habitats according to the geographic distribution of parental spawning and the patterns of larval transport. I assume that transport is also diffusive and may or may not provide a net directional or advective movement of offspring relative to the parental location (see description above); these two cases provide an important contrast.

2.3.1 No Net Advection of Offspring

The distribution of abundance in the unharvested state can be represented by a basin diagram as was developed in Chapter 1 (Figure 2.6). Because the population does not show DDHS, and because the larval stage is diffusive, the population extends symmetrically into the submarginal peripheral habitats. The central habitats produce an excess of offspring (the realized suitability is below the replacement line), which compensates for insufficient peripheral production.

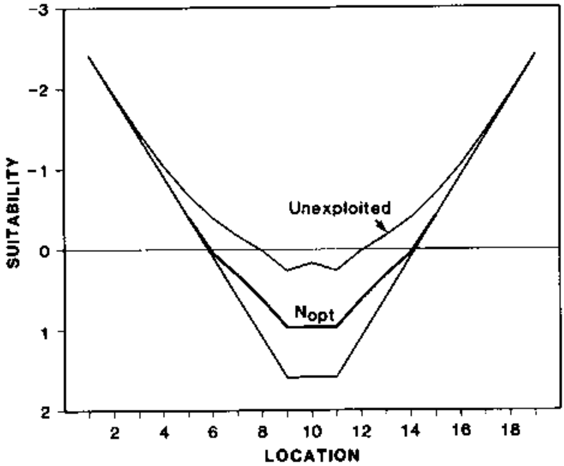

Figure 2.6 Basin diagram of an immobile population where offspring are subject to diffusion but no net drift. Local optimum abundances correspond to MSY levels shown in Figure 2.4.

The geographic distribution of abundance under free harvesting is shown in Figure 2.7. As described previously, free harvesting is assumed to produce a characteristically flat abundance profile over the harvested range. The production curve associated with free harvesting is very nearly symmetrical (Figure 2.8). Maximum sutainable yield is 3.97 and occurs at an F_{opt} of 1.46; the resource cannot sustain harvesting above an F_{max} of 3.20.

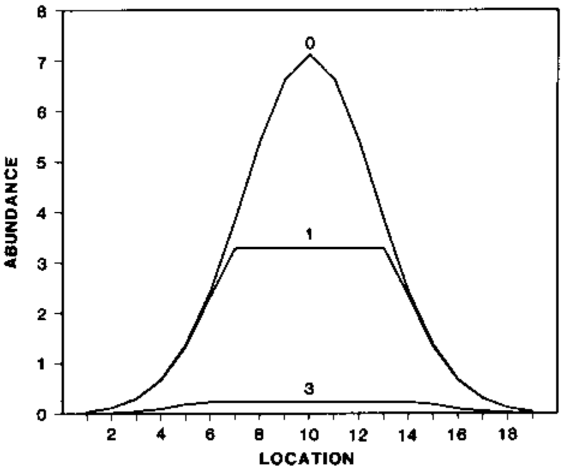

Figure 2.7 Distribution of an immobile population (no net drift of offspring) under free harvesting. Illustrated levels of fishing mortality are $F = 0, 1$, and 3.

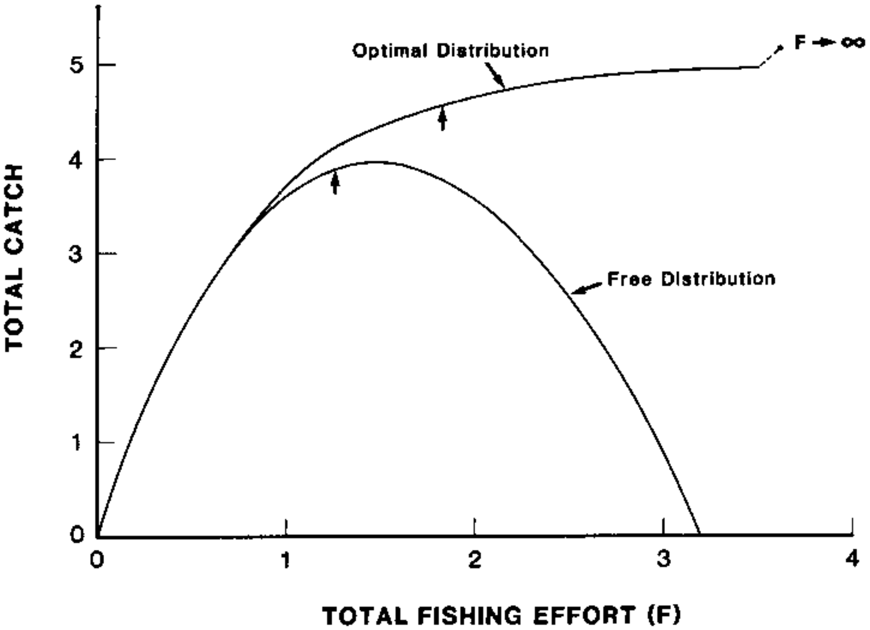

Figure 2.8 Production curves for an immobile population (no net drift). The upper curve results from geographic optimization, and the lower curve corresponds to a free distribution of effort. The arrows indicate locations of $F_{0.1}$ policies.

Optimal harvesting is in this case similar to that of the basin model with a viscous logistic population and can be determined analytically. Maximum productivity should be obtained when the abundance is optimal at each location. At maximum surplus production (the maximum difference between recruitment and replacement) from each cell, the slope of the stock recruitment curve is equal to the slope of the replacement line. Diffusive loss of potential recruits to habitats outside cells 1 and 19 must be included in this calculation. The optimum spawning abundances are shown in Figure 2.4. In peripheral cells 1–5 and 15–19, recruitment cannot exceed replacement and optimum spawner abundance is zero: all peripheral individuals are harvested. An iterative search for the optimal geographic harvesting strategy confirmed the above solution, where MSY is 5.16, or about 30 percent larger than MSY obtained from a free effort distribution.

The production curve for geographically optimal allocations of limited effort is shown in Figure 2.8. In agreement with the above solution, this production curve is asymptotic to a yield of 5.16 as F becomes very large. However, the curve lies above that for free effort at all levels of F greater than 1 and is indistinguishable for lower levels of harvesting intensity. The benefits of geographic optimization increase as total F increases, and are particularly great relative to an unregulated and overexploited ($F > 2$) resource.

A comparison of geographic distributions of fishing effort shows that under free harvesting (Figure 2.9), effort remains concentrated at the center of the resource, and at higher intensities there is little expansion of the fishing range. Under geographically optimal harvesting (Figure 2.10), the distribution of effort is central initially, but with increasing total F, fishing intensity soon becomes limited in the central locations, where abundance is not allowed to fall below the optimal level. Excess effort is shunted toward the periphery, particularly to marginal and submarginal locations with the highest abundances. In these locations the catch per effort is the highest, given the constraint that the impact on resource productivity must be negligible.

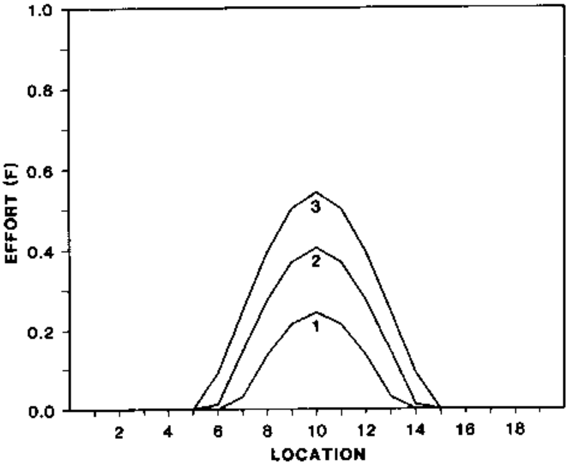

Figure 2.9 Free distributions of fishing effort for an immobile population (no net drift of offspring). Illustrated levels of fishing mortality are $F = 1, 2,$ and 3.

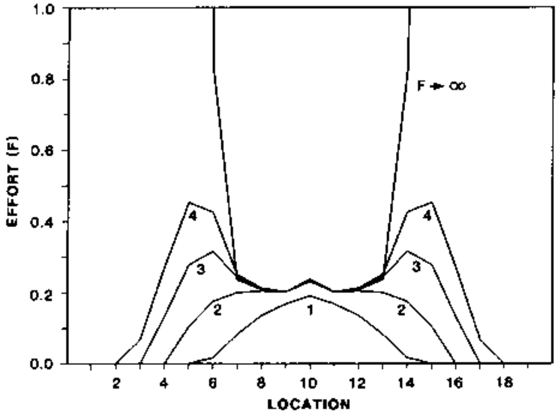

Figure 2.10 Optimized distributions of fishing effort for an immobile population (no net drift of offspring). Illustrated levels of fishing mortality are $F = 1, 2, 3,$ 4, and unlimited.

2.3.2 The Influence of Advection

The population in this simulation differs from the previous case only in that the distribution of recruitment locations is shifted two cells to the right (Figure 2.5). This simulation mimics a population spawning in the presence of a weak mean flow, so that relatively more recruits settle downstream of their parents. For an unfished resource, the resulting distribution of abundance is very similar in shape to that in the absence of advection (Figure 2.11), but the distribution is shifted about 2.5 cells downstream. The corresponding basin diagram (Figure 2.12) shows a very lopsided distribution of abundance in the habitat basin, with nearly half the population inhabiting habitat with submarginal realized suitabilities. This example shows the danger in naively assuming that the distribution of a population necessarily maps the distribution of favorable habitat, especially if the organism is not very mobile.

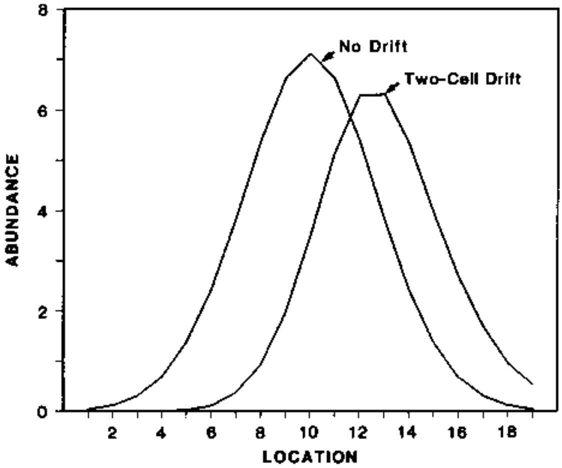

Figure 2.11 Comparison of distributions of unfished immobile populations without net drift of offspring and with two-cell net drift.

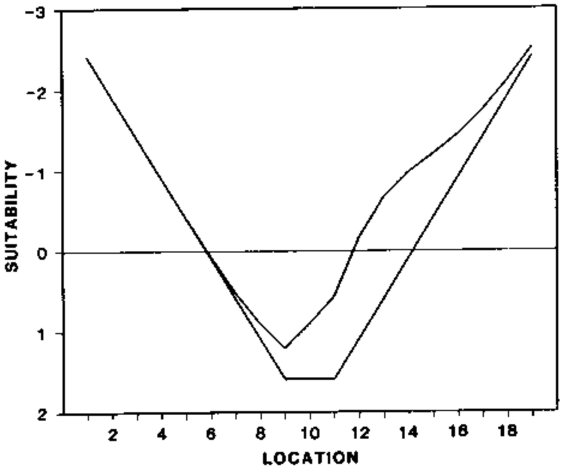

Figure 2.12 Basin diagram of an immobile population where offspring are subject to diffusion and a two-cell net drift.

Free harvesting again produces a nearly symmetrical production curve (Figure 2.13), although one somewhat less productive than in the previous case. Maximum sustainable yield is 2.99, occurring at an F_{opt} of 1.36, and F_{max} is 2.77. Geographic optimization again increases productivity, especially at higher total fishing intensities. The MSY of 4.76 is 59 percent higher than that obtained from unregulated free harvesting. The geographically optimum distributions of fishing effort are quite different from the previous symmetrical case, with the distribution of fishing effort being shifted downstream progressively with increasing total fishing intensity (Figure 2.14). As in the case of unregulated fishing effort, low levels of geographically optimized effort tend to be distributed similarly to abundance. At all fishing intensities, optimization results in the productive upstream segment of the population being conserved. Excess effort again is shunted into those unproductive downstream areas with the highest abundance.

There is little to be gained from attempting to optimize the geographic distribution of fishing effort if fishing intensity is at or below that producing MSY. However, substantial gains are possible for overexploited ($F > F_{\mathrm{MSY}}$) resources. Given a change to the optimum geographic distribution of effort, how soon are the benefits realized? Three simulated time trajectories of annual catches are shown in Figure 2.15. In the slightly overexploited case of $F = 1.5$ (cf. Figure 2.13), there is a brief ''windfall'' as harvests are taken from previously lightly exploited areas, and the yield quickly converges to the new equilibrium. In more severely overexploited cases, this ''windfall'' does not appear—actually, the brief increased catch from new fishing areas is offset by the decreased catches

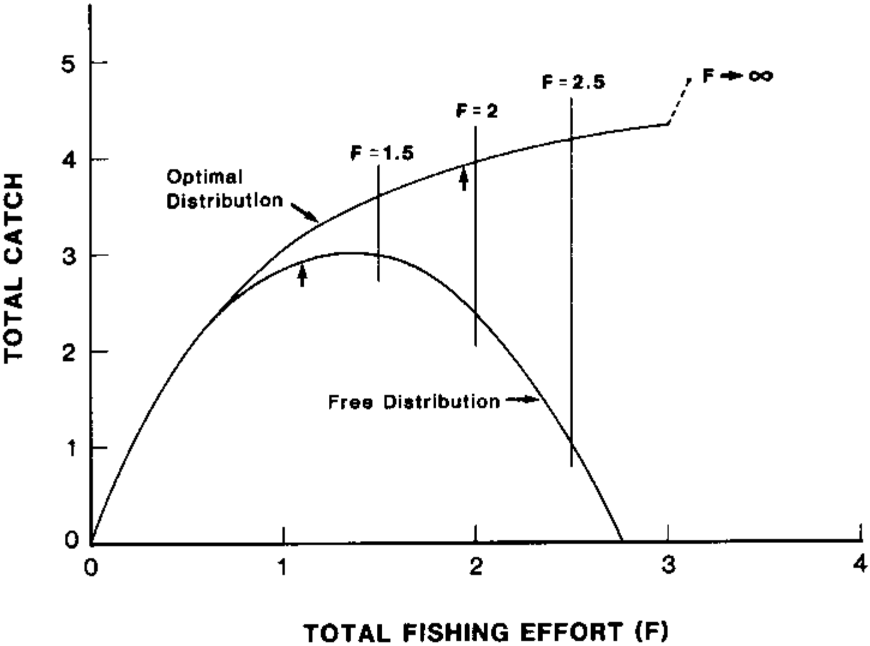

Figure 2.13 Production curves for an immobile population (two-cell net drift). The upper curve results from geographic optimization, and the lower curve corresponds to a free distribution of effort. The arrows indicate locations of $F_{0.1}$ policies.

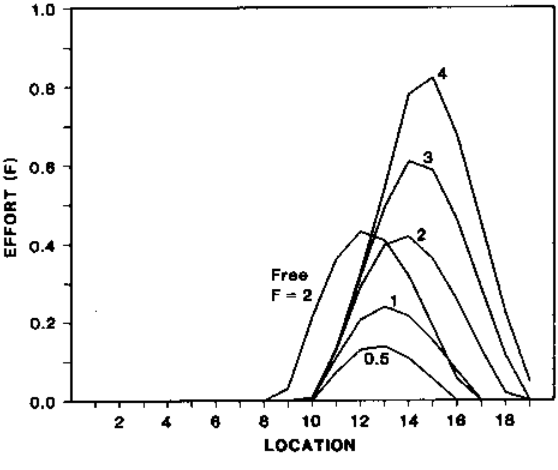

Figure 2.14 Optimized distributions of fishing effort for an immobile population where offspring are subject to a two-cell net drift. Illustrated levels of fishing mortality are free fishing $F = 2$, and optimized $F = 0.5$, 1, 2, 3, and 4.

from heavily restricted areas. Because of the new source of catchable fish, the transitional loss of catch appears to be smaller than those losses typically resulting from common changes in fishery regulations, such as changes in mesh size. As is normal for depleted resources, the rate of recovery is slower the greater the initial depletion. Whether the relative trajectories would be different for an age-structured model has not been investigated; presumably, similar "windfalls" would occur, but recoveries would be delayed by the time for individuals to grow from recruits to harvestable and/or reproductive size.

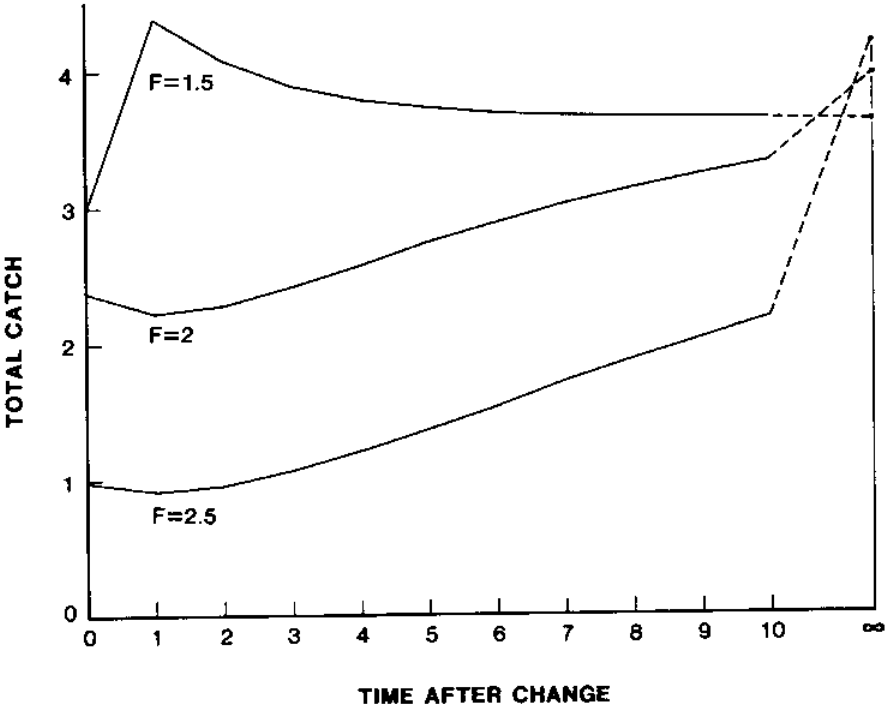

Figure 2.15 Catch trajectories following a change from free effort distributions to geographically optimized effort distributions utilizing the same total fishing effort. Locations on the related production curves are shown in Figure 2.13.

2.3.3 $F_{0.1}$ Harvesting Policies

Results of the simulations are compared in Table 2.2. Because MSY is not realizable at finite total fishing effort under the optimized strategies, another comparison is useful. Gulland and Boerema (1973) describe a popular management criterion, whereby fishing effort should not exceed the intensity at which the marginal yield from additional effort produces 10 percent of the marginal yield near zero effort (i.e., where the slope of the production curve is 0.1 the slope at the origin). This so-called $F_{0.1}$ policy provides a particularly useful rule of thumb for managing harvests that follow asymptotic yield curves similar to those generated by geographically optimized harvesting.

TABLE 2.2 Simulation results for immobile populations.

GEOGRAPHIC EFFORT DISTRIBUTION	FREE	OPTIMAL
Case: no net drift		
Pre-exploitation abundance	48.7	48.7
Maximum sustainable yield	3.97	5.16
(F_{MSY})	(1.46)	(∞)
(F_{MAX})	(3.20)	(∞)
Yield at $F_{0.1}$	3.89	4.60
($F_{0.1}$)	(1.24)	(1.82)
Case: two-cell net drift		
Pre-exploitation abundance	39.7	39.7
Maximum sustainable yield	2.99	4.76
(F_{MSY})	(1.36)	(∞)
(F_{MAX})	(2.77)	(∞)
Yield at $F_{0.1}$	2.92	3.93
($F_{0.1}$)	(1.09)	(1.96)

The $F_{0.1}$ harvesting levels for the production curves in Figures 2.8 and 2.13 also are summarized in Table 2.2. Because the slopes at the origin are the same whether or not harvesting is geographically optimized, $F_{0.1}$ values can be compared directly in each case. In the case of no advection, geographic optimization provides about 18 percent more yield at $F_{0.1}$, while allowing 47 percent more effort to be deployed. The case of two-cell advection shows even larger gains from geographic optimization under an $F_{0.1}$ management policy: yield increases by 35 percent, and allowable effort increases by 80 percent. Of course, in actual practice the desirability of these changes would have to be evaluated on the basis of more realistic management objectives.

2.3.4 Geographic Reproductive Value

The preceding simulations also provide a basis for determining location-specific impacts on the resources from modification of habitat. Individuals in various parts of the range make different contributions to following generations; this is especially apparent in the case of advection, where larvae from downstream spawning are washed out of the system. The simulations provide a basis for quantifying this phenomenon and for evaluating the importance of particular locations to the population.

By analogy to Fisher's (1958) concept of age-specific reproductive value, we can define a quantity called the geographic reproductive value. This quantity is the long-term equilibrium number of individuals in the population that are produced by an individual at a given location, and is expressed as a ratio where 1.0 signifies exact replacement.

In the present simulation model, I estimate geographic reproductive value by constructing a two-population model in which the dynamics of the two populations (called *A* and *B*) are identical in every respect, except that their location-specific abundances can be traced separately. At equilibrium of an all-*A* population, I introduce a very small quantity of type *B* to the location being evaluated (and subtract an equal amount from the local type *A* abundance). The simulation is then run until the geographic distribution and abundance of type *B* reach equilibrium. The geographic reproductive value of an individual at that location is the ratio of the final total abundance of type *B* to the quantity of type *B* that was introduced initially. Note that if the dynamics of the two populations is allowed to differ, equilibrium usually is not reached, and this ratio changes due to competitive exclusion of one or the other type in this simple model.

The geographic reproductive values corresponding to an unharvested resource with and without two-cell advection are shown in Figure 2.16. The traditional model, which assumes geographical homogeneity, would produce estimated geographic reproductive values of unity at every location. However, in the present model case of no advection, individuals in the three center cells have values of about 1.5, while values in the edge cells decline to zero. The contrast is even greater for the case of two-cell advection, where upstream individuals (those in cells 7 and 8) have geographic reproductive values of 9.5, but individuals at the center of abundance have geographic reproductive values approaching zero! This contrast of geographic reproductive values for upstream and downstream locations suggests that populations whose meroplanktonic larvae experience advective conditions may be under very strong selection pressure to develop behavioral or other mechanisms to counter the effects of that advective flow.

The importance of a particular habitat to the population, here termed *habitat value,* can be assessed as the product of the fraction of total abundance and the geographic reproductive values of individuals in that habitat. Summation of these products over all habitats must be equal to unity if the population is in equilibrium. In the simulated immobile population with no net advection of larvae, the central habitats account for about 45 percent of the total abundance, but they account for nearly 70 percent of the total habitat value (Figure 2.17).

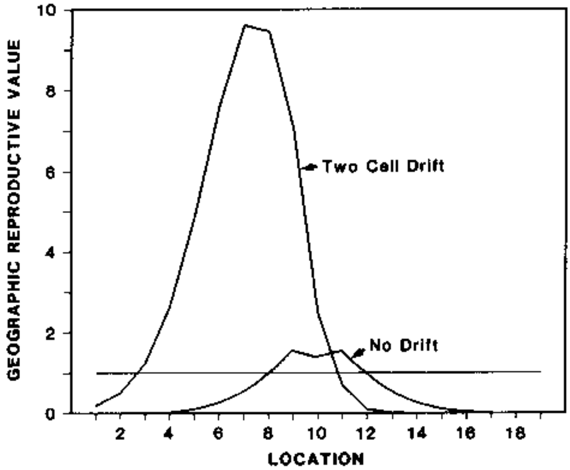

Figure 2.16 Geographic reproductive values for immobile populations where offspring are subject to diffusion, with and without two-cell net drift.

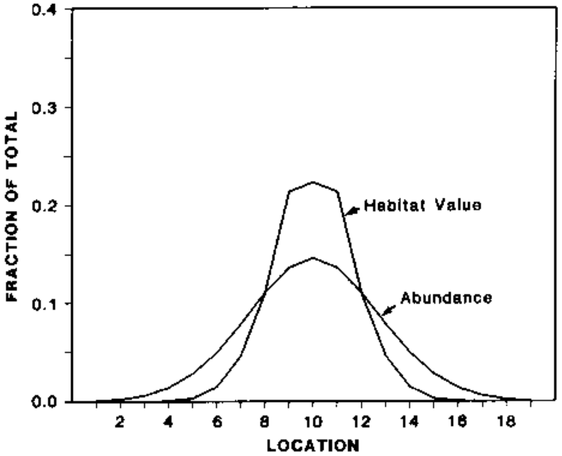

Figure 2.17 Distribution of abundance versus distribution of habitat value (see text) for an immobile population where offspring are subject to diffusion but no net drift.

The relationship is very different for the case of two-cell advection (Figure 2.18). Here, the habitat value peaks sharply in cell 9; this single cell accounts for 35 percent of the total habitat value despite its containing less than 5 percent of the total abundance. Actions impacting habitats at the center of abundance would have surprisingly little effect on the population, while impacts located on the sparsely populated upstream segment of the population could have substantial effects.

While consideration of geographic reproductive value and habitat value has obvious implications for traditional environmental impact analyses, these concepts are equally useful for evaluating potential effectiveness of positive actions such as creation of artificial reefs and other kinds of artificial habitat. For maximum effectiveness such a habitat enhancement might be located so as to balance its value as a fishing location

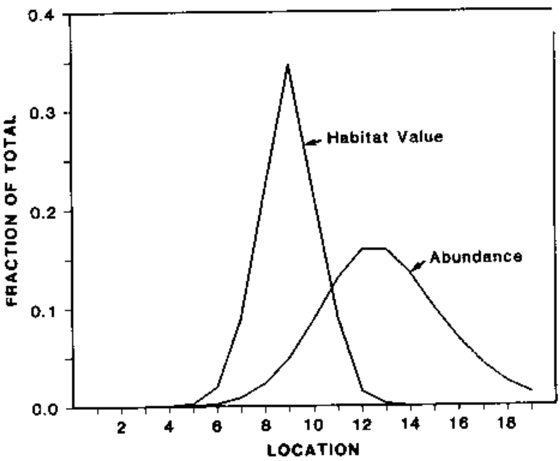

Figure 2.18 Distribution of abundance versus distribution of habitat value (see text) for an immobile population where offspring are subject to diffusion, with a two-cell net drift.

versus its value for enhancing the rest of the population by virtue of its habitat value. Comparison of Figures 2.17 and 2.18 shows that the pattern, distance, and direction of the advection of larvae can be a major consideration, particularly if the adults are immobile. In some cases these two objectives may be complementary, and in others they may be mutually exclusive.

Actual fishery cases illustrating these population behaviors are difficult to find, as typically free harvesting distributions tend to obscure the population geography (cf. Figure 2.7). One potential example is the clam fishery in Narragansett Bay, Rhode Island (Michael Prager, Old Dominion University, personal communication). Clams (species unknown) exist throughout the bay, but fishing is usually prohibited in the upstream portion of the bay due to contamination. This downstream fishery maintained consistently high yields for many years. When the upstream beds finally were declared safe and were opened to fishing, there was a brief bonanza, but overall production declined subsequently. When the upstream beds were once again closed, the fishery returned to its previous pattern of a productive downstream harvest.

2.4 MOBILE ORGANISMS WITH HABITAT SELECTION: INTERMEDIATE VISCOSITY

The case of very low viscosity, with rapid redistribution and mixing of the population, will not be treated. For a population with a simple life history and geographic structure, such as has been treated in the simulations, dynamics would be similar to the low-viscosity basin model with logistic dynamics as described in Chapter 1. To the extent that all locations of recruitment are equivalent, larval drift would be immaterial to a highly mobile species. Of course, drift (or lack thereof) may be important to survival through early, less mobile life stages (Parrish et al. 1981), in which case effects of drift would be included directly in defining the topography of the suitability basin. Also, in real cases mobile populations may nonetheless be defined by drift patterns, and corresponding life histories that are adapted to completing the reproductive cycle can be quite complicated (Sinclair 1988).

The following set of simulations treats the case of intermediate viscosity for the simple life history in the model. The fishery simulations incorporate four calls to the movement algorithm DDHS described in Table 2.1. This intermediate case may correspond to a variety of demersal fishes, such as flatfishes, which are mobile but are not energetic swimmers. Although this intermediate case seems to bridge the two extremes, it presents problems that do not necessarily occur for highly mobile or immobile organisms. In particular, the simulations suggest a tendency toward presence of unstable or neutral geographic configurations as well as toward multiple equilibria: fishermen can go to the fish or, alternatively, fishermen can harvest a ''hole'' in the population and let the fish come to them.

Corresponding ''optimal'' geographic distributions of fishing effort must be examined as to whether they are local optima, and as to whether they are reasonable or are artifacts of the mathematics used in the model. In the latter case, constraints may be placed on the model and on the nature of allowable solutions. Exploratory investigations showed that models incorporating adult diffusion rather than habitat selection are especially prone to multiple solutions. These multiple solutions are sensitive to the model specifications, and despite their popularity in the theoretical literature, models incorporating diffusion do not seem to provide any useful insights in the present context.

2.4.1 No Net Advection of Offspring

Again, with no net advection, the distribution of abundance is symmetrical. As would be expected from density-dependent habitat selection, the surface of the population in the basin diagram becomes flatter with increasing numbers of calls to the DDHS algorithm (Figure 2.19), as habitat selection counters the diffusive distribution of recruitment. The unfished population size could be interpreted as a carrying capacity that is determined by interaction of the basin topography, movement behavior of adults, and the drift or dispersal of the larvae. In this case of diffusion but no net advection of offspring, carrying capacity declines with increasing intensity of habitat selection (Figure 2.20).

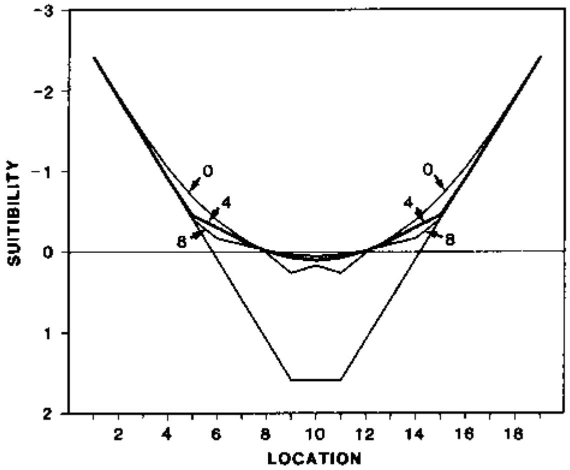

Figure 2.19 Basin diagram of viscous populations where offspring are subject to diffusion but no net advection. Viscosity is indicated by the specified number of applications of the movement algorithm; the dark line is the case (four applications) used in the fishery simulations.

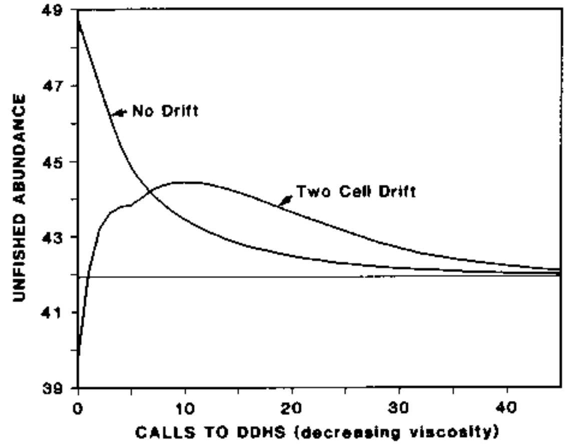

Figure 2.20 Influence of viscosity on unfished abundances or carrying capacities for populations with and without two-cell advection.

Although peripheral individuals occupy better habitat due to movement, elimination of the depression at the center of the population surface (Figure 2.19) results in decreased production of offspring. The extent of this decrease can be seen in Figure 2.4, where the right limb of the stock-recruitment curve for cells 9, 10, and 11 descends for adult densities exceeding 5. Also, habitat selection results in decreased utilization of peripheral, marginal habitat as places in which to live.

The following simulation employs four calls to the DDHS algorithm. Unconstrained harvesting policies (not illustrated) tend to exploit cells 9 and 11 heavily, while the relative intensity of fishing in cell 10 is lower for total F below 1.6 and higher for total F above that level. Apparently for free effort distributions with low total effort, the steep suitability gradients produced between cells 8 and 9 and between 11 and 12 result in a high influx of fish similar to the "overshoot" shown in cell 4 of the example in Table 2.1. This pattern is an artifact of the model and is unstable in the vicinity of $F = 1.6$, as shown by the shaded area in Figure 2.21.

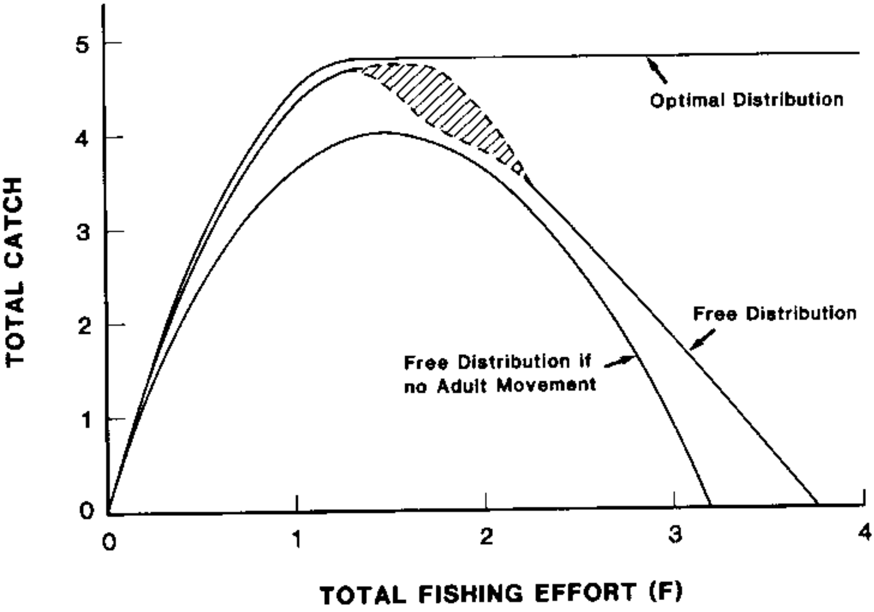

Figure 2.21 Production curves for viscous populations with no net drift of offspring. The upper curve results from geographic optimization, and the lower curve corresponds to a free distribution of effort. The arrows indicate locations of $F_{0.1}$ policies.

In the search for geographically optimum patterns of effort, I constrain the three center cells to have the same level of fishing effort. Up to the MSY level, both free and optimized effort distributions concentrate on the central three cells. At higher levels of total effort, the geographically optimized policy shunts all excess effort peripherally to cells 1–4 and 16–19, where almost no fish are harvested. Cells 5–8 and 12–15 are left unharvested, in contrast with the optimum under the case of no mobility. This peripheral shunting is logically equivalent to the usual management practices, which maintain effort at F_{MSY} by shortened seasons, inefficiencies, etc. Because fish in peripheral habitats tend to move toward the central favorable habitat, those fish potentially will reproduce in progressively better habitats. Fishing effort deployed in cells 5–8 and 12–15 would produce a low catch per effort due to the low abundance, while it would remove fish that would have improved their reproductive output substantially in the next season.

The ascending limb of the production curves for the free and optimized fisheries are nearly identical, but the right limb of the production curve for the geographically optimized fishery simply continues horizontally at the MSY level due to the shunting of excess effort (Figure 2.21). Because the ascending slopes are nearly identical, $F_{0.1}$ harvest policies are virtually identical for free and geographically optimized fishing (Table 2.3). Of course, the production curve for the free effort distribution descends at higher levels of effort. Both production curves are higher (more productive), skewed, and more resilient (able to sustain higher levels of F) than in the corresponding previous cases of no mobility. These differences are consistent with the properties that in Chapter 1 were predicted to arise from density-dependent habitat selection.

TABLE 2.3 Simulation results for mobile populations, with density-dependent habitat selection.

GEOGRAPHIC EFFORT DISTRIBUTION	FREE	OPTIMAL
Case: no net drift		
Pre-exploitation abundance	45.4	45.4
Maximum sustainable yield	4.79	4.79
(F_{MSY})	(1.66)	(ca.1.4)
(F_{MAX})	(3.79)	(∞)
Yield at $F_{0.1}$)	4.61	4.61
($F_{0.1}$)	(1.23)	(1.22)
Case: two-cell net drift		
Pre-exploitation abundance	43.8	43.8
Maximum sustainable yield	3.78	4.74
(F_{MSY})	(large, in cell 11)	(∞)
(F_{MAX})	(large)	(∞)
Yield at $F_{0.1}$	3.18	4.47
($F_{0.1}$)	(1.33)	(1.77)

2.4.2 Influence of Advection

Again, advection of larvae results in the population being shifted relative to the habitat basin, but the amount of shift is reduced as mobility increases (Figure 2.22). An increased number of calls to the movement algorithm can be interpreted equivalently as decreased viscosity. Using this interpretation, the basin diagram (Figure 2.23) shows the tendency for the simulated population to flow like a viscous liquid toward the central favorable habitat.

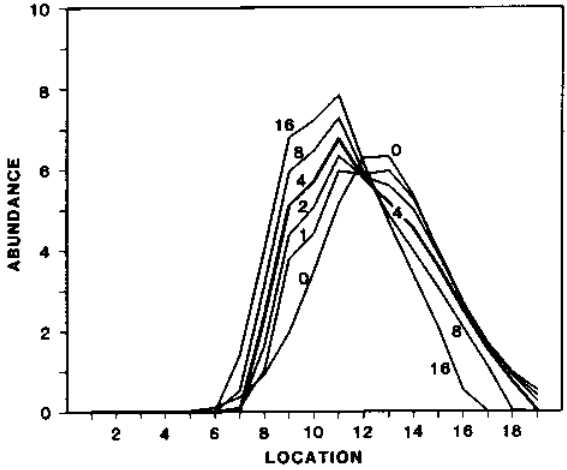

Figure 2.22 Distributions of unfished viscous populations with two-cell net drift of offspring and varying viscosities. Viscosity is indicated by the specified number of applications of the movement algorithm; the dark line is the case (four applications) used in the fishery simulations.

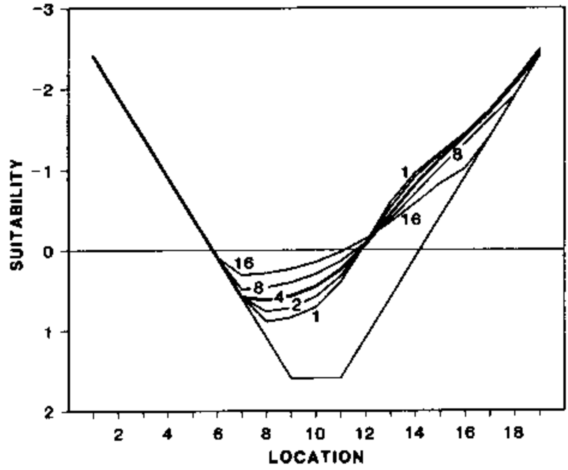

Figure 2.23 Basin diagram of unfished viscous populations where offspring are subject to diffusion and a two-cell net drift. Viscosity is indicated by the specified number of applications of the movement algorithm; the dark line is the case (four applications) used in the fishery simulations.

In contrast to the case of no net advection, equilibrium unfished abundances, or carrying capacities, initially increase as the intensity of habitat selection increases, or equivalently, as viscosity decreases (Figure 2.20). But as number of calls to the DDHS algorithm exceeds about 8, carrying capacity declines asymptotically. Although net advection of larvae lowers the carrying capacity for populations of relatively immobile individuals, advection may enhance carrying capacity slightly for more mobile populations. While it is premature to generalize, these simulations suggest that carrying capacity can vary unexpectedly with interactions between movement behavior and the environment, especially if conditions vary over time.

Again, four applications of the movement algorithm are used in the following fishery simulations. An unregulated fishery concentrates nearly all of its effort in cell 11. This is the location of highest abundance (Figure 2.22), and also is a location of very high influx of centrally migrating individuals that were recruited downstream. There are several poorly defined segments of the production curve similar to that shown in Figure 2.21, so the curve cannot be drawn clearly and $F_{0.1}$ policies are also unclear. The geographically optimized fishery produces a 25 percent larger MSY (Table 2.3), and the production curve again becomes asymptotic.

The optimum pattern of effort varies with fishing intensity (Figure 2.24). At all levels of effort, fishing is prohibited in upstream cells 1–9 and is very limited in cell 10. At low levels of effort, fishing is distributed evenly over the remainder of the population, again with a tendency to deploy additional effort farther downstream. Between a total F of 2 and 3, where the production curve has already flattened out, there is a large change in the optimum geographic distribution of effort: the fishery breaks into two segments, a central fishery in cells 12 and 13 and a downstream fishery in cells 15–19. Cell 14 is not fished.

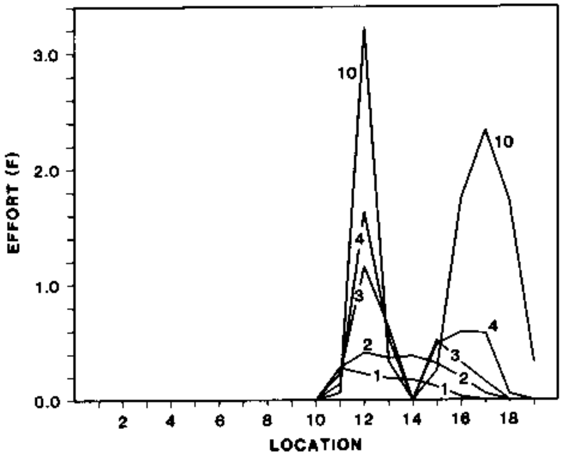

Figure 2.24 Optimized distributions of fishing effort for a viscous population and a two-cell net drift of offspring. Illustrated levels of fishing mortality are $F = 1$, 2, 3, 4, and 10.

This pattern seems to be analogous to the central and peripheral segments encountered in the previous case of no net advection. However, unlike the previous case, where the peripheral fishery caught very little, the downstream segment of this fishery produces 11–15 percent of the total yield.

2.5 DISCUSSION

The preceding simulations allow some tentative generalizations. The problem of geographically specific population dynamics results in computationally intensive models. The length of the simulations can be shortened considerably if an initial state is specified and a ten- or twenty-year time horizon is considered. Equilibrium solutions, such as were examined here, required between sixty and one hundred simulated years. Additional geographic structure, such as a more realistic two-dimensional suitability topography, will slow the execution of the simulations while requiring more time to reach equilibrium. The appropriate amount of simulated detail remains to be determined for a real resource, and available biological and oceanographic information may prove to be a limiting constraint.

Also, consideration of variability in patterns of drift and dispersal may require extensive computation. These simulations suggest that net drift may be very important to population dynamics and to optimal harvesting patterns. There are very few resources for which some directional drift does not occur. That drift, and the behavioral mechanisms by which the population counters it, should be examined carefully and incorporated into the simulations. For example, the mean pattern may not include infrequent but important events, such as reversals in current flow which episodically repopulate the upstream regions of the habitat. Waples (1986) shows how El Niño conditions may provide such upstream repopulations off southern California.

In view of our limited understanding of fish movements and of the mechanisms and stimuli involved (see Chapter 3), it may be appropriate to investigate various hypothetical models in a search for robust management policies. Again, experience with this simple simulation model suggests that simulations involving fish movement may tend to be somewhat "ill behaved." These simulated systems often possess multiple steady states, and solutions may depend on initial conditions as well as details of the mathematical algorithms used in the simulations; care must be taken in their construction and interpretation.

2.5.1 Fishery Management

It is unlikely that any of the very simple model populations and habitats portrayed in these simulations would correspond closely enough to a real fishery to be directly useful to management. If geographic optimization is considered for an actual fishery, an appropriately detailed model should be constructed. Yet, these simple simulations provide useful indications of which resources and fisheries would be good candidates for geographic optimization.

It is easiest to begin with those cases where geographic optimization is least likely to be worthwhile. Highly mobile organisms that move and mix throughout the range of the population on time scales of less than a year simply do not "stay put" long enough; local harvesting constraints have little effect. On the other hand, geographic contraction of the population coincident with decreased abundance may increase the risk of rapid overfishing by an unregulated fleet.

Also, in the traditionally ideal but practically rare case where the fishing fleet's potential effort is well matched to the production curve (e.g., where fleet capacity is at or below an $F_{0.1}$ level of fishing effort), geographic regulations are unnecessary. But if the fleet's potential exceeds F_{MSY}, or if management wants to maximize participation in the fishery, geographic optimization may be worthwhile. Geographic allocation of fishing effort should not be considered to be just another form of enforced inefficiency (e.g., shortened fishing seasons) unless its result is simply to occupy a position of lower fishing intensity on a production curve equivalent to that of an unregulated fishery. Geographic optimization is most likely to be useful where the exploited stage of the organism is not very mobile. Also, these simulations suggest that geographic optimization may be appropriate if the planktonic offspring of the exploited organism experience a directional drift that is not completely compensated by juvenile or adult movements. Geographic fishing strategies may be especially appropriate to optimizing transboundary fisheries, where criteria for optimality may vary considerably on opposite sides of the jurisdictional boundary.

2.5.2 Habitat Evaluation and Impact Assessment

One of the large unanswered questions in environmental management is, "What effects does habitat loss or habitat modification have on natural populations and their harvests?" Conventional fishery models, with their assumption of homogeneous populations, have not provided answers. This model's coupling of population dynamics with the geographic distribution of habitat suitabilities is a promising approach, but the model demands much more information and is far more difficult to implement than the usual fishery models. Indeed, full development of a geographic model is not appropriate for routine decisions, but guidelines for such decisions are indicated.

The viscosity of the resource is an important consideration in evaluating impacts. Impacts may be relatively local for highly viscous or immobile species, whereas for mobile species impacts may be borne by the entire population. Chronic impacts such as entrainment mortality of larvae by power plants, or reduced fecundity due to exposure to contaminants, would be locally contained for a viscous species. Even though the area of impact may be very local, much of the population of a mobile species may be exposed; total impact depends on the fraction of the population in the vicinity of the contaminant source and the rate of geographical mixing of individuals. In the case of impacts located near the edge of a population, contraction of population range with reduced abundance may provide a feedback mechanism by which progressively smaller fractions of the population are impacted, and a new equilibrium may be reached. Losses may be unexpectedly large for impacts located near the center of a population. There, mixing rates and the fraction of the population exposed are highest. Furthermore, a progressively greater fraction of the population is exposed to the impact as abundance decreases (cf. fishery collapse due to stock contraction).

In summary, some key considerations are raised by the previous simulations:

- *Is the population viscous, or is it highly mobile so that it mixes on short time scales and approaches homogeneity?* A viscous or immobile population potentially allows more specific answers to questions of local as well as population-level environmental impact. On the other hand, high mobility allows impacts to be diffused throughout the population, and simpler models may be used.
- *How diffusive is recruitment? Is recruitment subject to net directional movement or drift from the place of spawning?* If the resource is viscous, larval transport may cause the distribution of the adult population to reflect poorly the relative importance of habitats. Evaluation requires complicated models and geographically detailed oceanographic and biological knowledge. Impacts on upstream segments of the population may be deleterious to the population and harvest despite a relatively low abundance of impacted individuals. In choosing sites of refuges or artificial habitats, resource managers may wish to consider benefits from reproductive enhancement of the stock (improved habitat value) as well as more traditional concerns of changes in benefits from direct harvest.

3

APPLICATION OF THE BASIN MODEL

Stock expansion and contraction with large changes in abundance seems to be characteristic of clupeoid fishes (sardines and anchovies). Understanding the dynamics of this phenomenon is an important step in understanding how fisheries affect clupeoid resources.

From the viewpoint of the study of ecology, density-dependent habitat selection has seldom been the basis for field studies on a large geographic scale. In collecting fishery data, field observations are often made on the scale of an entire population spanning thousands of square kilometers. Owing to the extensive data on anchovy larvae collected by the surveys of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) over the past 35 years, and because of the unusually large dynamic range of abundance and geographic distribution exhibited by these larvae, the CalCOFI surveys provide an excellent opportunity to examine and apply the theory of density-dependent habitat selection developed in the preceding chapters.

This investigation consists of three segments. First, I examine the mechanisms that may be associated with habitat selection by spawning anchovies, with emphasis on those that cause a density-dependent decline in the suitability of spawning habitat. Second, I examine the geographic distribution of spawning and subsequent egg mortality rates with respect to the ideal free distribution. Finally, I use the CalCOFI time series of larva abundances as the basis for mapping the spawning anchovy's apparent habitat suitability basin.

3.1 THE NORTHERN ANCHOVY

Abundances of anchovy *(Engraulis mordax)* eggs and larvae (Figure 3.1) have been monitored systematically since 1951 by CalCOFI. The total abundance of larvae, which provides a rough index of adult spawning biomass (MacCall 1980a, Smith 1972), has varied 30-fold since observations began (Figure 3.2). More recently, Lo (1985) estimated an index of daily production of anchovy eggs which provides a better relative measure of spawner abundance because it reduces post-spawning sources of variability. Lo's index varies 1,000-fold over the same period (Figure 3.2). This extreme variability in presumptive abundance has been a source of concern in management of the anchovy fishery (MacCall et al. 1983). The changes in anchovy larva abundance have been accompanied by large changes in their geographic range as well as by changes in density at commonly occupied locations (Figures 1.12 and 1.13).

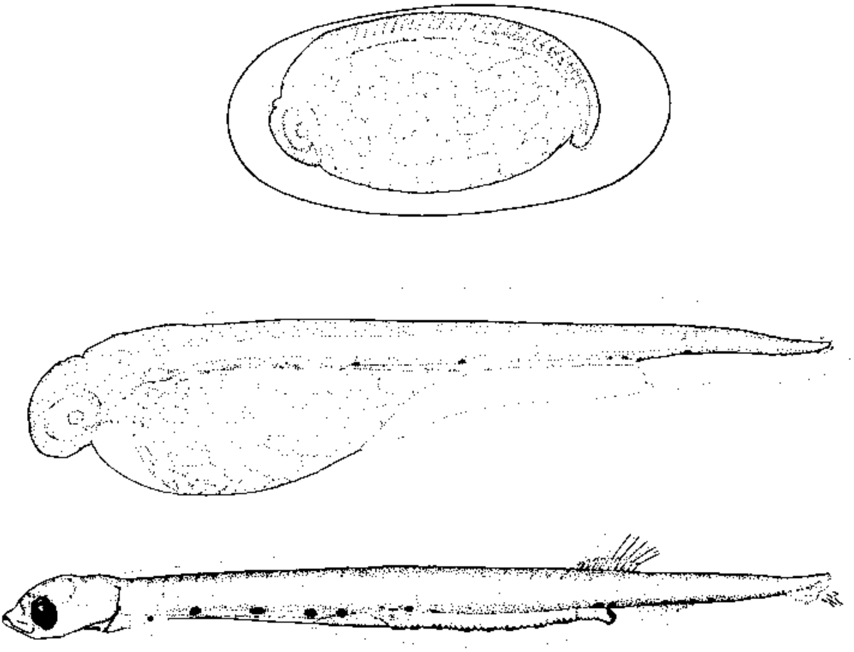

Figure 3.1 Anchovy eggs and larvae: *top*, egg, stage VII; *middle*, newly hatched larva, 2.5 mm; *bottom*, larva, 9.6 mm. Egg from Moser and Ahlstrom (1985), larvae from Kramer and Ahlstrom (1968).

The northern anchovy is a common schooling fish off the west coast of North America, ranging from the Queen Charlotte Islands, Canada, to the southern tip of the Baja California peninsula, Mexico (Miller and Lea 1972). The population is divided into southern, central, and northern subpopulations which show some genetic differences (Vrooman et al. 1981). The subject of this study is the central subpopulation, which nominally ranges from Punta Baja, in Baja California, to San Francisco, California (Figure 3.3). The actual boundaries are probably clinal and/or overlapping, and move north and south with changes in ocean climate

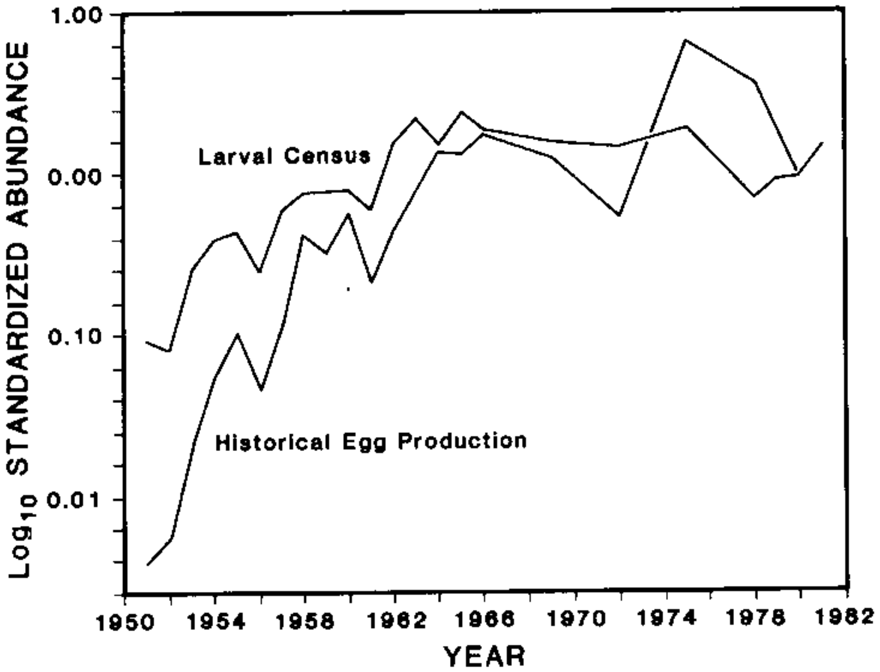

Figure 3.2 Indexes of the spawning biomass of the central stock of northern anchovy (log scale). Larval census indexes are from Stauffer and Charter (1982), and historical egg production indexes are from Lo (1985); both indexes have been standardized to a series mean of 1.0.

(MacCall et al. 1983). The fish do not make large seasonal migrations, and although tag returns show the potential for movements spanning the range of the subpopulation (Haugen et al. 1969), consistent geographic patterns of size at age indicate that longshore mixing is limited (Parrish et al. 1985).

The northern anchovy attains a maximum length of about 160 mm (SL) and a maximum age of six years; fish older than four years are very rare. The main spawning period is January through May, although some spawning occurs year-round. A large fraction of the one-year-old fish spawn in warm years, whereas spawning may be delayed to age two in very cold years (Methot 1986). Anchovies spawn approximately weekly during active spawning, and twenty or more batches may be produced by a fish in a season (Hunter and Leong 1981). The size of a batch of eggs is roughly proportional to body weight, but larger and older fish have a longer spawning season and produce a disproportionately large number of batches (Parrish et al. 1986). Hunter and Leong observed that stored fat in an average (16.4 g) female could support only about thirteen

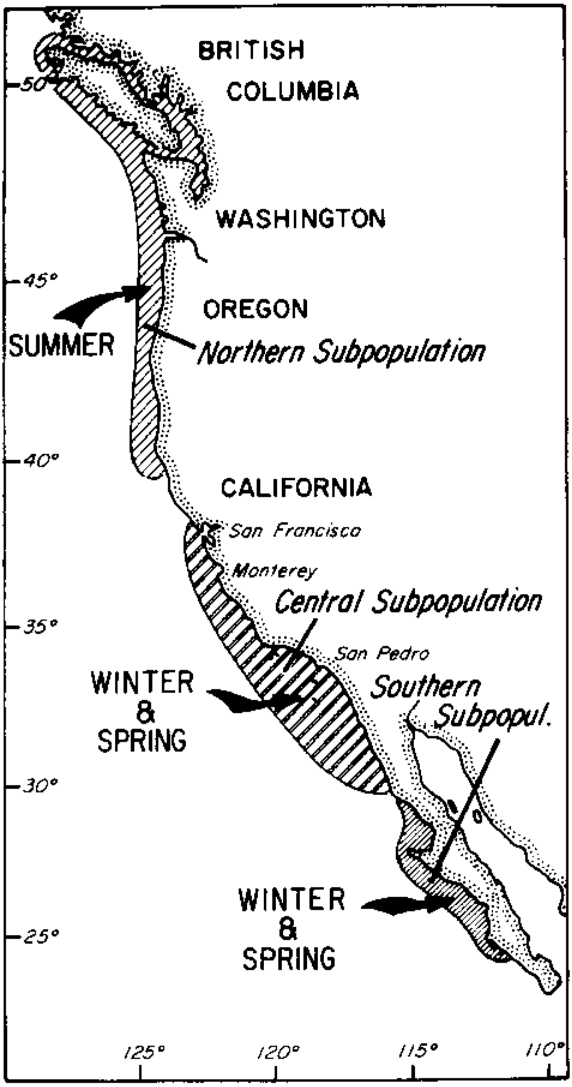

Figure 3.3 Northern anchovy subpopulations and their spawning seasons. From Smith and Lasker (1978).

batches of eggs, so a substantial amount of egg production must be supported by energy gained during the spawning season. Thus, there can be substantial demographic and environmental influences on the calibration of egg or larval production to parental spawning stock in any particular season.

Anchovies are omnivorous, feeding predominantly on zooplankton (especially copepods and euphausiids) and to a much lesser extent on phytoplankton (Loukashkin 1970). Although the northern anchovy is primarily a filter feeder, it also may be a particulate or selective feeder, depending on the size of the available food (CalCOFI 1967). When presented with a mixture of large and small food items, anchovies tend to adopt the feeding mode that results in the highest caloric intake (O'Connell 1972). They also consume their own eggs and larvae (Hunter and Kimbrell 1980).

Copepod eggs and nauplii are the commonest food items consumed by anchovy larvae (Arthur 1976). Unarmored dinoflagellates may also be an important larval food source, especially for first-feeding anchovy larvae. Adult anchovies frequently use these food sources as well, but the relative quantities present in adult stomachs (Loukashkin 1970) argue against their being a major source of adult forage.

To an anchovy larva, food edibility is determined by prey size, but nutrition is governed by species. Lasker (1978, 1981) has hypothesized that dense local concentrations of edible food items are required for successful first feeding, and that recruitment strength may be influenced strongly by formation and destruction of these microhabitats. Consistent with this hypothesis, Peterman and Bradford (1987) found a significant statistical relationship between larval anchovy mortality rate and frequency of calm periods with low wind speed during the spawning season, conditions that would favor formation and maintenance of larval feeding microhabitats.

3.2 MECHANISMS OF DENSITY DEPENDENCE

Density-dependent influences on larval growth and mortality rates can arise from two broad categories of interaction: larva-larva interactions, and adult-larva interactions (termed *stock dependence* by Cushing and Harris 1973). Larva-larva interactions are not likely to play an important role in survival of larval anchovies, as typical densities of fewer than one larva per liter are too low for larvae to encounter each other very often (or for their feeding ranges to overlap). Based on relative abundances, larval fishes are rare to very rare in plankton assemblages in the California Current, and nearly all of their significant interactions are likely to be with other zooplankton, whether they be prey, competitors, or predators (McGowan and Miller 1980).

3.2.1 Cannibalism

In contrast, there are ample opportunities for adult anchovies to interact with their eggs and larvae, directly and indirectly. Hunter and Kimbrell (1980) compared counts of anchovy eggs in stomachs with the rate they were being produced by the gonads. Based on their data, MacCall (1980b) concluded that cannibalism by the northern anchovy accounts for approximately 28 percent of the total egg mortality rate; the instantaneous rate of cannibalism (F_c) was estimated to be 0.11/day. Alheit (1987), supplementing the analysis of Santander et al. (1983), has determined that the rate of egg cannibalism by the Peruvian anchoveta, *Engraulis ringens*, may be about twice that seen in California ($F_c = 0.23$/day), but cannibalism accounted for only 22 percent of the total egg mortality rate due to much higher predation rates from other species. Both of these estimates suggest that cannibalism by adult anchovies is a significant source of egg mortality.

Adult anchovies also consume larvae, so cannibalism continues to be a source of larval mortality. Unfortunately, small larvae are digested very quickly in anchovy stomachs, preventing a similar direct assessment of mortality rates for larvae (Hunter and Kimbrell 1980).

These estimates of F_c allow evaluation of the significance of cannibalism to the stock-recruitment relationship of the anchovy. The Ricker curve (Equation 1.27) has a maximum when the density-dependent argument ($-bS$) has a value of unity (Ricker 1975). The component may be expressed as the integral of density (stock) dependent mortality coefficients (F_c) from time of spawning (t_S) to time of recruitment (t_R), so maximum recruitment occurs when

$$\int_{t_S}^{t_R} F_c(t)\,dt = 1 \; . \tag{3.1}$$

If this integral exceeds unity, recruitment will decline due to density-dependent effects, providing a convenient rule of thumb for evaluating the level of density dependence. In the above two cases, the integral of egg cannibalism rates from spawning to the time of hatching (ca. 3 days in California, 2 days in Peru) results in arguments of 0.27 and 0.46, respectively. Cannibalism of the egg stage alone accounts for a substantial fraction of the reference level of density-dependent mortality.

3.2.2 Random Encounter Model

MacCall (1980b) developed an independent argument based on a random filtering model. The specific rate of filter feeding cannibalism should be approximately

$$F_c = Npv/V \; , \tag{3.2}$$

where N is the number of adult fish, v is the average volume of water filtered per fish per unit time, p is the fraction of the time spent filtering, and V is the habitat volume. The volume of water filtered per fish is dependent on the size of the anchovy, but it is surprisingly large. Leong and O'Connell (1969) measured filtration rates in liters per minute (Figure 3.4).

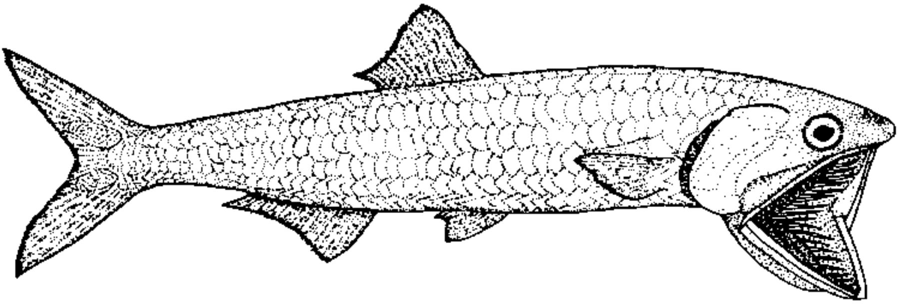

Figure 3.4 Adult anchovy showing filtering behavior.

The total egg mortality rate is

$$\frac{dE}{dt} = -E\left(M+F_c\right) , \tag{3.3}$$

where M is the mortality rate from other sources. After substituting Equation (3.2) for F_c and integrating, the number of eggs surviving the period of incubation to time of hatching (E_h) is

$$E_h = E_0 \exp(-M - Nvp/V)t_h , \tag{3.4}$$

where E_0 is the initial number of eggs spawned, and t_h is the incubation time from spawning to hatching. If the initial number of eggs spawned is proportional to the measure of abundance in the density-dependent term, this is a standard Ricker model.

As stated previously for the Ricker model, E_h reaches a maximum when the exponent of density-dependent mortality equals unity, in this case when $Nvpt_h/V = 1$, or when $Nvpt_h = V$. That is, the effective fecundity (measured as eggs hatched) is maximal when the local population filters a volume of water equivalent to the habitat volume exactly once during the length of time it takes the eggs to hatch. Note that the local density of fish producing maximum recruitment is independent of natural mortality, although the value of the maximum is not.

This somewhat surprising relationship provides a useful extension of the previous rule of thumb (Equation 3.1) for evaluating importance of density-dependent effects. Density-dependent effects (on the egg stage alone) are important if density of anchovies (N/V) approaches $1/vpt_h$. If N/V exceeds this level, E_h decreases despite further increases in N. In the case of the Peruvian anchoveta, this reference density is approximately 200 tons per square mile (Table 3.1). In California the reference density is approximately 250 tons per square mile, which is remarkably similar to the value calculated for Peru despite large differences in the individual parameters.

TABLE 3.1 Reference anchovy densities.

	PERU	CALIFORNIA
Mean fish weight (grams)	6.7[a]	14.6[b]
Filtration rate (liters per minute)	1.64[c]	2.54[c]
Time to hatching (days)	2[d]	3.15[e]
Total volume filtered per fish if $P = 1$ (liters)	4,700	11,500
Number of fish per ton	150,000	68,500
Volume filtered per ton (liters)	0.7×10^9	0.8×10^9
Habitat depth (meters)	40[a]	60[f]
Habitat volume per square mile (liters)	1.4×10^{11}	2.0×10^{11}
Fish density at maximum E_h (tons per square mile)	200	250

Source notes:

[a] Johannesson and Vilchez (1980).

[b] Six-year mean from Bindman (1986, Table 4).

[c] Leong and O'Connell (1969).

[d] Santander et al. (1983).

[e] Lo (1985).

[f] Interpreted from Mais (1974, Figure 12).

Of course, these estimated reference densities may not be very accurate. Likely values of p are certainly less than 1, affecting the reference densities inversely. Also, the assumption of independent random filtering is unrealistic for a schooling fish. However, anchovy schools orient their movement to local concentrations of food, thereby increasing their feeding efficiency. Koslow (1979) has shown that anchovy schools thoroughly remove all edible material from their paths.

On the other hand, incidence of eggs in anchovy stomachs seems to be higher than can be accounted for by the random filtering model (Hunter and Kimbrell 1980). Also, the effect of cannibalism on recruitment must include the larval stage. Hunter and Kimbrell report a 17 mm larva in one of the stomachs they examined, which indicates that larvae remain susceptible to cannibalism for at least one month after hatching. Although particulate feeding (which takes larvae) and filter feeding (which takes eggs) are mutually exclusive feeding modes for individual fish, Koslow's observations on anchovy schools indicate that both feeding modes co-occur within schools. As these various considerations seem to offset each other, I propose that the above reference densities be accepted as first approximations.

Judging by these criteria, observed densities of anchovies indicate that cannibalism is almost certainly an important density-dependent mechanism. Average Peruvian anchoveta densities encountered in hydroacoustic surveys reported by Johanneson and Vilchez (1980) exceeded 600 tons per square mile in the years 1973, 1976, and 1978. Moreover, in these years anchoveta abundance was a fraction of its historical levels. Johanneson and Vilchez also report local densities as high as 2,000 tons per square mile. Average anchovy densities in California are much lower. The peak abundance observed in 1975 corresponded to an average density of 235 tons per square mile in the center of the distribution, although many local densities were two to three times that level (S. J. Crooke, Cruise Report 75-A-1, California Department of Fish and Game, 220 Golden Shore, Suite 50, Long Beach, CA 90802).

The above calculations contain another useful implication: typical anchovy densities should result in any given parcel of water being filtered every few days. This rate of grazing is sufficient to cause food abundance to respond inversely to anchovy density. While it is unlikely that anchovies can detect egg and larval mortality rates, it is likely that anchovies respond to food levels. The latter behavior may be sufficient to generate an appropriate pattern of habitat selection which relates indirectly to egg and larval mortality rates. Moreover, if spawning is prolonged under good feeding conditions (see previous reference to Hunter and Leong 1981), habitat selection for optimum feeding conditions has an even more direct payoff.

3.3 THE IDEAL FREE DISTRIBUTION

One of the primary assumptions of Fretwell's (1972) "ideal free distribution" is that individuals distribute themselves such that all occupied habitats are equally "suitable," suitability being determined by both density-independent and density-dependent influences. Given rapid temporal variability in habitat quality, limited sensory capacity, and limited and delayed physical movement, individuals may at best only approximate an ideal free distribution.

The extent to which an ideal free distribution is achieved is seldom open to investigation because of difficulty in defining and measuring "suitability." The geographic distribution of anchovy spawning may allow a partial test of conformity to the ideal free distribution.

3.3.1 Egg Mortality Rate

In Chapter 1, I refined Fretwell's concept of "suitability" to be the marginal component of reproductive value conferred by selection of a habitat. Fecundity (m_x in life table notation) is an important component in calculation of reproductive value. If fecundity is measured in terms of offspring surviving to a nominal first age of census, the mortality rates of eggs and larvae from spawning to that age will have a large effect on reproductive value. From the preceding discussion, cannibalism appears to be an important component of these mortality rates and may be the major mechanism of density dependence. Also, the conditions governing egg mortality are in place at the time of spawning and potentially can be evaluated by the spawners (albeit indirectly, such as in the above forage-seeking hypothesis).

For the purpose of this investigation, I examine the hypothesis that egg mortality rate is the ultimate factor in selection of spawning habitat by the anchovy, even though immediate cues such as food abundance may govern fish behavior. If the hypothesis is valid, the ideal free distribution would predict a tendency toward similar egg mortality rates in all occupied habitats. Of course, effective fecundity as production of hatched eggs, which includes effects of feeding conditions, would be a better measure of habitat suitability, if it could be measured in the field. Also, other density-dependent behaviors and density-independent spawning behaviors (e.g., location-seeking behaviors favoring reduced larval drift, or simple temperature preferences, see Lasker et al. 1981) could cause deviations from an ideal free distribution based on egg mortality rates.

3.3.2 Apparent Egg Mortality Rate

Anchovy egg mortality rate was estimated from 1980 to 1985 as part of the ''egg production method'' of estimating adult anchovy abundance off California (Bindman 1986, Lasker 1985). Typically, anchovy egg abundance is sampled quantitatively at about 1,000 stations covering the range of the anchovy central population. Sampled eggs are preserved and are categorized by stage of embryonic development, allowing precise determination of ages. Mortality rates are then estimated by regression of abundance on age.

Picquelle and Hewitt (1983) give details of a survey conducted in February of 1982. The 1982 survey showed two separate anchovy egg concentrations, one off southern California and one off northern Baja California. Eggs occurred in lower abundance in the waters surrounding these two groups.

When the three regions are considered separately, abundances-at-age show very different apparent mortality rates (Table 3.2). The two high-density regions show similarly high apparent mortality rates (estimated by linear regression of log-transformed abundances-at-age), while the low-density region shows a much lower apparent mortality rate. The

TABLE 3.2 Anchovy egg abundance in three geographic regions, with estimated apparent mortality rates.

	1	**2**	**3**	
	Southern California	Northern Baja California	Surrounding waters	TOTAL
Mean density, day 1 eggs (eggs/0.05 m^2	27.9	15.1	3.3	10.3
Fraction of total population	0.42	0.39	0.19	1.00
Eggs-at-age				
Day-1	1,058	955	615	2,628
Day-2	459	881	710	2,050
Day-3	370	333	500	1,203
Total	1,887	2,169	1,825	5,881
Apparent mortality coefficient (per day)	−0.526	−0.527	−0.104	−0.391
(Standard error)	(0.179)	(0.258)	(0.143)	(0.082)

statistical confidence limits on these mortality rate estimates are very wide (only 1 degree of freedom, and large standard error) and would not support rejection of a null hypothesis that "mortality rates in the three regions are identical."

However, the pattern of apparent mortality rates is inconsistent with the hypothesis of density-dependent habitat selection and the ideal free distribution. If the true mortality rates in the three regions are different in the directions suggested by the estimates in Table 3.2, most of the spawning activity appears to be occurring in areas of unfavorable egg mortality, while apparently more favorable peripheral habitat is underutilized.

Alternatively, the abundances-at-age in the three regions may be influenced by oceanic transport and diffusion. There may be a net export of eggs from the high-density regions and a net import of eggs to the low-density region. These immigration/emigration effects could account for the differences in apparent mortality rates among regions. The question then arises, "Are probable rates of transport and diffusion high enough to account for a substantial exchange of anchovy eggs among regions?"

3.3.3 Simulation of Transport and Diffusion

Power (1986) developed a model of transport and diffusion for the coastal waters off California and northern Baja California. This transport model divides the area into rectangular cells (ca. 20 nautical miles on a side), whose corners correspond to standard CalCOFI stations (Figure 3.5). He has calculated long-term mean geostrophic flow across cell faces, and also has estimated wind-driven Ekman transport across those faces. In addition, he has included an eddy diffusivity coefficient based on reinterpretation of data from Okubo (1971). Details of the model are given in Power's (1986) paper.

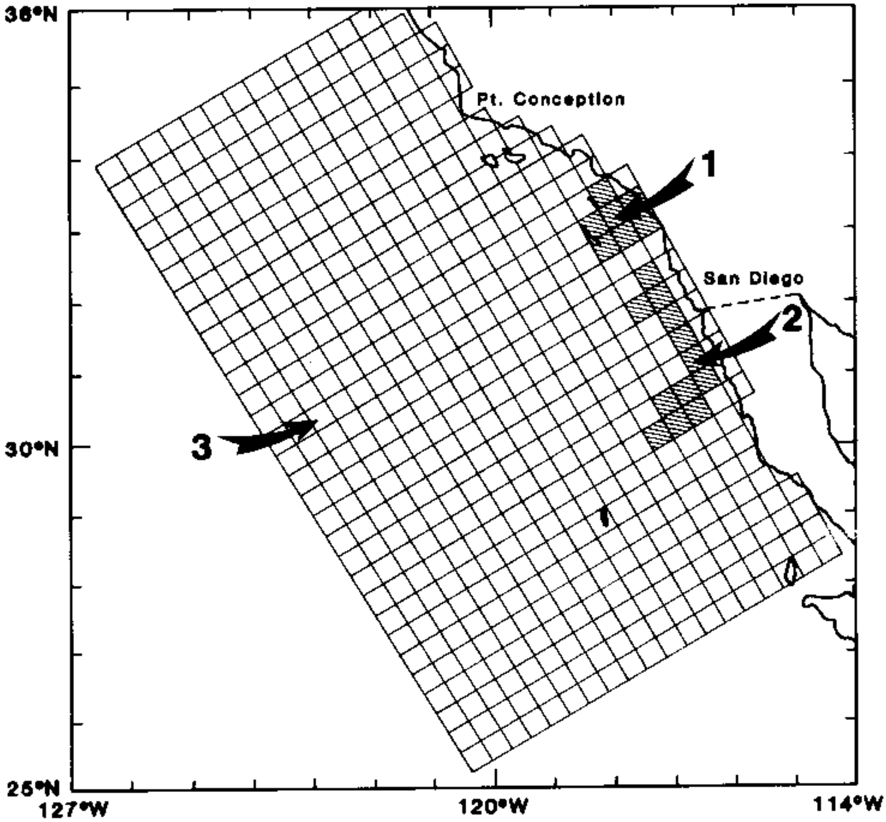

Figure 3.5 Cell diagram for the transport simulation. Modified from Power (1986).

Initial cell concentrations of anchovy eggs were based on density of day-1 eggs observed in the 1982 survey (Table 3.3). Power's transport model simulated advection and diffusion of eggs during a subsequent elapsed time of one and two days. For purposes of the simulation, the eggs were not subject to mortality; Ekman and geostrophic flow patterns were based on average conditions for the month of March. Results of the simulation show a net export of eggs from the high-density regions to the low-density region (Table 3.4). Notably, region 2 appears to lose eggs more rapidly than region 1. This is consistent with the much longer edge length of region 2 (24 cell faces) as compared with region 1 (12 cell faces, with one wholly interior cell). Also, region 2 is in an area of somewhat higher transport velocities.

TABLE 3.3 Initial concentrations of anchovy eggs input to the diffusion simulation (values in number/0.05 m^2). Location key is CalCOFI line and station corresponding to the northeast corner of the cell. Shaded values correspond to regions in Figure 3.5.

STATION:	**45**	**40**	**35**	**30**	**25**
Line:					
83.3	0	3.667	—	—	—
85.0	0	4.400	0	0.700	—
86.7	0.400	2.900	2.375	20.750	—
88.3	0.545	1.400	18.125	58.400	39.000
90.0	8.111	0.100	28.600	15.250	15.400
91.7	4.900	7.600	3.200	1.600	3.571
93.3	0	3.100	4.900	10.100	0.400
95.0	0.800	3.400	10.000	14.600	1.000
96.7	0	0	3.400	8.200	0
98.3	0	0	5.400	12.400	0
100.0	0	0	5.400	9.000	0
101.7	0	11.000	13.200	10.800	0
103.3	21.800	16.600	43.200	4.000	0
105.0	0	0	0.200	2.800	—
106.7	0	0.200	0	0	—

TABLE 3.4 Simulated changes in egg population distribution due to transport (no mortality).

		REGION		
TIME	**1**	**2**	**3**	**TOTAL**
0	0.42214	0.39055	0.18731	1.0
1	0.41379	0.34374	0.24247	1.0
2	0.40433	0.30487	0.29080	1.0

3.3.4 Mortality Rates Corrected for Transport

The simulation shows a substantial transport of eggs among egg density regions. If immigration and emigration are expressed in terms similar to exponential coefficients of mortality, the two factors may be combined in a simple manner to describe changes in abundance-at-age for a given region:

$$N(t) = N_0 \exp[-(Z+E)t] \,, \tag{3.5}$$

where $N(t)$ is abundance at time t, N_0 is initial abundance, Z is an exponential mortality coefficient, and E is an exponential coefficient of change due to transport, i.e., immigration and emigration.

The egg abundances-at-age in Table 3.2 allow estimation of combined coefficients (which previously have been referred to as "apparent" mortality rates) from change in relative abundance over unit time:

$$(Z+E) = \mathrm{Ln}\left[\frac{N(t+1)}{N(t)}\right] . \tag{3.6}$$

The simulation results similarly allow estimation of the immigration/emigration coefficient:

$$E = \mathrm{Ln}\left[\frac{p(t+1)}{p(t)}\right] , \tag{3.7}$$

where $p(t)$ is the fraction of the total population in the region at time t. Note that units of abundance cancel in both Equations (3.6) and (3.7), allowing a measure of relative abundance to be used in Equation (3.7). The mortality coefficient, Z, is then estimated by subtraction:

$$Z = (Z+E) - E \,. \tag{3.8}$$

Results are given in Table 3.5.

3.3.5 Discussion

The transport-corrected daily mortality coefficients are much more similar than the apparent mortality coefficients calculated from raw abundances-at-age. In particular, the mortality coefficient for low-density region 3 (-0.324/day) is quite close to the grand mean estimate (-0.391/day). These results suggest that much of the difference in apparent mortality rates among regions is accounted for by transport. The current velocities and eddy diffusion coefficient used in the simulation were nominal and reasonable, and are only rough estimates of true mean values. Moreover, transport patterns and intensities for any given time, such as February 1982, will differ substantially from the long-term mean. While confidence limits for these transport parameters are not available, the magnitude of their effect suggests that transport could easily account for the entire difference among apparent mortality rates.

TABLE 3.5 Transport-corrected mortality coefficients.

	REGION			
	1	2	3	TOTAL
Daily apparent mortality coefficient (from egg abundance-at-age)				
Age 0–1	−0.835	−0.081	+0.144	−0.248
Age 1–2	−0.216	−0.973	−0.351	−0.533
Mean	−0.526	−0.527	−0.104	−0.391
Daily immigration (+)/emigration (−) coefficient (from simulation)				
Age 0–1	−0.020	−0.127	+0.258	0.0
Age 1–2	−0.023	−0.120	+0.182	0.0
Mean	−0.022	−0.124	+0.220	0.0
Corrected daily mortality coefficient estimate				
Age 0–1	−0.815	+0.046	−0.114	−0.248
Age 1–2	−0.193	−0.853	−0.533	−0.533
Mean	−0.504	−0.404	−0.324	−0.391

As discussed earlier, it is probable that density-dependent deterioration of habitat suitability (measured as egg mortality rate) is not fully recognized by the fish, leading to an imperfect approximation of an ideal free distribution. In particular, anchovies may select habitats on the basis of food abundance, and density-independent factors such as water temperature clearly are associated with anchovy distributions in some years (Lasker et al. 1981). If habitat selection is based on density-independent cues, or on indirect density-dependent cues, it seems likely that egg mortality rates would tend to be higher in the densely occupied habitats, violating the ideal free distribution in a fairly consistent manner. The deviation of the estimated egg mortality rates from the hypothesized ideal free distribution is consistent with this supposition.

Finally, a better tentative measure of suitability would be "effective" fecundity, as production of hatched eggs. This measure would include effects of feeding conditions on egg production as well as on subsequent egg mortality. However, batch fecundities and spawning rates have been measurable only at the population level, and would be nearly impossible to measure in the field with enough precision to compare differences on a local scale.

3.4 MAPPING THE HABITAT BASIN

The changes in relative geographic distribution of anchovy larvae that accompanied the large historical changes in abundance (Figure 1.12) provide the basis for constructing a geographic map of apparent habitat suitability. This analysis consists of first developing a model for local density-dependent changes in habitat suitability and then using the assumption of an ideal free distribution to constrain the predicted distribution of anchovy larvae among habitats. Finally, I estimate the parameters of the model on the basis of larval abundance data from CalCOFI surveys and examine their statistical properties and relationships to oceanographic factors.

3.4.1 Variable-Habitat Ricker Models

Variable-habitat Ricker models can be developed in a manner analogous to the variable-habitat logistic models discussed in Chapter 1 and in the Appendix. In the logistic model the realized per capita growth rate, r^*, declines linearly with density. In the Ricker model, the realized spawning success, defined as the logarithm of the ratio of recruits to spawner abundance, declines linearly with spawner abundance.

As in Equations (3.2) and (3.3), the rate of decline of the abundance of individuals in a cohort is given by the differential equation

$$\frac{dN_h}{dt} = -N_h\left(M_h + c_h S_h\right) , \tag{3.9}$$

where N_h is abundance of offspring in habitat h at time t, M_h is the mortality rate in habitat h from causes independent of adult abundance, and c_h is a coefficient of mortality rate per unit of adult abundance (S). For a cohort of offspring, this differential equation has the solution

$$N_h = N_{0h} \exp\left[-\left(M_h + c_h S_h\right)\left(t - t_0\right)\right] , \tag{3.10}$$

where N_{0h} is abundance of offspring in habitat h at an initial time t_0, and is proportional to local adult abundance (S_h) at that time. By interpreting t_0 as time of spawning, this proportionality is the spawning fecundity, which, as described previously, contains habitat-specific and density-dependent components. The true form of density-dependent fecundity is not known, but an exponential decline with density appears to be reasonable and will be assumed. In support of this assumption, Tsukayama and Alvarez (1980) found that the fraction of Peruvian anchoveta that are mature declines exponentially with total adult abundance if ocean temperatures are warm (when food is scarce). During cold years, when food tends to be abundant, the fraction mature is independent of abundance. Recruitment occurs at a nominally specified age $T = t_{\mathrm{rec}} - t_0$ (e.g., one year), and the abundance of offspring surviving to recruitment ($R_h = N_{Th}$) is given by

$$R_h = N_{0h} \exp\left[-\left(M_h + c_h S_h\right)\right] , \tag{3.11}$$

where coefficients M_h and c_h have been redefined to include habitat-dependent and density-dependent fecundity effects as well as the fixed value of T. Also, the equation is redefined as pertaining to a cohort that was spawned in habitat h at a particular time. Whether or not all individuals remain in that habitat afterward, I assume that members of the cohort share similar growth and mortality rates as they drift as a loose group. Moreover, the largest part of the cohort's mortality is suffered in the few weeks following its creation, during which time it remains in the approximate vicinity of habitat h.

It is unlikely that offspring experience similar mortality rates at all ages. The parametrization of Equation (3.11) allows for variation in mortality rates-at-age, and requires only that those mortality rates remain linear in S_h and independent of N. A transformation of Equation (3.11) allows the Ricker model to be expressed as a linear combination of density-dependent and density-independent components similar to the logistic model in Chapter 1:

$$-\mathrm{Ln}\left(R_h / S_h\right) = Z_h = M_h + c_h S_h . \tag{3.12}$$

The Ricker model is usually applied to entire reproducing populations or to arbitrary large aggregations called "stocks." In this application to the CalCOFI data, the Ricker model is assumed to describe the stock-recruitment relationship for very local habitats, corresponding to CalCOFI stations (Figure 3.6), and the parameters reflect parental fecundities and mortality rates experienced by offspring spawned in each habitat. For a particular habitat (CalCOFI station, j) and time of spawning (year, i),

$$Z_{ij} = M_i + M_j + c_j A_{ij} , \tag{3.13}$$

where Z_{ij} is equivalent to Z_h in Equation (3.12) for offspring spawned at time i in habitat j (i.e., $h = ij$), and A_{ij} is similarly equivalent to S_h. The density-independent mortality coefficient has been divided into two additive components describing density-independent time (M_i) and habitat (M_j) effects, respectively. Interaction between these time and habitat components is ignored.

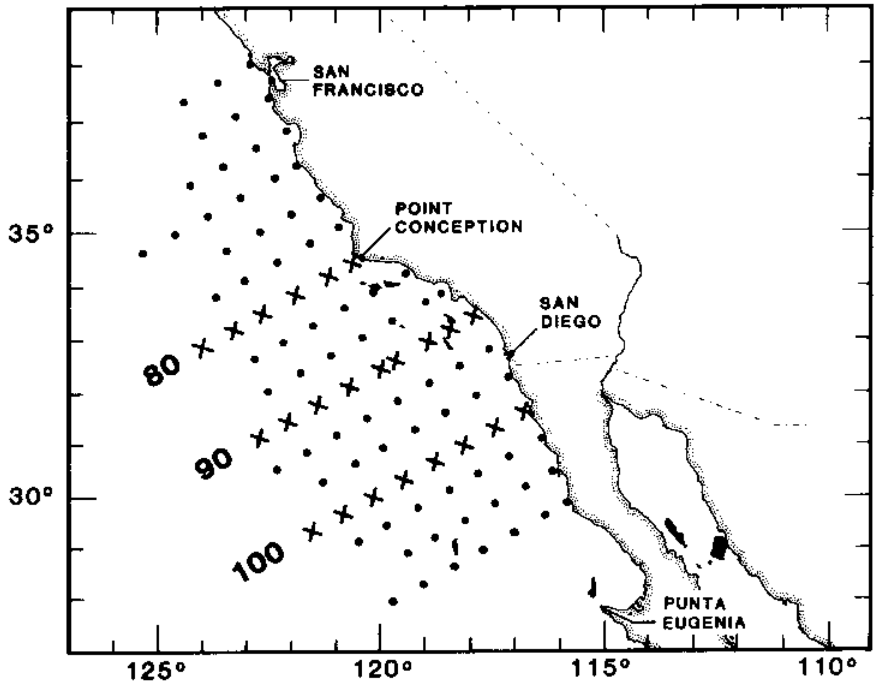

Figure 3.6 CalCOFI stations used in the analysis.

I assume that spawning adults distribute themselves among habitats according to an ideal free distribution whereby the spawning success (Z_{ij}) is the same for all occupied habitats. While I treat spawning success as a coefficient of mortality, it also includes habitat and density effects on fecundity. For simplicity, I assume that effects on fecundity can be approximated by the mortality model and can be subsumed into that model. Thus, use of spawning success as a measure of habitat suitability and as the basis for an ideal free distribution is equivalent to assuming that individual spawners have sought out the best habitats and therefore have distributed themselves so that the expectation of reproductive success (recruits per spawner) is equal everywhere. Thus, for all habitats at time i, I assume

$$Z_{ij} = Z_i^* , \tag{3.14}$$

which describes the ideal free distribution.

Two forms of variable-habitat Ricker model can be described corresponding to the "constant r" and "constant slope" forms of the logistic model described in Chapter 1 and in the Appendix. Assuming an ideal free distribution (Equation 3.14), the analog of the "constant r"

logistic model is a constant value of M for all j,

(3.15) $$Z_{ij} = M_i + M + c_j A_{ij} ,$$ "constant M"

and the analog of the "constant slope" logistic model is a constant value of c for all i and j,

(3.16) $$Z_{ij} = M_i + M_j + cA_{ij} .$$ "constant c"

These two models are shown in Figure 3.7.

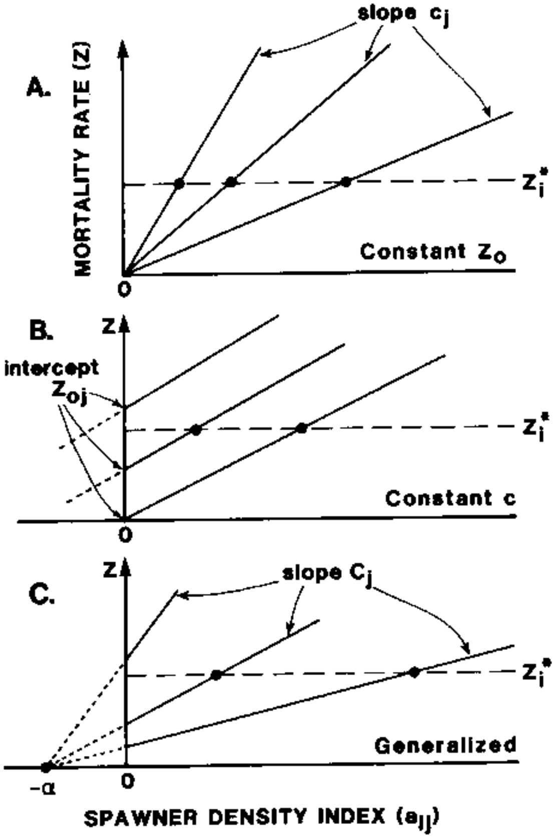

Figure 3.7 Three variable-habitat Ricker models. Solid dots indicate habitat distribution according to the ideal free distribution.

For purposes of predicting the abundance of adults in various habitats, Equations (3.15) and (3.16) can be solved for A_{ij}, given the constraint of Equation (3.14):

$$A_{ij} = \frac{Z_i^* - M_i - M}{c_j} \qquad \text{``constant } M\text{''} \tag{3.17}$$

$$\begin{aligned} A_{ij} &= \frac{Z_i^* - M_i - M_j}{c} \\ A_{ij} &= 0 \text{ if } Z_i^* < M_i + M_j \,. \end{aligned} \qquad \text{``constant } c\text{''} \tag{3.18}$$

In practice, adult abundance has not been measured in absolute terms; however, Lo's (1985) index varies proportionally to A_{ij}. Denoting this index by a_{ij}, we have

$$a_{ij} = kA_{ij} \,, \tag{3.19}$$

where k is an assumed constant of proportionality, the value of which is unknown. If k is constant for all times and habitats, Equations (3.17) and (3.18) become

$$a_{ij} = k\frac{Z_i^* - M_i - M}{c_j} \qquad \text{``constant } M\text{''} \tag{3.20}$$

and

$$\begin{aligned} a_{ij} &= k\frac{Z_i^* - M_i - M_j}{c} \\ a_{ij} &= 0 \text{ if } Z_i^* < M_i + M_j \,. \end{aligned} \qquad \text{``constant } c\text{''} \tag{3.21}$$

However, if k varies, its effect is indistinguishable from variation in the coefficient of density dependence, c or c_j. The consequences of this uncertainty will be addressed later in the discussion.

Also, actual values of the mortality coefficients M and Z are not known, but only the difference $Z_i^* - M_i - M_j$ is of importance to the model. For this reason the time-specific component of total mortality, M_i, may be subsumed into Z_i^*; the value of M_i has no effect on the habitat distribution (although it does affect resulting recruitment). Furthermore, it is not necessary to know the values of Z to predict values of a_{ij}: by choosing a value of $k = 1$ in Equations (3.20) and (3.21), Z is expressed directly in units of a_{ij}. The "constant M" model, which assumes that all M_j are equal, now gives the simple model

$$a_{ij} = \frac{Z_i^*}{c_j}, \qquad \text{(3.22)} \quad \text{“constant } M\text{”}$$

where parameters Z_i* and c_j have been redefined in appropriate units relating to the nominal measure of a_{ij}. The "constant c" model also can be simplified by rescaling, giving

$$\begin{aligned} a_{ij} &= Z_i^* - M_j \\ a_{ij} &= 0 \text{ if } Z_i^* < M_j \end{aligned} \qquad \text{(3.23)} \quad \text{“constant } c\text{”}$$

where Z_i* and M_j are in units of nominal adult abundance a_{ij}. Both of these models consist of a simple partitioning of predicted adult abundance into a time effect (Z_i*, which is actually a population size effect) and a location effect (M_j or c_j). In the "constant M" model, the interaction is multiplicative, while in the "constant c" model the interaction is additive.

These two models are rather restrictive. The "constant M" model is similar to the "constant r" logistic model and is unable to portray submarginal habitat or expansion and contraction of the population range (see Appendix). On the other hand, there has been a greater increase of density in the center of the anchovy's spawning habitat (note the logarithmic shading scale in Figure 1.12) than can be accounted for by the "constant c" model.

By adding another parameter to the simplified "constant M" model, I obtain a more general model analogous to the "fourth quadrant fixed point" logistic model described in the Appendix:

$$\begin{aligned} a_{ij} &= \frac{Z_i^*}{c_j} - \alpha \\ a_{ij} &= 0 \text{ if } \frac{Z_i^*}{c_j} < \alpha \end{aligned} \qquad \text{(3.24)} \quad \text{“generalized”}$$

This "generalized" model (bottom of Figure 3.7) closely resembles the "constant M" model, except that the relationship has been translated (i.e., the origin of the coordinate system is shifted) by a factor of $-\alpha$. Note that the scaling of M_j and c_j is defined by the value of α, as the equation must predict appropriate values of a_{ij}.

It is easily seen from Equations (3.22) and (3.24) that the "constant M" model is a special case of the "generalized" model wherein $\alpha = 0$. It is much less apparent from the equations, but somewhat more so from Figure 3.7, that the "constant c" model approaches being a limiting case of the "generalized" model, where α is very large. As α becomes large, the suitability lines for individual habitats in the "generalized" model become more nearly parallel, progressively approaching the pattern of the "constant c" model. The appropriate slope is obtained by the units of M_j and c_j so that the "focal point" at $-\alpha$ can be placed at any distance from the origin. Thus, if α is estimated to be large with respect to the mean value of a_{ij}, the best fit tends toward the "constant c" model, and if estimated α is small, the fit tends toward the "constant M" model.

3.4.2 Data and Parameter Estimation

Among the many physical and biological oceanographic variables that have been monitored routinely by CalCOFI surveys has been the abundance of anchovy larvae by size category per unit of sea surface area. The CalCOFI program has conducted plankton sampling at standard stations (Figure 3.6), and much attention has been given to standardization of the sampling operation (see Kramer et al. 1972 for details). The "central subpopulation" of the northern anchovy is considered to range from San Francisco southward to Punta Baja, Baja California (Figure 3.3). Accordingly, this study uses observations from CalCOFI lines 60 to 110 (Figure 3.6).

In order to reduce the effects of drift, I restricted counts of anchovy larvae to individuals less than 8 mm in length. The corresponding ages of these larvae would range from four days (newly hatched) to about two weeks, with the modal age being about one week (Methot and Kramer 1979). In choosing to use larvae smaller than 8 mm, several operational trade-offs were considered. Smaller larvae, being younger, will tend to be nearer the original spawning location and, in that respect, are more representative of the adult spawning distribution. As shown in the preceding larval drift model, transport can be substantial, and over days or weeks the initial distribution will tend to be "smeared."

On the other hand, problems with random variability become severe if the nominal measure of abundance is restricted to smaller larvae. Eggs and early larvae are very patchy in distribution, whereas diffusion reduces the patchiness of older larvae (Hewitt 1982). Also, sizes of counts increase as larger larvae are included, increasing effective sample size. Eggs and the smallest larvae are subject to additional variability, as significant fractions can be lost from the net by extrusion through the meshes (Lo 1983).

This study assumes that local larval abundance reflects local adult abundance. A correction is needed to preserve this relationship among years. Mortality rates of eggs and larvae have been shown to increase with increased overall larval abundance so that standing stock of larvae is not proportional to the initial rate of production, and therefore is not proportional to changes in adult abundance among years (Hewitt 1982, Lo 1985). Accordingly, I developed scaling factors for each year based on estimated adult abundance for that year. The estimates of adult abundance are described by MacCall and Methot (1983) and are the anchovy abundance estimates used in the Northern Anchovy Fishery Management Plan (MacCall et al. 1983). These abundance estimates are based on Lo's (1985) estimates of historical anchovy egg production and have been modified by constraints from changes in observed age composition. The yearly scaling factors were developed from the ratio of estimated adult abundance to a regionally stratified census of larvae smaller than 8 mm. The regions and months (January through April) are the same as those used by Lo (1985). The yearly scaling factors were adjusted for a 1954 value of 1.0, so that adult abundance was expressed in terms of 1954 larval equivalents. Thus, nominal adult abundance is given by

$$a_{ij} = n_{ij} H_{ij} s_i \, , \tag{3.25}$$

where n_{ij} is the count of larvae smaller than 8 mm from sample ij (year i, station j), H_{ij} is the "standard haul factor" adjusted for fraction of the catch sorted, being a multiplier which converts the larva count to estimated abundance beneath 10 m^2 sea surface area (Kramer et al. 1972), and s_i is a year-specific scaling factor which converts the abundance of larvae to an index of adult abundance in units of 1954 larval abundance equivalents. Cruises and yearly scaling factors are given in Table 3.6.

Parameters of the "generalized" model (Equation 3.24) were estimated by the method of maximum likelihood. The assumed probability density function is based on the observed count of larvae (n_{ij}) in the sample and is a continuous approximation to the distribution of discrete larva counts. Cassie (1968) reviews the statistical distributions of plankton samples, and concludes that "for practical purposes the log-normal does as well as any." Accordingly, I assume that larval abundances are distributed log-normally about predicted abundances (Figure 3.8). Rearrangement of Equation (3.25) gives the predicted count of larvae in sample ij:

$$n_{ij} = \frac{\hat{a}_{ij}}{H_{ij} s_i} \, , \tag{3.26}$$

where $\hat{a}_{ij}$ is given by the "generalized" model (Equation 3.24). For purposes of parameter estimation, α is added to both sides of Equation (3.24), giving

$$\hat{a}_{ij} + \alpha = Z_i^* / c_j \, . \tag{3.27}$$

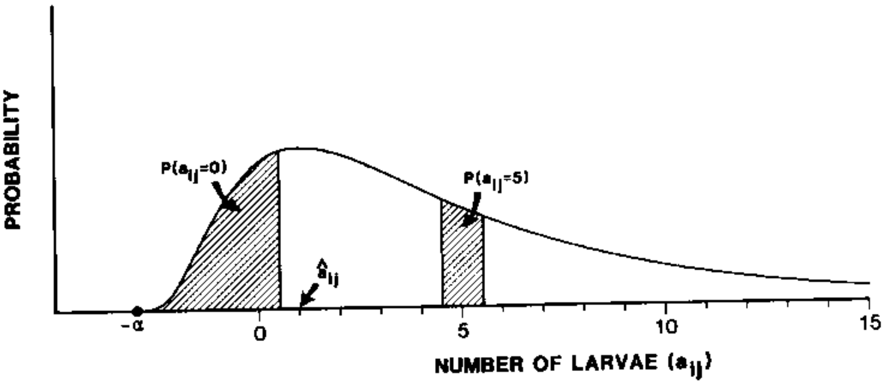

Figure 3.8 Log-normal approximation to the probability distribution of discrete larva counts. The mode and variance are functionally specified by the estimated year and station parameters.

TABLE 3.6 CalCOFI cruises and scaling factors used in parameter estimation.

	JANUARY	FEBRUARY	MARCH	APRIL	ABUNDANCE SCALING FACTOR
1954	●	●	●	●	1.000
1955	●	●	●	●	1.153
1956	●	●	●	●	2.032
1957	●	●	●	●	1.452
1958	●	●	●	●	3.434
1959	●	●	●	●	2.014
1960	●	●	●	●	3.468
1961	●	—	—	●	3.033
1962	●	—	●	—	1.476
1963	●	—	—	●	2.102
1964	●	—	—	●	5.378
1965	●	—	—	●	3.122
1966	●	●	—	●	6.270
1969	●	●	—	●	2.518
1972	●	●	●	—	6.996
1975	●	—	●	—	5.611
1978	●	—	●	●	4.130
1979	●	●	●	●	16.411
1980	—	—	●	●	4.750
1981	●	●	—	●	2.730
1982	—	●	●	—	3.654

Equation (3.27) is the "generalized" model translated by α, which makes the problem of estimation equivalent to that of the "constant *M*" model.

The probability density function is

$$(3.28a)\quad P\left(n_{ij}=I\right)=\frac{1}{\sigma_{\hat{a}_{ij}}\sqrt{2\pi}}\int_{I-0.5}^{I+0.5}\exp\frac{1}{2}\left\{\mathrm{Ln}\left[\left(IH_{ij}s_i+\alpha\right)/\left(\hat{a}_{ij}+\alpha\right)\right]/\sigma_{\hat{a}_{ij}}\right\}^2 dI$$

$$I=1,2,3,\ldots$$

and

$$(3.28b)\quad P\left(n_{ij}=0\right)=\frac{1}{\sigma_{\hat{a}_{ij}}\sqrt{2\pi}}\int_{-\infty}^{0.5}\exp\frac{1}{2}\left\{\mathrm{Ln}\left[\left(IH_{ij}s_i+\alpha\right)/\left(\hat{a}_{ij}+\alpha\right)\right]/\sigma_{\hat{a}_{ij}}\right\}^2 dI,$$

where the standard error $\sigma(\hat{a}_{ij})$ is defined in terms of log-transformed values of $(\hat{a}_{ij} + \alpha)$,

$$(3.29)\qquad \sigma_{\hat{a}_{ij}} = \sigma_0 + \sigma_1\,\mathrm{Ln}\left(\hat{a}_{ij}+\alpha\right).$$

This parametrization of the standard error as a function of the predicted abundance provides additional flexibility in the description of the probability density function, partially compensating for the arbitrary assumption of a log-normal distribution.

The likelihood function $\mathscr{L}(\theta)$ is calculated under log-transformation (maximization of the sum of the logarithms of the terms is equivalent to maximization of the product of the terms):

$$(3.30)\qquad \mathscr{L}(\theta) = \Sigma\,\mathrm{Ln}\left[P\left(n_{ij}=I\right)\right]\Big|\theta$$

where θ denotes the vector of estimated parameters (σ_0; σ_1; α; Z_i^*, i = 1, 2, 3, . . . ; c_j, j = 1, 2, 3, . . .), and the sum is taken over the number of sample observations. The maximum of $\mathscr{L}(\theta)$ was determined by IMSL subroutine ZXCGR, a conjugate gradient method requiring only first derivatives of $\mathscr{L}$ with respect to estimated parameters.

Estimation of parameter values requires at least one nonzero observation ($n_{ij} > 0$) at each station j. Otherwise, all of the probabilities for that station are given by Equation (3.28b), which is maximized by estimating an infinitely unsuitable habitat. Thus, the data were screened to include only stations with at least one nonzero observation. Also, station and year parameters always appear in the form of a ratio, Z_i^*/c_j; this ratio is unaffected if all Z_i^* and c_j values are multiplied by a constant. In order to establish a fixed scale for these parameter estimates, the 1954 value of Z_i^* was arbitrarily fixed at 1.0, reducing the number of estimated parameters by one. The 1954 abundance was the lowest in the time series, so estimates of Z_i^* are unlikely to fall much below 1.0; importantly, negative values of Z_i^* cannot be allowed (for comparison, see the constraints on the constant-r and FQFP logistic models in the Appendix). In order to maintain the property of Z_i^* and c_j being positive numbers throughout the iterative maximization of the likelihood function, these parameters were passed to subroutine ZXCGR in the form of log-transformed values.

The iterative maximization of the likelihood function was very slow. The slowness was due to several reasons: (1) there were many observations; (2) the gradients of $\mathscr{L}(\theta)$ with respect to the estimated parameters are small (i.e., the response surface is "flat"); (3) there is a large covariance among estimated parameter values, particularly with respect to α; and (4) gradient methods tend to be slow.

Consequently, parameter estimation was divided into three stages. In the first stage a smaller data set involving selected stations was the basis for estimating all parameters. In the second stage this small data set was resampled using a jackknife procedure to estimate bias and standard errors of estimated parameters. In the third stage a larger data set including many more stations was used to estimate the parameters, but parameters σ_0, σ_1, and α were held constant at the values determined in the first stage.

3.4.3 Results

A subset of the observations was chosen based on the well-sampled stations of CalCOFI lines 80, 90, and 100, giving 23 stations (Figure 3.6). A total of 1,312 observations were made at these stations on 63 cruises extending over the 21 survey years from 1954 to 1982 (Table 3.6). These data form the basis for estimating 46 parameter values (Table 3.7). Details of the statistics and parameter estimates are given by MacCall (1983). The model and estimated parameters provide a statistically significant reduction in the unexplained sum of squares, as shown by an F-test ($F_S = 5.43$; $F_{0.01} = 1.59$; $d.f. = 45, 1{,}266$). Of course, given this many degrees of freedom, a significant F-statistic is relatively easy to obtain.

Maximum likelihood estimates very often provide biased estimates of parameter values. The jackknife procedure is one way of estimating the magnitude of probable bias, and approximate standard errors can be obtained in the same analysis. The grouped jackknife estimate of bias and standard error are described by Miller (1974). This 23-station subset of the observations was divided temporally into five groups for purposes of calculating jackknife statistics. Information on suitability of peripheral stations (c_j) is obtained only in years of high population size,

TABLE 3.7 Parameter estimates based on subset of 23 stations.

PARAMETER NAME	**MAXIMUM LIKELIHOOD ESTIMATE**	**JACKKNIFE**	
		Estimate	**Standard error**
σ_0	3.922	3.939	0.0373
σ_1	−0.282	−0.276	0.0137
α	5.879	6.157	1.5803
Ln *Z* (year)			
1954	(defined as 0.0)		
1955	0.373	0.391	0.0343
1956	−1.259	−1.289	0.0221
1957	0.729	0.726	0.0312
1958	2.911	2.926	0.0691
1959	−0.346	−0.256	0.1236
1960	1.846	1.765	0.0892
1961	0.634	0.769	0.1502
1962	2.400	2.589	0.1754
1963	2.235	2.526	0.1441
1964	2.850	2.838	0.0923
1965	3.755	3.845	0.1161
1966	4.407	4.383	0.1134
1969	3.411	3.429	0.0625
1972	1.441	1.393	0.1054
1975	3.644	3.461	0.1404
1978	1.863	1.848	0.0791
1979	3.834	3.858	0.1543
1980	2.842	2.767	0.0869
1981	2.309	2.168	0.1095
1982	2.775	2.718	0.1692

or Z^*, requiring that the groups be balanced. The years (excluding reference year 1954) were ranked by their estimated values of Z_i^*. Five subsets of four years each were defined by choosing years of rank R, $R + 5$, $R + 10$, and $R + 15$, where $R = 1, 2, 3, 4, 5$. This selection procedure assures that each subset contains a roughly equal representation of the range of population size effects (Z_i^*). The five subsets were of roughly equivalent sample size (Table 3.8).

Jackknife estimates of standard errors are given in Table 3.7. Standard errors of parameters σ_0, σ_1, and α are relatively small, supporting their treatment as given constants in the third stage of parameter estimation. Also note that the estimate of α is significantly different from zero (a distance of 3.9 standard errors, Student's t_{4df} : $P < 0.01$), allow-

TABLE 3.7 Continued.

PARAMETER NAME	MAXIMUM LIKELIHOOD ESTIMATE	JACKKNIFE Estimate	JACKKNIFE Standard error
– Ln *c* (line-station)			
80– 51	2.734	2.666	0.3907
80– 60	0.335	0.451	1.1149
80– 70	−1.194	−0.926	1.0769
80– 80	−3.511	−3.575	1.0803
80– 90	−5.551	−5.539	0.6497
80–100	−5.824	−5.952	0.9053
90– 30	4.824	4.612	0.2692
90– 37	5.395	5.375	0.0638
90– 45	4.820	4.808	0.2404
90– 55	2.765	2.905	0.5830
90– 60	2.209	2.317	0.3451
90– 70	−1.001	−0.809	0.9348
90– 80	−2.318	−2.182	0.8274
90– 90	−2.979	−2.791	1.0203
90–100	−2.902	−2.930	0.5017
100– 30	4.172	4.092	0.2872
100– 40	3.295	3.227	0.3021
100– 50	1.247	1.127	1.0297
100– 60	−1.431	−1.327	0.8894
100– 70	−3.699	−3.651	1.1393
100– 80	−3.664	−3.728	0.4666
100– 90	−8.485	−8.625	0.5885
100–100	−5.413	−5.437	0.4685

ing rejection of the null hypothesis that the observations may have arisen from a "constant M" (i.e., $\alpha = 0$) model lacking expansion and contraction of range. Standard errors for the year parameters, Z_i^*, are relatively small, but some of those for station parameters (c_j), especially on the periphery, are quite large (Figure 3.9).

The third stage of parameter estimation uses 4,948 observations from 97 stations extending from CalCOFI line 60 to line 110. Parameters σ_0, σ_1 and α were held fixed at the maximum likelihood values estimated in stage 1. The station values from the 117 estimated parameter values (see MacCall 1983 for numerical values) are plotted as geographic contours in Figure 3.10. Standard errors were not estimated, but relative values developed in the previous stage of estimation (Figure 3.9) provide

TABLE 3.8 Subsets of observations, 1955–1982, used for jackknife estimation.

GROUP	YEARS DELETED	SAMPLE SIZE*	WEIGHTING FACTOR
1	1956, 1962, 1969, 1972	1,044	0.9786
2	1959, 1960, 1975, 1982	1,047	0.9814
3	1955, 1965, 1978, 1980	1,087	1.0189
4	1961, 1963, 1964, 1979	1,110	1.0405
5	1957, 1958, 1966, 1981	1,046	0.9805

* Sample size with no deletions: 1,312.

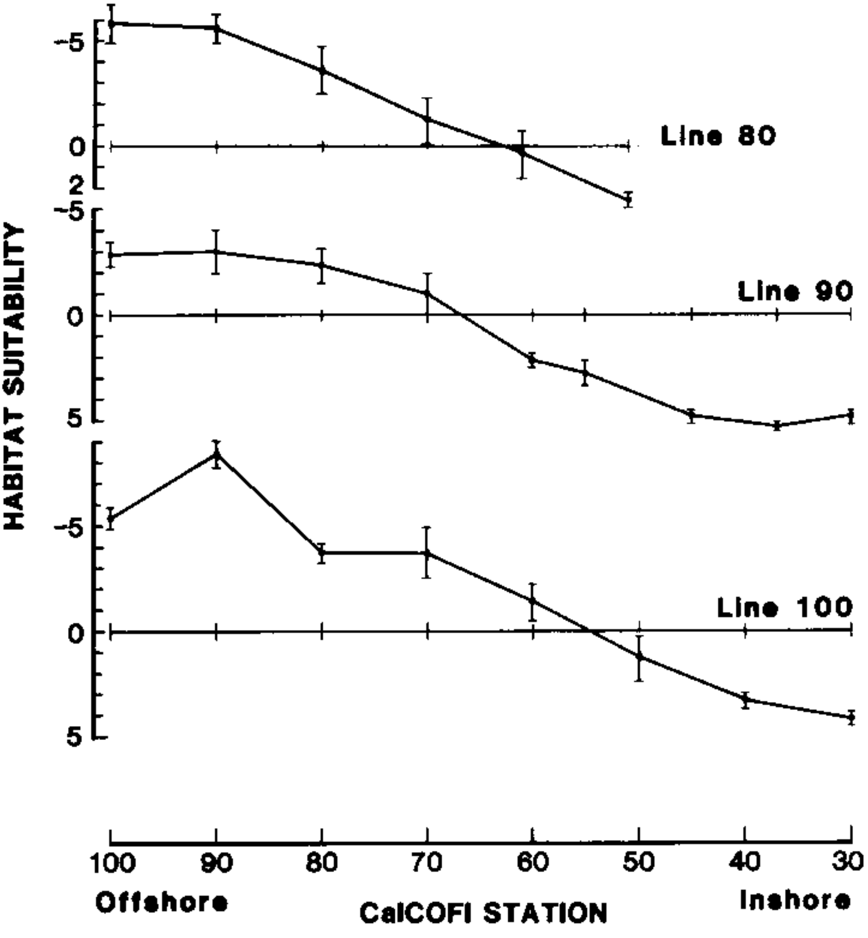

Figure 3.9 Estimated habitat parameters (Ln c_j) and standard errors for the subset of 23 stations. Values are plotted as increasing downward so that the plots depict transects through the habitat suitability basin.

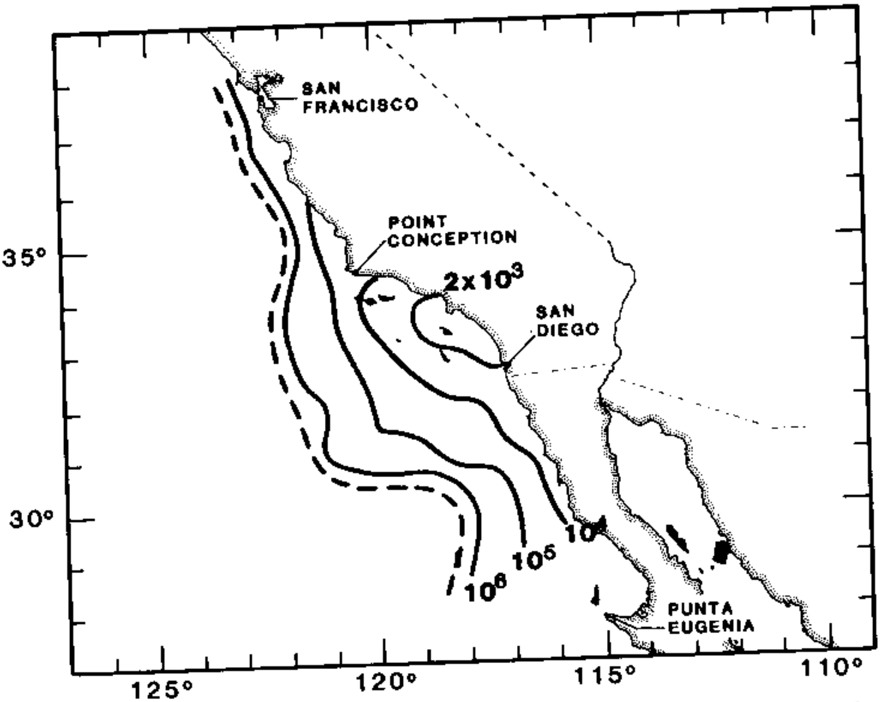

Figure 3.10 Approximate spawning habitat suitability contours for the central subpopulation of northern anchovy, showing the nominal edge (see text) of the larva distribution at various spawning biomasses (in tons). The dashed line is the nominal edge of the larva distribution at an estimated population carrying capacity of about two million tons.

an approximate guide. Standard errors for year parameters should decrease due to the increase in sample size, while standard errors for many of the added stations are probably larger because those stations tend to have somewhat fewer occupations than the 23 stations used in the previous stage.

3.4.4 Errors

The anchovy habitat model is based almost entirely on egg and larva information. Even the scaling factors given in Table 3.6 are themselves derived from this source. Yet I have attempted to make a variety of inferences about the adult population and its habitat from this single source of information. It is appropriate to consider sources and types of error in this analysis and their effects upon the inferences that are made.

The best understood type of error is that associated with sampling the larvae, a topic that has been discussed by Cassie (1968), Hewitt (1982), Lo (1985), and many others. Anchovy eggs are contagiously distributed at spawning, but the eggs and larvae disperse progressively with time until the onset of schooling behavior. The log-normal probability density function advocated by Cassie (1968) adequately addresses sampling variability. As usual, a portion of the error variability in the estimated parameter values is due to this source. However, in this analysis there are several other types of error about which much less is known.

Misspecification of the model is probably a major source of error but cannot be fully evaluated because the ''true'' model specification is unknown. The simple linear relationship between habitat suitability (measured as spawning success) and spawner or larval density may not adequately describe the true relationship, and almost certainly misrepresents the behavioral mechanisms governing habitat selection. The model used here must be considered a low-level approximation. There is no certainty that the Ricker model is itself a correct description of the stock-recruitment relationship. Indeed, the largely multiplicative rather than additive pattern of changes in abundance at central and peripheral locations more closely resembles that expected from an ideal free distribution under a Beverton and Holt stock-recruitment model (see Figure 1.11). In any case, there are enough other causes for an *apparently* multiplicative model (see below) that it is unlikely that the stock-recruitment model could be inferred reliably from these data.

Another type of model misspecification is the assumption of a constant or invariant basin topography. The true topography almost certainly varies within and among years. Further error may arise from viscosity properties of the spawning anchovy population (Chapter 1) combined with dispersive recruitment due to meroplanktonic eggs and larvae (Chapter 2): the population may not be near an ideal free distribution even though it may continually be attempting to approach that state. Also, to the extent that anchovies distribute themselves with respect to physical stimuli that are not affected by fish density, expansion and contraction of range will be weakly associated with estimated Z_i^*, and again the best fit to the distribution of larval abundances should tend toward the multiplicative ''constant M'' model.

The errors arising from these sources should tend to be spatially correlated, providing a potential tool for their analysis. For example, principal components analysis or factor analysis could help identify geographical regions for which anomalously high or low larval abundances covary consistently. A very complicated maximum likelihood model could attempt to account for spatial correlation directly, although the model would be difficult to fit as well as specify.

Diffusion of the larvae away from the locations at which they were spawned is another source of error falling into this general category of spatial misspecification. The current strengths estimated by Power (1986) suggest that movements of 30 to 60 km may easily occur during the average one-week period between spawning and capture of the larvae by the CalCOFI sampler. Diffusion should tend to result in an apparently multiplicative model.

Further sources of error (e.g., variable fecundity and mortality rates) involve violation of the assumed proportionality between larval abundance and abundance of spawning adults. Similarly, variability in the location-specific slopes or coefficients of density dependence (c_j) results in changes in the geographic distribution of larval abundance, which is independent of total abundance. Actual suitability curves are less constrained than the "generalized" model with its constant value of α.

There are several likely sources of variability in fecundity. The scaling factors in Table 3.6 attempt to remove only the variability in the standing crop of small larvae arising from changes in mortality rates of eggs and larvae. Anchovy surveys conducted from 1980 to 1985 have shown a moderate range of daily population fecundity measured as eggs produced per day per gram of adults (Bindman 1986). The coefficient of variation has been about 18 percent, and the highest value has been slightly less than twice the smallest value. However, these fecundities reflect the approximate peak of spawning and do not necessarily represent variability in the average fecundity over the four-month period used in this study. In fact, there are several reasons to suspect that average fecundity is more variable, including large age-dependent changes in spawning duration and potential influence of the current feeding rate discussed in the biological description at the beginning of the chapter.

Much less is known about variability in the coefficient of density dependence or, what is more important to this model, variability in the strength of the mechanism of "perceived" density dependence (i.e., the presumably density-related stimuli which are perceived by the fish and which influence their choices of spawning habitat). As was shown in the first chapter, an increase in the coefficient of perceived density dependence will cause an expansion of range and a decrease in local densities within the range: the peripheral areas become more attractive if suitability decreases in the central area due to the increased coefficient of density dependence (Figure 1.4), except in the special case of the "constant *M*" model. The extent of bias from this source is unknown, but all model fits should be biased toward the multiplicative "constant *M*" model.

Decreased food abundance is likely to result in increased cannibalism due to increased time spent feeding by the adults, but it also may result in switching to the alternative feeding mode. The response of food levels to foraging intensity by the anchovy could conceivably lead to a relationship between c_j and M_j similar to that given by the fitted model: The zero-density intercept, or density-independent component of habitat suitability (M_j) should vary with the amount of food provided by that habitat if no adults were present, and the slope, or per capita coefficient, of perceived density dependence (c_j) may tend to be steeper for habitats with low initial food levels because relatively larger amounts of time must be spent feeding.

3.4.5 Interpretation of the Estimated Parameters

The relatively small estimated value of parameter α results in a model that closely resembles the "constant M" model. That is, changes

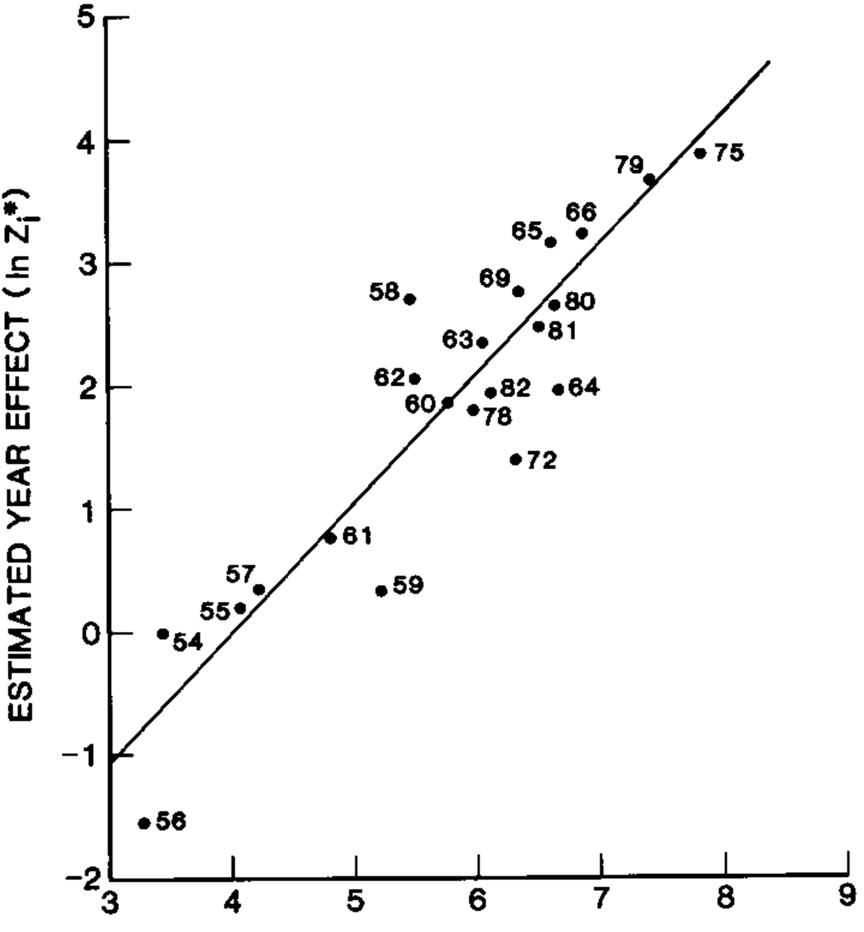

Figure 3.11 Log-log relationship between estimated year effect (Z_i*) and anchovy abundance (spawning biomass, B_i).

in larval density at stations of high suitability account for most of the change in total abundance, while expansion and contraction of range account for a small portion of the change.

The local stock-recruitment model used in this analysis (Equations 3.12, 3.13) assumes that egg and larval mortality rates increase linearly with local density of adults, and accordingly with density of spawned eggs. Because of differential occupation of habitats with changes in total population size, the linearity does not necessarily hold for total population size. However, the slope of a log-log plot of estimated yearly Z_i^* values against estimated anchovy spawning biomasses (Figure 3.11) appears to be very close to 1.0, indicating approximate proportionality of change. This indicates that the small value of α results in a model sufficiently close to the "constant M" form that differential occupation of habitat would be expected to have little effect on the stock-recruitment relationship. However, more direct investigations of anchovy egg and larval mortality rates do show a curvature (Hewitt 1982, Lo 1985) in the relationship between larval mortality rates and spawning biomass. The slope of a log-log GM functional regression (Ricker 1973) of Lo's estimated mortality coefficients on egg production rate is 0.257, indicating a strongly curved relationship between the untransformed variates.

The difference between the basin model and the above empirically estimated mortality rate-biomass relationships is consistent with the discussion of suspected biases toward a "constant M" model fit. While the concept of the geographic model has clear bearing on the theory of population dynamics, these comparative results suggest that the fitted model may be of limited value for inferring particular models of population dynamics.

Despite the relatively small estimated value of α, the model predicts a substantial expansion and contraction of range with changes in total abundance. Habitat corresponding to the nominal edge of the range (c_{edge}) is given by solution of Equation (3.24) for $a_{ij} = 0$:

(3.31a) $$c_{\text{edge}} = \frac{Z_i^*}{\alpha} ,$$

or, after log-transformation,

(3.31b) $$\text{Ln}\left(c_{\text{edge}}\right) = \text{Ln}\left(Z_i^*\right) - \text{Ln}(\alpha) .$$

Note that the nominal edge of the spawning area is a very imprecise and biased predictor of the edge in any actual year. The edge condition that $a_{ij} = 0$ indicates that the probability of observing no larvae slightly exceeds 0.5. (The cumulative probability to the mode of the log-normal distribution is 0.5; the nominal edge of the population is defined by the mode occurring at zero larvae, but the integral in Equation (3.28b) extends to 0.5 larvae.) Consequently, the expected value for the observed number of larvae is always greater than zero and is consistent with the fact that larvae sporadically occur well beyond the nominal edge of spawning habitat as defined here. Further imprecision in this description of the edge of the population arises from many of the sources of error discussed earlier, particularly changes in the true basin topography, in fecundity, and in the coefficients of density dependence.

Log-log regression of Z_i^* on spawning biomass (Figure 3.11) gives the estimated relationship

$$\mathrm{Ln}\left(Z_i^*\right) - 1.056\,\mathrm{Ln}\left(B_i\right) - 4.24 \,, \tag{3.32}$$

where spawning biomass in year i (B_i) is in units of thousand tons. Using these estimated regression parameters and the estimated value of α = 5.879, the nominal edge of the range of anchovy spawning habitat can be expressed as a function of spawning biomass:

$$\mathrm{Ln}\left(c_{\mathrm{edge}}\right) = 1.056\,\mathrm{Ln}(B) - 6.01 \,. \tag{3.33}$$

The quantity of habitat of various suitabilities is conveniently

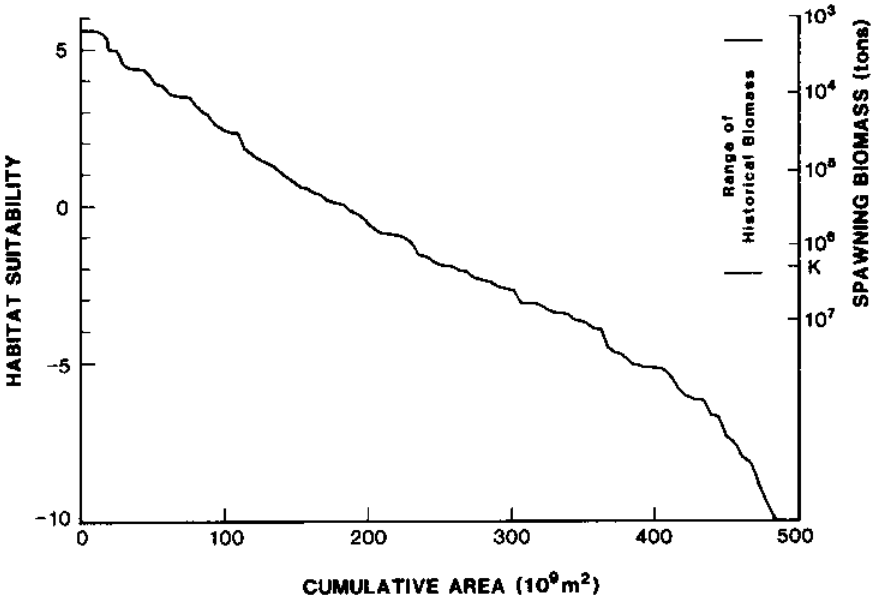

Figure 3.12 Hypsogram relating suitability (Ln c_j) and quantity of spawning habitat. Relationship between spawning biomass and area within the nominal edge of the occupied range (see text for definition) is based on the regression in Figure 3.13.

summarized by a hypsogram. Each open-ocean CalCOFI station was assumed to represent a habitat area of 40 nmi by 40 nmi, or 5,500 km^2. Inshore stations were assigned an arbitrary area of one-half this amount; stations 90.55 and 90.60 were assigned two-thirds; and station 82.47 was assigned one-quarter of the area of an open-ocean station (cf. Figure 3.6). The resulting hypsogram (Figure 3.12) shows the area inhabited by spawning anchovy to increase almost linearly with the logarithm of spawning biomass.

At the estimated unfished equilibrium spawning biomass of 1.9 million tons (MacCall and Methot 1983) spawning would extend over about 250,000 km^2. At very large spawning biomasses the estimated amount of marginal habitat appears to decline sharply. The precision of this portion of the hypsogram is very low, as presence of larvae in these marginal habitats is subject to high random variability, and stations were included for estimation only if there was at least one positive larval occurrence. Therefore, there is likely to be more marginal habitat than is shown by the hypsogram, as many equally suitable peripheral stations may have been excluded from estimation by random effects.

At spawning biomasses below about 1,000 tons, spawning should tend to contract into a few most favorable locations, and density-dependent effects would become negligible. This final contraction of a declining population is typified by the behavior of the Pacific sardine *(Sardinops sagax caerulea)* when its population fell below 10,000 tons in the 1960s and 1970s (MacCall 1979, Mais 1974). At this low abundance most of the sardine population seems to have consisted of a few large schools occupying consistent locations in or near southern California's larger estuaries such as San Diego Bay.

3.4.6 Relationship of Basin Topography to Oceanographic Variables

Three oceanographic variables have been monitored routinely at CalCOFI stations: small plankton volume (milliliters of small plankton per 1000 m^3 filtered by the net; methods are described by Kramer et al. 1972), and temperature and salinity at a nominal depth of 10 m. I have calculated means of these observations for the same 4,948 station occupations used in the basin model fitting. The geographic patterns of these variables can be compared with the topography of estimated anchovy spawning habitat parameters in Figure 3.10. No single oceanographic factor correlates well over the entire range of anchovy spawning habitat. Habitat suitabilities perceived by the anchovy are very likely to be determined by a mix of factors whose relative importance varies among locations and conditions, a mix that probably differs most at opposite ends of the population's range (Brown 1984).

Small plankton volume increases nearly tenfold from south to north (Figure 3.13). The only region where small plankton volume appears to correlate with the spawning basin is in the southern end of the study area. Off northern Baja California mean plankton volume is very high inshore and declines sharply to low values offshore. The spawning habitat basin appears to be similarly constricted inshore in that area.

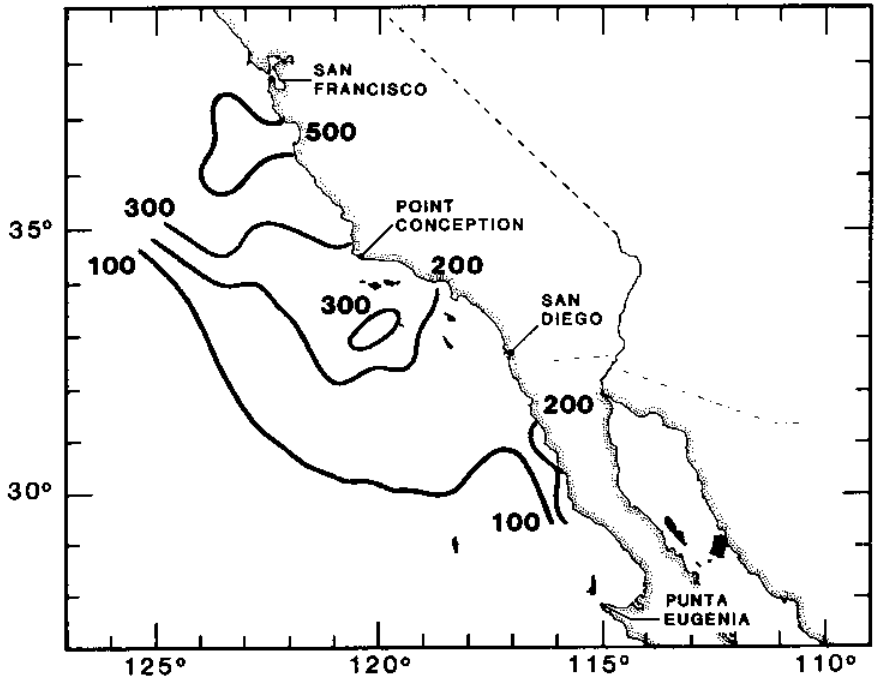

Figure 3.13 Mean small plankton volumes (milliliters per 1,000 m^3) for the samples used in the analysis.

Mean 10 m temperature (Figure 3.14) shows a similar pattern off northern Baja California, suggesting a relatively narrow inshore band of upwelling which supports the increased plankton abundance. Mean temperature isotherms in the northern part of the Southern California Bight appear to correspond to the inshore topography of spawning habitat, as Lasker et al. (1981) have shown more directly. The pattern of mean 10 m salinity (Figure 3.15) shows a similarity to the spawning habitat topography off Central California, where it indicates upwelling of relatively more saline underlying water. Salinity shows no correspondence elsewhere.

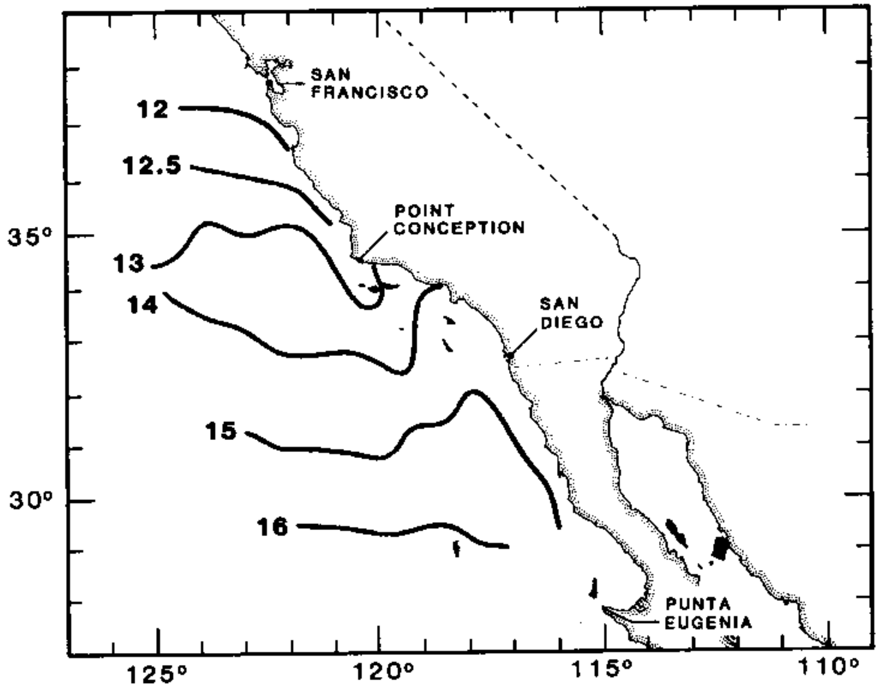

Figure 3.14 Mean temperatures (degrees Celsius) at a depth of 10 m for the samples used in the analysis.

Each physical variable, therefore, appears to correspond to some portion of the spawning habitat basin topography. However, these correspondences are of little more than heuristic value; inference of causal or even statistical relationships is inappropriate.

Oceanographic factors other than those discussed above may also be related to real or perceived suitability of anchovy spawning habitat. Lasker (1978, 1981) maintains that vertical stability of the water column is necessary for the formation of strata of larval fish forage sufficiently dense that first-feeding larvae are able to avoid starvation. The waters of the Southern California Bight tend to be more stable than surrounding waters due to lower wind speeds and a stronger thermocline (Husby and Nelson 1982).

Another somewhat related factor that is thought to influence anchovy reproductive success is the likelihood of adverse transport of the planktonic larvae (Parrish et al. 1981). Off California there is risk of wind-driven Ekman transport away from shore, and southwestward transport by the California Current. The water circulation in the Southern California Bight is often gyral, and the probability of retaining planktonic larvae is higher than in the areas to the north and south. This retention is

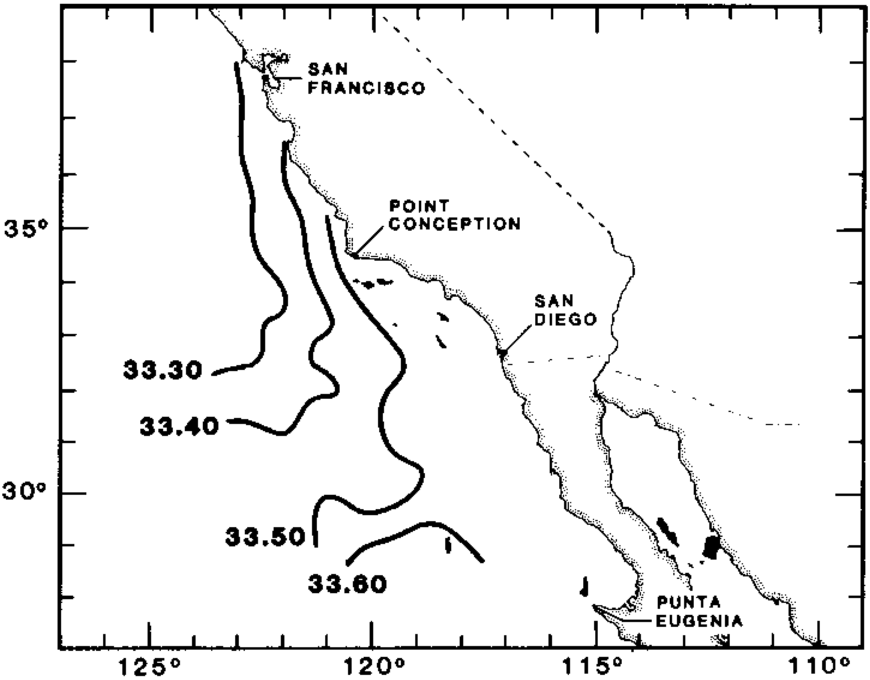

Figure 3.15 Mean salinities (parts per thousand) at a depth of 10 m for the samples used in the analysis.

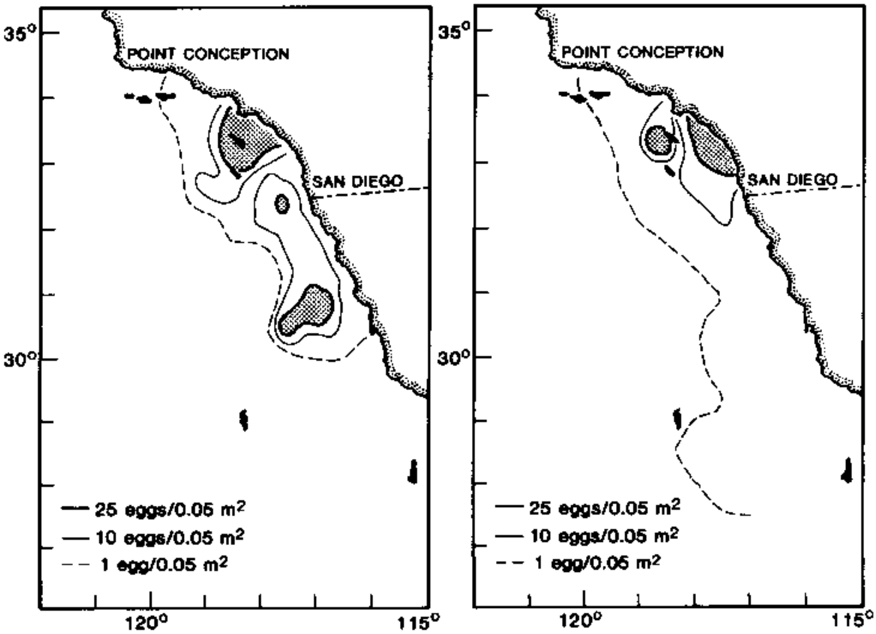

Figure 3.16 Anchovy egg distribution in 1982: *left*, initial distribution; *right*, distribution after 30 days of simulated transport.

demonstrated by simulating 30 days of transport using Power's (1986) model, given the initial egg distribution in 1982 from Table 3.3 (Figure 3.16). Marginal spawning habitats outside the Southern California Bight are progressively more subject to adverse transport, whereas the highest retention of eggs and larvae coincides almost exactly with the most favorable habitat in the estimated basin topography (Figure 3.12).

Parrish et al. (1983) compare oceanographic factors and pelagic fish spawning areas in four major eastern boundary currents and conclude that "spawning grounds tend to lie in coastal indentations where wind-induced transport and turbulence are reduced and continental shelf width tends to be greater. The spawning grounds of the largest populations tend to be located downstream (equatorward) of upwelling centers." The estimated anchovy spawning basin clearly shows these characteristics and is congruent with the habitat features described by Parrish.

4

SUMMARY AND CONCLUSION

Fishery modeling has been slow to develop a functional or quantitative awareness of population geography (but see Sinclair 1988). Once a ''unit stock'' has been defined, geography is often ignored except with regard to management options involving area closures. Indeed, geography has not been easy to incorporate into useful, practical models of population dynamics.

Ecologists have long considered geographic aspects of population dynamics, but the more successful models have been applicable at local scales corresponding to habitats or communities. Few field studies at the population level have been attempted, partly because of the time and expense of large-scale population studies spanning periods long enough to observe substantial variability in abundance. In this respect, observational data obtained from monitoring of exploited populations provide rare opportunities for ecological investigation of relationships between population geography and dynamics.

The ''basin model'' describes a potential interrelationship between geography, movement, and growth dynamics at the population level. Although it presents a grossly simplified and abstract view of population behavior, the model conveys a strong intuitive image which allows a holistic grasp of an entire suite of important considerations: abundance, distribution and geographic structure, movement, and population growth. While the model can be cast easily in mathematical terms, allowing quantitative prediction and rigorous examination of its properties, it also can be understood without resort to mathematics.

The analogy of populations to a viscous liquid flowing under the influence of gravity in a physical basin allows dynamics of population movement and habitat selection to be visualized in terms of common experience. Not only does the ideal free distribution arise naturally in this analogy, but it is achieved in a way that reflects underlying biological behavior as well: individual organisms, like molecules of a viscous liquid, need only move in response to local gradients. The dynamics of population growth are reflected in a tendency for the volume of liquid to increase or decrease so that the surface of the liquid seeks a level corresponding to neutral suitability, or zero growth, at which time the volume of liquid corresponds to the carrying capacity of the basin. Thus, the carrying capacity is established indirectly, being the population size that fills the basin to the neutral reference level. Changes in carrying capacity arise mainly from changes in the density-independent factors which dictate the basin's shape and level with respect to the neutral level of zero growth, but they also can arise from changes in the intensity of density dependence.

Clearly, not all biological populations will conform to this model. It may be best suited to marine fish populations, but with minor modifications it can be extended easily to a much wider range of organisms, including plants as well as animals.

The basin model is best suited to populations with a clear central-peripheral density gradient, which Rabinowitz (1981) associated with wide geographic range and broad habitat specificity. Similarly, it is best suited to populations inhabiting relatively continuous habitats, although a model incorporating fine-scale structure or grain of habitat variability could be elaborated. The basin model allows a flexible representation of habitat suitability, and it may be possible to reconcile the model with alternative ecological theories that do not invoke density dependence. Nearly all theories of population dynamics must account for a population's range, and this basin representation of habitat suitability may be especially useful for this purpose (cf. Brown 1984).

The model is easily extended to specific cases, but as the habitat model becomes more detailed, perhaps including temporal as well as spatial variability, so must the representation of movement dynamics. As shown in the population simulations explored in Chapter 2, the basin model can easily incorporate complicated or detailed models that include behavioral as well as physical mechanisms of dispersal and/or movement. Portrayal of the interaction of population density and habitat suitability need not be restricted to logistic models. Simple resource-based models such as Schoener's (1973) and Getz's (1984) per capita approaches are attractive in that they potentially account for the actual mechanisms determining habitat suitability.

The phenomenon of biological invasions has long received attention from theoretical as well as descriptive viewpoints (e.g., Mooney and Drake 1986). The geographic pattern of an invasion over time would seem to provide an ideal set of observations on which to develop a basin model of the invader's habitat. Moreover, the rate of spread would provide useful inferences about movement dynamics, information that is often difficult to obtain for established populations.

Beginning with Fisher (1937), a series of theoretical investigations of traveling frontal waves from logistically growing diffusive populations (see review by Okubo 1980) has evolved. These often difficult mathematical investigations have focused on various specifications of movement dynamics, and usually have assumed homogeneous habitat. Consideration of gradients in habitat quality, as portrayed in the basin model, would make these frontal wave problems even more difficult mathematically, but it could add a needed element of realism which would relate directly to the study of real biological invasions and range expansions.

Further possibilities include multispecies basin models, involving competition and/or predation. The logistic model of population dynamics is the basis for a variety of well-established simple multispecies models, and extension of the basin model in this direction should be straightforward. Models of population genetics involving competing alleles could be developed along similar lines: Fisher's original frontal wave model (1937) portrayed the spread of advantageous genes within a population. Competing alleles could result in alternative geographic fitness basins (e.g., sickle-cell anemia as an extreme case), setting up conditions for maintaining heterozygosity or clinal variations in gene frequencies. The basin model also can generate conditions favoring increased homozygosity, for example, the representation of conditions leading to centrifugal speciation discussed in section 1.3.1.

An aspect of the model most needing further investigation is its behavior in view of imperfect orientation and movement of individuals. Not only is it reasonable to expect the orientation of individuals to be imperfect but, as discussed in section 1.3.2, there is theoretical reason to believe that there are selection pressures that run counter to perfection of orientation; peripheral habitats are more extensively colonized if orientation is imperfect, and it is these peripheral habitats which are conducive to speciation (see sections 1.2.4 and 1.3). The preceding treatment of movement has assumed that imperfect orientation confers a diffusive component to population behavior, but other behavioral models could lead to different results. There also may be a relationship between selective values of oriented versus diffusive movement and the temporal and geographic grain of basin variability; spatial variability should favor diffusive movement, whereas temporal variability would favor oriented movement.

While it is easy to think of theoretical extensions of the basin model, it is much more difficult to envision ways of testing or validating the basin model. Direct measures of habitat suitability remain elusive, especially as linked to reproductive success in the basin model. Indirect validation, by means of consistently successful predictions, may be more likely.

Aside from the biological invasions mentioned above, natural fluctuations in abundance tend to be confounded by the large-scale spatial coherence of environmental conditions. Thus, widespread areas including both central and peripheral segments of populations may benefit from improved climate, making it difficult to separate abiotic from biotic factors in range expansions.

Once again, observations of exploited populations may provide answers not available from the unexploited populations studied by most ecologists: Exploitation reduces the abundance of a population "artificially," while the habitat quality presumably remains otherwise unchanged. Decreases in exploited populations (especially fish) are often associated with range contractions despite the fact that formerly occupied habitat remains available and otherwise as attractive as it was prior to exploitation.

Of course, explanations based on other effects of exploitation must be considered: for example, exploitation also decreases the average life span and could result in range contraction due to reduced time over which diffusion acts from a central nursery area. Nonetheless, the world's fisheries contain many cases of parallel populations in various states of exploitation, and they provide many opportunities for examining the predictions arising from the basin model.

The basin model has particular promise for management of some exploited populations, and for conservation of depleted populations where critical habitat is often an issue. A current problem in conservation biology is that of optimal design of preserves: whether many small preserves or a single large preserve is more likely to succeed in preventing extinction (Goodman 1987).

Without entering into that debate, it would seem that the basin model provides some useful insights. Are the preserves to be near the center or toward the periphery of the original range? Clearly, preserves near the center should be superior. If preserves must be created near the periphery of the original range due to loss of central habitat, it might be advantageous to site those preserves at diametrically opposed locations.

Not only would this help to preserve independence of environmental fluctuations among the sites but it would also utilize any tendency toward negative correlation between changes in habitat suitability at opposite ends of the range. This negative correlation is most easily seen in a north-south orientation, where climatic (e.g., temperature) deterioration at one end of the range would tend to be accompanied by amelioration at the other end of the range.

The model's utility for fishery management is most direct for relatively immobile organisms. For example, Stevenson (1986) commented on the difficulties in managing the Atlantic surf clam *(Spisula solidissima)* fishery: "Currently a vessel can only fish one day every two weeks.... Obviously fishermen would prefer some other system." She goes on to say that it has taken strong enforcement to prevent extensive "cheating" by fishermen. MacCall (1986) suggested that the surf clam fishery on the U.S. Atlantic coast might benefit from a geographic management strategy which completely closes the center of the range but allows unlimited harvesting toward the edges (or downstream). Besides resembling the optimal effort distributions in Figure 2.10, this strategy might have benefits of easier and less costly enforcement. An inadvertent application of this type of management may have occurred in Narragansett Bay, where pollution afforded protection to what may be the upstream productive segment of the clam population (see section 2.3.4).

The basin model may also provide some guidance in evaluating the utility and placement of artificial habitat. I must warn that our technological ability to create artificial habitat is still very questionable, especially in the case of fragile habitats such as wetlands. Yet other examples such as artificial reefs often have been successful. With continuing human population growth and encroachment of urban centers on habitats such as wetlands, we may expect increasing pressure to attempt mitigation of habitat loss by creating "equivalent" artificial habitat in less economically desirable areas. Again, the basin model may provide guidance in choosing sites for these attempts.

The fact that the basin model offers practical advice to the field biologist and resource manager as well as insight to the theoretician is evidence that it bridges the major realms of biological science. Whether that bridge is useful can only be judged by the traffic it bears.

APPENDIX
SPECIFICATION OF LOGISTIC MODELS

The logistic model has long been a favorite tool of biomathematical modeling, theory, and resource management. Kingsland (1982) gives a detailed review of its early historical development. The logistic model is concise, mathematically tractable, and often a good first approximation for more complicated density-dependent models; Lotka (1925) showed that it is equivalent to a truncated Taylor series expansion of the general population growth model $dN(t)/dt = f[N(t)]$.

Recent investigations in theoretical ecology have allowed parameters in the logistic model to vary in order to simulate the effects of habitat variability in space or time. Of these two forms of variable-habitat logistic models, variability in time has received the most attention during the past decade, mainly due to the arcane but well-developed mathematics of diffusion equations and stochastic calculus. Treatment of spatially varying logistic models has lacked a unifying methodology and has not yet developed a coherent body of literature.

In both temporally and spatially varying cases, results of analyses have been influenced profoundly by the form or parametrization of the logistic model employed. This problem has received scattered comment in the literature on temporally varying logistic models but has been overlooked in the literature on spatially varying models. Here I examine some of the difficulties encountered by various forms of variable-habitat logistic models, and argue that the conventional r and K parametrization has been of serious disutility.

LOGISTIC MODEL

The logistic model assumes that the per capita growth rate of the population, $r^*(N)$, declines linearly with increasing abundance or density, N. Thus, $(dN/dt)/N = r^*$, and in the conventional notation of r and K

$$r^*(N) = r[1 - (N/K)] \, , \tag{A.1}$$

where r is the "intrinsic rate of increase," being the per capita population growth rate at vanishingly small density, and K is the "carrying capacity," being the asymptotic abundance toward which the population grows or declines (i.e., an attracting point). When this form of logistic model is used to describe average dynamics of an entire population, parameters r and K are necessarily positive and the slope of $r^*(N)$ is appropriately negative.

As the model itself is an abstraction, potential mechanisms underlying the linear density dependence of the logistic model are seldom considered explicitly. A useful exception is offered by Schoener (1973), who develops a linear model from energetic considerations. Schoener postulates that "reproductive rate per individual beyond maintenance and replacement is proportional to the net energy harvested by the individual minus that energy needed for maintenance and replacement." Schoener also assumes that the rate of energy input may vary among habitats but is not reduced by direct impact of foraging. Given the energy supplied by a particular habitat, energy input to an organism is influenced only by the fraction of activity time spent feeding, which decreases with increasing population density due to time-consuming interactions with other individuals. Schoener gives a long list of assumptions illustrating the numerous restrictions needed to justify even such a simple growth equation.

In the present general discussion there seems little to be gained from further exploring specific mechanisms to support an abstract model. However, it is worthwhile to examine interpretations of the parameters r and K in Equation (A.1) and how they can be extended from population parameters to habitat-specific parameters.

The most popular form of the variable-habitat logistic model has been that with fixed r and habitat-specific variable K (Figure A.1). I suspect that, to some extent, this popularity has been due to misleading semantics. The term "intrinsic" rate of increase connotes an innate property of the species, independent of the vagaries of habitat.

Kiester and Barakat (1974) noted that there are two divergent views of the nature of r. The first, exemplified by MacArthur and Wilson (1967), assumes that r is a genetically determined (i.e., truly intrinsic) constant, being the maximum growth rate in an "ideal" environment. As a corollary, this view requires that variations in carrying capacity reflect density-dependent effects on population productivity (e.g., in their words, "the efficiency of resource utilization"), because of the assumed constant nature of r. The alternative view, held by Birch (1948) and elaborated by Enright (1976), has been that maximum r must relate to a de-

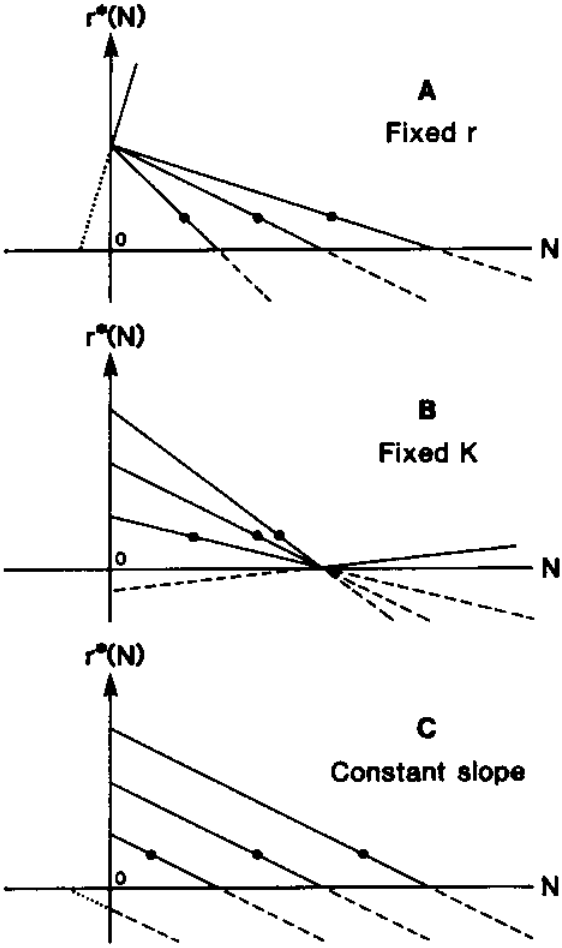

Figure A.1 Simple variable-habitat logistic models: *A*, constant *r* model; *B*, constant *K* model; *C*, constant-slope model. Solid dots indicate habitat distribution according to the ideal free distribution. Dashed lines indicate submarginal habitat. Dotted lines indicate impossible region ($N < 0$).

fined set of physical conditions, i.e., a defined habitat, and these conditions vary over space and time.

From the point of view of variable-habitat logistic models, the interpretation of MacArthur and Wilson is untenable; clearly, some habitats are more favorable (viz. higher *r*) than others when density is arbitrarily low. Enright further argued that variations in carrying capacity are necessarily determined by variations in both density-dependent and density-independent factors. It is the sum of these two contributions to per capita growth rate that is important, so that a decrease in density-independent factors requires a complementary increase in density-dependent factors (hence increased density) to restore the nominal equilibrium that underlies the concept of carrying capacity. Enright's argument requires a positive covariance between *r* and *K*. The density-independent factors which contribute to a change in *r* at low density will, at carrying capacity, have to be compensated by a change in density-dependent factors, especially density itself (viz. *K*).

VARIABLE-HABITAT LOGISTIC MODELS

Being linear in *N*, a logistic model for a particular habitat or time is fully specified by two parameters. In modeling habitat variability it is convenient to hold one of the parameters constant while varying the other. Most commonly, the function $r^*(N)$ is constrained to pass through a specified point, (r^*,N), usually either $(r,0)$, where *r* is assumed to be constant, or $(0,K)$, where *K* is assumed to be constant (see Figure A.1).

Rarely are other fixed points used. Schoener's (1973) logistic model has a fixed point at a population density where all time would be spent on intraspecific interactions; at this population density r^* is less than zero, placing the fixed point in the second quadrant (Figure A.2). Accordingly, this model will be called a "second quadrant fixed point" (SQFP) model. It is also conceivable that the fixed point could be placed in the fourth quadrant ($r^* > 0$, $N < 0$), given the appropriate constraint on the sign of the slope. The latter model is shown in Figure A.2, and will be called the "fourth quadrant fixed point" (FQFP) model. While the

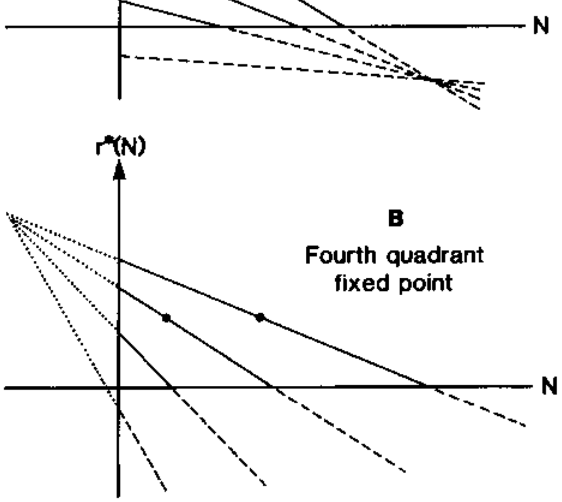

Figure A.2 Generalized variable-habitat logistic models: *A*, second quadrant fixed point (SQFP) model; *B*, fourth quadrant fixed point (FQFP) model.

fixed point conceivably could be placed in the first quadrant ($r^* > 0, N > 0$), a strong argument against this model is its negative covariance between r and K.

The one alternative to the fixed point parametrization is a fixed slope model, which is also a special case of Schoener's (1973) model wherein loss of time due to intraspecific interactions is negligible. The constant-slope model may be written

$$r^*(N) = r - bN , \tag{A.2}$$

where b represents a constant per capita decrease in realized per capita growth rate, and r has the same interpretation as before (Figure A.1). Algebraic solution of Equation (A.2) for $r^*(K) = 0$ gives $K = r/b$, which has the proper covariance, as discussed previously. In this model, carrying capacity is not a direct measure of some quality of the habitat, but rather is the abundance which causes r^* to be zero due to density effects on the realized growth rate. Indeed, much of the historical discussion of the significance of r and K is of questionable relevance to the constant-slope form of the variable-habitat logistic model because of this coupling of r and K.

EVALUATION OF ALTERNATIVE FORMS

Empirical curves of per capita growth rate or fitness versus population density for various species would provide a useful basis for comparison. For example, Whitham (1980) measured per capita reproductive success of aphids as related to leaf size (habitat quality) and number of aphid galls per leaf (population density). He equated reproductive success to fitness, and the resulting curves are well approximated by a constant-slope logistic model, and are even better approximated by a SQFP logistic model. Another example is provided by the variable-habitat anchovy spawning model in Chapter 3, which corresponds to the FQFP model.

Lacking other empirical evidence for "biological realism," it is useful to review and compare theoretical and mathematical properties of the three common forms of variable-habitat logistic model (Table A.1). The most popular form has been that with fixed r and variable K (Figure A.1). The failings of this model, in particular its requirement that all habitats be equally advantageous at low density, were discussed previously.

The alternative fixed point model of constant K and variable r (Figure A.1) appears mainly in the literature on temporally varying habitats (Table A.1). No justification other than mathematical convenience is usually offered, but the model could be used as an approximation for the dynamics of some territorial species (Morisita [1952, 1971] found ant

TABLE A.1 Comparison of simple variable habitat logistic models.

	CONSTANT r	CONSTANT K	CONSTANT SLOPE
Per capita growth rate (r_i*)	$r - rN_i/K_i$	$r_i - r_iN_i/K$	$r_i - DN_i$ $b = r_i/K_i$
Examples			
t:time varying s:spatially varying u:unspecified	Gadgil 1971(t,s) Rosenzweig 1971(u) Fretwell 1972(t) Kiester and Barakat 1974(t) Roughgarden 1974(s) Feldman and Roughgarden 1975(t) Boyce and Daley 1980(t)	Levins 1969(t) Tuckwell 1974(t)	May 1973(t) Kiester and Barakat 1974(t) Feldman and Roughgarden 1975(t) Slatkin 1978(t)
Evaluation			
$N \approx 0$	All habits equal	Well behaved	Well behaved
$N \approx K$	Well behaved	All habits equal	Well behaved
$N > K$	Well behaved	Inverted ranking of growth rates	Well behaved
$r < 0$	Inappropriate to model	Positive slope (K is repelling)	Well behaved
$K < 0$	Positive slope (K is repelling)	Inappropriate to model	Well behaved
Density-dependent habitat selection	No differential suitability (constant habitat distribution); unable to model submarginal habitat	Well behaved only if $r > 0$ and $N < K$; suitabilities are reversed if $N > K$; differential suitability disappears near K; unable to model submarginal habitat	Well behaved

lions to behave in this way), and also as a special case of Schoener's (1973) model. The constant-K model behaves very poorly in the case of $N > K$. While K remains an attracting point, the order of habitat quality is inverted: that with the highest r gives the lowest $r^*(N)$. This artifact has not affected most temporally varying models of this form, since their dynamics do not allow the value of K to be crossed by the trajectory of $N(t)$ for a given set of initial conditions. It could easily prove to be a problem in spatially varying models that allow N to be determined by additional dynamics such as immigration from surrounding habitats.

Submarginal Habitats

As noted earlier, r and K are necessarily positive when used to describe average dynamics of an entire population. However, when the logistic model is used to describe dynamics in a local habitat (time or space), there is no biological reason that r and K must always be positive. It is easy to conceive submarginal conditions in which local abundance would decline even at N near zero (i.e., $r < 0$). A realistic linear model still requires that the slope of $r^*(N)$ be negative, so that the per capita rate of increase (although already negative) further declines with increasing population density. Carrying capacity still corresponds to the population size or density at which r^* would be zero, but a negative K would indicate that this condition cannot be met by an actual population in that habitat. Both fixed-r and fixed-K forms of variable-habitat model are incapable of portraying this condition realistically: if either r or K is negative, the slope becomes positive and K becomes a repelling point (see Figure A.1). Interestingly, the common parametrization of the Lotka-Volterra competition equations, e.g.,

$$r^*(N_i) = r_i\left[\frac{K_i - \Sigma a_{ij}N_j}{K_i}\right], \tag{A.3}$$

where a_{ij} is a "competition coefficient" relating to the effect of species j on species i, is a multispecies extension of Equation (A.1) and suffers the same difficulty in portraying submarginal habitats. This problem with fixed-r or fixed-K forms of the variable-habitat logistic model has occasionally been mentioned (e.g., Slatkin 1978 and Turelli 1977), and a common although unsatisfactory solution has been to restrict the variance of the stochastic parameter so that negative values are arbitrarily improbable.

The constant-slope form of the variable-habitat logistic model (Equation A.2, Figure A.1) overcomes many of the difficulties with fixed-point forms of the model. First appearing in simplified form ($b = 1$)

as a mathematical convenience (May 1973), it has been used in most later treatments of temporally varying habitats. Besides being well behaved at all values of N, submarginal habitats are modeled easily by a negative value of r. The corresponding value of K is also negative, and remains an attracting point (though unattainable) due to the negative slope of $r^*(N)$.

The other fixed-point models (SQFP and FQFP) share some of the problems of fixed-r and fixed-K models, but with lesser severity. In a spatially varying application of the SQFP model (Figure A.2), N could exceed the value of the fixed point, but because this must occur at $r^* < 0$, the likelihood of that condition is reduced. The FQFP model (Figure A.2) has no problem with negative values of r, but maximum r must not exceed the value of the fixed point.

IMPLICATIONS FOR HABITAT SELECTION

It is instructive to compare the common forms of variable-habitat logistic models in light of the DDHS theory of Fretwell and Lucas (1970) and Fretwell (1972). Their theory predicts that in an ''ideal free distribution'' individuals differentially occupy available habitats so that realized ''suitability'' is equal for all occupied habitats. Here suitability corresponds to realized per capita growth rate, $r^*(N)$, so the predicted abundance in each habitat is given by $N(r^*)$ as shown by the solid dots in Figures A.1 and A.2.

The fixed-r, variable-K model indicates that all habitats would be colonized even at very low total population size, with no further colonization of marginal habitats as overall abundance increases. Rather, abundance is distributed among all the habitats in proportion to their carrying capacities, and the relative distribution *does not vary with abundance*. Because of this property, the dynamics of the entire population retain the linear properties of the logistic model.

All other forms of variable-habitat logistic models result in nonlogistic behavior of the overall population due to differential occupation of habitats as total population size varies, the habitat with the highest r being colonized first. In the variable-r, fixed-K model, this differential disappears as K is approached, and order of habitat suitabilities (hence order of habitat occupation) is reversed if total population size exceeds K. Again, the constant-slope model is consistently well behaved: Differential occupation of habitats occurs at all levels of abundance, even if K is exceeded, under which conditions submarginal habitats are colonized.

CONCLUSION

I submit that for theoretical modeling, the constant-slope form of variable-habitat logistic model is better than the fixed-*r* or fixed-*K* forms in nearly every respect. While the literature on temporally varying logistic models seems to be in substantial agreement with this conclusion, treatments of spatially varying habitats (e.g., Gadgil 1971 and Roughgarden 1974) and unspecified variable-habitat models (e.g., Oksanen et al. 1981 and Rosenzweig 1971) have seldom used the constant-slope form of spatially varying logistic model. The constant-slope form is particularly well suited to spatially varying models, whereas the fixed-*r* and fixed-*K* forms are unable to represent submarginal habitat. The other fixed-point forms (SQFP and FQFP) offer greater representational flexibility, but they also entail greater mathematical complexity and so are unlikely to see widespread use.

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