

4. DEMOGRAPHIC AND SPATIAL FACTORS IN EVALUATION OF RISK

4.1 Overview

Species extinction risk can be evaluated by considering two separate, but related, types of information: (1) information about the dynamics and distribution of the species itself, and (2) information about threats confronting the species, including their intensity, trends and responses of the species to them (Crawford and Rumsey, 2009). This chapter evaluates information associated with the recent condition and distribution of a species itself. An approach that has been applied to listing and recovery of Pacific salmon under the U.S. Endangered Species Act (McElhany et al., 2000) is based on general conservation biology principles and provides a useful framework for considering the extinction risks to the 82 candidate coral species. The approach entails evaluating the following four species parameters at a variety of spatial scales: (1) abundance, (2) productivity, (3) spatial structure, and (4) diversity.

The initial step in applying this approach involves identifying the population units for analysis. In this context, a “population” is defined as a unit that is “relatively demographically isolated” and is the most biologically appropriate unit for many types of abundance and trend analyses (McElhany et al., 2000). The overall species status is a function of the status of the individual populations and groups of connected populations. Two key challenges in applying this method to corals are the general lack of information for identifying these population units and their colonial and fragmenting nature that leads to multiple genetically identical “individuals.” As a consequence, status and trend data have typically been reported at the scales of the original studies, which were frequently either smaller or larger than a demographic population. In very few cases have studies considered the actual number and demographics of distinct genets (Ayre and Hughes, 2000; Baums et al., 2005; 2006; Connell et al., 2004).

While there were generally insufficient data to define population structures for each of the 82 candidate coral species, it was still useful to consider species condition in terms of abundance, productivity, spatial structure, and diversity. All else being equal, a species with high abundance is at less extinction risk than a population at low abundance because small populations are more vulnerable to the negative impacts of environmental fluctuations, genetic problems, catastrophic events, and other issues. Higher productivity is perhaps a more important indicator of low extinction risk. Productivity is defined here as the tendency of the population to increase in abundance if perturbed to low numbers and is often expressed as “recruits per spawner” at very low levels of adult population density, although the term “recruit” can be difficult to apply in the case of corals, which reproduce both sexually and asexually (see Section 2.2.1). This is the productivity definition commonly used in fisheries and is a direct measure of population resilience (Mangel et al., 2010). This definition is distinct from the concept of “primary productivity” used for photosynthetic organisms (such as a coral-algal-microbial holobiont) to describe the conversion of sunlight and carbon dioxide into organic compounds for organismal growth and reproduction. It is useful to note that productivity (*sensu* fisheries) is often a better indicator of extinction risk than overall abundance—a large population can be quite vulnerable if it lacks resilience and, conversely, a relatively small population can be robust if it has high productivity (Fig. 4.1.1). This is one of the reasons it can be difficult to predict a species vulnerability to extinction based on its current abundance (another reason being potential “extinction debt,” discussed below).

The life-history strategy and pattern of productivity can affect extinction risk. Species that are short-lived with high productivity (classic “r-selected” species; MacArthur and Wilson, 1967) might show great variability in abundance driven by short-term environmental fluctuations but are relatively resistant to extinction as long as mean productivity remains high and they do not experience too many bad seasons relative to the required recovery interval. Species that are long-lived with relatively low or episodic productivity (classic “k-selected” species) may show relatively stable adult populations in the face of environmental fluctuations but are quite vulnerable to extinction if adult survival declines or if productivity declines below the already naturally low levels. The relatively low levels of successful reproduction in some long-lived coral species, where partial mortality regularly occurs, may not keep pace if adult mortality increases substantially (Soong and Lang, 1992; Szmant-Froelich, 1985). Species with this strategy are described as displaying a “storage effect” as they carry over reproductive potential across multiple breeding seasons (Edmunds, 2002; Warner and Chesson, 1985). Many of the 82 candidate coral species have this long-lived, low or episodic productivity life-history strategy making them highly vulnerable to trends of increased mortality or catastrophic mortality events. Because abundance and productivity have such interactive effects on extinction risk (Fig. 4.1.1) and because they are often both estimated from the same time series data, the BRT addressed these two parameters together. Trends in abundance represent a “realized” productivity (McElhany et al., 2000) and are also considered in this chapter. Trend data can be very informative when evaluating extinction risk. However, extrapolating from trend information requires an assumption that the biological and environmental processes that operated in the recent past will continue into the future

(the “stationarity assumption”). If directional changes, phase shifts, catastrophic events, or other features are expected in the future that are not captured in the time frame in which the existing trends were determined, these types of data provide less confidence as a basis for estimating extinction risk. In the case of an expected increase in anthropogenic threats, the stationarity assumption is violated and a simple extrapolation of historic trend data will tend to underestimate risk.

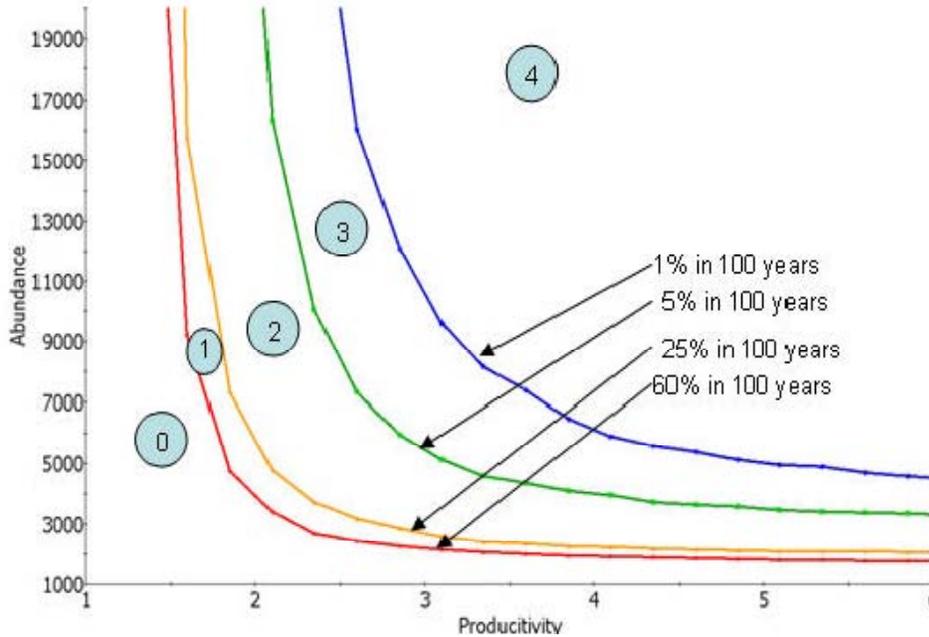


Figure 4.1.1. A conceptual “viability curve” illustrating the relationship between abundance and productivity. The y-axis indicates population abundance for adults of a hypothetical species, and the x-axis indicates population productivity in terms of the number of offspring per adult if the population is very small. A single-colored curve shows combinations of abundance and productivity with the same extinction risk (McElhany et al., 2007).

Spatial structure is important at a variety of spatial scales. At small spatial scales within the range of a single population, issues of gamete density and other Allee effects can have significant impacts on population persistence (Allee effects are discussed more extensively in the section below on Critical Risk Thresholds). At larger spatial scales, geographic distribution becomes important for “spreading the risk” among multiple populations. A larger geographic range can buffer a population or a species from correlated environmental fluctuations or catastrophic events. A large geographic range also provides a hedge against large-scale directional environmental change (e.g., climate change) because it is more likely that some areas of the range will be less affected by the threat. However, isolation of populations in wide-ranging species can reduce gene flow and the potential for larval connectivity, reducing the likelihood of recovery from mortality events. Thus, a robust spatial structure includes a wide geographic range, with substantial connectivity maintaining proximity of populations and individuals within the range.

Diversity affects species viability across spatial scales, from genotypic diversity within a single population to morphological variation over the entire species range. In this context, “diversity” describes both genetic variation and phenotypic variation; both influence population viability, but in different ways. Within a population, diversity helps buffer against environmental fluctuations. At all spatial scales, genetic diversity provides the raw material for evolutionary response (i.e., adaptation) to directional environmental change (e.g., climate change). Based on their colonial nature, ability to resume growth following partial colony mortality (often forming multiple new colonies), and ability to produce new colonies by fragmentation, corals may exist in large numbers on a reef but have very little genotypic diversity. While high abundance still reduces the risk of extinction for coral populations, a lack of diversity may limit the ability of corals to outcross during sexual reproduction or may reduce or preclude fertilization in species that do not self-fertilize. In an extreme case all colonies of a coral species on a particular reef would be clones of the same sex in a gonochoric species, and the coral might be numerically abundant but sexual reproduction would be impossible. The limited number of genotypes also suggests that many “individuals” in the population are vulnerable to

the same environmental threats (e.g., a specific disease), and an event that would be a minor reduction in a more genotypically diverse population could be catastrophic in one that is genotypically depauperate.

In evaluating the extinction risk for the 82 candidate coral species, the BRT applied the concept of a “Critical Risk Threshold (CRT).” The Critical Risk Threshold describes a condition where the species is of such low abundance, or so spatially disrupted, or at such reduced diversity that extinction is extremely likely. In the final section of this chapter, the key factors that influence the Critical Risk Threshold are summarized.

4.2 Abundance and Productivity of Corals

Information related to coral abundance and productivity can be divided into six types: (1) qualitative abundance estimates, (2) quantitative species abundance estimates, (3) time series of species-specific percent cover, (4) time series of percent cover at the genus level, (5) estimates of changes in percent cover based on extrapolation and expert opinion, and (6) estimates of juvenile recruitment. Unfortunately, very few abundance, productivity, or trend data were available for the 82 candidate coral species at the time of the review. Most of the data that did exist failed to adequately elucidate the effects of global threats on a species across its entire range. Relevant information for each species was presented in the individual species accounts (Chapters 6 and 7). Here, an overview of the information considered for this analysis is presented.

Qualitative abundance estimates (e.g., “common” or “rare”) for the candidate species were available from several sources. The sources most commonly used by the BRT were Veron (2000), Carpenter (2008), and online IUCN species accounts (IUCN, 2010). These estimates provided relatively little information for evaluating extinction risk. While it is true that, in general, “rare” species are more vulnerable than common ones, some species are naturally rare and have likely persisted in that rare state for tens of thousands of years or longer. Classifying a species as “common” does not necessarily indicate it has a low risk. For example, the Caribbean *Montastraea* species considered in this Status Review Report were listed as “common” (Veron, 2000), yet trend information indicated substantial declines and relatively high risk. Indeed, it is likely that naturally “rare” species have intrinsic characteristics that maintain viability at lower abundance that depleted “common” species (i.e., those which have declined to low abundance) lack. However, naturally rare species may generally be at greater risk of extinction than naturally more common species when confronted with anthropogenic threats (Magurran, 2009). Presence and absence data are another type of qualitative abundance data; these are useful for establishing the potential range of a species. If repeated over time, presence/absence surveys can provide some quantitative indication of trend (i.e., change in frequency of occurrence).

Quantitative abundance estimates were available for only a few of the candidate coral species. Richards (Richards, 2009; Richards et al., 2008b) estimated total effective population size (Wright, 1931) for a number of Pacific *Acropora* species based on extrapolation from local surveys and an assumption that effective population size was a fixed percentage of census size. These data suffered from substantial uncertainties based on small survey sample sizes relative to the scale of the extrapolation, uncertainties in estimating the extent and quality of reef habitat, and uncertainties about the relationships between census counts and effective population sizes. The Richards data are also limited in that they do not inform changes over time. However, the data are useful in helping to distinguish among the different species of *Acropora*, particularly given the limitations in coral cover data that could show trends (see below).

The most informative data are time series observations of species-specific abundance (most commonly percent cover), because these data provide direct evidence of temporal changes in the focal species. Unfortunately, these data were less common than one might expect. The majority of the 82 candidate coral species occur in the Indo-Pacific (75), but many literature reports and long-term monitoring programs reported coral percent cover only to genus level or morphological group (e.g., branching, massive, encrusting) within a genus because of the substantial diversity within many genera and difficulties in field identification among congeners. These genus-level data were considerably less informative for evaluating the extinction risks to species and generally were not included as part of the BRT individual species accounts in Chapters 6 and 7. In the Caribbean, most of the candidate coral species were too rare to document meaningful trends (e.g., *Dendrogyra cylindrus*), commonly identified only to genus (*Mycetophyllia* and *Agaricia* spp.) or potentially misidentified as different species (e.g., *Montastraea annularis* complex). Time-series data were available for the candidate *Montastraea* species partially because they make up such a predominant part of live coral cover. Even for these species, the time-series observations at the species level were often of very short duration (they were not separated as sibling species until the early 1990s and many surveys continue to report them as *Montastraea annularis*

complex) and cover a very limited portion of the species range (e.g., the time-series only monitors a subsection of a single national park).

The IUCN report (IUCN, 2010) and the accompanying publication in *Science* (Carpenter et al., 2008) were the primary analyses referenced in the petition to list 83 corals. That work relied on extrapolating species-specific extinction risks from estimates of total coral cover and habitat types at very broad geographic scales. The uncertainties introduced by this extrapolation were substantial. The regional estimates of status and change in coral cover often were based on nonquantitative expert opinion, which does not necessarily make them wrong, just uncertain. Perhaps a greater source of uncertainty in that analysis was the assumption that the trends in individual species would be the same as that estimated for overall change in total coral cover. It is not apparent that individual species would always increase or decrease in direct proportion to the overall change in coral cover within a given habitat type; the diverse ecology and life history of the range of candidate coral species would seem to suggest otherwise. The problem is exacerbated by the potential mismatch between the broad spatial scale of the total coral cover estimates and the actual geographic distribution and microhabitat requirements of individual species. Although the expert panel approach used by IUCN may provide a general picture of changes in total coral cover, it would not necessarily provide a very precise estimate of trends in individual species.

For some of the candidate *Montastraea* species, data were available on juvenile recruitment (summarized in Edmunds et al., 2011). These data provided valuable information on rates of successful sexual reproduction and the potential for the species to replace itself. Interpreting recruitment data can be challenging because recruitment may be naturally episodic for some species, which will require many years or decades of observation to detect trends in population dynamics (Edmunds and Elahi, 2007). Individuals from species with a mean life expectancy of many decades may only need to successfully replace themselves infrequently to maintain a stable population.

4.3 Spatial Structure of Corals

As discussed in Chapter 3 on the threats facing the 82 candidate coral species, the impacts of climate change and ocean acidification are of central importance in evaluating the Critical Risk Threshold. The BRT considered a broad geographic distribution across a variety of habitats and microhabitats within a reef to be a significant buffer against the potential impacts of ocean warming and acidification. At large spatial scales, broad latitudinal distributions were considered important as a buffer against ocean warming, as it indicates a relatively wide thermal tolerance and a potential ability to persist through thermal anomalies and as thermal isoclines shift poleward. High-latitude reefs may serve as either refugia or climate-change hot spots (Riegl, 2003), and corals may have the potential to expand their latitudinal distributions with ocean warming (Precht and Aronson, 2004; Yamano et al., 2011). However, the BRT determined that insufficient data existed to adequately address potential range changes at the level of the candidate coral species. Additionally, there are limits to latitudinal buffering as entire ecosystems shift in response to climate change and other factors, so geographic range is only a limited predictor of extinction risk. Additionally, studies on the range of habitats suitable for reef development indicate that factors other than temperature, such as light availability (Kleypas, 1997) or aragonite saturation state (Guinotte et al., 2003), will likely limit the potential of poleward expansion. Finally, local microhabitat variability has been considered to provide potential refugia (Fabricius et al., 2004; Skirving et al., 2010) or a range of conditions that might provide for greater genetic adaptation within a species (Barshis et al., 2010; Baskett et al., 2009a). Although it is only a limited predictor, estimates of current geographic range were among the few pieces of information available for many of the candidate species and, therefore, were of relatively high influence in the BRT's evaluation of Critical Risk Thresholds².

Data on the geographic distributions of the 82 candidate coral species were obtained from four main sources: (1) IUCN maps (www.iucnredlist.org), (2) Veron's survey of corals (Veron, 2000), (3) an evaluation of the U.S. distribution of candidate coral species (Kenyon et al., 2010b), and (4) personal communication of observations from BRT members, BRT-solicited subject matter experts, and other researchers with direct knowledge of the candidate coral species. BRT members expressed considerable uncertainty and skepticism regarding some of the reported species distributions. Much of this uncertainty arose from basic taxonomic uncertainty among the corals (discussed in Section 2.1) and the difficulty

² It should be noted that, while the Individual Species Accounts in Chapters 6 and 7 include an assessment of the species' occurrence in U.S. waters, it was the species' global range of occurrence, not U.S. occurrence, that was considered as a factor in estimating the extinction risk for the candidate species. The U.S. Endangered Species Act requires extinction risk for invertebrates to be assessed range-wide.

in identifying species in the field. Where questions arose, they are discussed in the individual species accounts (Chapters 6 and 7).

4.4 Diversity in Corals

Genetic and phenotypic diversity help buffer a species against negative effects of environmental variability. In general, a species with high diversity is more likely to have some individuals with traits suitable for altered local conditions at a particular place and time than a population with reduced diversity. Phenotypic diversity can be important even in the absence of clear genetic diversity as it indicates a certain plasticity that may allow for persistence in multiple environments and habitats; loss of the ability to produce certain phenotypes may result in increased risk. Genetic diversity is important as the raw material for evolutionary change in response to environments with directional change (e.g., from climate shifts). Loss of this genetic diversity could be considered an increased risk factor (e.g., Hughes and Stachowicz, 2004).

Unfortunately, few data are available about diversity within the 82 candidate coral species. In many cases, the species themselves have not even been unambiguously identified (see Section 2.1), much less any analyses of within-species variability. However, as described in Section 4.2, estimates of effective population size are available for some species of *Acropora* (Richards, 2009). Small effective population size can infer relatively low genetic diversity or potential population genetic bottlenecks, such as inbreeding and mutation accumulation (Lynch et al., 1995). As described above, there is considerable uncertainty regarding these estimates of effective population size in corals generally, and the candidate species in particular. However, even after considering the uncertainty, these analyses suggest low effective population sizes for the rarer species (Richards, 2009)—much lower than might be suspected, given their relatively large geographic ranges. These effective population size estimates are discussed in the appropriate individual species accounts (Chapters 6 and 7).

Another piece of relevant information regarding within-species diversity of corals (and further reducing estimated effective population size below census size) is the level of asexual reproduction. Scleractinian corals can reproduce either sexually by dispersal of gametes or clonally by asexual fragmentation. Although survival often depends on fragment size, fragmentation can be extremely important in supporting local abundance, or in recovering from physical damage, such as storms. Asexual reproduction simply creates more copies of the same genotypes, and these clones may help a species survive disturbances in the short term. However, the loss of genetic diversity resulting from a lack of sexual reproduction could reduce the long-term viability of a species (Honnay and Bossuyt, 2005). In the *Monastrea annularis* complex, successful replacement of adults through sexual reproduction is not common and levels of recruitment from asexual fragmentation have rarely been determined (Edmunds et al., 2011; Foster et al., 2007). It is unclear whether the levels of sexual reproduction and recruitment are changing in the *Monastrea annularis* complex. Detecting trends is difficult because sexual reproduction and recruitment are assumed to be episodic, since it has never been observed at an appreciable level (Edmunds et al., 2011), with supposed long, irregular (and therefore largely unobserved) intervals between successful recruitment events. Whatever the trend, the overall levels of larval recruitment are very low (Edmunds et al., 2011), leading to potential concerns about low levels of diversity.

Finally, reef-building corals are functional holobionts and there is substantial diversity of the symbiotic zooxanthellae and microbial components. The BRT did not formally address this level of diversity in the species analyses, as it is beyond the scope of the petition. However, the BRT acknowledges that the ability to host, for example, multiple clades of zooxanthellae may provide the ability to adapt to different environmental conditions and addressed this in individual species accounts when relevant information was available. This is clearly a complex issue that remains poorly understood. While genetic variability among zooxanthellae has been found across reefs, among reefs, and geographically (Baker et al., 2001; Fabricius et al., 2004; LaJeunesse, 2002; LaJeunesse et al., 2004a; LaJeunesse et al., 2003), the ability (or lack thereof) to either incorporate new zooxanthellae or retain them after stress events may control adaptation (Coffroth et al., 2010; LaJeunesse et al., 2010; LaJeunesse et al., 2009; Thornhill et al., 2006).

4.5 Critical Risk Threshold

Absolute extinction is often defined as occurring when there are zero individuals of a particular species alive. Prior to that end point, a species may be considered “functionally extinct” where extinction is inevitable, although some individuals may still be alive. For example, if the only individuals left are male, the species will go extinct—it is only a matter of time. In the case of corals, a clonal colony can potentially survive for decades or centuries and functional extinction could occur well before absolute extinction. It may not always be apparent when a species is functionally extinct. For example, a species may contain both males and females but they may be somehow genetically incompatible

individuals (e.g., cannot self-fertilize, or both carry the same recessive lethal alleles) or they may be so far apart physically that natural reproduction is impossible. The species also may have entered some other “extinction vortex” where absolute extinction is inevitable or very likely because of depensatory feedback loops. In a depensatory feedback loop, individual survival decreases with smaller population size, so that as the population gets smaller, more individuals die or fail to reproduce leading to an even smaller population size and even lower survival and reproduction, until eventually, and perhaps after a long time, reaching extinction.

The BRT distinguishes between situations where extinction is inevitable, which the BRT calls functional extinction, and situations where extinction is extremely likely because of depensatory feedback or other processes that the BRT refers to as “critical risk.” Some researchers have used the term functional extinction in situations the BRT would describe as critical risk (e.g., Sekercioglu et al., 2004). The distinction is important because, according to the BRT’s definition, a functionally extinct population is doomed, whereas there may be potential for recovery of a population at critical risk. Successful recovery of a species considered at critical risk may require significant management intervention, occurrence of unusually favorable natural conditions, or both. The BRT’s task did not include estimating or predicting possible future changes or effects of changes that could foster recovery, but such conditions could occur. The BRT, therefore, used the more inclusive concept of critical risk, but in practice it is likely difficult to distinguish between a functionally extinct species and one at critical risk. Because of this difficulty, the BRT evaluated the likelihood of the species falling below a “Critical Risk Threshold” (CRT) within a specified period of time, rather than the likelihood of the species becoming absolutely or functionally extinct.

Extinction thresholds may also be difficult to detect because of “extinction debt.” The term extinction debt was originally coined to describe a phenomenon observed in a specific multispecies meta-population model where extinction of competitively dominant, but poorly dispersing species is predicted to occur at a substantial time lag after a habitat destruction event (Loehle and Li, 1996; Tilman et al., 1994). Extinction debt has been broadened from the original specific meta-population model to describe the general situation where delayed extinction represents an ecological “debt” to be paid in the future for current habitat destruction (Kuussaari et al., 2009). Analyses suggest that long-lived corals may be vulnerable to extinction debt (Stone et al., 1996), making detection of risk extremely challenging since apparently healthy but patchy coral populations may in fact be headed toward inevitable extinction within a few generations because of habitat destruction (or resultant recruitment failure). Extinction debt theory also predicts that competitively dominant and often quite abundant species are particularly vulnerable to delayed extinction as compared to rare species that are less-effective competitors, but good dispersers.

In modeling extinction risk based on projections from abundance time series, it is common to estimate the probability of a population declining to a “Quasi-extinction Threshold” rather than absolute extinction (Engen and Sæther, 2000; Ginzburg et al., 1982; Holmes et al., 2005; Jenouvrier et al., 2009). The Quasi-extinction Threshold corresponds to a low abundance (or high rate of decline) considered to represent a situation of conservation concern or an abundance where processes outside the scope of those included in the model become important (e.g., demographic stochasticity). Although there is no uniform way of setting Quasi-extinction Thresholds, values in the literature vary considerably depending on prevailing conservation concerns, model structure, and the life history/historical abundance of the species in question (Ellner et al., 2002). While the conceptual bases for describing Quasi-extinction Threshold and Critical Risk Threshold are similar, the BRT has chosen to not use the term Quasi-extinction Threshold because of its association with a particular type of modeling and because it is often applied at the population scale. Quantitative population and productivity data were available for very few of the 82 candidate coral species, making such modeling problematic, dubious, or even impossible in cases with no data. The BRT’s application of the Critical Risk Threshold concept was not restricted to a quantitative model and was applied at the species, rather than population, scale.

The BRT defined a Critical Risk Threshold as a condition where the species is of such low abundance, or so spatially disrupted, or at such reduced diversity that extinction is extremely likely within a defined timeframe. The Critical Risk Threshold level is influenced particularly by the effects of depensatory processes, environmental stochasticity, and catastrophic events. Depensatory processes include reproductive failure from low density of reproductive corals and the effects of genetic processes, such as inbreeding. Environmental stochasticity results from “normal” levels of environmental variation, whereas catastrophes result from severe, sudden, and chronic, but new (e.g., climate change), deleterious environmental events. The BRT did not define Critical Risk Threshold as a single abundance number, density, spatial distribution or trend value, but rather as a qualitative description encompassing multiple metrics. Critical Risk Thresholds vary among species based on life-history parameters and other characteristics.

4.5.1 Critical Risk Threshold and depensatory processes

Several key depensatory processes affect extinction risks in corals. This section describes the depensatory processes that were taken into account by the BRT in determining Critical Risk Thresholds for each of the 82 candidate coral species. The first is **fertilization**. Most coral species, including all of the candidate species, are sessile and cannot move closer to each other for spawning, and when they release their spawn into the water column, ocean currents dilute the gametes as they are transported to downstream locations. Experimental studies have indicated a level of proximity among colonies that is required for a reasonable chance of fertilization. For broadcast-spawning corals, these studies have indicated that eggs must be released within a relatively short distance (2–5 m) of a spawning male for successful fertilization to occur (Lacks, 2000; D. Levitan, Florida State University, FL, pers. comm., March 2010). It is not clear the extent to which these experimental studies on a few individual species can be extended to all corals, particularly since it is known that many naturally rare species occur at lower densities than the limits found in these studies. Considering the diversity and heterogeneity of coral reefs and the distances among corals of the same species in nature, the results of these studies seem unrealistically small. It has been pointed out by Oliver and Babcock (1992) and Coma and Lasker (1997) that many aspects of the natural histories of scleractinian corals and octocorals are adaptations of sessile colonies to maximize the potential for successful fertilization. Synchronous spawning, buoyant gamete bundles that accumulate at the sea surface, and timing of spawning during periods of low water motion (Van Woesik, 2010) might result from selective pressure for gamete concentration and may increase the distance at which spawning can be successful. Nevertheless, dilution and dispersion by ocean currents makes it reasonable that sessile coral colonies must be within a few tens of meters of a colony of another compatible parent (e.g., opposite sex for gonochoric species and/or different genotype for any coral) for successful fertilization to occur. Levitan et al. (2004) argued that the genetic isolation among species of *Montastraea* involves separation in time of spawning by 2 hours even though gametes are viable for as long as 6 hours. The dilution and dispersion by ocean currents within the 2-hour time difference effectively separates these species. If populations of coral colonies become less densely distributed, their effective population sizes decrease substantially even though the absolute numbers of colonies might remain high.

Second, **fecundity** affects fertilization success, population recovery, and population connectivity. In a synergistic interaction among threats, the initial number of gametes spawned influences the rate at which sufficient dilution and dispersion of gametes occurs. However, anthropogenic physical disturbance, chemical pollution, and other factors reduce the fecundity of corals by decreasing the size distribution of corals and by reducing the energy available for producing gametes. Fertilization reportedly decreases after pollution and bleaching events (Omori et al., 2001). As colonies become more sparsely distributed with smaller size distributions, lower fecundity per polyp, and potentially reduced fitness of the gametes produced, the fecundity of the population decreases and the probability or rate of fertilization decreases. Gardner et al. (2003) analyzed data from 263 sites across the wider Caribbean and found an 80% decline in coral cover (which might be taken as a proxy for population fecundity) from 1977 to 2001. Studies that monitored coral recruitment from 1977 to 1993 in Jamaica (Hughes and Tanner, 2000) and 1979 to 2004 in Curaçao (Bak et al., 2005) indicated a substantial decline in coral recruitment over the same three decades. Declining coral cover (low population fecundity) thus could lower production of planulae, leading to lower coral recruitment, which would provide lower replenishment of adult colonies and thereby further decrease population fecundity and production of planulae—a positive feedback process that accelerates population decline over the geographic area.

Third, declining corals are influenced by **disrupted metapopulation processes**. Depensatory processes can reduce interconnections among populations by three mechanisms: (1) increased distances among populations, (2) establishment of toxic barricade waters, and (3) decreased fecundity. For fish, the maintenance of local populations is often dependent on frequent arrival of dispersed larvae (Cowen et al., 2006; Steneck, 2006). As coral populations are extirpated by habitat damage, disease, bleaching events or other factors, the distance between the remaining populations increases (Fig. 4.5.1). Thus, it is less likely that the remaining populations can exchange larvae needed for maintenance or adaptation. This can lead to further loss of populations, creating even greater interpopulation distance leading to a depensatory spiral and possibly further local extirpations. Populations do not need to be completely extirpated to have reduced connectivity. Lowered population fecundity also reduces the probability of sufficient larvae recruiting to a reef with a depleted population (Cowen et al., 2006; Steneck, 2006). As fecundity decreases, the distance at which a population can effectively provide larvae to rescue other populations decreases (Fig. 4.5.2). Thus, drops in fecundity and connectivity are synergistic. Also, anthropogenic runoff and effluents can act as barriers to larval dispersal, effectively isolating populations of normally high gene-flow species (Puritz and Toonen, 2011). This can reduce connectivity, causing or reinforcing the depensatory effects of habitat fragmentation. Genetic isolation by human coastal populations is “most likely caused by larval mortality from the substantial contemporary augmentation of freshwater, particulate and/or pollutant load” (Puritz and Toonen, 2011). Even if the geographic distance among populations does

not change, the effective distance among populations can be changed by altered ocean circulation patterns, such as are projected to result from climate change (see Section 3.2.5).

The particular life history strategy of a coral species can affect vulnerability to disrupted metapopulation processes, however, it is not readily apparent whether brooding or broadcasting species are most at risk. Brooding larvae are capable of almost immediate settlement and most successful settlement appears to be in close proximity to spawning locations. However, the fact that most brooders have zooxanthellae implies that they may be capable of distant dispersal. So, while brooders predominantly settle near their parents, they are also capable of some long distance settlement. Brooding corals may be favored on semi-isolated reefs because of extended larval competency periods (Harriott, 1992). Although this suggests that brooders should be less vulnerable to extinction as well as having lower species origination rates (Johnson et al., 1995), preferential survival of brooders during the Oligocene/Miocene extinction in the Caribbean may have been more as a result of enhanced survival of brooded lecithotrophic larvae than extended larval competency (Edinger and Risk, 1995). Brooders may also have reduced genetic variability, especially if they are capable of self-fertilization. However, the trade-off for brooders may be improved larval survival because of the increased likelihood that they will settle in a compatible environment. This advantage may be reduced as the climate changes giving broadcasting species an advantage in environments where reefs and coral communities span a wider range of environmental conditions (Glynn and Colley, 2008).

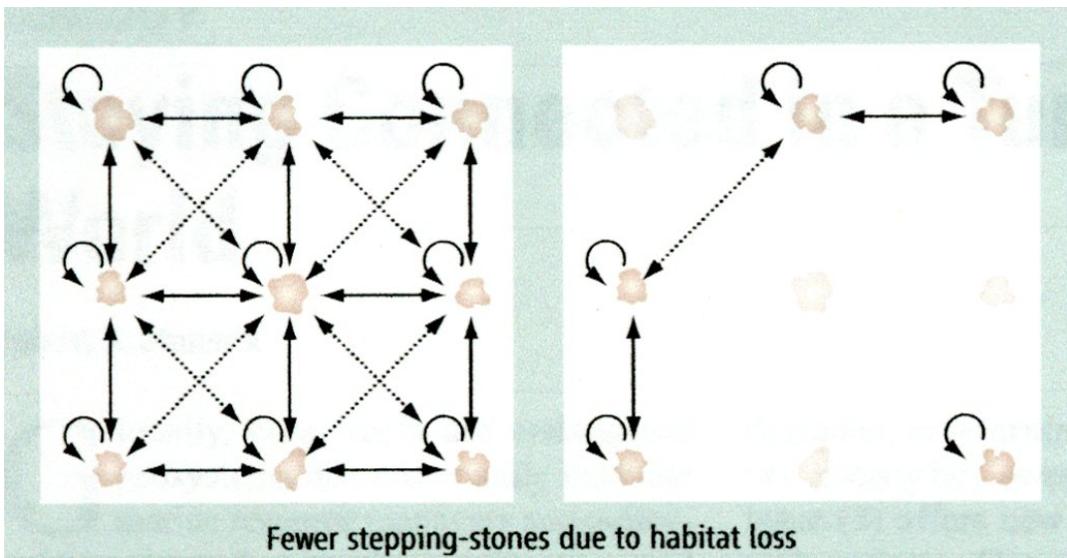


Figure 4.5.1. In a damaged ecosystem (illustrated in panel on the right) increased distances between patches can lead to recruitment failure (Nakamura et al., 2011).

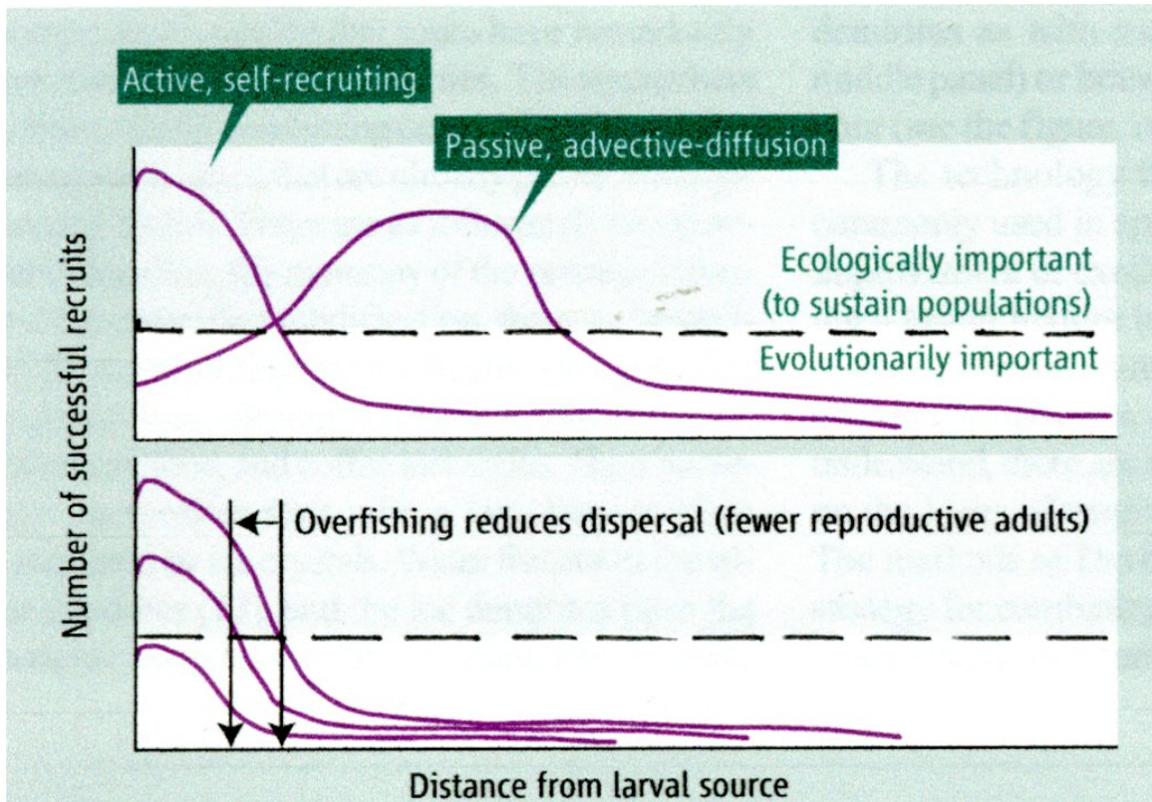


Figure 4.5.2. Number of successful recruits for population replenishment (area above the dotted line) declines as harvesting or ecological disturbances reduce the abundance of reproductive adults (Figure from Steneck, 2006).

The fourth process is **predation**. While predation on corals most often results in only partial mortality, the probability of overpredation (a second predation event before the first has healed or lost individuals are replaced) decreases exponentially with increased coral abundance and increases linearly with increased healing time (Fig. 4.5.3). As with fertilization, fecundity, and connectivity, the probability of escaping overpredation increases with colony abundance and individual size (Jayewardene et al., 2009). Pollution and climate change can potentially increase the healing time (Fisher et al., 2007) required for lesions resulting from predator bites and these factors can thereby reduce the threshold time required to reach overpredation (Fig. 4.5.3). On a healthy coral reef, the frequency of predation on corals can be intense, but the corals are able to sustain their population (Jayewardene et al., 2009); however, as coral populations decrease the predators focus on the few remaining colonies and predation becomes depensatory. This scenario assumes a Type II predator-prey functional response (Holling, 1959), where predators consume more prey per capita when the prey are at low density (Fig. 4.5.4). This effect has been observed on coral reefs during crown-of-thorns seastar predation outbreaks after mass-bleaching events (Glynn, 1985a). This is likely to occur if the predators have no alternative prey or it can occur as a result of predator concentration.

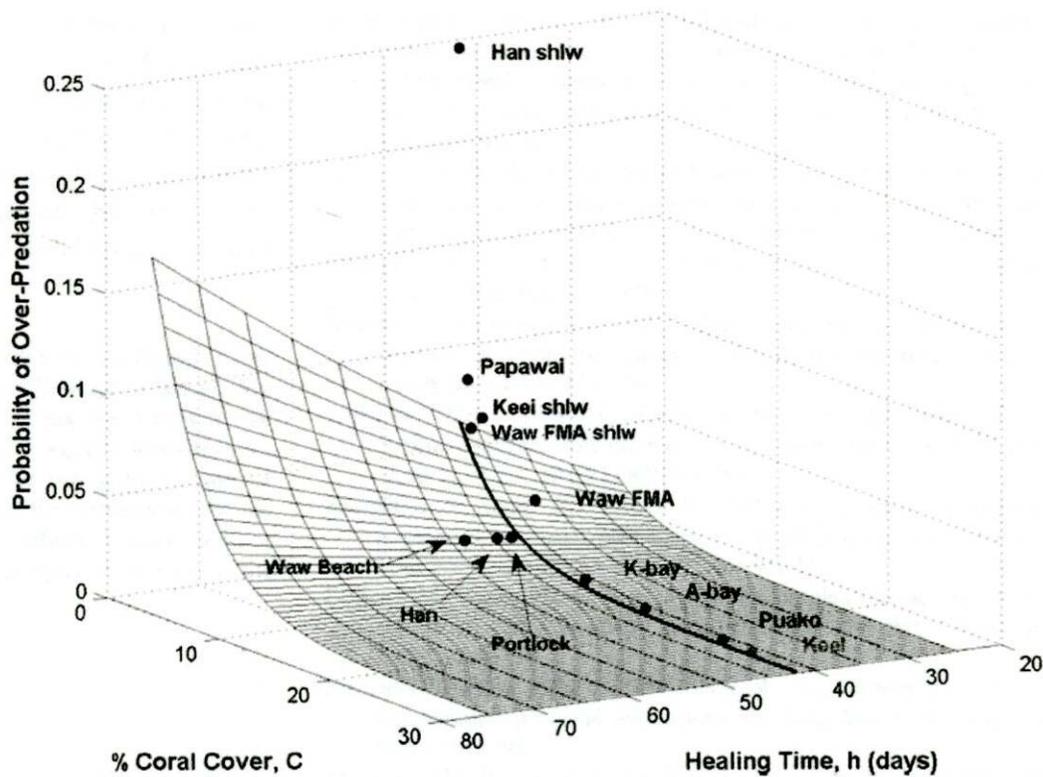


Figure 4.5.3. Probability of overpredation in relation to coral cover and healing time from lesions from bites of predators (Jayewardene et al., 2009).

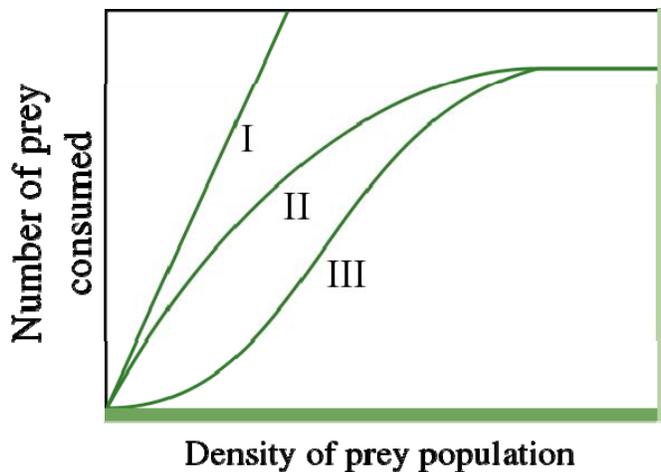


Figure 4.5.4. Predator-prey functional response types (Holling, 1959).

Fifth, **macroalgal phase shifts** (Fig. 4.5.5) impair adult and early life stages of corals (see Section 2.3.4. “Phase shifts.”). Just as predators can outpace the recovery abilities of prey at low population levels, once algae cover more space than the herbivore populations can effectively graze, the process becomes depensatory. This is because the algal population can expand making it even less likely that the algae can be controlled by herbivores (Williams et al., 2001), yielding reduced recruitment habitat for coral larvae. Macroalgae further impair coral populations by many mechanisms (McCook et al., 2001). Some seaweed species have allelopathic effects on both coral adults and settling larvae. Some filamentous algae create sediment traps that make hard substrata inaccessible to settling larvae or smothers recently established recruits (Birrell et al., 2005). Macroalgal thalli can cause bleaching and death to coral tissue in direct contact

(Rasher and Hay, 2010) and can reduce coral larval settlement in their vicinity (Kuffner et al., 2006). Other lab experiments show that macroalgal tissues impair corals not in direct contact, presumably by stimulating enhanced microbial loads by leaking carbon (Smith et al., 2006). Some algae may also trigger disease when in direct contact with coral (Nugues et al., 2004b). These mechanisms all represent potentially depensatory pathways as corals become more rare.

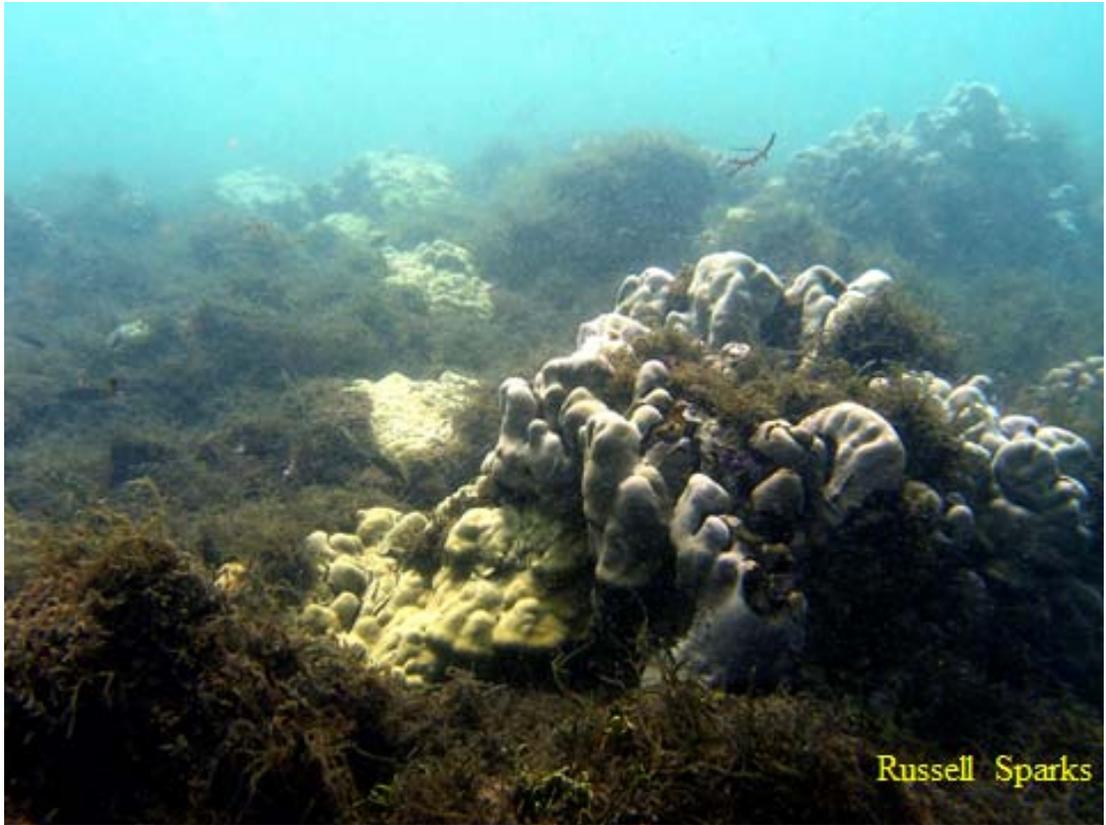


Figure 4.5.5. Macroalgae overgrowing corals on an overfished reef in western Maui.

The sixth process on coral reefs is **bioerosion and its resultant decrease in topographic complexity**. As corals are killed by episodic disturbances such as large waves from cyclones, large-scale predation by crown-of-thorns seastars or mass-bleaching events, large areas of carbonate skeleton are cleared of living coral tissue, facilitating increased bioerosion. Partial colony mortality increases the vulnerability of corals to bioerosion (Scoffin et al., 1997). Bleaching can also result in greater concentration of bioeroding organisms, intensifying the destructive process (Glynn, 1988b; Reaka-Kudla et al., 1996) and even push reefs from net growth into a state of net erosion (Johnson et al., 1995). Bioerosion is self-reinforcing because it weakens the skeleton and makes the coral more vulnerable to wave action and other stressors. When damaged by wave action, detached corals can become projectiles that can affect other corals and facilitate further bioerosion, a depensatory process. As the three-dimensional topographic complexity is reduced to a more two-dimensional framework or rubble, the amount of habitat for herbivorous fishes is reduced. Algae also do better on unstable substrata than do corals, further reducing the ability of corals to occupy space.

The seventh process, **decreasing colony size**, is depensatory as the size distribution of corals becomes smaller through slower growth and partial mortality, effects that can be caused by human activities and climate change. As the colonies become smaller, the potential area of contact on their circumferences becomes greater relative to the living surface area of the corals. For example, sediment stress (Nugues and Roberts, 2003), bleaching and fishing (McClanahan et al., 2008), and disease (Richardson and Voss, 2005) can all reduce coral colony size through partial mortality of large colonies or recruitment of small colonies after mass mortalities. However, mortality and reproduction are size-dependent in corals. For example, small corals are less susceptible to disease but more prone to total mortality if they become infected (Nugues, 2002). Larger colonies have larger eggs and more eggs per polyp (Hall and Hughes, 1996; Nozawa et al., 2006; Villinski, 2003), and most corals have a minimum physical size at which they are capable of

reproduction (Soong and Lang, 1992; Szmant-Froelich, 1985). The minimum reproductive size could lead to loss of sexual reproduction in damaged populations. However, there are some circumstances in which small colony sizes are advantageous. For example, smaller colonies of *Oculina patagonica* appear less vulnerable to bleaching than larger colonies (Shenkar et al., 2005). Size-structured population models indicate that coral colony size dynamics can increase population extinction risk as a consequence of small decreases in recruitment rate (Sweatman et al., 2011).

While normally not considered compensatory, there are cases where **disease** can be considered the eighth and final compensatory process. In most cases, higher host density leads to an increase in disease likelihood. For example, in one case, relatively high (30% cover) density has been found as a requisite condition for disease outbreak prediction (Heron et al., 2010). However, there are potential cases where low density can lead to increased risk of disease. Raymundo et al. (2009) observed a higher frequency of diseases on corals of heavily fished reefs than in marine reserves. They hypothesized that intensive fishing may have removed the apex predators, releasing some of their prey, corallivorous chaetodontids, to become more abundant and transmit more coral disease as they fed. As the corals became less abundant, the released corallivores focused on the few remaining colonies and the spread of disease became compensatory. This is a complex, four-way, nonlinear interaction that illustrates the complexity of understanding compensatory processes.

4.5.2 Critical Risk Threshold and sexual reproduction

Several of the compensatory processes described above could result in the loss of successful sexual reproduction within the species. Sexual reproduction plays an important role in maintaining genetic and genotypic diversity, which can be advantageous in heterogeneous environments (Becks and Agrawal, 2010). The BRT considers a species that has lost the ability for successful recruitment of sexually produced progeny to be below the Critical Risk Threshold, even if it can still reproduce asexually. The BRT does not expect that species will lose the ability to produce gametes but rather through a compensatory process (or processes), sexual reproduction results in no new recruits that enter the population. A species in this situation would likely be far along an extinction trajectory. This issue is of some concern in species such as those of the *Montastraea annularis* complex that show very low levels of successful sexual reproduction (Edmunds et al., 2011; Hughes and Tanner, 2000).