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RECRUITMENT AND THE LOCAL DYNAMICS OF OPEN MARINE POPULATIONS

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ABSTRACT

The majority of marine populations are demographically open; their replenishment is largely or exclusively dependent on a supply of juveniles from the plankton. In spite of much recent research, no consensus has yet been reached regarding the importance of recruitment relative to other demographic processes in determining local population densities. We argue 1. that demographic theory suggests that, except under restrictive and unlikely conditions, recruitment must influence local population density to some extent. Therefore, 2. the question as to whether the size of a particular population is limited by recruitment is misguided. Finally, 3. the effect of recruitment on population size can be difficult to detect but is nonetheless real. A major weakness of most existing studies is a lack of attention to the survival of recruits over appropriate scales of time and space. Acknowledgment of the multifactorial determination of population density should guide the design of future experimental studies of the demography of open populations.

INTRODUCTION

Recruitment, in the broadest sense, is the addition of new individuals to populations or to successive life-cycle stages within populations. This process is clearly important for understanding a range of ecological phenomena, from the

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genetic structure of populations (1, 46, 64, 81, 140), to population dynamics (the subject of this review), to community structure (10, 75, 104, 110, 125, 128, 165). While interest in recruitment of marine populations has a long history (58, 161, 175), the last decade has seen renewed interest and substantial progress in this area. This resurgence stems in part from the recognition 1. that most local populations of marine organisms are demographically open, where local recruitment is uncoupled from local reproduction by a dispersive larval phase, and 2. that marine species are often organized into non-equilibrial communities whose structure and dynamics depend on the interactions of a suite of biotic and abiotic processes that affect both recruitment and postrecruitment survival (29, 47, 95, 103, 104, 126, 128, 154, 160). Thus, for open marine populations, recruitment is generally defined more restrictively as the addition of individuals to local populations following settlement from the pelagic larval phase to the benthic or demersal early juvenile phase. Recruitment, in this case, is analogous to births in closed populations.

Seven recent reviews of recruitment in marine species (10, 42, 47, 50, 95, 110, 127) attest to the rapid growth of interest in this topic. However, no consensus has yet been reached regarding the relative importance of recruitment and other processes in determining the dynamics of local, open populations of marine species (42, 65, 87, 110, 172). Therefore, our goals are fourfold: 1. to review demographic theory as it applies to recruitment and subsequent population density in open populations; 2. to review methods for investigating the importance of recruitment relative to other processes in driving the dynamics of these populations; 3. to examine how issues of temporal and spatial scale affect the interpretation of the importance of recruitment in setting local population size; and 4. to suggest a protocol for future studies of the dynamics of open populations of marine species. We limit our review mainly to the substantial literature published since 1980 for temperate and tropical reef fishes and for intertidal and subtidal invertebrates living on hard substrata.

GENERAL CONCEPTS

Population Dynamics in Open Systems

Understanding the processes that underlie local population dynamics requires knowledge of the rates of birth (here recruitment), death, immigration, and emigration. In open marine populations, various combinations of these demographic rates could be examined for both the pelagic phase and the benthic or demersal phase; usually they are studied only after settlement into the adult habitat. For most benthic invertebrates and demersal fishes, the local production of offspring has little or no direct role in setting local population size because larval recruitment from elsewhere provides the only substantial input of new individuals. If recruitment fails, the local population will decline to extinction, regardless of local fecundity. Conversely, the local population will persist as long as recruitment continues, even if these adults produce no viable offspring. As a result, a local population cannot be regulated by its own fecundity, even if density-dependent effects on local reproductive output are evident (e.g. 54, 74). Postsettlement movement of juveniles and adults is potentially important in local population dynamics only for highly mobile species; they can safely be ignored for most sessile species. However, localized dispersal of benthic stages does occur among marine invertebrates that are capable of detachment or that undergo fragmentation (76), and also among some nonterritorial reef fishes (118, 119, JL Fredrick, unpublished data).

Historically, fisheries studies have provided the major focus on the dynamics of marine species (3, 5, 35, 36, 50, 68, 117, 121, 138, 144–146). Documenting strong year classes in various fish stocks, Hjort (67) was the first to articulate the idea that variation in larval survival may drive adult population dynamics. However, much of this research is not directly relevant to understanding local dynamics because fisheries biologists consider entire stocks (of fish, molluscs, crustaceans, etc), which, by definition, are reproductively closed. Recruitment in fisheries also typically refers to individuals entering the exploitable stock, which usually occurs at the subadult or adult stage. Consequently, a linear relationship is often postulated between recruitment and subsequent stock size (35, 36). In contrast, most population studies of marine invertebrates and reef fishes occur at localized sites, where fecundity and recruitment, estimated at the time of settlement, are decoupled.

The theory required to understand population dynamics is fundamentally different for open versus closed systems, and the appropriate choice of models is clearly scale-dependent. For example, at a sufficiently large spatial scale groups of open local populations become closed at the level of the "metapopulation" [i.e. an interconnected group of subpopulations linked by dispersal (59)]. Metapopulations, however, are not the subject of this review for three reasons. First, and most importantly, field studies of benthic invertebrates and demersal fishes generally have been conducted at the level of local populations. Thus, linking empirical studies with population dynamics theory can only be done presently at a relatively small spatial scale. Although an immense potential for dispersal exists between subpopulations during the larval stage (46, 91, 132, 133, 140), much more work on rates of larval exchange between local populations is required before metapopulation models can be tested for marine species (54). Second, many terrestrial-based metapopulation models are not directly relevant to marine populations because they assume the subpopulations are mostly closed, with only infrequent dispersal between patches (38, 60). In contrast, for most sessile invertebrates and fishes, the length of larval life ensures that virtually all local recruitment is from elsewhere. Third, most existing metapopulation theory addresses systems in which subpopulations are subject to high probabilities of extinction followed by rapid recolonization (54, 60). Local marine populations appear to be much more persistent; typically they do not go extinct and are reestablished on a regular basis, except at very small spatial scales (e.g. 26, 28). Only a handful of metapopulation models incorporate these features, which are therefore directly applicable to marine systems (11, 22, 27, 80, 111, 122).

Limitation vs Regulation

Confusion is evident in the marine literature regarding definitions associated with population limitation and regulation. Limitation occurs when any process adds individuals to or subtracts individuals from a population (142). In contrast, regulation occurs when at least one demographic rate is density-dependent—i.e. per capita rates of birth (recruitment) or immigration decrease, or the rates of death or emigration increase, as population density increases (62). Regulation leads to bounded fluctuations in population size, such that a population neither increases to infinity nor goes extinct (16, 107). A single process such as recruitment may limit a population if it is density-independent in one instance but regulate the population if it is density-dependent in another.

Recruitment to open populations typically varies spatially and temporally by several orders of magnitude (e.g. reviews in 42, 47 for reef fishes, and 31, 160 for benthic invertebrates). For a large peak of recruitment to result in not even one more adult, exact compensation is required, which could only occur if the strength of density-dependent mortality increased with density (143). The empirical evidence indicates that density-dependent postrecruitment mortality is unlikely to increase to such an extent that it completely eliminates a recruitment signal, i.e. fluctuations in recruitment invariably account for some of the variation in local density. Therefore, given that the dynamics of all open populations are driven to varying extents by both recruitment and mortality, a multifactorial approach is required to evaluate the contribution of recruitment relative to other limiting and regulating processes in setting population density (e.g. 65, 66, 74, 87, 88, 99, 166).

The importance of recruitment in determining local population size cannot be resolved by measuring rates of recruitment without additional knowledge of subsequent mortality patterns (89). However, as noted by Underwood & Denley (160), it is often assumed that the amount of recruitment in many marine organisms is so large that it could not possibly be limiting. This approach is unconvincing unless the postrecruitment survival rate is measured, and it can be demonstrated that even more recruits would not result in a further increase in local population size. Of course, patterns of mortality are much more difficult to measure in the field than is recruitment, particularly for mobile organisms such as fish. This logistical difficulty probably accounts for the greater emphasis on recruitment in studies of reef fishes compared to sessile invertebrates (where mortality of marked individuals is relatively easy to record). However, studying reef fishes has the advantage that newly settled individuals are relatively easy to identify to species compared to many sessile invertebrates.

THEORY OF OPEN POPULATION DYNAMICS

Conceptual Models

Although the importance of recruitment has been recognized repeatedly through this century (reviewed in 58, 161, 175), it was not until 1981 that Doherty (39) formalized the recruitment-limitation hypothesis, asserting that "the planktonic supply of larvae, far from being endless, may often be the limiting factor that forces future population size" (p. 470). At the time, many researchers believed that larval supply was generally sufficient to saturate habitats with juveniles, so that postsettlement competition was inevitable unless mediated by postsettlement predation or physical disturbance. As originally presented, the recruitment-limitation hypothesis stated simply that low rates of settlement could limit densities below levels where substantial competition occurred. Subsequently, Doherty & Williams (47) provided explicit predictions of the recruitment-limitation hypothesis, including that 1. postrecruitment mortality should be density-independent, 2. differences in the sizes of consecutive cohorts resulting from annual pulses of recruits should be preserved in the age-structure of populations without distortion, and 3. local population size should be highly correlated with variations in recruitment (i.e. recruitment determination sensu 51). As demonstrated below, however, the first and third predictions are not necessary conditions for the limitation of population size by recruitment, and the second may be true even if postrecruitment mortality is density-dependent. Clarifying these concepts is a major goal of this review.

Larval supply and subsequent settlement are difficult to measure due to problems of defining the number of larvae capable of settling at a particular place and time, and of counting small and/or cryptic individuals. Consequently, recruitment has come to be operationally defined as the initial sighting of a recently settled juvenile in the adult habitat (30, 89, 116). By this definition, recruitment necessarily incorporates early postsettlement losses (31, 89). Early mortality is often very high (reviews by 65 for reef fishes; 31, 169, 176 for invertebrates). To account for this pattern, Victor (163) proposed the dichotomy between primary and secondary recruitment limitation. Primary recruitment limitation is identical to Doherty's (39) original formulation, i.e. due to limited larval supply, the density of new recruits at the time of settlement is below levels where competition for limiting resources occurs. Secondary recruitment limitation is said to occur when the initial density of new recruits is sufficient for competition to occur if they were all to survive, but subsequent mortality reduces their density below any competitive threshold before they reach the adult stage. In this context, however, "recruitment" refers strictly to the number of older juveniles (up to several years postsettlement) entering the adult population, rather than larval input to the benthic population.

Mathematical Models

Hughes (73) and Roughgarden et al (123) were the first to model local population dynamics of corals and barnacles, respectively, using an external input of recruits rather than an intrinsic birth rate. More recent modeling studies have used the same approach for coral-reef fishes (166), bryozoans (74), and kelp (4, 108). These models demonstrate that local populations may be regulated, not just limited, by recruitment. A form of regulation occurs because, for a given absolute recruitment rate, the per capita recruitment rate into the adult population is higher when the density of a local population is low. In order for the per capita rate to remain steady across a range of adult densities, the number of recruits per unit area would have to increase over time in direct proportion to the increase in adult density. This is unlikely, except where recruitment is strongly aggregative (7, 69, 84, 112, 113, 152, 153). Thus, in many circumstances, the per capita recruitment rate is likely to decline as population size increases, i.e. recruitment is effectively density-dependent (4, 71, 73, 74, 166). This mechanism of regulation is not due to density dependence in the conventional sense, because no biological interaction is necessary for it to occur, but it is nonetheless real. In addition, density-dependent interactions may occur among recruits or between recruits and adults, which will cause a further depression of per capita recruitment rates at higher density. Few field biologists are aware of the implications of changes in the rate of per capita recruitment because of the convention of measuring inputs on an areal basis (e.g. per hectare or per m^2). In contrast, mortality is rarely expressed as the number of deaths per unit area; instead it is routinely quantified as a percentage (i.e. a per capita rate). This historical mixture of currencies has hampered studies of the relative roles of recruitment and mortality in limiting and regulating local, open populations.

A density-related decline in per capita recruitment into local populations cannot regulate an entire metapopulation. For regulation to occur at this larger spatial scale, "true" density dependence (in recruitment, fecundity, or mortality) must operate among the local populations or in the plankton. Most existing metapopulation models include density dependence at some level (72, 107, PL Chesson, personal communication). Indeed, model metapopulations with density-independent dynamics take the same random walk to extinction as do local populations (23).

To date, models of open population dynamics have demonstrated that 1. a local population may fluctuate around an equilibrium level due to regulation by recruitment even in the absence of density-dependent mortality (4, 73, 74), and 2. when recruitment limitation occurs, by definition variation in recruitment will cause fluctuations in total population size (166). This correlation is the most common empirical test of the influence of recruitment on population size. However, computer simulations show that 3. even minor variation in rates of mortality will decouple the relationship between recruitment and population size (or year-class strength) (166). Finally, 4. where recruitment is inhibited by adults, cyclical variations in local population size can result from the time lag between recruitment and adulthood (4, 123). Thus, competition can result in wide fluctuations in numbers that might easily be mistaken as the result of peaks and troughs of recruitment. Clearly, many of the criteria used in field studies to characterize the effect of recruitment have been inadequate.

A Graphical Model of Open Population Regulation

To clarify the above issues, consider a simple graphical model of the dynamics of a local, open population (Figure 1). As noted earlier, the obligatory density-related decline in per capita recruitment will regulate a local population, even where postrecruitment mortality is density-independent (73, 166). The lack of density-dependent mortality will allow peaks of recruitment to translate directly into peaks in adult numbers, with no damping of fluctuations (Figure 1A). If mortality is high, large fluctuations in recruitment will obviously translate into relatively smaller fluctuations in the number of adults, compared to longer-lived organisms receiving the same variation in recruitment. Conversely, if mortality is low, the total number of adults will be the result of many recruitment events that remain “stored” in the population, resulting in a larger population size (24, 165). Consequently, fluctuations in total adult numbers in response to recruitment will be most evident in short-lived taxa that have one or a few dominant age-classes generated by recruitment pulses. Where density-independent mortality is variable, the correlation between recruitment peaks and the resultant number of adults will be scrambled and difficult to detect, especially in longer lived organisms. Thus, it is no accident that many existing empirical demonstrations of recruitment limitation are based on studies of relatively short-lived taxa whose populations are comprised of only a few cohorts (e.g. 74, 151, 162, 163), or those in which mortality rates are remarkably uniform (44).

Where density-dependent mortality occurs, it will tend to damp out large peaks in recruitment. However, the population size is still likely to rise and fall in response to peaks and troughs of recruitment, even if the correspondence

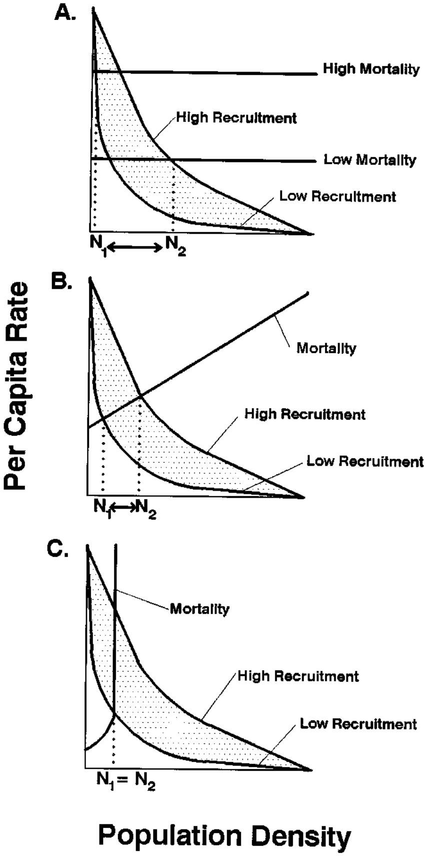

Figure 1 A graphical model of local population regulation in an open system. Recruits are generated elsewhere and arrive in numbers independent of local adult density. Unless the number of recruits increases in direct proportion to adult population density, the per capita recruitment rate must decline as the number of established individuals increases, i.e. per capita recruitment is effectively density-dependent. At very low population density, the per capita recruitment rate increases sharply, converging toward infinity when there are no established adults. Conversely, as adult density increases, the per capita rate of recruitment declines asymptotically toward zero. The stippled area bounded by the high and low recruitment curves represents variable recruitment levels. Three situations are illustrated: In (A), mortality is density-independent, and the local population is regulated solely by recruitment. Population size will fluctuate in response to changes in mortality or recruitment, between N_1 (low recruitment, high mortality) and N_2 (high recruitment, low mortality). In case (B), mortality is weakly density-dependent, which will partially damp out large peaks in recruitment, but the population size will still reflect recruitment fluctuations. Finally, in case (C), mortality is strongly density-dependent and increases in strength with increasing population density. This is the only case where population size will not reflect recruitment fluctuations.

between recruitment and population size is not perfectly linear (Figure 1B). For example, density-dependent mortality may be sufficiently strong to ensure that a doubling of the per capita recruitment rate results in only a 10% increase in population size. In this case, the local population is clearly regulated both by recruitment and by mortality. This is probably the most common case for marine invertebrates and fishes, in which density-dependent mortality is not uncommon, but in which its strength varies insufficiently to completely eliminate large pulses of recruitment. Complete elimination of large recruitment pulses would occur only if every recruit died above a certain threshold density that was exceeded even in years of poor recruitment (Figure 1C). Thus, the often-stated dichotomy that local population size is determined either by recruitment limitation or by density-dependent mortality is misguided. Certainly, an empirical demonstration of density-dependent mortality does not rule out the likelihood that recruitment is also important, nor does an empirical demonstration of recruitment effects on population size rule out the possibility that density-dependent mortality or emigration affects population size.

EMPIRICAL STUDIES OF OPEN MARINE POPULATIONS

Various interacting processes have the potential to influence the dynamics of open marine populations. Their relative importance will depend in part on where and when the study is conducted, and the spatial scale and temporal duration of the study. Much disagreement in the ecological literature stems from the use of spatial or temporal scales that differ among studies (21, 37, 109, 170, references in 56 and 135). For example, processes affecting larval supply and recruitment can operate at scales much larger than postsettlement processes such as competition and predation (47, 102). Hence, large-scale studies may overemphasize the former processes, and small-scale studies the latter. The relative importance of different processes may also depend on whether researchers are interested in total population size or the densities of reproductively mature adults (see 87), and on their operational definition of recruitment. Collectively, these differences constrain the way we define populations and which parameters we measure. Here we consider how operational decisions made prior to commencing a study can affect our interpretation of what drives the dynamics of local, open populations.

Selecting Study Sites

Ideally, several sites should be chosen that span a representative range in recruitment levels (e.g. 31, 55, 70, 86, 99, 115, 151). However, recruitment limitation has frequently been tested in habitats where rates of replenishment are unusually low. For example, rates of recruitment by the coral-reef fish *Pomacentrus* *moluccensis* onto lagoonal patch reefs of the southern Great Barrier Reef (44) are less than those onto contiguous reef slopes (BD Mapstone, unpublished data). The relative impact of recruitment fluctuations on population size is likely to be greater in the former habitat than in the latter. Conversely, Connell (31) argued that many experimental results on barnacles may have underestimated the importance of recruitment because workers frequently select high density sites where recruitment rates are relatively low and levels of competition and predation are high. Since sites are likely to vary in their rates of larval supply (98, 105) and/or the availability and quality of settlement habitat (e.g. benthic invertebrates: 34, 96; reef fishes: 17–19, 21, 92–94, 129, 155, 167), generalizations based on a single location will be inadequate.

Selecting Spatial and Temporal Scales

The minimum spatial scale for studying local population dynamics is constrained by the need for reliable estimates of recruitment and mortality. For mobile organisms, the area examined must be large enough to assume postsettlement movement is negligible, or at least measurable, throughout the life of the cohort. Where population densities are low, larger areas will be required to obtain reliable estimates of recruitment and mortality.

The relative importance of various processes may change with scale, so that a multiscale approach is required for a full understanding of population dynamics. In marine populations, density-dependent effects on mortality rates are often detected in small-scale experiments (e.g. for invertebrates: 31, 33, 148, 158, 159; for reef fishes: 8, 14, 51, 52, 78, 82, 85, 119, 120, 134, 147, 156, 157). It is quite possible that these effects may be less important in regulating numbers at larger scales, particularly in mobile animals where density-dependent emigration can ameliorate competition and where competition may occur only at a limited number of sites (see also 63). However, investigating the relative importance of limiting and regulating processes on very large spatial scales is problematic because all parameters must be estimated by scaling up from small-scale observations. For example, the dynamics of marine populations on a single habitat-type within a coral reef (e.g. 44, 86, 131), cannot be assumed to be representative of patterns at the scale of entire reefs.

The optimal temporal scale for determining the relative importance of recruitment and mortality in population dynamics is set by the longevity of a cohort (61, 75). The biggest effect of a new cohort on local population size occurs immediately after settlement. Because this impact diminishes with time, an inappropriately short time-scale may lead to an overestimate of the importance of recruitment. The time-scales of most marine population studies have not been justified, and few workers have provided estimates of longevity for the species under investigation (but see for example, 28, 48, 75).

Measuring Population Densities and Recruitment

The local densities of juveniles and adults are crucial variables in population studies. Since a cohort is always most abundant at settlement, it should not be surprising if the total local population size (i.e. all age classes combined) fluctuated in response to recent pulses of recruitment, particularly in short-lived species. Therefore, knowledge of the size and density of the resultant adult population is required to adequately assess the extent of local population regulation. For organisms with patchy spatial distributions, standard sampling techniques based on areal counts may underestimate the importance of density-dependent processes. This underestimation occurs because individuals at the center of aggregations experience higher densities compared to those at the edge. For juveniles in particular, it may be more appropriate to estimate the average density experienced by randomly chosen individuals rather than average densities based on quadrats or transects (83).

How recruitment is defined and measured is critical to testing and understanding the role of both pre- and postsettlement processes and the extent to which these processes are dependent or independent of population density. Measures of larval supply, settlement, and subsequent survival through to the adult population are all relevant response variables in experimental studies. However, methods of quantifying rates of delivery of larvae to benthic populations have only recently been developed (25, 41, 53, 105, 136, 178), and the manipulation of larval supply is extremely difficult. Furthermore, because settlement is typically sporadic, often sparse, nocturnal and/or cryptic, difficulties in measuring rates of settlement have forced most ecologists to adopt the standard operational definition of recruitment: the number of individuals that have settled and survived between census intervals (30, 89, 116).

Reef-fish ecologists have measured recruitment across time-scales ranging from hours to years, often using recruitment as a proxy for settlement. The median duration between censuses was 6 days in 105 published studies surveyed for this review. For some sessile invertebrates, quantifying recruitment is relatively easy, because settling stages can be detected shortly after metamorphosis, and settlers attach to both natural and artificial substrata (e.g. 12, 31, 49, 55, 57, 100, 101, 174). For others, however, recruits cannot be identified as to species until they attain diagnostic morphological characteristics months or years after settlement (e.g. 28, 75, 77).

The length of time between settlement and when recruitment is estimated can affect in a variety of ways interpretations of how population density is determined. First, the greater the time lag, the more likely patterns of abundance established at settlement will be modified by postsettlement mortality. For both reef fishes and sessile invertebrates, most studies of postsettlement mortality have reported highest mortality rates within the first few days after settlement (e.g. fish: reviewed in 65; see also 6, 9, 20, 66, 94, 156; invertebrates: 31, 169, 176). During this brief period, mortality may be sufficiently strong or variable to modify patterns of abundance established at settlement (e.g. 13, 15, 32, 66, 93, 94, 156). Furthermore, species differ markedly in early postsettlement mortality rates (45, 48, 130), which may alter patterns of relative abundance established at settlement (13, 20). The greater the lag between the occurrence of settlement and the measurement of recruitment, the more likely juvenile and subsequent adult densities will be positively correlated. Thus, long delays between settlement and measured recruitment can overestimate the importance of recruitment in determining the number of adults.

The frequency with which recruitment is sampled can also substantially influence estimates of the mean and variance of recruitment (e.g. 6, 90, 106) and can make comparisons of studies with different intensities of sampling virtually impossible. Of course, the ideal sampling frequency is a continuous record of arrival of settlers. Examples are provided by Yund et al (178) and Gaines & Bertness (53), who adapted sediment traps for use as passive, continuous samplers of barnacle larvae.

Another method of estimating recruitment in studies of reef fishes is the back calculation of daily settlement rates from circuli of otoliths (inner ear stones), which has become a common technique (reviewed by 164). No comparable method is yet commonly used in recruitment studies of invertebrates, although high-frequency banding (e.g. daily growth bands) could potentially be used in some taxa. Of the 28 published studies of reef fishes that estimated daily recruitment, 30% were based on otolith back-calculations. Such estimates assume constant mortality through time (i.e. across settlement episodes) and little measurement error (114, 162). These assumptions become increasingly tenuous with increased duration between settlement and the collection of fish for otolith samples (97). Therefore, this method of estimating recruitment and/or settlement rates should be avoided unless these assumptions can be met.

Relative Importance of Recruitment and Postrecruitment Processes

Field tests of the relative importance of recruitment and patterns of mortality can be observational or experimental. Neither approach is superior. They provide complementary information, and both are useful for testing theory or parameterizing models. Observational studies provide information on natural rates of recruitment and mortality, and changes in adult population size. However, experimental manipulations are necessary to examine the relative contribution of these factors to determining population size. The relative importance of factors in experiments (judged from statistical effect sizes) must be evaluated in the context of long-term observational data at larger spatial scales. For example, competition may show strong effects in experiments, but recruitment may not always reach a level that leads to competition in the field (see 86).

EFFECTS OF RESIDENT POPULATIONS ON RECRUITMENT In most published studies of open marine populations, a tacit yet untested assumption is that recruitment is determined solely by the incoming supply of larvae competent to settle, i.e. that recruitment is not a product of competent larvae interacting with resident populations. Correlations between recruitment and adult densities, both negative (e.g. 149, 177) and positive (e.g. 99, 151, 163), can provide evidence that such interactions are important. Experimental manipulation of resident densities has demonstrated that residents may facilitate (7, 69, 84, 112, 113, 134, 152, 153), inhibit (52, 113, 124, 134, 139, 153), or have no effect on recruitment (40, 84, 93, 155, 171). So far, experimental tests have been restricted to small patches of habitat. We do not know whether the significant effects that have been detected would be detected at larger spatial scales. Likewise, it is not clear whether nonsignificant results genuinely indicate no effect, or merely stem from high variability among small patches, inadequate sample sizes, or both.

NATURAL PATTERNS OF RECRUITMENT, JUVENILE MORTALITY, AND SUBSEQUENT ADULT DENSITIES The extent to which local populations are influenced by patterns of recruitment and mortality may be partially revealed by detailed demographic observation. Numerous studies of marine organisms provide estimates of population size, recruitment, and mortality monitored over multiple sites and/or years (e.g. 2, 20, 28, 74, 75, 77, 79, 141, 173). Data on mortality rates, however, are often limited or absent, especially from studies of mobile organisms such as fish, in which monitoring of individuals is difficult. The relationship between the abundance of recruits and adults over time (with an appropriate lag phase based on the time to maturity) has been used to distinguish between recruitment limitation and density dependence. If adult population size tracks recruitment levels, variable recruitment can be inferred to be the major determinant of population variation (e.g. 43, 44, 55, 151, 171). Alternatively, if adult population size is stable despite fluctuating recruitment, density dependence is likely to predominate (e.g. 86). The absence of a relationship between recruit and adult densities, however, does not necessarily imply that recruitment does not affect adult numbers. Instead, variable mortality, emigration, and/or postsettlement immigration may obscure the relationship (99, 118, 119, 166). In addition, the form of the relationship observed in a particular population may change through time. For instance, in a study of the goby *Sagamia* *geneionema*, Sano (personal communication) detected significant relationships between recruitment and adult densities in some years but not others.

To explore the consequences of various combinations of demographic variables, consider the graphical model in Figure 2. As noted previously, if mortality is density-independent, fluctuating recruitment will be translated directly into fluctuating numbers of adults (Figure 2, Case 1 or 2). Thus, the absence of a relationship between recruitment and subsequent mortality is usually attributed to density-independent mortality (163). However, it is only in situations in which mortality is constant from site to site (and/or generation to generation) that a strong linear relationship between recruitment levels and the size of the resulting adult population will be observed (Case 1C). If mortality is density-independent, but highly variable, patterns of recruitment will be modified by mortality, and there will be a relatively poor relationship between recruitment and subsequent adult population size (Case 2C). In this case, knowledge of mortality rates and factors affecting mortality could provide a better predictor of population size than recruitment, even though the population is recruitment-limited in the sense that, if an individual cohort of recruits was larger, on average more individuals would subsequently be added to the adult population.

If mortality is density-dependent but highly variable (Figure 2, Case 3A), there will be an indistinct or "density-vague" (150) relationship between recruitment and adult numbers (Case 3C), which might be difficult to distinguish from the situation in which mortality is primarily density-independent and variable (Case 2C). With constant density-dependent mortality (Case 4A), cohorts of different strength will tend to converge in size, and the number of adults derived from increasing recruitment will tend toward an asymptote (Case 4C), as observed in some species (e.g. 8, 52, 82, 86, 156), or even generate a unimodal relationship (117).

PATTERNS OF RECRUITMENT REFLECTED IN THE AGE STRUCTURE OF ADULT POPULATIONS If larval supply of a species is variable and early mortality is not strongly density-dependent, then age-class strength should be variable among years, with the size of each cohort reflecting the recent history of recruitment. This observation has been the basis of much research into the role of recruitment in marine populations (e.g. 43, 44, 162, 163, 168). Variable and persistent age-class strength, however, can also occur in populations subjected to density-dependent processes (70). Therefore, persistent age-class structure is not diagnostic of density-independent mortality. Furthermore, variable postrecruitment mortality may be sufficient to hide the relationship between recruitment and year-class strength, even in the absence of density-dependent mortality (Figure 2, Case 2C). Future experiments which manipulate the magnitude of successive cohorts may enable us to better evaluate the effect of fluctuating

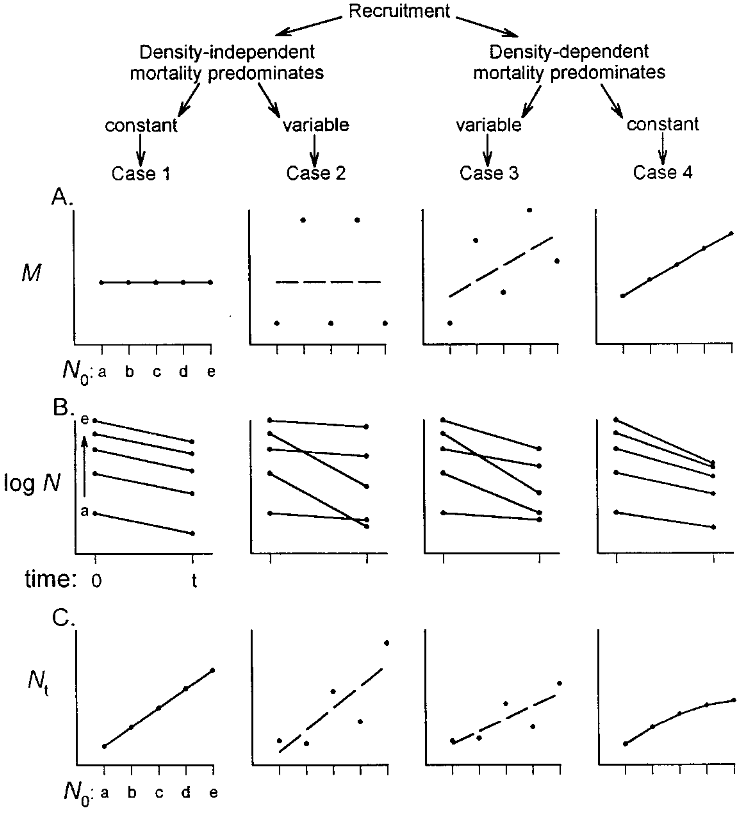

Figure 2 The effect of postrecruitment mortality on local population dynamics when mortality is constant and density-independent (Case 1), variable and density-independent (Case 2), variable and density-dependent (Case 3), or constant and density-dependent (Case 4). Following a fixed pattern of recruitment at time 0 (five cohorts of density *a* through *e*), we illustrate the patterns of, *A*, per capita mortality rate (*M*) as a function of recruitment density (N_0), *B*, the resulting survivorship curve of log *N* as a function of time from initial density at time 0 to later densities of juveniles or adults at time *t* , and *C*, densities of adults and juveniles (N_t) as a function of N_0 (the recruit-stock function). Between-cohort variation in mortality can cause unclear relationships (dashed curves) between recruitment and mortality both in terms of slope and curvature (Cases 2A and 3A), as well as unclear recruit-stock relationships (Cases 2C and 3C). Note that all recruit-stock functions must pass through the origin, so the illustrated curves are only portions of entire functions. Note also that all these plots are for cohorts and, therefore, do not consider the cumulative affects of recruitment and mortality of sequential cohorts on total population size.

recruitment on age-distributions as well as the overall population size. Differences in the initial strength of cohorts will tend to disappear over time if density-dependent mortality is strong or to persist if it is weak or absent.

RECRUITMENT MANIPULATIONS: EFFECTS ON JUVENILE MORTALITY AND SUBSEQUENT ADULT DENSITY The most direct approach to testing the effects of varying recruitment on subsequent population size is to manipulate levels of recruitment and monitor changes in the size of cohorts with different starting densities (e.g. 40, 51, 83). Ideally, recruitment into several cohorts will be manipulated over a number of years (86). In these experiments, recruitment must be manipulated in a realistic way, and the experimental units should be large enough to provide realistic measures of mortality rates under different conditions.

MULTIFACTORIAL EXPERIMENTS Ultimately, assessment of the importance of recruitment relative to other biological processes in determining population densities in open marine populations will require the use of multifactorial experiments (65, 87, 99). To test whether patterns of recruitment are modified by particular postrecruitment processes, such as competition or predation, recruitment must be manipulated in conjunction with these other processes. For example, to test the relative importance of recruitment and postsettlement predation, levels of recruitment must be manipulated, in both the presence and absence of appropriate predators. There are at least four possible outcomes of such an experiment. First, postrecruitment mortality may be density-independent regardless of the level of predation. Second, prey mortality may be density-dependent where predators are rare or absent (due to competition or a mortality agent other than competition), but density-independent where predators are common (due to the reduction in competition caused by reduced prey densities). Third, prey mortality may be density-independent where predators are rare or absent (due to low rates of recruitment), but density-dependent where predators are common. Finally, prey mortality may be density-dependent regardless of the level of predation, indicating either that competition (or a mortality agent other than predation) operates independently of predation, or that density-dependent mortality is the result of, for example, competition in the absence of predation but is the result of predation when predators are present. To date, this multifactorial experiment has been conducted on two species of damselfishes (*Chromis cyanea* in the Bahamas, Hixon and Carr unpublished data; and *Pomacentrus amboinensis* on the northern Great Barrier Reef, Jones & Hixon, unpublished data). For both species, mortality was density-independent in the absence of predators, but was weakly density-dependent in their presence.

FUTURE DIRECTIONS

Key issues remain unresolved in each of three main areas regarding recruitment. First, understanding of why recruitment varies in space and time is still limited. In particular, we need to understand better the causes of variation in production and survival of larvae, the processes that transport them, and mechanisms of habitat selection (see 91, 137). Second, the extent to which temporal and spatial variation in recruitment underlie variation in adult populations remains poorly understood. Third, and perhaps the most difficult and important question to answer for benthic and demersal populations, concerns the relative importance of recruitment vs postrecruitment processes in determining population size and structure. That is, to what extent does abundance in natural populations depend on recruitment, the process that establishes initial patterns, in comparison to factors such as competition, predation, facilitation, or disturbance—the processes that can modify these patterns? As noted above, the relative importance should be examined by multifactorial experiments in which recruitment and postrecruitment processes are manipulated simultaneously. A major problem in executing such experimental designs will be the manipulation of recruitment in realistic ways. Increasingly, investigators are finding ways to study and manipulate the early life history stages of both fishes and invertebrates, and we are optimistic that this trend will continue.

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