Importance of Recruitment Processes in the Dynamics and Resilience of Coral Reef Assemblages

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Abstract

Recruitment is now widely recognized as a fundamental process governing spatial patterns, dynamics, and maintenance of marine invertebrate communities. Moreover, recruitment is a critical factor for successful recovery following disturbances and thus resilience of ecosystems. Over the last decades, tropical coral reefs, which are one of the most diverse ecosystems on Earth and provide goods and services to ~500 million people, have been confronted with various types of natural and anthropogenic disturbances, causing widespread mortality of reef-building coral species. In this context, understanding processes of coral recruitment and their patterns in time and space is a fundamental step to understand, detect, and predict the effects of climate change on reef ecosystems. Despite major advancements in the last three decades, our understanding of some critical phases of coral recruitment processes remains too limited for their integration into management and conservation actions that are urgently needed for this unique ecosystem. Here, we synthesize and analyze existing literature on coral recruitment to determine the state of knowledge, identify knowledge gaps, and suggest future lines of research. We particularly focus on the spatiotemporal variability of recruitment and its controlling factors, the relative importance of pre- and post-settlement events and life strategies in the maintenance of adult assemblages, and the critical role of recruitment for the recovery and resilience of disturbed reef communities.

Keywords

Coral reefs • Scleractinian corals • Recruitment • Post-settlement processes • Regulation • Resilience

1 Introduction

1.1 The "Coral Reef Crisis"

Coral reefs are one of the world's most iconic marine ecosystems, often referred to as "rainforests of the sea." They act as natural breakwaters, protecting coastal areas and provide important economic, social, and esthetic goods and services, which are critical to the survival of ~500 million people (Moberg and Folke 1999). As tropical rainforests, coral reefs are characterized by an exceptional biodiversity and complexity and are among the most productive ecosystems on Earth. Hermatypic scleractinian corals, with their endosymbiotic single-celled algae (zooxanthellae), are the primary framework builders of the reef ecosystem and are a key component of coral reef health and diversity. As trees, corals build a complex tridimensional structure and provide essential or important habitat for hundreds of thousands of reef-dwelling organisms. Due to the sedentary nature of corals and their narrow tolerance range for environmental conditions, reef ecosystems are highly vulnerable to acute stressors and may change rapidly in their structure and functioning (Hughes and Connell 1999; Harrison and Booth 2007). Like many marine ecosystems, coral reefs are becoming increasingly exposed to various chronic and/or episodic threats and are expected to be highly vulnerable to future climate change (Hughes et al. 2003; Edmunds et al. 2014). While some physical and biological disturbances are a routine part of reef community dynamics, there is growing concern that the frequency and severity of various types of natural and anthropogenic disturbances, which have increased over the last three decades, will continue to do so (Hoegh-Guldberg et al. 2007). Among the broad range of large-scale disturbances that affect coral reefs, thermally induced coral bleaching events, cyclones, and outbreaks of keystone species, such as the coral-killing sea star *Acanthaster planci* in the Indo-Pacific, have the potential to significantly alter the biological and ecological processes that maintain coral communities (De'ath et al. 2012; Kayal et al. 2012). Coral reefs are also under increasing pressure from the combined effects of local human-induced stressors including overfishing, water pollution, dredging activities associated with coastal development, tourism, and recreational impacts (Grigg and Dollar 1990). Consequently, coral reefs have been affected by widespread mortalities of keystone organisms and habitat degradation and in many cases have undergone a striking phase shift in community structure. Classically, these phase shifts have involved the replacement of stony corals by algae, which results in the deterioration of the ecosystem goods and services previously supplied by corals (Harrison and Booth 2007). In the context of "confronting the coral reef crisis" (Bellwood et al. 2004), understanding the processes that maintain coral populations is of critical importance to better evaluate the resilience of reef ecosystems (defined here as the ability of an ecosystem to recover its structure and functions after a perturbation; see further developments of this concept in the "companion chapter ► The Resilience of Marine Animal Forests" by Bianchi et al.) and to understand, detect, and predict the effects of climate change. These outcomes are also crucial to identify appropriate actions for coral reef conservation and management (Mumby and Steneck 2008; Anthony et al. 2015).

1.2 The Importance of Recruitment Processes

Coral assemblages often show strong spatiotemporal variations which are governed by a variety of interacting physical and biological processes that vary in frequency, intensity, and spatial scale (Hughes and Connell 1999; Harrison and Booth 2007). Among these processes, recruitment is widely recognized as being fundamentally important in the dynamics of local populations and recovery following disturbances, though both pre- and post-settlement processes may also influence the local abundance and spatial distribution of adult assemblages (Caley et al. 1996; Cowen et al. 2000; Doropoulos et al. 2015). In fact, the supply of coral larvae, their successful settlement and metamorphosis, and their subsequent survival and growth can have a marked influence on local population structure. The relative contribution of these processes vary greatly across geographic scales given dissimilarities in adult coral assemblages, local hydrodynamics, disturbance history, competition, and sources of predation (Hughes et al. 2000). In some cases, spatial heterogeneity of adult distribution can be largely influenced by stochastic variations in early recruitment rates (Caley et al. 1996; Cowen et al. 2000). But post-settlement mortality in scleractinian corals is generally high (up to 90 % within the first year), thereby representing a critical process for coral population dynamics, that can greatly distort patterns established at settlement (Vermeij and Sandin 2008; Penin et al. 2010). One of the key questions for ecologists then is to determine the degree to which spatial heterogeneity in the abundance of adult corals is influenced by pre- vs. post-settlement processes and to identify major intrinsic and extrinsic biological and physical factors that drive these patterns.

1.3 Complexities of the Coral Life Cycle

With the high complexity of their life cycles and the inter- and intraspecific diversity of their life strategies, scleractinian corals are a challenge for demographic and population dynamics studies (Hughes and Jackson 1985; Kayal et al. 2015). Like most marine invertebrates, corals have a bipartite life cycle in which larvae develop as plankton before settling and attaching to the substratum (Fig. 1). As seeds for trees, coral larvae are the predominant means for dispersal and colonization of new habitats, enabling recolonization following disturbance and genetic exchange among subpopulations (Caley et al. 1996; Cowen et al. 2000). In addition to the typical recruitment, growth, and mortality processes observed in other benthic organisms, most corals have a clonal life-form and undergo fragmentation, fission, fusion, and partial mortality (i.e., shrinkage or negative growth), which distort age-size relationships (Hughes and Jackson 1985; Harrison and Wallace 1990). Moreover, corals are exceedingly small in size at settlement compared to their adult form and have a long life span. Most corals require several years of benthic life to become sexually mature (i.e., become "adults"). The nonreproductive benthic phase of corals, which can last for up to 5 years, can thus be separated into a recruit and a juvenile stage, that are ecologically very different (Fig. 2; see Penin et al. (2010) for further distinctions between recruits and juveniles). Sizes vary by up to an order of magnitude between these stages, and many processes such as growth and mortality are size dependent in corals (Vermeij and Sandin 2008; Kayal et al. 2015). In addition, organisms interacting through competition or predation with recruits are likely to be different from those interacting with juveniles and/or have differing severity in their effect on recruits vs. juveniles. Consequently, juvenile corals can be seen as immature colonies from several successive cohorts, providing a short-term history of settlement patterns combined with early post-settlement growth and mortality, whereas early recruits reflect variability in larval supply (Penin et al. 2010). Most studies conducted on recruitment and post-settlement mortality of corals have focused either on recruits

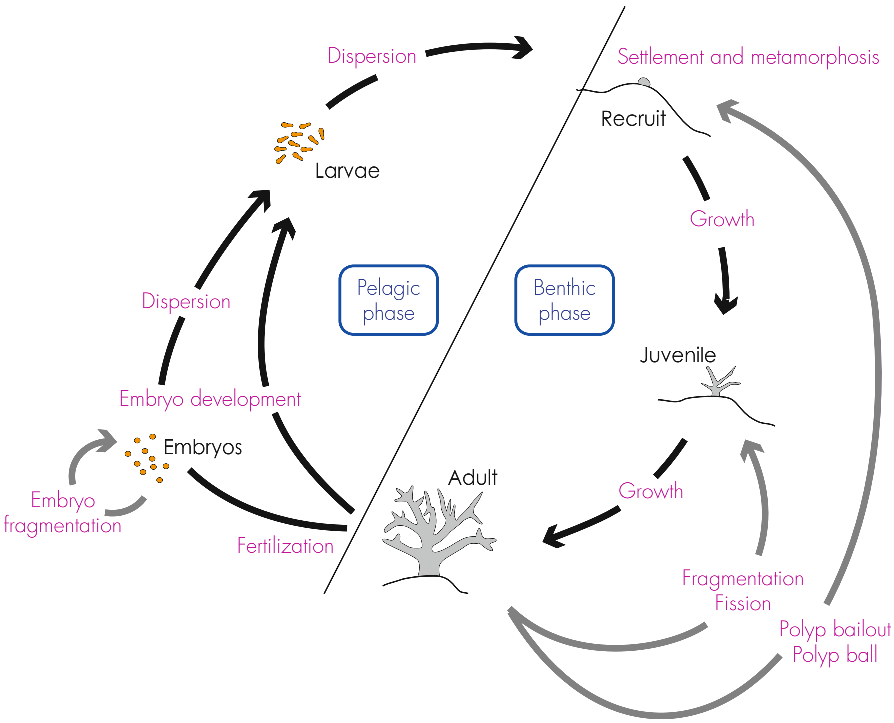

Fig. 1 Coral life cycle showing the critical pelagic and benthic phases. Most of the coral species have adult colonies that are attached to the substratum. Sexual reproduction occurs in two forms: fertilization and brooding of the larvae within the polyp and external fertilization and development. Several modes of asexual reproduction are known, such as fragmentation, fission, polyp bailout, polyp balls, asexual brooded planulae, and embryo fragmentation. Following their pelagic phase, coral planulae must settle, metamorphose, and grow to form the next generation of adults

or juveniles, but rarely on both partly because the techniques used to investigate each stage differ (i.e., deployment of artificial substrates and observations under microscope in the laboratory for early recruits vs. in situ survey for juveniles). Consequently, the relative importance of events occurring during each of these stages remains largely unknown.

1.4 Objectives of This Chapter

Since the 1980s, several studies have been conducted on recruitment and post-settlement processes in corals that have led to major advances in our understanding of the ecology of coral populations and communities that form coral reefs. However, some critical phases of these processes have yet to be examined. The recent decline of some coral reefs and their vulnerability to future climatic changes suggest the need to develop new areas of research, not only to improve our fundamental

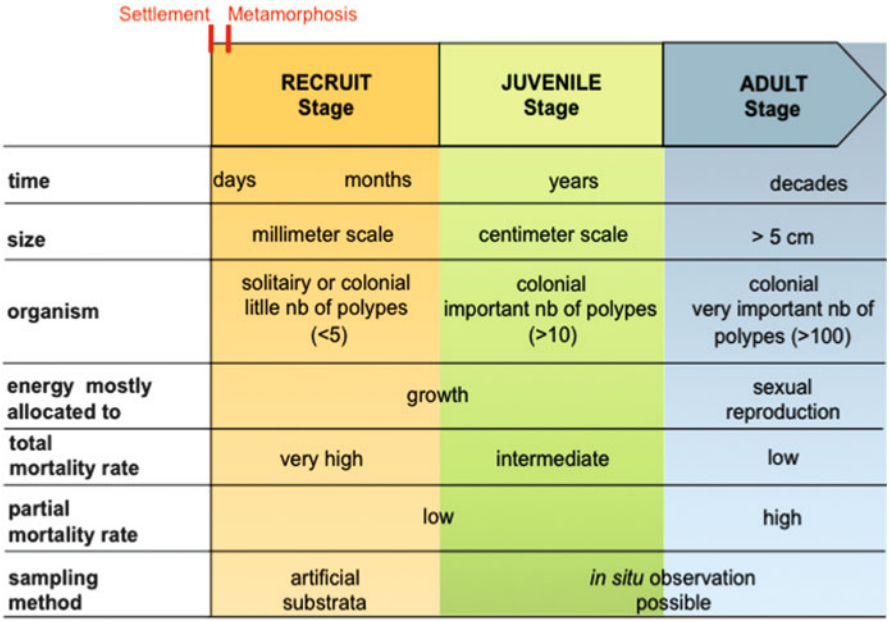

Fig. 2 Main characteristics of the recruit, juvenile, and adult phases in coral reefs. Recruits are invisible to the naked eye on natural substrata, generally aged less than 1 year, whereas juveniles are observable in situ (>1 cm) and typically aged at least 1 year. Growth and mortality are size dependent in corals. Total mortality is very high during the first months of the benthic life and decreases with increasing size of coral colonies. Large adult colonies are mainly affected by partial mortality

knowledge but also to help implement adequate conservation actions. In this chapter, we synthesize and analyze existing literature on major advances in our understanding of recruitment process in corals (variability in recruitment, post-settlement and regulation processes, importance of recruitment in recovery and resilience). Our intention is not to achieve an exhaustive review of the literature, but rather to determine the state of knowledge, identify major gaps, and suggest future lines of research.

2 Spatiotemporal Patterns of Recruitment and Major Controlling Factors

One of the most striking characteristics of coral recruitment is its strong spatial and temporal variability at almost every scale investigated. Patterns of recruitment also vary among coral taxa in relation to their life history traits. This high variability in coral recruitment is partly explained by the numerous biological and physical factors (i.e., "positive" and "negative" cues) that may influence the abundance and distribution of coral recruits.

2.1 Spatial Patterns

Marked spatial variation in recruitment patterns has been recorded at various scales, from geographic (i.e., between Indo-Pacific and Atlantic reefs; see Ritson-Williams et al. 2009) to local scales (i.e., within reefs or between sites of the same region), and even within sites, among adjacent settlement tiles, and between upper and lower surfaces of tiles (Fisk and Harriott 1990; Hughes et al. 2002; Adjeroud et al. 2007). At local scales, recruitment patterns and settlement preferences often vary with hydrodynamic and wave energy exposure and with depth gradients (Ritson-Williams et al. 2009; Edmunds et al. 2010). Some of the physical factors associated with these patterns include sedimentation, water quality, availability and composition of adequate substrate, the preference of larvae for certain wavelengths of light or substrate color, and sound (Vermeij et al. 2010; Mason et al. 2011). Biotic interactions such as predation or allelopathy may also greatly influence spatial patterns of coral recruitment (Ritson-Williams et al. 2009). In particular, competing algae may affect coral recruitment and adult distribution through space pre-emption, overgrowth, and chemical cues (Kuffner et al. 2006; Dixson et al. 2014). Conversely, some encrusting coralline algae enhance recruitment success of coral species through the production of chemical cues that induce larval settlement and metamorphosis (Ritson-Williams et al. 2009). Specifically, preferred encrusting coralline algae tend to exhibit poor antifouling defense strategy, thus providing a substratum that is suitable to early post-settlement survivorship of corals (Harrington et al. 2004). At regional scales, spatial variation in the fecundity of coral species may explain a large part of the variation in recruitment, as it was demonstrated for *Acropora* on the Great Barrier Reef (Hughes et al. 2000). In the Indo-Pacific, the oceanic island of Mo'orea and several subtropical reefs in Taiwan, Hong Kong, Gneering Shoals, or Houtman Abrolhos Islands are characterized by low recruitment rates (~40 recruits m^{-2} $year^{-1}$ at Mo'orea; Adjeroud et al. 2007) which are an order of magnitude lower than those found on tropical Western Pacific reefs (~200 to 700 recruits m^{-2} $year^{-1}$ and up to 4590 recruits m^{-2} $year^{-1}$ in the central Great Barrier Reef; Hughes et al. 1999). Moreover, the relative contribution of the different families of recruits differs highly at this scale. In Mo'orea and most subtropical reefs in the Indo-Pacific, recruits are typically dominated by Pocilloporidae (>60 %) with Acroporidae representing less than 15 %, whereas on tropical Western Pacific reefs, Acroporidae are more abundant, representing up to 85 % of the recruits (Fisk and Harriott 1990; Hughes et al. 2000). Despite the low recruitment rates and the rarity of Acroporidae recruits at Mo'orea and some subtropical reefs, adult densities and living coral cover may reach relatively high values similar to those recorded on some reefs of the GBR (Hughes et al. 2002). These results suggest that low levels of recruitment are compatible with a relatively abundant adult population for some species. One of the hypotheses to explain this outcome is that early post-settlement mortality in coral populations is particularly reduced at these reefs. Alternatively, these results may indicate a higher contribution of fragmentation, one of the several asexual reproductive modes of corals, in the maintenance of local populations of some species, which can also be a major driver in recovery after perturbations (Roth et al. 2013).

For example, recent observations suggest that populations of branching *Acropora* in French Polynesia produce a high number of fragments that possess a 90 % chance of survival and reattachment, while other species like massive *Porites* use fission and fusion processes to maintain their local populations (Kayal et al. 2015).

2.2 Temporal Changes

Monitoring surveys have all demonstrated that the density of recruits varies among seasons and years (Fisk and Harriott 1990; Adjeroud et al. 2007). This interannual and seasonal variability of coral recruitment appears to be mainly related to the spawning patterns of coral assemblages. Specifically, changes in climatic and oceanographic conditions affect the fecundity, pre-settlement mortality (which is highly weather dependent), dispersal, and early post-settlement events (Harrison and Wallace 1990). Small sublethal changes in the fecundity of corals could also result in major reductions in recruitment. These changes in coral fecundity may be caused by the effects of large-scale perturbations such as thermally induced bleaching events or chronic stressors such as water pollution, which result in the depletion of the larval pool at regional scales (Mumby 1999; Adjeroud et al. 2007). This interannual variability in fecundity, settlement rates, and post-settlement events may therefore result in “good” and “bad” years for recruitment. In fact, adult population densities seem to be the results of 10-year averages of variation in larval production and early juvenile mortality, and present-day populations probably reflect successful recruitment events that occurred years or decades earlier (Hughes et al. 1999). Some authors even suggest that some coral populations may rely on sporadic episodes of high recruitment for their maintenance and recovery (i.e., the “storage effect”; Warner and Chesson 1985).

2.3 Perspectives

Major advances have been made in characterizing the spatiotemporal patterns in coral recruitment, and the interactions of various and complex biophysical drivers of this variability have been identified for some reefs. However, the evolutionary and ecological factors that may explain the high variation in recruitment rates at geographic scales are still unclear. The link between interannual variation in fecundity, larval supply, and successful recruitment at regional scales remains poorly understood. The recent progress on coral recruitment mainly concerns a few subsets of coral taxa from a few families (mainly Acroporidae, Pocilloporidae, and Poritidae in the Indo-Pacific) indicating a critical lack of information concerning recruitment of other taxa that are also major components of adult assemblages. This is primarily due to the difficulty in identifying early coral recruits because at this stage of development, the micro-architecture of the corallum is not sufficiently developed to allow high-resolution identification (Babcock et al. 2003). It is also plausible that some coral taxa do not recruit on the artificial settlement tiles used in some recruitment surveys. These taxa may also rely on occasional episodes of high recruitment (that have few chances to be detected in classical recruitment surveys that rarely exceed 5 years) or on asexual reproduction for their maintenance. Nonetheless, efforts need to be placed on monitoring these "rarely recruiting taxa" in order to avoid over-simplifications and to allow more holistic examination of mechanisms of population regulation within coral communities. This will require the development of approaches to better discriminate early recruits (Hsu et al. 2014). Another critical information gap concerns the origin of recruits. If population genetic studies have greatly improved our knowledge on connectivity among established subpopulations of corals, the question of self- vs. allorecruitment remains open. This future line of research calls for the development of genetic tools for corals, such as the DNA parentage analysis which has been successfully applied to reef fishes. This challenging task, coupled with the monitoring of the spatiotemporal variability in recruitment rates, will provide an insight into the extent to which larvae recruit into populations on their natal reef, or are dispersed between reefs, leading to the identification of potential reef "sources" and "sinks" at regional scales.

3 Post-settlement Events, Regulation Processes, and Life Strategies

A critical step in understanding the dynamics and regulation of coral populations is to determine the relative contribution of pre- and post-settlement processes (Fig. 3). Pre-settlement processes, such as distribution and abundance of larvae, integrate regional scales (i.e., up to several hundreds of kilometers), whereas post-settlement processes like competition or predation occur at a much smaller scale (i.e., within reef habitats). As a consequence, the relative importance of pre- and post-settlement events may appear to be very different depending on the scale considered, and a high variation in mechanisms of population regulation is expected among regions. Moreover, the relative contribution of pre- and post-settlement processes in the dynamics of adult populations varies greatly among coral species within the same reef, underlying the importance of intrinsic life history strategies in mechanisms that maintain local populations.

3.1 Post-settlement Events and Regulation Processes

For many benthic organisms, rates of mortality are very high during the first days or weeks following settlement, which has significant implications on population structure, dynamics, and recovery capacity after disturbance (Gosselin and Qian 1997). However, in situ studies addressing the effects and mechanisms of positive and negative settlement cues are limited (Penin et al. 2010, 2011). This is mostly due to the very small size of newly settled coral recruits and their preference for cryptic habitats, which make their observation difficult. The major sources of mortality of early recruits are unsuitable environmental conditions, competition, and predation.

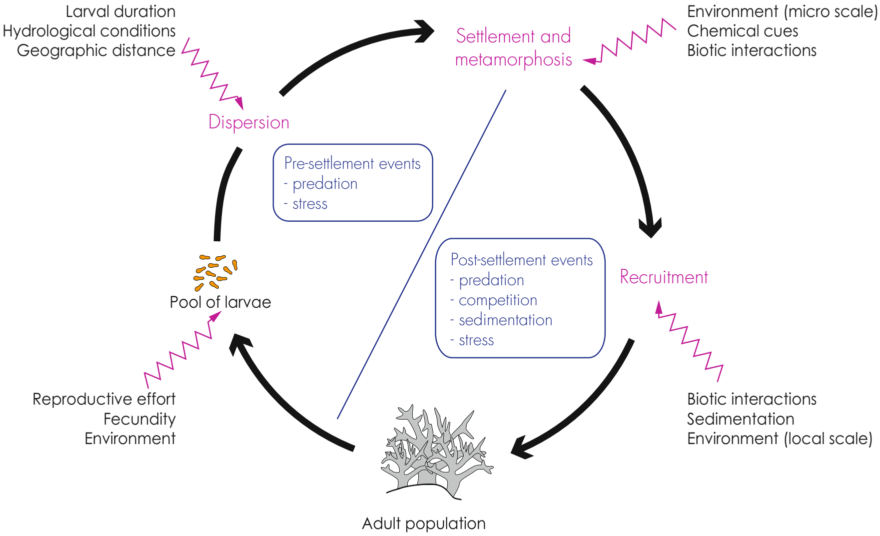

Fig. 3 Major factors influencing larval dispersal, settlement, and recruitment of corals. Dispersion patterns of larvae are largely determined by their physiology (duration of the planktonic phase, competency period, vertical distribution in the water column), the prevailing hydrological conditions (mainly hydrodynamic patterns), and geographical distances. Settlement and recruitment patterns are influenced by factors acting at the local and/or at the small spatial scales. Pre-settlement mortality is mainly due to predation by fishes, whereas predation by fishes and sea urchins is a major component of the post-settlement mortality. Competition is also playing an important role in recruitment patterns, particularly when space occupancy is high

Effects of competition on early benthic stages of corals have received little attention. However, the presence of adult corals and other benthic organisms such as turf algae has been shown to increase early post-settlement coral mortality (Ritson-Williams et al. 2009). Conversely, established coral colonies can also benefit early survivorship through creation of diverse habitats and provision of refuges from multiple stresses (Ritson-Williams et al. 2009). Sedimentation also limits early survivorship through abrasion or burial of colonies (Hunte and Wittenberg 1992), and sediment trapping can be an indirect reason for the detrimental effect of competition with turf algae (Penin et al. 2011). Since they are very small at settlement, coral recruits mostly face incidental predation linked with dislodgement by grazers during their first days or weeks of benthic life. Grazing is an important ecological process in coral reefs, benefiting corals in their competitive interactions with algae (Mumby et al. 2007). However, altering grazer abundance, through caging experiments, for example, demonstrates a potentially strong effect of incidental predation on recruitment success (Penin et al. 2011). Contrasting effects of grazing on early post-settlement survivorship have been revealed in different reefs. When grazer abundance is low, algae grow and compete with early settlers, trapping sediment thus increasing early post-settlement mortality. Conversely, high grazer abundance reduces the development of turf algae, but induces incidental predation on coral recruits. The current consensus is that the presence of macrograzers is beneficial for coral resilience, tipping the scales of coral/algal interactions in favor of corals, enhancing coral recruitment and growth, and improving recovery after disturbances (Bellwood et al. 2004; Mumby et al. 2007). However, there is a critical need to further examine the "collateral damage" made by grazers to the different life cycle stages of corals and to better understand the cost/benefit ratio of grazing processes on coral reef resilience (Rotjan and Lewis 2008).

3.2 Supply-Side Ecology

The relative contribution of early recruitment patterns and post-settlement events may vary among coral reefs. The contribution of larval supply and early recruits to the structure of the adult assemblages is evident in some situations, while post-settlement events and differential rates of post-settlement growth and mortality appear to have a stronger effect on other reef systems. Divergences between recruitment patterns and adult assemblage distribution may also be due to contrasting effects of environmental factors and perturbations on these different life stages. Mortality is size specific, and some disturbances do not have the same impact on all size classes (Kayal et al. 2015). Contrasting patterns of distribution of adults and recruits may also indicate that asexual reproduction plays an important role in population maintenance as suggested for the branching *Acropora* corals. The positive link between spatial distribution of adult and recruit abundances may be viewed as an indication of strong stock-recruitment relationships (where the adults drive the number of recruits), recruitment-limitation relationships (where recruits drive the number of adults), or as the result of preferential settlement of recruits near established adult colonies. On the contrary, strong dissimilarities in spatial patterns between recruits and adult corals have been used to argue that coral populations are not strongly regulated by patterns of recruitment, but rather are highly dynamic. Correlations between adult abundance and local densities of coral recruits are generally expected for species with short competency periods (most brooding species) or in closed systems where larvae are not dispersed far away from the natal reef. However, this relationship is likely to break down in large open systems where advection tends to mix larvae from natal and distant reefs, particularly for broadcast spawning species with long larval durations (Caley et al. 1996; Cowen et al. 2000). One of the implicit assumptions of the hypothesized recruitment-limitation relationship is that juvenile and adult patterns are temporally constant, such that current patterns of adult coral abundances were generated by patterns of recruit and juvenile abundances similar to contemporary levels. However, recruitment rates and early post-settlement mortality can fluctuate greatly among successive years (Hughes et al. 1999; Adjeroud et al. 2007). It is thus necessary to determine whether observed relationships between juvenile and adult abundances are temporally consistent through the implementation of long-term monitoring programs routinely measuring recruitment rates and juvenile abundance. Moreover, the effects of larval input on adult abundance may be difficult to detect because adult abundance reflects the accumulation of recruits over many successive cohorts and infrequent years of very high recruitment might have a disproportionate influence on adult abundance. Scientific opinion regarding the extent to which coral populations are open or closed has varied in recent decades. Since the majority of coral reefs are broadcast spawners with potentially long dispersal capacities, coral populations were largely considered open and driven by recruits from distant locations (Caley et al. 1996; Cowen et al. 2000). But recently, there has been renewed interest in the possibility that populations of a broad range of taxa, including scleractinian corals, can be remarkably closed even though they have dispersive larvae (van Oppen et al. 2008; Cowen and Sponaugle 2009). In fact, the current consensus is that populations of many marine organisms occupy a gradient from fully open to fully closed, with their position on this gradient determined by a complex assortment of biological and physical processes.

3.3 Life Strategies

Several studies underline discrepancies among coral taxa in terms of maintenance processes that are most likely linked to differences in life history traits such as reproduction strategies, stress tolerance, growth capacities, or competitive abilities, each modifying maintenance processes (Penin et al. 2010). For example, Pocilloporidae corals tend to settle in disproportionate abundance compared to other families in places like the Central Pacific and subtropical or equatorial locations, but then most likely show higher rates of early post-settlement mortality (Adjeroud et al. 2007). This may be linked to the fact that this family is represented by opportunistic genera, capable of high recruitment, but presenting high turnover and mortality. In these reefs, Pocilloporidae clearly represent the opportunistic species, with higher recruitment rates, high potential for larval dispersal and colonization, fast growing, and low resistance to perturbations. For these taxa, post-settlement events seem to be preponderant. On the opposite, taxa like massive Poritidae usually show a resistant life strategy with the production of fewer offspring endowed with a higher capacity for survival (Penin et al. 2010; Kayal et al. 2015). Their populations are characterized by slow growth, slow turnover among individuals, large-size colonies, and lower rates of decline in presence of harsh conditions and catastrophic events. For these species, higher abundance of recruits appears to lead directly to higher abundance of juveniles and adults. A third group is characterized by species displaying high aptitudes to preempt space and resources in optimal environments through faster individual growth and asexual propagation by fragmentation. This group, referred to as competitive, is illustrated by some Acroporidae species with high proportions of clonality and high susceptibility to disturbances (Kayal et al. 2012, 2015). For this group, the preponderance of recruitment or early-stage mortality in population maintenance is still unclear.

3.4 Perspectives

Understanding the relationships between recruitment and population structure is challenging in many marine systems where propagules have the potential to travel long distances and populations are structured through a diversity of pre- and post-settlement events (Caley et al. 1996; Cowen et al. 2000; Cowen and Sponaugle 2009). For corals, this area of research is relatively recent, and further studies are clearly necessary to elucidate the relative importance of larval supply and settlement and early post-settlement mortality in shaping juvenile and ultimately, adult coral assemblages. Future lines of research should clarify the contradictory role of herbivores and grazers on post-settlement survivorships of recruits and juveniles. This is a critical point as many management actions focus on reducing fishing pressures, which generally induce an increase in the densities of herbivores and grazers. Another critical step is to integrate spatiotemporal variation in coral fecundity and density-dependent interactions to adequately test the mechanisms of population regulation. Future studies would also be more effective by taking into account the size-structure of adult colonies within populations which better reflects fecundity than simply adult colony densities. At present, the great majority of coral health monitoring programs focus mainly on the interannual variability of coral cover. Integrating all the critical phases of recruitment processes (pre- and post-settlement events) in classical monitoring programs clearly represents a challenge and requires considerable sampling effort with the development of simple techniques to monitor various processes such as coral fecundity. This is clearly the most effective way to increase our knowledge on regulation of coral populations and their replenishment capacities after disturbances.

4 Recruitment, Recovery, and Resilience

Coral reefs throughout the world are increasingly threatened by a combination of various large-scale disturbances and local stressors that are exceeding their capacity for resilience. The resulting global trajectory of declining reef ecosystems is calling for the need for practical tools to estimate coral persistence. In this context, coral recruitment represents an adequate, integrated, and effort-efficient indicator of the potential of populations to replenish. In this section, we describe how quantitative information on coral recruitment and recent modeling approaches can help estimate resilience of coral populations.

4.1 Recruitment Rate as Indicator of Resilience

A major goal in coral ecology and conservation is to identify early indicators of species performances that reflect their ability to persist. Such ecological indicators of resilience should be versatile in a way that can be implemented in diverse reef environments while remaining comparable between various systems. In addition, indicators of coral health need to be relatively simple to monitor and be both cost- and effort effective. Finally, a good indicator should integrate species success in multiple steps of their life cycle since diverse large-scale disturbances and local stressors affect corals not only during their adult sessile phase but also during other life stages (Harrison and Booth 2007; Anthony et al. 2015). The recruitment process plays a fundamental role in the maintenance of coral species as it drives both the continuous turnover of individuals within established populations and the episodic replenishment of populations following mass mortality events (Hughes and Tanner 2000; Hughes et al. 2000; Doropoulos et al. 2015). The larval phase and early recruitment represent the most critical periods in the coral's life, given the high rates of per capita mortality and sensitivity to alterations in their environment. Furthermore, adult corals surviving disturbance and stress often show reduced fecundity and growth given the higher needs for energy allocation to tissue reparation and colony maintenance, subsequently resulting in decreased reproductive outputs and recruitment rates (Anthony et al. 2015). Thus, coral recruitment represents an interesting indicator of population health and capacity for replenishment, as it integrates the effects of both acute disturbances and gradual deterioration of reef conditions on multiple life stages. However, efficiency of this indicator remains to be tested, as few studies have examined the impacts of large-scale disturbances or reef degradation on the interannual variability in coral recruitment.

4.2 The Importance of Recruitment for Recovery

Following major disturbances, recovery of coral populations is often based on a combination of newly settling larval recruits and growth and propagation of surviving corals (Harrison and Booth 2007). The relative importance of larval recruitment vs. growth and regeneration of remnant corals to reef recovery is however highly system specific, as it depends on the nature and intensity of disturbances, the species composition of the considered assemblage, and the level of connectivity with adjacent fecund populations (Hughes and Tanner 2000; Doropoulos et al. 2015). In theory, maintenance of isolated populations relies more on survival and regeneration of corals across mortality events, which is locally influenced by the ability of the species to resist and respond to disturbances and the availability of refuges (Baskett et al. 2010; Anthony et al. 2015). In contrast, populations exhibiting higher recruitment rates are more likely to show higher potential for recovery and resilience from intense mortality events and recurrent disturbances (Riegl and Purkis 2009; Muko et al. 2014). However, this theoretical relationship between recruitment rates and the capacity for recovery is far from simple (Gilmour et al. 2013). For example, despite showing relatively low recruitment rates compared to other regions (Adjeroud et al. 2007), coral assemblages around Mo'orea are among the few that have shown the ability to recover from severe and recurrent disturbances (Adjeroud et al. 2009). This outcome suggests that elevated recruitment rates are not necessarily a prerequisite for population maintenance and successful recovery of reefs. Additional empirical research from diverse reef systems is required to tear apart the importance of larval recruitment and growth of remnant corals in recovery trajectories following disturbances.

4.3 How Much Recruitment for Persistence?

Despite the obvious theoretical importance of recruitment in populations replenishing, it is actually difficult to evaluate the specific recruitment threshold that can guarantee persistence of a given population. This is mostly due to the complexity of the underlying machinery that drives population dynamics and the relatively long temporal scales at which demographic processes are playing (Kayal et al. 2015). Identifying the most critical stages in species life cycle, a prerequisite for effective species management, requires robust analytical tools to efficiently account for such complexity. This is particularly the case for species with clonal life histories like most corals, with numerous population processes that potentially contribute to population maintenance (see Fig. 4 step 1). Recent advancements in computational modeling have embraced a new line of research for population studies that aim to evaluate the importance of different population processes in species dynamics and persistence. Two different types of data-based models can be distinguished, descriptive and simulative. Descriptive models transcribe ecological observations into mathematical equations, allowing estimation of patterns and testing hypothesis from empirical data (Fig. 4 step 2). Such models are commonly used to evaluate trajectories of coral populations and variability in coral performance in different population processes across time, space, taxa, and development stages and to link observed dynamics with environmental drivers. For example, patterns of coral recruitment have recently been related to the density of local populations in different reef systems (Hughes et al. 2000; Doropoulos et al. 2015; Kayal et al. 2015). Simulative models allow projecting beyond observations to test for consequences of hypothetic scenarios on future trends (Fig. 4 step 3). Such models typically use in situ observations on species dynamics and estimations of species performance in different population processes calculated from descriptive models on empirical data. Three major types of simulative models have been developed on coral population dynamics: transition matrix models (Hughes and Tanner 2000; Baskett et al. 2010; Doropoulos et al. 2015), individual-based models (Riegl and Purkis 2009; Muko et al. 2014), and integral projection models (Madin et al. 2012). These simulative approaches have notably allowed comparing the projected trajectory of coral populations with differing levels of recruitment and post-settlement regulation. In particular, sensitivity analyses constitute interesting components of simulative models, as they allow evaluating quantitatively the importance of each or any given variable in the modeled outcome. As such, implementation of sensitivity analysis in data-based models has evaluated the relative importance of recruitment, versus survival and growth at different life stages, in specific coral populations (Riegl and Purkis 2009; Muko et al. 2014; Doropoulos et al. 2015). By comparing

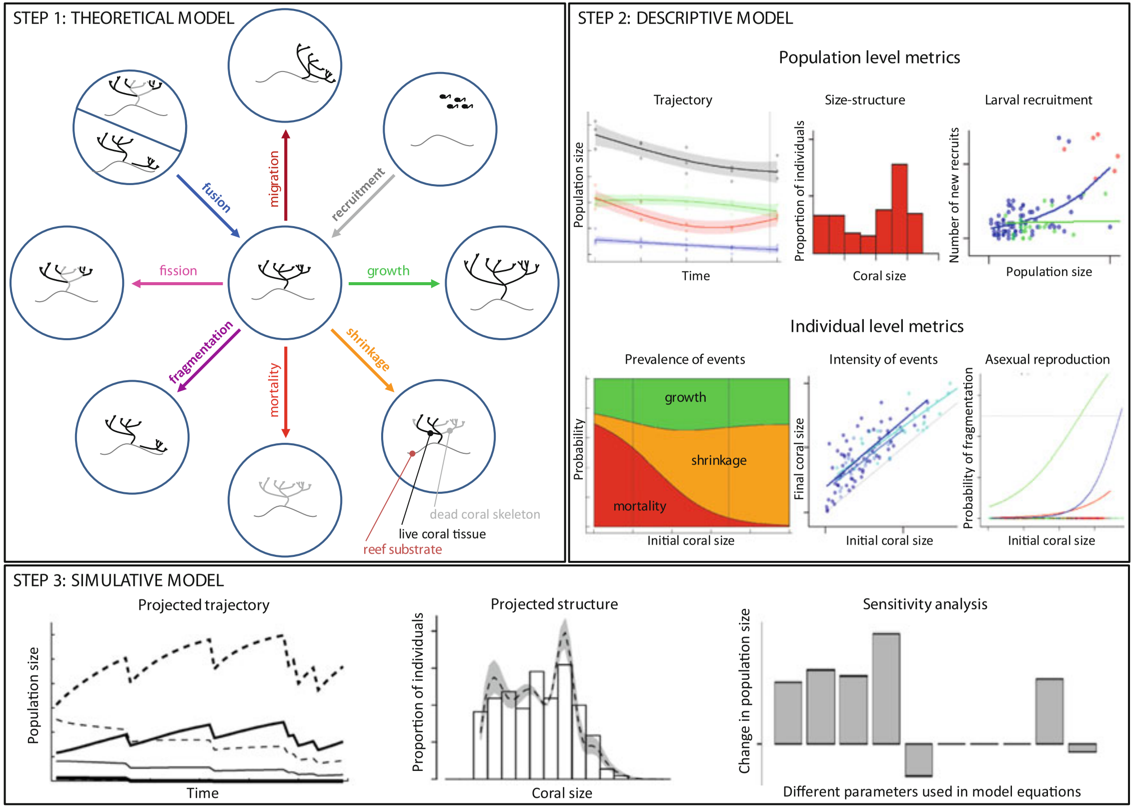

Fig. 4 Schematic illustration showing the different steps involved in quantifying the importance of recruitment and other demographic processes in coral population maintenance and future trends. The example of the construction of an integral projection model is shown here where individual coral dynamics are

observed patterns of recruitment with the estimated thresholds required for population maintenance, these approaches may greatly help to estimate resilience capacities of coral communities. Broadening the application of such models across various reefs will greatly help to identify, locally, the most critical life stages in species maintenance and the most vulnerable populations. Additionally, it will provide a more extensive understanding of how the relative importance of recruitment compared to post-recruitment processes varies with differing environments and future scenarios. However, building such population models necessitates a huge sampling effort for gathering the required amount of data on the different demographic processes and their variability (Fig. 4), which is currently only implementable in a few study systems.

4.4 Perspectives

In the present context of increasing disturbance regimes and reef degradation, quantitative knowledge on recruitment patterns can provide information on the recovery capacity of coral populations and can benefit conservation (Harrison and Booth 2007; Anthony et al. 2015). Increasing empirical data on coral recruitment in diverse reef systems will provide additional material to assess how recruitment varies across multiple disturbance events and changes in assemblage composition and reef environment. Increasing amount of quantitative data on corals is being available throughout the planet from long-term monitoring programs to short-term studies. Computational modeling is providing increasingly powerful tools that can more realistically transcribe complex ecological data and processes into powerful descriptive and simulative models (Baskett et al. 2010; Madin et al. 2012; Kayal et al. 2015). Management of coral reef ecosystems will particularly benefit from adaptive learning approaches to coral dynamics at multiple scales, from that of local assemblages to planetary dynamics (Anthony et al. 2015). Furthermore, population genetics investigations that quantify the dispersal, connectivity, and degree of openness of coral populations can greatly improve population models. Such models can be used to identify critical steps in species life cycles and develop finer indicators

Fig. 4 (continued) quantified and related to the size of the colonies constituting the population. The theoretical model in step 1 identifies the different demographic processes that contribute to coral dynamics. The complexity of this theoretical model varies with life history of the considered species. Descriptive models in step 2 are used to transcribe observed dynamics into mathematical metrics and to estimate the prevalence and intensity of each of the demographic processes as a function of individual or population size. The representativeness of this approach depends on the sampling effort, as increasing observations on individual corals allow better estimates of natural variability as captured across time, space, and development stages. Simulative models in step 3 use estimations from the descriptive models to project coral dynamics under different scenarios. Sensitivity analysis performed on these simulations allows quantifying the importance of each of the demographic processes in the dynamics of populations. Steps 1 and 2 adapted from Kayal et al. (2015), step 3 from Riegl and Purkis (2009) and Madin et al. (2012)

of population health and resilience. Moreover, resilience capacities can be better characterized through holistic multidisciplinary approaches that consider reef ecosystems in their entirety, not as simplistic single-population systems. Similarly, the dynamics of both ubiquitous and rare species needs be considered to identify ecological keystone species and to avoid system collapses and erosion of biodiversity.

5 Conclusions

Our knowledge of coral recruitment processes has greatly improved in the last three decades. However, as other complex ecological mechanisms involving a variety of intrinsic and extrinsic controlling factors acting at various scales, our understanding in this area of research is far from being sufficient in correctly addressing conservation and management issues. For several reefs and coral taxa, consistent data on the spatiotemporal patterns of recruitment rates and some of their controlling factors are now available. But this type of information should now be collected for those several coral taxa lacking data to avoid oversimplifications of mechanisms of population maintenance. Moreover, the spatial origin of locally recruiting corals is unknown, and no consistent data are available to estimate the relative contribution of auto- vs. allorecruitment in the maintenance of local populations. Similarly, the link between variation in fecundity, larval supply, and successful recruitment has been poorly addressed. Therefore, even if we intuitively feel that recruitment is an important aspect in the recovery and resilience of coral assemblages after disturbance, the underlying mechanisms remain hypothetical. Additional empirical research coupled with modeling approaches are clearly necessary to determine the importance of recruitment processes in the persistence of coral assemblages under various scenarios of future environmental changes.

By increasing our knowledge on some key phases of coral recruitment processes, more effective conservation and management actions could be implemented. For example, by determining the spatiotemporal patterns of recruitment and by identifying potential “source” and “sink” reefs, managers could identify the most effective areas to protect and the critical periods during which potential stressors should be minimized. Moreover, additional information on the contradictory role of herbivores and grazers on survivorship of recruits will also clarify the expected cascading effects of fishery management. Coral recruitment is an interesting indicator of coral reef health and resilience and should be more widely considered in monitoring surveys. This is clearly a challenging task, but given the vulnerability of coral reefs to future changes, it becomes a necessary goal for successfully managing these marine animal forests.

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6 Cross-References

▶ Complexity and Biodiversity in Caribbean Coral Reefs
▶ Corals as Architects of the Oceans
▶ Demographic Trends of Gorgonian Corals: Hints for Management and Conservation
▶ Resilience of the Animal Forest

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