CHAPTER 1

The Merging of Metapopulation Theory and Marine Ecology: Establishing the Historical Context

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I. Introduction
II. Differences and Similarities between Marine and Terrestrial Systems
A. Describing Actual Spatial Population Processes and Structures
B. A Framework for Asking Research Questions
C. A Paradigm for Population and Conservation Biology
D. Applications to Marine Populations
III. History and Effects of Predominant Research Questions in Marine Ecology
IV. Conservation and Fisheries Management Influences on Marine Ecology
A. Scale of Study
B. Spatial Resolution
C. Marine Protected Areas
V. Summary
References

I. INTRODUCTION

The metapopulation concept, first formalized by Levins (1969, 1970), has roots dating back to the work of Andrewartha and Birch (1954), and MacArthur and Wilson (1967). The origin and subsequent evolution of this concept into an important component of modern ecological theory have been described by Hanski and Simberloff (1997), and Hanski (1999). Previous discussions were

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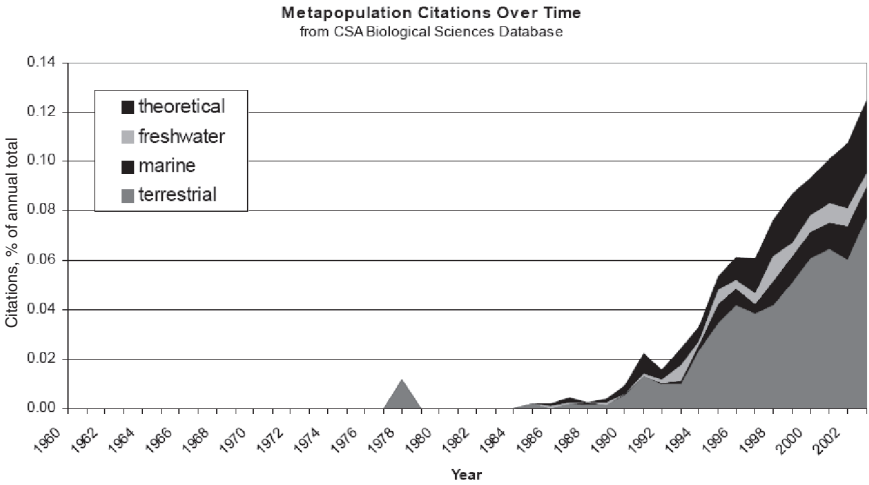

FIGURE 1-1. The pattern of growth in citations to **metapopulation** in the CSA's Biological Sciences database, by ecosystem studied. "Theoretical" studies are those that discussed metapopulation concepts or theory but could not be assigned to a specific habitat. Terrestrial studies greatly outnumber either freshwater or marine ones, and theoretical studies also exceed the total of aquatic studies. Citation search and figure provided by W. Figueira.

largely focused on theoretical developments and on applications of the metapopulation concept in terrestrial systems. Our goal here is to examine the use of metapopulation concepts and theory in marine systems. In doing so, we will be setting the stage for this volume.

Despite the first appearance of the term *metapopulation* in Levins' papers more than three decades ago, the concept was not widely used until the early 1990s, and it exhibited a steady increase in usage through the mid 1990s (Hanski and Simberloff, 1997), with no apparent plateau in citations into the early years of this century (Hanski and Gaggiotti, 2004). Applications of metapopulation theory to aquatic ecology appeared in the early 1990s, not long after the exponential increase in metapopulation citations generally (Hanski and Gaggiotti, 2004), but these references were to freshwater systems (Figueira, 2002), and use of metapopulation concepts in marine systems was rare prior to the mid 1990s (Fig. 1-1). These have since increased dramatically (Figueira, 2002; Grimm et al., 2003). For example, in the first of two edited books on the ecology of coral reef fishes (Sale, 1991), there is but a single reference to metapopulations, and that is only a parenthetical note (Doherty, 1991, p. 264). In contrast, the second book (Sale, 2002a) contains metapopulation references on 25 pages (approximately 6% of all pages), spanning eight different chapters by different authors on different topics.

Citations using metapopulation concepts in marine systems are now about as common as those referencing freshwater systems, although they remain but a minor fraction of terrestrial metapopulation citations (Figueira, 2002). Unlike the case for terrestrial studies, the rate of marine citations of metapopulation concepts does not appear to be increasing greatly. This is despite the fact that more than 70% of the earth's surface is covered by marine habitat and a considerable proportion of global biodiversity dwells in the sea.

In this chapter, we consider three general explanations for the pattern of use of metapopulation ideas in marine ecology. First we examine whether there are fundamental differences between marine and terrestrial systems (apart from the surrounding medium) that render theory developed primarily in one context of limited use for the other. We do this through a critical assessment of how metapopulation theory is used in terrestrial ecology and suggest likely differences in application of metapopulation theory to marine systems.

We then explore whether the slow adoption of a metapopulation paradigm in marine ecology might have been a direct consequence of the pattern of development of ideas and questions in marine ecology. The early absence and eventual integration of metapopulation theory into marine ecology might be driven by a change in the types of questions investigated by marine ecologists, because not all ecological issues fall directly within the domain of metapopulation ecology. An early focus by marine ecologists on topics outside this domain provides a simple explanation for why adoption of metapopulation concepts lagged. We examine this possibility through a historical review of marine ecology during the past 30 years.

Finally, we examine the extent to which marine environmental management and conservation may have helped initiate and now continue to drive the application of metapopulation theory. Scientific inquiry rarely unfolds in a vacuum. Instead, science is often heavily shaped by the rest of human society (Diamond, 1997). Hanski (1999) has described how the development of metapopulation ecology as a whole was spurred by applications in environmental conservation, and we explore this in the context of marine conservation.

Before proceeding, we must have a clear definition of a metapopulation. This clarification is necessary to identify how a given characteristic of marine systems, research topic in marine ecology, or marine management issue fits into our perception of a metapopulation. Recently, Smedbol et al. (2002) and Grimm et al. (2003) have put forth arguments to the marine ecology and fisheries science communities that metapopulations should be defined in the spirit of the classic Levins model, with real likelihood of extinction of local populations a necessary feature. In contrast, we have all put forth arguments for a different perspective (Hanski and Simberloff, 1997; Hanski, 1999; Hanski and Gaggiotti, 2004; Kritzer and Sale, 2004)—one we will adopt here. Metapopulation ecology has grown considerably since Levins' landmark papers, and modern metapopulation research

often considers more than simply local presence or absence of organisms. Even without local extinctions, metapopulation structure has implications for abundance of local populations, as well as those populations' age, size, and genetic structures. We define a metapopulation as a system in which (1) local populations inhabit discrete habitat patches and (2) interpatch dispersal is neither so low as to negate significant demographic connectivity nor so high as to eliminate any independence of local population dynamics, including a degree of asynchrony with other local populations.

II. DIFFERENCES AND SIMILARITIES BETWEEN MARINE AND TERRESTRIAL SYSTEMS

How have ecologists used the metapopulation framework in the study of terrestrial populations, and are these approaches applicable to marine systems? Our purpose here is not to imply that the terrestrial comparison is somehow fundamental for marine ecology, and even less that marine ecologists should try to emulate what terrestrial ecologists have already done. But given the 15-year experience of terrestrial metapopulation ecologists, it is worth asking, in this context, about the current standing of the field. We distinguish three ways of using the metapopulation concept, although the boundaries are not necessarily sharp. These are its use to describe spatial processes and structures in actual populations, its use as a framework for asking research questions, and its use as a paradigm for population and conservation biology.

A. Describing Actual Spatial Population Processes and Structures

Many species on land live in highly fragmented landscapes (Hanski, 1999), in which suitable habitat accounts for only a small fraction, often a few percent, of the total landscape area and mostly occurs as small, discrete patches. Such situations are common, especially for invertebrates, many of which are habitat specialists and have small body size, high rate of population increase, and short generation time—all factors that make it likely that the species has a metapopulation structure (Murphy et al., 1990). Small body size means that the number of individuals in even small fragments of habitat may be large enough to constitute a local breeding population, especially because small species tend to have lower migration rates than large ones (excluding very small organisms that disperse passively and very widely; Finlay and Clarke, 1999; Finlay, 2002). A high population growth rate implies that, after population establishment, local populations quickly grow to the local carrying capacity, unless they go extinct. Short

generation time means, among other things, that stochastic events are not buffered by great longevity of individuals, which would reduce the risk of population extinction. Finally, habitat specialists with short generation times are likely to be greatly affected by interactions between large-scale weather perturbations and local environmental conditions.

Butterflies have been studied most intensively in the metapopulation context. These satisfy the aforementioned criteria but also possess features that make them especially amenable to field studies (for a review see Thomas and Hanski, 2004). Numerous other terrestrial species have comparable spatial population structures, although studying many of them would be much more difficult than investigating butterflies. For example, thousands of species of insects, fungi, mosses, and other taxa live in dead and decaying tree trunks in forests. Individual decaying logs represent discrete habitat patches, containing local populations of species that necessarily are organized as a metapopulation because of the ephemeral nature of the habitat (Hanski, 1999).

Richard Levins' (1969, 1970) simple metapopulation model captured the bare essentials of the dynamics of species that exist regionally in a balance between local extinctions and recolonizations of currently unoccupied habitat patches. Since then, the theory has developed in many directions, recently reviewed in the edited volume by Hanski and Gaggiotti (2004). The theoretical development that remains closest in spirit to Levins' original concept with local extinctions and recolonizations has been dubbed the *spatially realistic metapopulation theory* (Hanski, 2001; Hanski and Ovaskainen, 2003; Ovaskainen and Hanski, 2004). The key elements of this theory are a finite number of patches (infinite in the Levins model), variation in patch qualities (identical in the Levins model), and variation in patch connectivities resulting from inevitable differences in their spatial locations and distance-dependent migration in most species (all patches equally connected in the Levins model). These features lead to sufficiently realistic models for many real metapopulations to allow statistically rigorous estimation of model parameters (for a review see Etienne et al., 2004), which, in the best cases, allow the construction of predictive models (Wahlberg et al., 1996; Moilanen et al., 1998; Hanski, 2001; Thomas and Hanski, 2004). One limitation that remains is that these models do not include a description of local dynamics, hence the label *(stochastic) patch-occupancy models* (SPOM). Because the emphasis in SPOMs is in the dynamics of assemblages of many small local populations, they cannot profitably be applied to systems consisting of a small number of populations or populations of very large size (Baguette, 2004). Spatially realistic simulation models have been advocated as an efficient tool for the latter situations, and many applications of generic simulation models have appeared in the conservation literature (Akcakaya et al., 2004). Unfortunately, such models tend to be so complex that there are hardly ever sufficient data to estimate the model parameters properly, and the modeling that has been done seldom takes into

account uncertainty in parameter values (Hanski, 2004; for an example that does incorporate uncertainty in parameter estimates see Dreschler et al., 2003).

In summary, the defining feature of the terrestrial systems in which spatially realistic metapopulation models have been successful is a highly fragmented landscape structure. The theory has been useful because such highly fragmented habitats are common in terrestrial systems, and they are becoming increasingly common because human land use practices tend to fragment habitats that were more continuous in the past. Apart from the quantitative analysis of real metapopulations referred to earlier, the theory has allowed more qualitative analysis of key phenomena, such as the extinction threshold for long-term persistence (Hanski and Ovaskainen, 2000) and the transient dynamics following perturbations (Ovaskainen and Hanski, 2002; Hanski and Ovaskainen, 2003).

B. A Framework for Asking Research Questions

Over the years, the perceived success of the metapopulation approach has invited applications to systems for which the value of the concept is less clear. Practically all populations have a patchy distribution at some spatial scale, making the metapopulation approach tempting, but patchy populations differ in many ways from each other. Two questions in particular are worthy of closer scrutiny here. First, to what extent is patchiness of populations attributable to patchiness of the physical environment? And second, at what spatial scale does patchiness occur?

Metapopulation theory is primarily a theory for cases when the spatial structure of populations is imposed by habitat patchiness. One of us has even viewed current spatially realistic metapopulation theory as an amalgamation of classic metapopulation theory and landscape ecology (Hanski, 2001; Hanski and Ovaskainen, 2003). If a species has a patchy population structure in the absence of obvious habitat patchiness, there must presumably be some other key factor or process that causes this spatial structure. In this case it would be most unlikely that fundamental understanding of the system could be gained by ignoring such a key process and applying theory that assumes habitat patchiness. Thus, one important message is that rather than focusing on the spatial patterns, one should focus on the processes that underlie those patterns (Hanski, 1999).

That being said, it is nonetheless clear that if the population is patchily distributed, for whatever reason, the patchy population structure has important implications for population dynamics, maintenance of genetic variation, evolutionary response to environmental change, and so forth. Thus, at one level, it is useful to recognize "metapopulation structure" in the sense of spatially structured population, regardless of the causes of that structure (which remains a key research question), because this leads to new questions.

Turning to the issue of spatial scale, metapopulation theory also requires that local populations are at least potentially connected via migration. If the patchiness is at such a large scale that different geographic populations are hardly at all connected to each other, these populations represent practically independent entities, and migration among them makes no real difference for their dynamics. Migration on a large spatial scale may be interesting and important, but it is not addressed by metapopulation theory.

The first questions to ask about metapopulations include what difference it makes that interactions are localized within local populations. Levins (1969, 1970) gave a partial answer for ecology with his model—an example of a so-called island model with an infinite number of identical patches and populations. Other examples of island models include Wright's (1931) population genetic island model and Maynard Smith's (1974) haystack model in evolutionary theory. The island models have allowed researchers to ask questions about the consequences of spatial population structure in the very simplest setting. More recently, researchers have asked questions about the role of dissimilar attributes of local populations in metapopulations (several chapters in Hanski and Gaggiotti, 2004). In ecology, these questions were asked partly in response to criticism of the simplicity of the Levins model (Harrison, 1991, 1994), and this led to the spatially realistic metapopulation theory described earlier. In population genetics, the island model has the unfortunate and unrealistic feature of equalizing the contributions of all local populations (demes) to the next generation, which greatly inflates the effective size of the metapopulation in comparison with what is likely to exist in reality (Whitlock, 2004). The question of effective metapopulation size has been posed but is still without a satisfactory answer. Research on source–sink population structures, when focused on the actual patterns of migration and gene flow among local populations, has opened a new avenue for research that touches, for example, the process of local adaptation (Kawecki, 2004). Observations about the demographic effects of inbreeding in small local populations have stimulated a new round of research on the significance of inbreeding for population persistence (for a review see Gaggiotti and Hanski, 2004). Even this short list of examples demonstrates that the metapopulation concept has stimulated a wide range of important research questions.

C. A Paradigm for Population and Conservation Biology

It is striking how suddenly metapopulation theory became adopted as a new conceptual and theoretical framework (paradigm) for conservation biology. Papers published in the early 1990s made it clear, either explicitly (Hanski, 1989; Merriam, 1991) or implicitly (Wilson, 1992; Noss, 1993), that the metapopula-

tion concept had replaced the dynamic theory of island biogeography as the leading conservation paradigm. Hanski and Simberloff (1997) have examined the reasons for this "paradigm shift." One reason was the perception that island theory is an equilibrium theory whereas metapopulation theory is not. In reality there is no such difference: The core models by MacArthur and Wilson (1967) and Levins (1969) are special cases of a single, more general model (Hanski, 2001).

However, the primary reason why metapopulation theory appeared to provide a better framework for conservation than island theory was the absence of a mainland and mainland populations in the former. In island theory, no species that is present in the mainland pool will go extinct on an island, because there is always the possibility of recolonization from the mainland. Such a vision is not adequate for a fragmented landscape, from which species may and do go permanently extinct. Indeed, only metapopulation theory posed the key question about an extinction threshold, which depends both on the structure of landscapes and on the biological properties of species (Hanski, 1994).

D. Applications to Marine Populations

The three roles of the metapopulation concept in the study of terrestrial systems may all apply to marine systems: Metapopulation theory may provide an effective modeling tool to analyze the actual spatial population dynamics and structures of marine populations, metapopulation theory may be a helpful framework in which to ask new research questions, and metapopulation theory may represent a useful new paradigm.

Application of realistic metapopulation models to actual marine populations is dependent on the physical structure of the habitat, in the same manner as in terrestrial situations. Such applications are therefore restricted to species that have discrete local populations on shores or on the seafloor. Examples include populations of barnacles on rocky shores (Iwasa and Roughgarden, 1986), of crabs in estuaries (Botsford et al., 1994), of various demersal fishes (McQuinn, 1997; Stephenson, 1999), and of animals such as seals that occupy terrestrial breeding colonies but spend their time otherwise at sea. A recent study of the gray seal metapopulation in the Orkney Islands contributed not only to a better understanding of seal biology, but to metapopulation biology in general. Gaggiotti et al. (2002, Gaggiotti, 2004) have developed Bayesian methods to extract information in multilocus genotypes to infer patterns of migration of seals among breeding colonies. This work is especially valuable in showing how effectively to combine ecological (demographic) and genetic information in the same analysis.

Many marine species have highly dispersive juvenile stages, and hence dispersal and gene flow may be widespread (see the following section). In this

feature, they appear different from many terrestrial populations. This need not restrict the usefulness of the metapopulation approach, because it can accommodate a broad range of rates of dispersal. However, in cases when dispersal is so extensive as to homogenize the demography of the set of local groups, it has nothing to tell that a conventional, spatially nonstructured, demographic analysis would reveal.

One obvious way in which metapopulation theory may help to guide marine ecological research concerns the question of patchiness. Patchiness is a common feature of the vast majority of both terrestrial and marine populations, although the cause of patchiness is often less clear for the latter. Although it is important to understand the causes of patchiness in marine just as in terrestrial systems, it is both valid and necessary to ask questions about the consequences of observed patchiness. A metapopulation approach provides one way to do this.

Finally, we see a genuine difference between terrestrial and marine environments when it comes to considering the nature of human impacts. The primary threat of human activities to terrestrial biodiversity, although clearly not the only one, is posed by habitat loss and fragmentation. Most habitats in modern landscapes in areas with high human population density are already highly fragmented, and becoming more so. It appears obvious that a theory that is specifically focused on the dynamics of species in such highly fragmented landscapes is not only useful, but essential, for research and management. The situation in marine environments is different. Although patchy loss of habitat, leaving remnant patches untouched, may result from effects of storm-tossed debris on rocky shores, or from crown-of-thorns starfish outbreaks or bleaching on coral reefs, each of these agencies can result in widespread degradation if extreme (Connell et al., 2004), and anthropogenic impacts on marine habitats generally result in degradation and homogenization of habitat across broad areas. Coastal pollution tends to spread out over large areas downstream of the source (Rabalais et al., 2002), and commercial trawling has been documented to simplify and homogenize the predominantly biogenic structure of benthic habitats over extensive areas of continental shelves (Thrush and Dayton, 2002).

Rather than any effects on habitat, the major human impact on marine systems is arguably overfishing (Reynolds et al., 2002). This reduces abundance and truncates age distributions of target and by-catch populations, and its effects vary spatially in correspondence with the spatial variation in fishing pressure. Although fishing pressure is rarely spatially homogeneous, certain types of management action (particularly, the use of protected areas or regional seasonal closures) are spatially explicit and serve to create or strengthen spatial variation in fishing pressure, with the result that populations come to be more patchily distributed, and more variable demographically, than they were before (Polunin, 2002). Thus, although patchiness of populations may be increasing in many marine populations, the reasons are largely different than in terrestrial systems. Therefore, the

metapopulation paradigm, if and when it helps guide marine research, most likely will have distinct uses from those that serve in terrestrial systems. This also means that marine ecologists are likely to make their own novel contributions to the development of metapopulation concepts and theory.

III. HISTORY AND EFFECTS OF PREDOMINANT RESEARCH QUESTIONS IN MARINE ECOLOGY

Marine ecology seems always to have been the younger sibling of terrestrial ecology. Although marine ecologists have appreciated the substantial differences between the marine and the terrestrial environment, and their consequences for ecology, terrestrial ecology was always there to offer the tested paradigms. Fisheries science, and chemical and physical oceanography all contribute ideas and approaches, but terrestrial paradigms have prevailed, particularly for those aspects of marine ecology that concern populations and communities. Given this pattern, it was perhaps inevitable that marine ecologists would incorporate metapopulation theory into their work, but do so after its embrace by their terrestrial colleagues. What is interesting in exploring the progress of marine ecology, is to see how and why terrestrial concepts become incorporated into the marine context. Our adoption of a metapopulation paradigm grew out of an enthusiastic rediscovery of the powerful effects on populations of larval dispersal and subsequent recruitment.

The early days of marine ecology, a half century or more ago, were a time for detailed descriptive studies that cataloged what species lived where, their characteristics, their trophic interactions, and the circulation of energy and materials through their ecosystems. Studying marine systems called for innovative methods that usually involved machinery to grab samples and haul them into boats, where the ecologists would examine what was caught and try and make sense of what it might have been doing before it was abruptly interrupted. During this period, ecologists probably developed a greater appreciation for the unique properties of marine systems than was evident later on in what might be called the *hypothesis-testing phase* of marine ecology. This began with hesitant steps early in the 20th century, and really came of age in the 1970s and 1980s.

Doing proper, hypothesis-testing science requires that you have some ability to manipulate the system being studied. To do such science in the marine environment initially required a retreat to its edges—those parts of the marine world that were more or less accessible to the scientist. Thus we find that the science of marine ecology is strongly rooted on the intertidal rocky shore; in the shallow sub- and intertidal mud flats, salt marshes, and estuaries; and on rocky and coral reefs. Some brave souls persisted in studying plankton and neuston of the open ocean, but it was virtually impossible to do experiments out there, and the tax-

onomy was horrendous. Even today, the gap (as reflected in patterns of citation and conferences attended) between the "blue water" biological oceanographers and the coastal marine ecologists is arguably larger than the gap between the latter and terrestrial ecologists. The development of the science of marine ecology during the last 50 years has been driven from the edges, as is well illustrated by a recent text on marine ecology (Bertness et al., 2001) that, in its eight chapters (of 19 total) dealing with "community types," deals exclusively with inshore and benthic systems.

Two of the most profound features of the ocean are its vastness and its continual motion. Even drifting passively, marine organisms are able to travel long distances during relatively short periods of time. Ignoring for the moment the creatures that occupy the pelagic zone throughout their lives, those demersal, and sessile plants and animals that live on firm substrata are overwhelmingly organisms with pelagic dispersive (usually egg or larval) stages. As a result, local populations, occupying particular shores, bays, estuaries, or reefs, can be extensively interconnected by the dispersal of their propagules. Following pelagic life, larvae settle to suitable substrata and are recruited to populations of juveniles and adults living there. The importance of this fact of life was clearly recognized by ecologists studying marine communities at the mid century (e.g., Scheltema, 1974; Thorson 1950, 1966), but it was largely neglected by those who interpreted observations and experimental results on demersal and often sessile organisms using the concepts of terrestrial ecology. During the '60s and '70s, the prevailing assumption was that larvae were always available to replenish populations.

Intertidal ecology moved from description to experimentation, with the pronounced zonation on shores acting as a major driver. This universal and conspicuous pattern was initially interpreted using tolerances of individual species to emersion and submersion. When that did not suffice (because too many well-zoned species could tolerate conditions far more extreme than any they would experience on a shore), the competitive and predatory interactions among them became the chief focus of attention (Underwood and Denley, 1984). Some of the finest field experimentation anywhere has been that done to explore the interactions of plants and animals of the rocky shore. Yet most of it dealt with the sessile and sedentary organisms easy to find stranded at low tide, as if they existed in nicely contained local communities, and it ignored, until the mid 1980s, the fact that local "populations" of barnacles, mussels, or whelks were the product of large numbers of individual settlement events bringing single larvae to that shore from places outside (at least on the scale of tens of meters at which the ecological studies were done; Morgan, 2001).

A similar pattern of maturation of the science can be seen in coral reef studies (where zonation was also an early fascination), and in studies of subtidal mud flats, sea grass beds, mangroves, and other coastal marine environments. Open-water studies evolved very differently, and never had the impact on the wider

science of ecology, perhaps because experimentation was so much more difficult. Deep-sea studies evolved slowly because of the technical difficulties and expense, but included experiments and focused on local biotic interactions in much the same way that intertidal studies did (Etter and Mullineaux, 2001). In the 1960s and '70s, to pose experimentally testable hypotheses, marine ecologists worked with demersal and sessile species, and studied processes that took place on very local scales—often scales of centimeters. The vastness and continual motion of the oceans were fine for sunset watching at the end of the day, but they did not contribute to the science.

Classic field experiments that had profound impacts on the development of community ecology examined the competitive interactions of barnacles of different species (e.g., Connell, 1961a,b, 1978), and the predatory interactions of mussels, whelks, and starfishes (e.g., Paine, 1966; Dayton, 1971). Superficially simple but important concepts, such as escapes in space or in growth, or that of disturbance as an agent to maintain community structure, came from such studies. More complex studies involving urchins, kelp, and sea otter (e.g., Estes and Duggins, 1995), or the creatures that colonize fouling plates (e.g., Sutherland, 1974) gave us alternate stable states, and the related idea that ecological changes could be sudden phase shifts as well as gradual successional processes. Yet it was not until late in the 20th century that marine ecologists remembered that profoundly important feature of virtually all the organisms they studied—pelagic dispersal of larval stages and subsequent settlement to juvenile and adult demersal and sessile populations.

The idea that recruitment of dispersive larvae to populations of sessile or sedentary juveniles and adults was an important ecological process was "discovered" virtually simultaneously by marine ecologists working on rocky shores and on coral reefs. On the rocky shores, Dayton's (1971) early work, which drew attention to the importance of disturbance to maintaining community structure, indirectly recognized that it was settlement and recruitment of larval stages that led the recovery from disturbances. In an important review, Connell (1985) pointed to the likelihood that recruitment processes would be found to be quite variable, and play a role in the development and maintenance of intertidal communities. However, it was not until Caffey's (1985) work that a serious effort to document spatial and temporal patterns of settlement or recruitment of intertidal organisms was undertaken. Note that it has been traditional in marine ecology to measure recruitment very close to the time of settlement from the pelagic stage, rather than later in life, as is more typical of fisheries science, when the interest is in recruitment to the catchable population—typically a size-related event.

Caffey set out to quantify spatial and temporal patterns in settlement and in recruitment about one month after settlement for the barnacle *Tesseropera rosea* on a series of rocky shores extending over 500 km along the east coast of Australia. His nested design demonstrated profound (order of magnitude) spatial

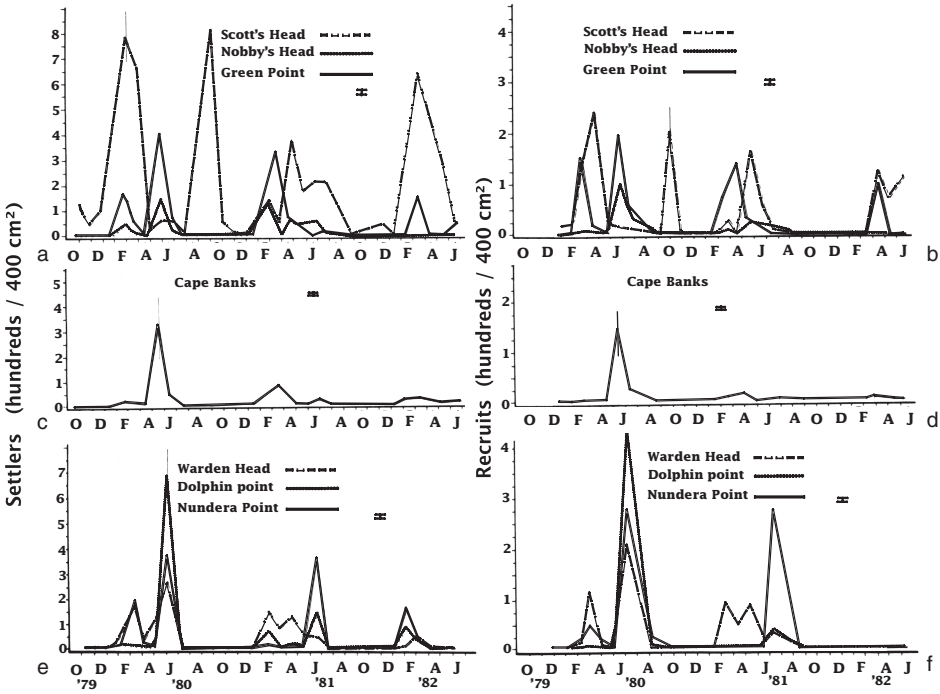

FIGURE 1-2. Geographical and temporal variation in patterns of settlement and recruitment of the barnacle *Tesseropora rosea* on rocky shores of New South Wales, Australia. Settlement was defined as the density of animals 30 days old or less at sampling; recruitment was density of animals 30 to 60 days old at sampling. Graphs represent the mean rates of settlement (over 24 replicates) and recruitment (over 12 replicates) at each shore. (Figure redrawn from Caffey, 1985, and with permission of the Ecological Society of America.)

variations in settlement on scales of less than 3 m, 20 to 50 m, and 10 to 500 km, and very considerable variance in the relationship between settlement and recruitment one month later (Fig. 1-2). His study also demonstrated large differences in the spatial patterns in two successive years. Other intertidal researchers had begun to monitor recruitment and settlement on local scales, and over short time periods, but Caffey's work was the first to show the rich patterns in these processes for an intertidal organism. Nearly simultaneously, and continuing over several more years, Roughgarden et al. (1985, 1988) demonstrated equally complex patterns in barnacle recruitment on the California and Oregon coasts, and they were able to relate some of this variability to regional-scale processes, particularly the effects of wind-induced coastal upwellings.

On coral reefs, Sale (1977), in proposing lottery competition as the mechanism permitting coexistence of territorial damselfishes, had argued for the impor-

tance of, but had not attempted to quantify, variability in settlement. However, Williams and Sale (1981) monitored the settlement of a broad range of fish species to coral colonies of the same type that had been set out in four grids on the shallow sandy floor of a lagoon about 2 km in diameter. Grids of corals were about 1 km apart, and daily collections of all fish settling to them were made over two successive summer settlement seasons. The results showed pronounced variation among sites, within and between years, and among species.

Both on reefs and in intertidal areas there followed a period of intense study of settlement and recruitment dynamics using a variety of species of organism. The fact that recruitment was highly variable in time and in space, and seemingly on many scales, was confirmed numerous times, and Hjort (1914) was suddenly being cited with enthusiasm by marine ecologists. Throughout these investigations, there has been a broadly accepted appreciation that the larvae settling to local sites have been supplied at least partially, and perhaps substantially, by populations located elsewhere. Local marine populations are open, and their recruitment is subsidized by neighboring populations.

If documenting the variability in recruitment was easy, developing explanations for that variability has been far more difficult. Roughgarden's (Roughgarden et al., 1988) early success in explaining a considerable portion of recruitment variation of barnacles has been repeated for other organisms and locations, but there have been many more studies that were unable to identify causal factors of any importance (Caley et al., 1996). The reason for this appears to be that the process of larval dispersal and subsequent settlement is a strongly biophysical process, with multiple interacting causes, in all except those species with behaviorally simple larvae that are pelagic for only hours. The movement of water is complex at any but the global scale, particularly close to shores and substrata where the demersal and sessile species live, and it varies with time as well as space. The larvae may well be passively transported when very young, but they undergo rapid development and are frequently highly adapted for their pelagic existence. Fish and crustacea, in particular, may be pelagic for months, and are very capable pelagic organisms by the end of this period. To understand the path followed by a long-lived larva, it is necessary to have detailed knowledge of a complex and variable hydrodynamics, and of a set of sensory and behavioral skills that change as larval life progresses (Sale and Kritzer, 2003). One consequence of this difficulty in specifying causes of recruitment variation has been an inability to specify either the spatial scale on which local populations are interconnected or the extent of the subsidy of recruitment to each local population as a result of dispersal from other sources.

Recognition that openness and larval dispersal play major roles in the ecology of marine populations and communities leads logically to the consideration of metapopulation ideas. Perhaps because marine ecologists have tended to focus their studies on quite local populations and communities, executing experimen-

tal treatments on replicate 1-m^2 plots or replicate small boulders on rocky shores or replicate small patch reefs or coral heads on coral reefs, attention to metapopulation concepts was slow to develop. Such attention began during the 1980s with the rediscovery of recruitment dynamics and a move to larger spatial scales. Roughgarden et al. (1985, 1988) sampled barnacles over approximately 100 km of the central coast of California. Caffey (1985) did the same across 500 km of Australian coasts. Doherty and colleagues (Doherty and Williams, 1988; Fowler et al., 1992) sampled reef fish recruitment at sites on sets of reefs spread across 1000 km of the Great Barrier Reef. Hughes et al. (2002) documented recruitment dynamics and adult population sizes for corals across the same 1000-km range. Each of these studies has concerned recruitment dynamics primarily, and population structure secondarily, if at all. But each provides data consistent with a metapopulation paradigm, and Roughgarden and Iwasa (1986, Iwasa and Roughgarden, 1986) were the first to use a metapopulation model explicitly. Although marine ecologists currently have trouble applying metapopulation theory, chiefly because of the difficulty of quantifying the larval dispersal that provides the connectivity among local populations, the value of the metapopulation paradigm is widely recognized, and the need to develop techniques for measuring connectivity among marine populations is broadly recognized as a high priority for this science (Kritzer and Sale, 2004; Sale, 2004).

IV. CONSERVATION AND FISHERIES MANAGEMENT INFLUENCES ON MARINE ECOLOGY

A. Scale of Study

The preceding section documents shifts in the focal questions of academic marine research from within-patch dynamics that occur in isolation from other populations to within-patch dynamics influenced by replenishment from unidentified external sources, to demographic linkages among distinct populations. Concurrently, the spatial scale of study has increased to often oceanwide scales (e.g., Hughes et al., 2002; Planes, 2002; Mora et al., 2003). In contrast, fisheries science has long adopted very large-scale perspectives. For example, the broad geographic scope of Sinclair's (1988) stimulating essay on population ecology of northern temperate marine fisheries species is comparable to that adopted 20 years earlier by Harden Jones (1968) in his classic text on fish migration.

The historical large-scale approach of fisheries science is likely due in part to the large geographic areas that fisheries management agencies are charged with overseeing, as well as the larger areas from which scientists can obtain data through fishery-dependent sampling. At any rate, the metapopulation concept is fundamentally about ecology at large scales, and the larger geographic scope of

fisheries science seems to have created a research climate conducive to adopting metapopulation theory once that theory had found its way into marine science. For example, Shepherd and Brown (1993) called for metapopulation thinking in managing abalone fisheries several years before the documented increase in general marine metapopulation references (Grimm et al., 2003). Also, Botsford and coworkers' studies of commercially harvested crab stocks were among the first to make use of the metapopulation concept in a marine context (Botsford, 1995; Botsford et al., 1994, 1998; Wing et al., 1998; and Chapter 9). Of course, the earliest marine metapopulation studies were not conducted in a fisheries context (Iwasa and Roughgarden, 1986; Roughgarden and Iwasa, 1986), but those are the exceptions rather than the rule. Although fisheries science and academic marine ecology have often operated across an unnecessary divide (Sale, 2002b), the influence of metapopulation approaches in fisheries on broader marine ecological research must be acknowledged.

B. Spatial Resolution

The historically larger focal scale of fisheries science certainly helped facilitate incorporation of a large-scale approach such as metapopulation ecology, but fisheries science had held that broad-scale perspective for many years before metapopulation theory was invoked explicitly. This is due in part to the fact that metapopulation ecology is not simply about ecology at large spatial scales, but also considers in detail the spatial arrangement of and relationships among local populations.

Fisheries science initially tended to downplay consideration of smaller scale structure among local populations. Although Atlantic herring biologists have examined spatial patterning related to migration and the distribution of herring "races" since the mid 1900s (reviewed by McQuinn, 1997), comparable attention to other species has been slower to emerge. However, the 1980s saw a groundswell of studies examining stock structure of a variety of marine fisheries resources, particularly the identification of substocks within a larger management area (e.g., Fairbairn, 1981; Shaklee et al., 1983; Grant, 1985; Oxenford and Hunte, 1986; Cooper and Mangel, 1999). Investigation of stock structure has now become a standard component of fisheries science (Begg et al., 1999). Molecular genetics has been a prominent tool in this area, but morphometric, life history, and other approaches have also played important roles (Begg and Waldman, 1999).

Initially, resolving spatial structure of marine fish stocks was primarily a descriptive exercise in distinguishing between discrete spawning units. Now, there is often greater attention to the dynamics within and interactions among distinct substocks, which are akin to local populations in metapopulation termi-

nology and therefore invite a metapopulation perspective. For example, McQuinn (1997) reviewed a wide range of data on genetics, morphometrics, life history traits, and population dynamics of Atlantic herring. He then developed a metapopulation model that explains how seasonally distinct spawning populations exchange individuals as a consequence of within-cohort variability in development rates, yet retain their characteristic behavioral traits through social transmission of behaviors to immigrants from other spawning populations. The utility of merging dynamic ecological processes with spatial patterns in distribution and migration has invoked calls for increased application of metapopulation theory to fisheries science (Stephenson, 1999; Frank and Brickman, 2000).

The spatial arrangement and interrelationships of local populations in metapopulation ecology (or of substocks in fisheries science) is necessarily interwoven with the structure and distribution of marine habitats that support those populations. In the United States, the amendment of the Magnuson-Stevens Fishery Conservation and Management Act that introduced the need to identify and protect "essential fish habitat" as a management responsibility has spurred an increase in attention to the topic in the latter half of the 1990s. Recognition of essential habitat has implications for regulating human activities that might affect adjacent marine areas (e.g., Dewey, 2000) and for planning restoration efforts (e.g., Coen et al., 1999). This focus on habitat is necessarily spatially explicit and perhaps has helped direct interest to the substock structure within fishery stocks.

The most widespread application of essential fish habitat research is direct protection of that habitat through use of marine protected areas (MPAs), or areas permanently protected from development or extractive activities (e.g., Conover et al., 2000, and associated papers). Attention to essential fish habitat may not have had a direct influence on the integration of metapopulation ecology and marine ecology; however, it has at least had indirect influence through fostering MPA research, which is probably the largest single contribution of marine management science to the integration of metapopulation ecology and marine ecology.

C. Marine Protected Areas

The potential benefits and optimal design of MPAs are arguably the most actively researched and vigorously debated topic in contemporary marine conservation biology and fisheries science (Polunin, 2002; Lubchenco et al., 2003; Willis et al., 2003; Sale et al., 2005). MPAs are not a new concept. Beverton and Holt (1957) discussed area closures in fisheries management in their classic monograph, and MPAs have existed in many locations across the globe well before the explosion in their popularity since 1990. However, MPA literature prior to 1990 was focused largely on the role of MPAs in protecting pockets of biodiversity, iso-

lated from human activity. For example, Polunin et al. (1983) and Minchin (1987) report inventories of organisms found within MPAs in Bali and Ireland respectively, and Salm (1984) offered guidelines of MPA locations that should ensure they contain representative biodiversity. This objective of sequestering biodiversity from human impacts does require attention to spatial ecology, but it utilizes the static equilibrium perspective that informed terrestrial SLOSS debates (Soulé and Simberloff, 1986; Simberloff, 1988) along with a classical view that emphasizes the role of internal biotic interactions rather than dispersal across boundaries in maintaining community structure. It does not call upon the perspective of a dynamic, interconnected patch network that characterizes metapopulation ecology.

As discussed earlier, renewed attention by ecologists in the 1980s to patterns of recruitment variability focused both on consequences (e.g., Iwasa and Roughgarden, 1986; Roughgarden and Iwasa, 1986; Sale, 1988; Victor, 1983), and causes, including larval production, dispersal, and pelagic survival processes (Underwood and Fairweather, 1989; Sale, 1990). This change brought "pure" marine ecology closer to the domain of fisheries science (Doherty, 1991; Rothschild, 1998). The shift also led Fairweather (1991) to consider the implications of larval production, dispersal, and recruitment patterns for management using MPAs, and Roberts and Polunin (1991) to call for increased attention to the services MPAs can provide to unprotected areas outside their borders. Around the same time, Polacheck (1990) and DeMartini (1993) began to model small-scale linkages between MPAs and adjacent fished areas through adult movement. A perspective that views marine populations as grouped into metapopulations has now become well established (Fig. 1-3). Man et al. (1995) provided the first marine fisheries model explicitly couched within the metapopulation framework. Numerous other marine metapopulation modeling studies exploring fisheries management issues soon followed (Supriatna and Possingham, 1998; Cooper and Mangel, 1999; Crowder et al., 2000; Tuck and Possingham, 2000; Lipcius et al., 2001; Sanchirico and Wilen, 2001; Lockwood et al., 2002; Smedbol and Wroblewski, 2002; Wilen et al., 2002). Mathematical models are important stimuli for development of both empirical research and theory, and this growing body of literature addressing metapopulation models to MPAs has no doubt provided important stimuli for metapopulation-oriented marine research.

V. SUMMARY

Marine ecology overwhelmingly concerns those benthic or demersal populations that are found in association with solid substrata. Such populations are frequently distributed patchily, along with the habitats they occupy. Our knowledge of pelagic populations is less extensive, and although they also appear to be

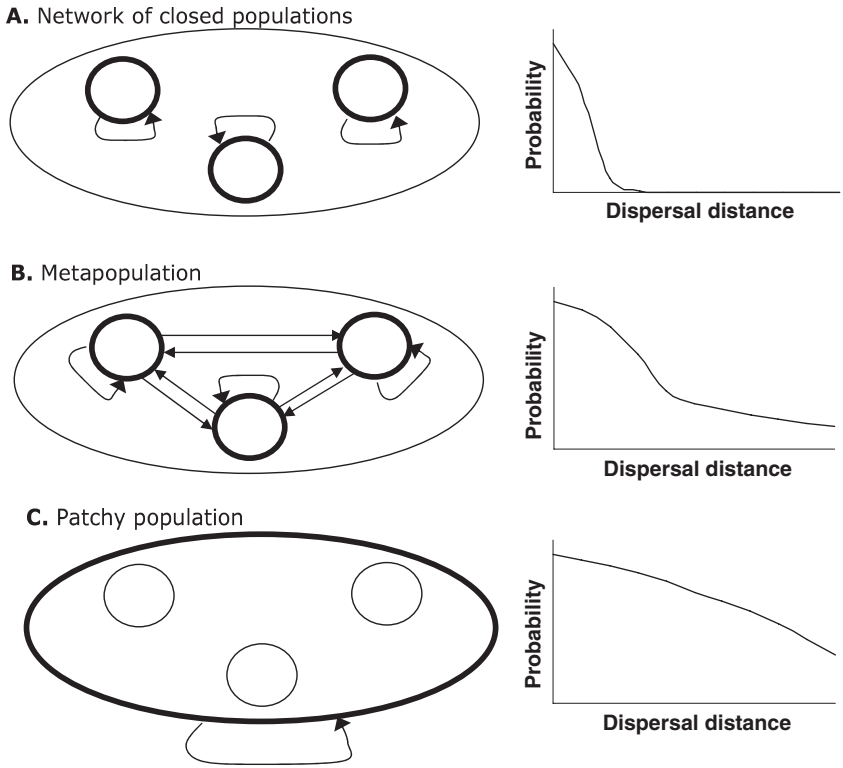

FIGURE 1-3. The way in which the extent of larval dispersal, relative to interpopulation spacing, determines the nature of the linkages among a set of local populations. These variously form a set of independent, closed populations (A); a metapopulation (B); or a single, large, but spatially subdivided population (C). Diagram from Kritzer and Sale (2004) with permission of Blackwell Publishing Ltd.

patchily distributed, it is unclear to what extent habitat factors usually drive this patchiness.

Although it might be logical for marine ecology and fisheries management science to interact closely, there has been a long history of marine ecology borrowing concepts and theories from terrestrial ecology. The recent adoption of metapopulation theory is a case in point.

Metapopulation theory, in its terrestrial context, is highly relevant to the description and exploration of sets of small populations scattered over small patches of suitable habitat—a condition that applies to a broad and growing range of species as human impacts continue to reduce and to subdivide patches of formerly more contiguous habitat. It deals explicitly with the dynamics of small

populations that interact through dispersal of individuals among them, and considers dynamics both at the local population and at the wider metapopulation scale. Terrestrial ecologists use metapopulation theory to model actual populations, as a framework for guiding research questions, and as a paradigm against which to view population ecology.

Although marine and terrestrial systems have in common the fact that populations are patchily distributed, it is clear that marine systems differ from terrestrial ones. In marine systems, the causes of the patchy distributions are not always so clearly related to patchiness of habitat, and most human impacts tend to reduce, rather than increase, patchiness of habitat. Nevertheless, it is clear that there are many situations in which metapopulation theory has much to offer marine ecology. Time will tell how useful this theory becomes in marine ecology and management.

Marine ecology came to adopt metapopulation theory by way of its rediscovery of the importance of larval dispersal and recruitment dynamics. Prior to the 1980s, marine ecologists examined local populations with little reference to their interactions with nearby or distant populations of the same species. This changed with the recognition that recruitment dynamics were sufficiently variable that they played a major role in structuring local populations in terms of abundance and age distribution. Given that recruitment was perceived as coming largely, if not entirely, from outside the local population, it was perhaps logical that metapopulation concepts would be embraced.

The worldwide trend toward overfishing and the loss of fisheries, and the growing interest in marine conservation, have led to a search for management tools that will protect marine species, and particularly those with fishery value. The use of spatially explicit management strategies, such as the use of no-take marine fishery reserves and other types of MPA is being widely advocated and enthusiastically endorsed at a time when marine ecologists are becoming interested in the use of metapopulation theory to model the populations with which they work. As a consequence, metapopulation theory is now being applied frequently to marine systems. The following chapters illustrate the current "state of play" and provide glimpses of the likely future.

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