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The Prevalence and Importance of Competition Among Coral Reef Fishes

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Keywords

intraspecific competition, interspecific competition, density dependence, coexistence, resource limitation, climate change

Abstract

Although competition is recognized as a core ecological process, its prevalence and importance in coral reef fish communities have been debated. Here we compile and synthesize the results of 173 experimental tests of competition from 72 publications. We show that evidence for competition is pervasive both within and between species, with 72% of intraspecific tests and 56% of interspecific tests demonstrating a demographically significant consequence of competition (e.g., a decrease in recruitment, survival, growth, or fecundity). We highlight several factors that can interact with the effects of competition and make it more difficult to detect in field experiments. In light of this evidence, we discuss the role of competition in shaping coral reef fish communities and competition's status as one of several processes that contribute to species coexistence. Finally, we consider some of the complex ways that climate change may influence competition, and we provide suggestions for future research.

1. INTRODUCTION

Competition is a fundamental process in ecology and the foundation of many classic ecological theories, from formulations of population growth to models of interacting species to explanations of coexistence and the structure of communities. It has been invoked to explain almost every spatial and temporal pattern in ecology, from local resource subdivision to global patterns in biodiversity and from the outcome of brief encounters between individuals to long-term adaptation and coevolution. Competition can be defined as the “interaction between individuals brought about by a shared requirement for a resource in limited supply, and leading to a reduction in the survivorship, growth, and/or reproduction of the competing individuals concerned” (Begon et al. 1986, p. 203). However straightforward this seems, the role of competition in ecology remains one of the most hotly debated topics in the field (Simberloff 1982, Roughgarden 1983). It has divided ecologists over key issues such as the mechanisms of coexistence and the importance of competition versus other ecological processes, density-dependent versus independent processes, and contemporary versus historical factors in ecology. Our understanding of the significance of competition has been greatly advanced by field experiments, with a large body of empirical research showing that both intra- and interspecific competition commonly influence the demographic drivers of distribution, abundance, and community structure (Connell 1983, Schoener 1983, Underwood 1986, Gurevitch et al. 1992). Although a general rule as to when and where competition is and is not important has yet to be formulated, experiments continue to refine and expand our understanding of this ubiquitous yet elusive process.

Coral reef fish communities have been fertile ground for testing established theory and developing new ideas concerning the ecological role of competition (Sale 1980, Jones 1991, Jones & McCormick 2002, Hixon 2011, Forrester 2015). Pioneering researchers in the early 1970s were fascinated by the diversity of reef fish communities and the mechanisms of coexistence under conditions of seemingly intense competition for living space. Not surprisingly, the established view from terrestrial systems—that coexistence and stability stem from competition-induced niche partitioning (MacArthur & Levins 1967)—was transposed to coral reefs (Smith & Tyler 1972, 1973). However, this theory of limiting similarity was not a comfortable fit with early observations on the ecological overlap among reef fishes and the apparent instability of reef communities. In the mid-1970s, Peter Sale (1976, 1977) proposed his lottery hypothesis as an alternative model of competitive coexistence. This novel and contentious theory argued that competing species with identical resource requirements and similar competitive abilities could coexist through chance colonization of vacant space. The theory assumes that space is a limited resource and that the first-available recruit from any species recolonizes the vacant space left when an individual dies. Debate over the importance of niche partitioning versus lottery competition dominated the early growth of this field, peaking in the early 1980s (**Figure 1**). Coral reefs provided a natural laboratory for field experiments, and the first critical tests of competition for shelter sites (Robertson & Sheldon 1979) and living space (Robertson et al. 1981) were published during this time.

Challenges to the assumption that reef fish communities are limited by the availability of space emerged during this period of intense debate. Talbot et al. (1978) proposed that disturbance and predation keep communities in a nonequilibrium state below carrying capacity, which reduces the intensity and importance of competition. In the early 1980s, another new model of reef fish population dynamics and community structure was put forward: the recruitment limitation hypothesis (Doherty 1983, Victor 1983). As with the lottery hypothesis, this idea emphasized the importance of variable recruitment, but it also argued that larval settlement is insufficient to lead to resource limitation or density-dependent population regulation resulting from competition. It was based on empirical observations of the degree to which fluctuations in recruitment drive

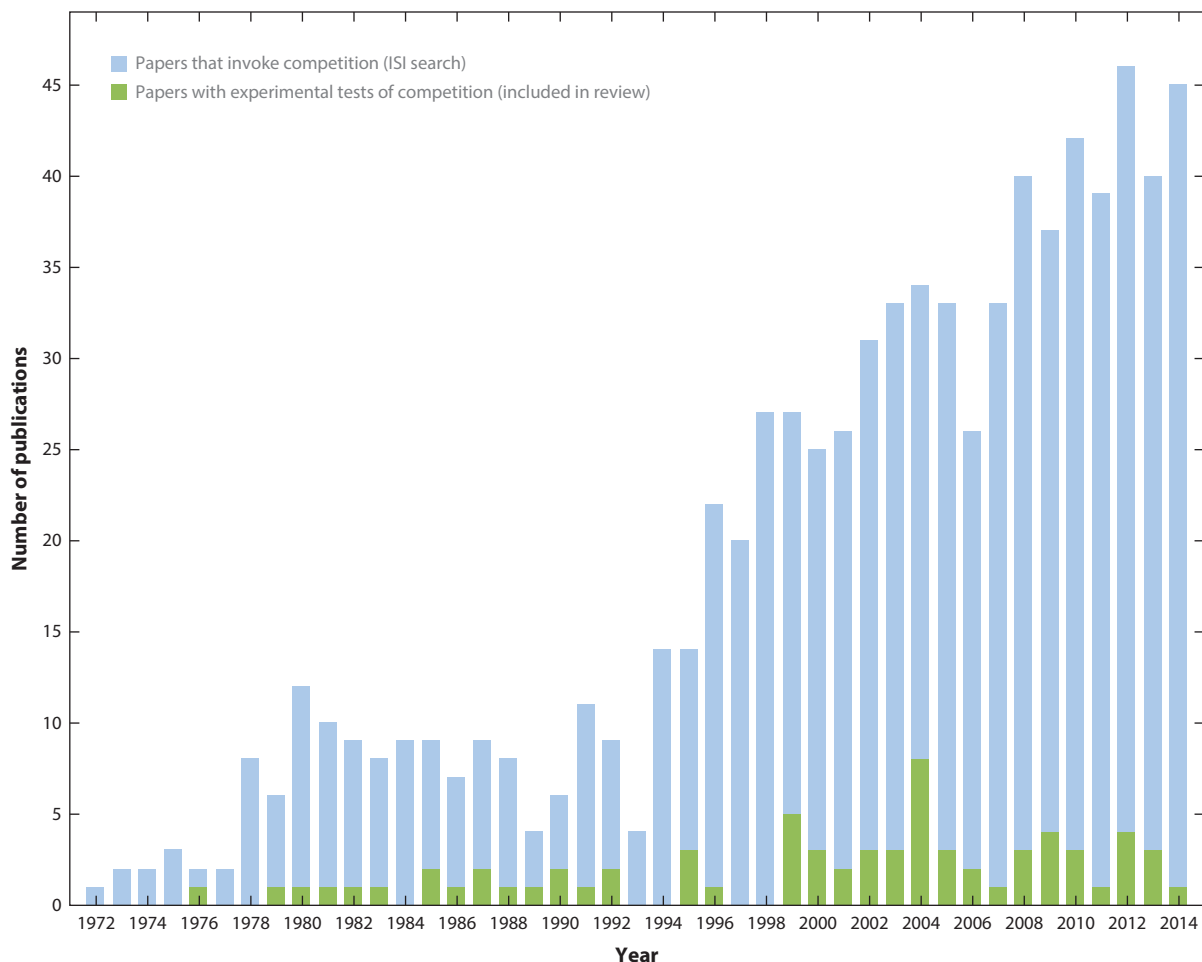


Figure 1

Trends over the past 42 years in the annual number of publications that have invoked (*blue bars*) or experimentally tested (*green bars*) competition within or among coral reef fish species. The number of papers that have invoked competition was determined through an ISI Web of Science survey using the search term [(competit* AND coral* AND reef* AND fish*) OR (resource AND partitioning AND coral* AND reef* AND fish*) OR (resource AND sharing AND coral* AND reef* AND fish*) OR (stability AND coral* AND reef* AND fish*) OR TOPIC: (space AND sharing AND coral* AND reef* AND fish*) OR (resource AND limitation AND coral* AND reef* AND fish*)] for the years 1972–2014. The results of this search were then manually filtered to exclude papers not focused on coral reef fishes, reducing the list from 1,133 to 707. The final tally ($n = 724$) includes additional references cited in the two key books on coral reef fishes (Sale 1991, 2002) that were not picked up in the survey. The number of publications that provided experimental tests of competition ($n = 72$) was determined using the criteria outlined in the review.

adult population size, as well as pioneering experiments that failed to detect evidence of inter-specific competition (Doherty 1983). By the end of the 1990s, it also became widely accepted that predation is another major factor reducing populations to below carrying capacity (Hixon 1991). During the period 1985–1995, the view that competition was rare in reef fish communities was pervasive and research attention waned (**Figure 1**). However, despite a preoccupation with recruitment and predation, studies on competition never completely ceased. This period saw the

first demonstrations of intraspecific competitive effects on survival (Jones 1987a,b) and the effects of interspecific competition on reef fish distributions (Robertson & Gaines 1986, Clarke 1989).

By the early 1990s, the dichotomous views of the past had weakened, and a pluralistic view that recruitment, predation, and competition may all interact to influence reef fish ecology gained increasing acceptance (e.g., Hixon 1991, Jones 1991). Rather than single-factor models, the next decade was dominated by discussion of the relative importance and strength of density-dependent and independent processes and their underlying causes (Jones 1990, Caley et al. 1996, Hixon & Webster 2002). Although the density-dependent effects of predation dominated the literature, the study of competition regained momentum (**Figure 1**). Evidence accumulated that competition could drive patterns of abundance and distribution across coral reef habitats (Robertson 1996), influence energetic factors such as growth and reproduction (Forrester 1990, Jones & McCormick 2002), and strongly affect mortality (Hixon & Webster 2002).

Interest in competition has continued to grow, and a large body of literature addressing this process has been published over the past 15 years (**Figure 1**). Increasing attention has been fuelled in part by the global degradation of coral reef habitats and the likely exacerbation of competition as a result of declining resources (e.g., Bonin et al. 2011). Forty years on, a review of studies on competition in reef fishes is clearly needed, one which will enable us to appreciate the diverse ways in which competition affects populations and communities and recalibrate our understanding of the significance of this process. This review provides a comprehensive synthesis of the roles of both intra- and interspecific competition in structuring coral reef fish populations and communities. Specifically, we (*a*) evaluate the different approaches from which we can reliably infer competition and compile those papers that provide adequate tests; (*b*) synthesize the evidence for both intra- and interspecific competition and the strength of these effects on key demographic parameters; (*c*) discuss how competition interacts with and may be confounded by other factors, such as habitat quality and predation; (*d*) revisit the old debates with new data, including evidence supporting early views such as resource partitioning and the lottery hypothesis; and (*e*) assess the likely future role of competition among reef fishes in a changing world.

2. WHAT CONSTITUTES GOOD EVIDENCE FOR COMPETITION?

Although theoretical and observational studies are valuable for generating predictions about the role of competition in ecological communities, manipulative experiments are necessary to provide definitive evidence (Connell 1983, Underwood 1986). Ideally, these experiments demonstrate an effect of competition on a vital demographic parameter (e.g., recruitment, survival, growth, fecundity). At the very least, they must demonstrate that competitors produce changes in patterns of abundance, distribution, or resource use that are indicative of changes to the vital parameters. The experimental approaches that can be applied fall into three general categories: competitor density manipulations, resource availability manipulations, and dominance experiments (see the sidebar, Experimental Approaches for Measuring Competition).

For this review, we thoroughly searched the literature and included studies if they met the following three criteria: (*a*) They were field- or laboratory-based experimental studies of coral reef fishes; (*b*) they involved a competitor density manipulation, resource manipulation, and/or dominance test; and (*c*) they measured a demographically significant consequence of competition (e.g., a change in abundance, distribution, resource use, recruitment, survival, growth, or fecundity). Although a total of 724 studies of reef fishes over the past four and a half decades have invoked competition, our selection criteria produced a total of only 72 papers, across at least 50 species, that provide direct experimental evidence for intra- and/or interspecific competition among coral reef fishes (**Figure 1**). Most of these papers include multiple experimental tests of


EXPERIMENTAL APPROACHES FOR MEASURING COMPETITION

In competitor density manipulations, researchers either add or remove competitors from experimental plots on natural reefs or stock them in various densities on experimental reefs. The simplest version of this type of experiment involves manipulating competitor presence/absence, but an even better approach is to establish three or more competitor density treatments, as this allows for tests of density dependence in demographic parameters. The densities chosen should reflect those that occur naturally for the study species and include treatments at the higher end of this range.

Resource availability manipulations can be useful for identifying the specific resource that is limited in a study system. The availability of a resource is either supplemented or reduced, and then changes in at least one demographic response variable are measured.

Dominance experiments involve replicated trials that place a pair of competitors together and test for dominant-subordinate relationships, as indicated by a shift in resource use by the subordinate individual in the presence of the dominant individual. Experiments that only show evidence of aggression do not provide good evidence of competition unless they also demonstrate a consequence in terms of resource use or a fitness parameter.

competition because competitive effects were tested across several species, different life history phases, or different experimental approaches. For these papers, each experimental test of competition on a focal species was cataloged on a per experiment basis for each life history stage tested. For example, if the reciprocal effects of two species on each other were tested in an experiment, this would be recorded as two separate tests of competition (one for each focal species). The resulting 173 experimental tests of competition form the basis for this review. We have compiled a database that includes information on the original citation, the type of experiment, the species and life stages, the response variables measured, and the outcome, as well as notes on the primary conclusions of the authors. This database is provided online, in both spreadsheet format (**Supplemental Table 1**; follow the **Supplemental Material** link from the Annual Reviews home page at <http://www.annualreviews.org>) and as an interactive figure (**Supplemental Figure 1**), so that it may serve as a resource for further exploration of the literature and concepts we review here.

 Supplemental Material

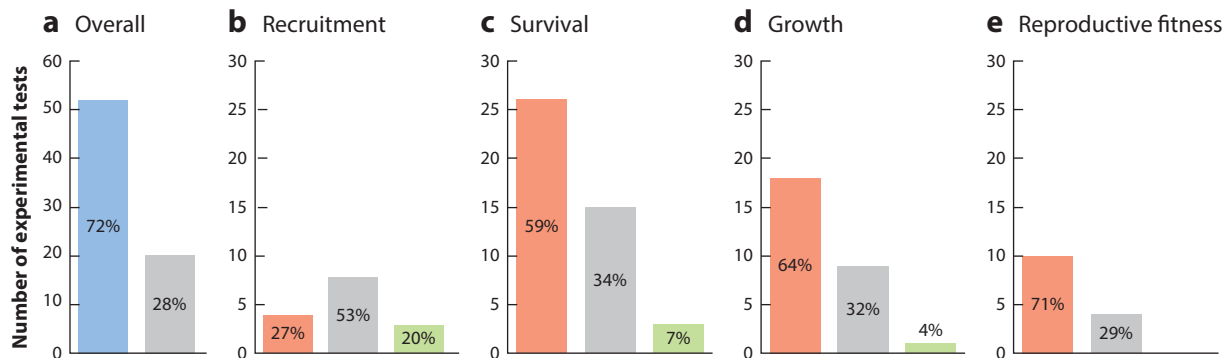
3. EVIDENCE FOR INTRASPECIFIC COMPETITION

A review of 75 experimental tests of intraspecific competition from 52 publications revealed that 72% of experiments provided evidence that this process influences the local distribution, resource use, or demographic rates of coral reef fishes (**Figure 2a**). Most experiments examined effects of intraspecific competition during the juvenile stage, either as a result of changes in the density of the juveniles themselves (30 experiments) or adult conspecifics (22 experiments). An additional 21 experiments tested for intraspecific competition among adults. Given that these experiments were conducted on 29 different focal species from five families (**Supplemental Table 1**), it is clear that reef fishes are commonly affected by intraspecific competition.

3.1. Distribution and Resource Use

Sixteen experiments explored changes in the local distribution and resource use of reef fishes resulting from competitive interactions with conspecifics (**Supplemental Table 1**). Most of these experiments demonstrated shifts in the distribution or resource use of planktivores following the manipulation of dominant competitor densities (Coates 1980, Forrester 1991, Webster & Hixon 2000, Webster 2004, Whiteman & Côté 2004). In all cases, dominance hierarchies were

Intraspecific competition



Interspecific competition

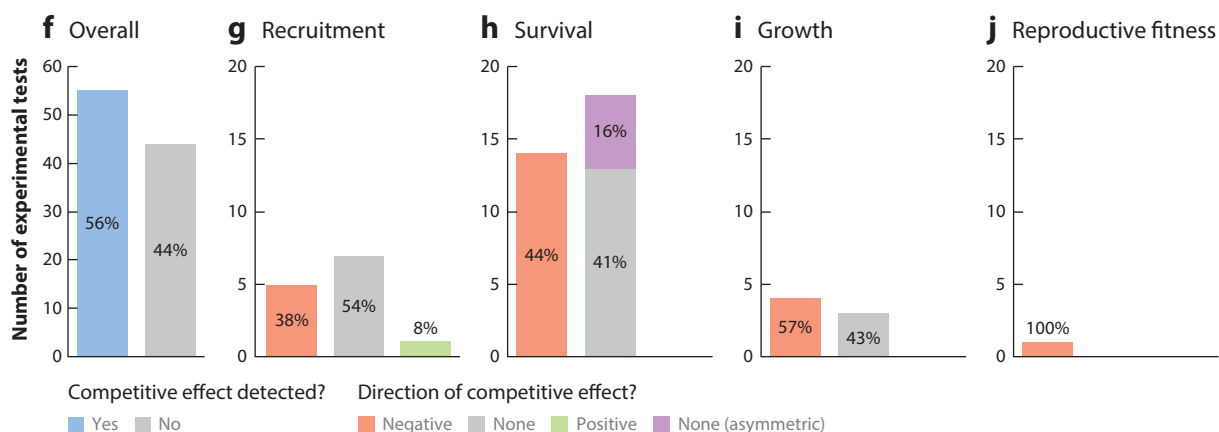


Figure 2

Summary of the evidence for intra- and interspecific competition among coral reef fishes from the 173 experimental tests included in this review. Overall counts, (a) intraspecific and (f) interspecific, indicate the number of experimental tests that found evidence of competition across all response variables (e.g., a change in abundance, distribution, resource use, recruitment, survival, growth, or fecundity). Panels b–e (intraspecific) and panels g–j (interspecific) show competition's effect on the four key demographic parameters: recruitment, survival, growth, and reproductive fitness. A negative effect (*red bar*) indicates a decline in that response variable as a result of competition, and a positive effect (*green bar*) indicates an increase in that response variable with an increased density of competitors. In the case of (b) interspecific competitive effects on survival, we distinguish between tests on a focal species that found no evidence of competition (*gray bar*) and tests in which the focal species was dominant in an asymmetric competitive pairing (*purple bar*).

established based on body size, with larger fish excluding smaller ones from access to preferred feeding positions or larger prey items. Intraspecific competitors may also exclude subordinates from accessing high-quality refuges (Buchheim & Hixon 1992, Hobbs & Munday 2004, Coker et al. 2012). For example, conspecific damselfish may compete for prime predator refuges within coral colonies (Holbrook & Schmitt 2002), and larger gobies may usurp smaller conspecifics in protective shrimp burrows (Thompson 2005).

3.2. Recruitment

Increasing evidence exists that recruitment (i.e., the input of juveniles into a population) is affected by competitive interactions with conspecifics. Since Sale (1976) first investigated this issue,

14 experiments have evaluated how competitors affect the input of new recruits. Given that recruitment is inherently difficult to measure, it is perhaps not surprising that approximately half of these experiments failed to detect an effect of intraspecific competitors (**Figure 2b**). This may indicate that resident conspecifics do not influence the settlement and/or early postsettlement mortality of some coral reef fishes (Doherty 1983, Forrester 1999, Webster 2003). However, Forrester (1995) demonstrated that recruitment patterns are sometimes strongly influenced by conspecifics, with the number of recruits of the bridled goby, *Coryphopterus glaucofraenum*, decreasing by a third across a naturally occurring range of adult densities. Although adult gobies do not appear to discourage settlement, they occupy a finite number of shelter holes, which leaves new settlers more vulnerable to predation (Forrester 1995, 1999). This negative influence of adults on the availability of shelter sites for settling juveniles has also been described for two damselfish, *Dascyllus flavicaudus* and *Dascyllus trimaculatus*; the presence of resident conspecifics reduces the density of recruits by 94% and 74%, respectively (Schmitt & Holbrook 2000). However, in some cases the presence of conspecifics may enhance rather than reduce recruitment (**Figure 2b**). Sweatman (1985) demonstrated that the presence of conspecific adults increased the number of settlers for three damselfish species, presumably because adult presence indicated a high-quality habitat.

3.3. Survival

Measured in a total of 44 experiments, survival is by far the most common response variable used to assess the effect of intraspecific competition among coral reef fishes. Although many early studies failed to detect an effect of intraspecific competitors on survival (Robertson & Sheldon 1979; Doherty 1982, 1983; Jones 1987a), two experiments by Jones (1987b, 1988) provided the first indication that intraspecific competitors could induce density-dependent mortality in reef fishes. Negative effects of conspecifics on survival have subsequently been demonstrated in 59% of experiments (**Figure 2c**). The most commonly implicated resource in competition-induced, density-dependent survival is shelter space from predators. Such competition is especially intense among small-bodied species that are closely associated with specific shelter sites, including gobies (Forrester 1995; Forrester & Steele 2000, 2004; Wilson 2005; Samhouri et al. 2009), blennies (Buchheim & Hixon 1992), wrasses (Caselle 1999), and damselfish (Schmitt & Holbrook 1999a, 2007). The death of competitors is usually attributed to predation rather than injuries sustained during interactions with competitors. Holbrook & Schmitt (2002) provided the first conclusive evidence that competitive interactions are the underlying source of density-dependent predation mortality. Infrared underwater video revealed that subordinate damselfish competitors were displaced to high-risk peripheral areas as they jostled for shelter space at the center of coral colonies. This intense competition led to density-dependent mortality because as the density of conspecifics increased, a larger proportion of individuals were displaced into shelter sites with a higher risk of predation. Although most experimental work has demonstrated negative effects of conspecifics, a small proportion of experiments (7%) have shown positive effects of conspecific density on survival (**Figure 2c**). Survivorship of the juvenile damselfishes *Dascyllus albisella* and *Pomacentrus amboinensis* was enhanced in larger groups (Jones 1988, Booth 1995). However, in both cases, increased densities of conspecifics came at the cost of reduced growth and delayed maturation, leading the authors to conclude that although group living may be beneficial, drawbacks associated with intraspecific competition do exist.

3.4. Growth and Reproduction

Of the 28 experiments that have measured intraspecific effects on growth, 64% observed negative effects of competition (**Figure 2e**). Doherty (1982) provided the first evidence that conspecific

densities could influence growth: The average body size of the damselfish *Pomacentrus wardi* is smaller in large groups than in smaller groups. By individually tagging fish, Jones (1987a,b) later confirmed that juveniles of the congener *P. amboinensis* not only grew less at higher densities but also that this translated into delayed maturation. Given that conspecifics often have a near-complete overlap in resource requirements, competition over food is frequently cited as the mechanism underlying reduced growth at increasing conspecific densities (Jones & McCormick 2002, Hixon & Jones 2005). Alternatively, several studies have demonstrated that crowded individuals expend more energy and have increased metabolic costs than less crowded fish. Fish at high densities engage more frequently in aggressive interactions, cover more distance while foraging, and spend more time searching for shelter, all of which may reduce growth (Booth 1995, Forrester et al. 2006, Johnson 2008, Samhouri 2009, Samhouri et al. 2009). A single study has described a positive effect of conspecifics on growth. In this study, the presence of larger conspecifics enhanced growth of the damselfish *Dascyllus aruanus* (Booth 2004). However, this effect was only seen on food-supplemented reefs, suggesting that conspecifics enhance growth only when food is abundant. The study is unique in that it highlights how the availability of resources may alter the strength of intraspecific competition in reef fishes.

Strong evidence also exists that intraspecific competition can influence reproduction in coral reef fishes, with 71% of 14 experiments observing reduced reproductive fitness due to competitors (**Figure 2e**). Early studies demonstrated a delay in age of maturation due to reduced growth (Jones 1987a, Forrester 1990, Booth 1995), whereas more recent experimental work has shown decreased rates of egg clutch production (Samhouri 2009, Forrester et al. 2011) and smaller clutch size (Wong et al. 2008) and larval size (McCormick 2006) when fish breed among higher densities of conspecifics. In an unprecedented 8-year study covering multiple generations of the bicolor damselfish, *Stegastes partitus*, Hixon et al. (2012) demonstrated that fecundity decreases with increasing conspecific density, but this competitive effect was mediated by habitat structural complexity. Adult damselfish living on reefs with high habitat complexity and ample refuge space from predators displayed density-dependent egg production, whereas damselfish on reefs with low habitat complexity displayed density-independent egg production.

4. EVIDENCE FOR INTERSPECIFIC COMPETITION

Because early studies failed to detect interspecific competition, the initial perception was that competition among coral reef fishes occurred primarily within species rather than between them (Jones 1991). However, our knowledge of interspecific competition among reef fishes has grown considerably and now includes information from 98 experimental tests in 34 publications (**Supplemental Table 1**). These experiments have been conducted on 39 focal species from five families. Fifty of the experiments examining interspecific competition were performed on adults (**Supplemental Figure 1**), and the remaining 48 tested the effect of interspecific competition during the juvenile stage, whether in the presence of heterospecific juveniles (29 experiments) or adults (19 experiments). More than half (56%) of these studies detected an effect of interspecific competitors on at least one demographic response variable (**Figure 2f**), which indicates that interspecific competition among reef fishes is much more prevalent than once thought.

4.1. Distribution, Abundance, and Resource Use

With 58% of 43 experiments demonstrating effects of interspecific competitors (**Supplemental Table 1**), ample evidence exists that interspecific competition can influence the spatial distribution of coral reef fishes, both across reef zones (Robertson & Gaines 1986, Robertson 1995) and

among microhabitats (Ebersole 1985, Clarke 1989, Srinivasan et al. 1999, Munday et al. 2001, McCormick & Weaver 2012). These interactions are usually highly asymmetric, with the distribution of one species in the pair strongly affected by the presence of the other but not vice versa. A removal experiment by Robertson & Gaines (1986) is a prime example. They tested competitive relationships among five species of surgeonfish that exhibited high dietary overlap and defended feeding territories along a reef slope. Of the 27 interacting species pairs, only 3 had competitive relationships that were not strongly asymmetric. In most pairings, one species was consistently more aggressive and defended territories that would otherwise be used by the subordinate species. Strong competitive asymmetries are also evident in experiments that have demonstrated effects of interspecific competitors on coral reef fish abundance (Robertson 1996; Schmitt & Holbrook 1999b, 2003; Munday et al. 2001; Holbrook & Schmitt 2004). In the first study to demonstrate interspecific competition among juvenile coral reef fishes, Schmitt & Holbrook (1999a) manipulated the presence of two coral-associated damselfishes, *D. flavicaudus* and *D. aruanus*, on experimental patch reefs and compared population growth rates after 3 months. The population size of *D. aruanus* declined by ~55% in the presence of *D. flavicaudus*, a striking result when compared with the 50% population growth observed in the absence of this competitor. By contrast, the presence of *D. aruanus* had a negligible influence on the population growth of *D. flavicaudus*, highlighting the asymmetry in this competitive pairing.

4.2. Recruitment

Since Doherty's (1983) pioneering experiment, which found no effect of the removal of the territorial damselfish *P. wardi* on the recruitment of a congener, only a handful of other studies have examined the potential for interspecific competitors to influence the recruitment of coral reef fishes. Sweatman (1985) was the first to present experimental evidence that the presence of interspecific competitors influences recruitment patterns, with the richness and abundance of an assemblage of coral reef fish recruits tending to be higher on artificial reefs without resident *D. aruanus* and *Dascyllus reticulatus* damselfish. Similarly, studies by Almany (2003, 2004) have shown that prior residence by adult damselfishes can influence the recruitment of other species. The negative effects of these prior residents on recruitment were apparent primarily for other damselfish species, whereas their effect was neutral or positive for wrasse, butterflyfish, and surgeonfish (**Figure 2g**).

4.3. Survival

As with intraspecific competition, survival is the most common demographic response variable measured to assess interspecific competition among reef fishes. Although a handful of early studies (Doherty 1982, 1983; Jones 1987b, 1988; Munday 2001) found no evidence of its effect, 44% of the 32 experimental tests to date have detected a significant negative effect of interspecific competition on the survival of a focal species (**Figure 2b**). Of the 18 experiments that did not find evidence of interspecific competition, 15% involved dominant asymmetric competitors: Although these species had strong effects on another species, reciprocal tests showed that subordinate competitors did not affect their survival (**Figure 2b**). Carr et al. (2002) found that the survival of juvenile bicolor damselfish (*S. partitus*) was density dependent only in the combined presence of congener *Stegastes leucostictus*, adult conspecifics, and predators; this suggests that interspecific competitors are important in population regulation. In this case, density-dependent mortality was induced by interference competition for shelter space with the highly aggressive beaugregory damselfish, *S. leucostictus*. Bonin et al. (2009) conclusively demonstrated an effect of an interspecific competitor on the survival of a coral reef fish. They manipulated the densities of two damselfishes with similar

microhabitat preferences and found that survival of juveniles of the damselfish *Chrysiptera parasema* (recently revised as *Chrysiptera arnaza*; Allen et al. 2010) was substantially reduced when they shared a reef microhabitat with a more dominant damselfish, *Dascyllus melanurus*. In a subsequent study of these two species, Boström-Einarsson et al. (2014) showed that per capita survival of *C. parasema* decreased with increasing density of *D. melanurus* (i.e., was density-dependent) and that this effect of interspecific competition was stronger than that of intraspecific competition. Likewise, a series of studies have shown that the presence of interspecific competitors can reduce the survival of juvenile wrasses (Geange & Stier 2009, Geange 2010, Geange et al. 2013). Notably, the outcome of competition between two wrasses depends on the sequence of their arrival onto the reef. When juveniles arrive simultaneously, *Thalassoma quinquevittatum* is the dominant competitor and the survival of *Thalassoma hardwicke* decreases by 196% in its presence. However, even if *T. hardwicke* has only 5 days prior residence, it becomes the dominant species in the pairing and decreases *T. quinquevittatum* survival by 93% (Geange & Stier 2009). Hence, the outcome and strength of competition between species may vary depending on the particular conditions under which it occurs.

4.4. Growth and Reproduction

In contrast to the burgeoning literature on survival, only eight experiments have measured sublethal effects of interspecific competition among reef fishes (**Figure 2i,j**). The first experimental tests failed to find any evidence of interspecific competitive effects on growth (Jones 1987b, 1988). However, Clarke (1992) demonstrated that competition between the spinyhead blenny, *Acanthemblemaria spinosa*, and the roughhead blenny, *Acanthemblemaria aspera*, influenced both growth and fecundity. Where these two species co-occur, the competitively dominant spinyheads exclude the roughheads from occupying shelter holes positioned higher above the substratum (Clarke 1989). These higher positions are preferred by both species because they have greater availability of planktonic food. Clarke's (1992) resource manipulation experiment showed that the consequences of occupying shelter holes closer to the substratum were a reduction in feeding rate, spawning frequency, and clutch size for both species. A subsequent aquarium experiment suggested that the lower metabolic demands of the subordinate competitors, the roughheads, allowed them to persist in the lower-quality microhabitat despite the costs of competition. To the best of our knowledge, this remains the only study to illustrate an effect of interspecific competition on reproductive fitness (**Figure 2j**), although since that time two other studies have demonstrated interspecific effects on growth. Munday (2001) found that a tradeoff in competitive ability and the magnitude of fitness consequences allowed a coral-dwelling goby that was an inferior competitor to persist in a lower-quality microhabitat, and Forrester et al. (2006) manipulated the densities of two gobies and found that the growth of both species declined with increasing densities of the other. Despite the lack of attention, interspecific competition clearly has the potential to influence growth and reproduction in coral reef fishes through competition for food.

5. THE RELATIVE STRENGTH OF INTRA- VERSUS INTERSPECIFIC COMPETITION

From our review of the literature, it is clear that both intra- and interspecific competition can significantly influence coral reef fish distribution, abundance, and demographic rates. But is one of these processes more important than the other? Comparing the strength of intra- and interspecific competition (Gurevitch et al. 1992) can provide insight into the relative importance of these processes in structuring reef fish communities. Intraspecific competition might be expected to

be more intense than interspecific competition because conspecifics exhibit greater overlap in resource use. However, when strong competitive asymmetries exist, dominant species may have greater effects on subordinate species than intraspecific competition does. Although it has long been recognized that intra- and interspecific competition should be measured simultaneously to judge their relative importance (Underwood 1986), experiments that do so are still incredibly rare in the coral reef fish literature (but see Forrester et al. 2006, Boström-Einarsson et al. 2014).

To address this knowledge gap, we calculated standardized effect sizes (Cohen's d) with 95% confidence intervals (Nakagawa & Cuthill 2007) across studies that measured competitive effects on the survival of a focal species at a particular density level in both the presence and absence of interspecific competitors. In each calculation, the estimate of survival with only conspecifics present was considered the control and the survival estimate with interspecific competitors present was designated the treatment. Positive values of d indicate that intraspecific competition was stronger than interspecific competition (i.e., survival was lower in the presence of conspecifics than in the presence of heterospecifics at that density level), and negative values of d indicate that interspecific competition was stronger than intraspecific competition (i.e., survival was lower in the presence of heterospecifics than in the presence of conspecifics). Five studies had experimental designs that permitted this comparison and reported the necessary statistics for effect size calculation. Four of these papers measured the effects of competition across several pairs of competing species or in several habitat types, yielding a total of 15 effect size values for comparison (Figure 3). For several species pairings (e.g., the wrasses *T. hardwicke* versus *T. quinquevittatum* and *Gomphosus varius* versus *T. quinquevittatum*), strong competitive asymmetries led to significantly stronger intra- or interspecific effects on survival, depending on the focal species considered. However, for most interactions (9 out of 15) the 95% confidence intervals around the effect sizes spanned zero, indicating that intraspecific and interspecific effects on survival were not significantly different in magnitude (Figure 3). This outcome is similar to that reported by Gurevitch et al. (1992), who found no difference in the strength of intra- and interspecific effect sizes in their meta-analysis of competition experiments on primary producers and carnivores. Admittedly, this is a small sample size from which to draw conclusions. The lack of experiments that have manipulated both intra- and interspecific competitors across multiple densities means a critical gap remains in our knowledge.

6. FACTORS THAT COMPLICATE THE DETECTION OF COMPETITION

6.1. Resource Identification and Limitation

Identifying the specific resources that individuals compete for can be challenging. Perhaps because of this, few of the studies we reviewed attempted to do so. Although it is possible to demonstrate that competition is occurring without identifying the underlying resource involved, a problem can arise when interpreting the results of an experiment. The authors of several studies have argued that resource limitation did not drive competition, even though they observed strong effects of competitors (e.g., Forrester et al. 2006, Geange & Stier 2009, Samhouri 2009). Their hypothesis is that behavioral interactions due to crowding, rather than a lack of resources, are the underlying cause of reduced growth or survival. This interpretation is sometimes supported by resource manipulation experiments that fail to show effects of altered resource availability. Although we agree that crowding incurs energetic costs and can increase the risk of mortality, we caution against interpretations that disregard resource limitation as the underlying cause of competition. The very behaviors that result in the observed costs of competition (e.g., increased aggression or moving farther from shelter) are motivated by the search for, acquisition of, and

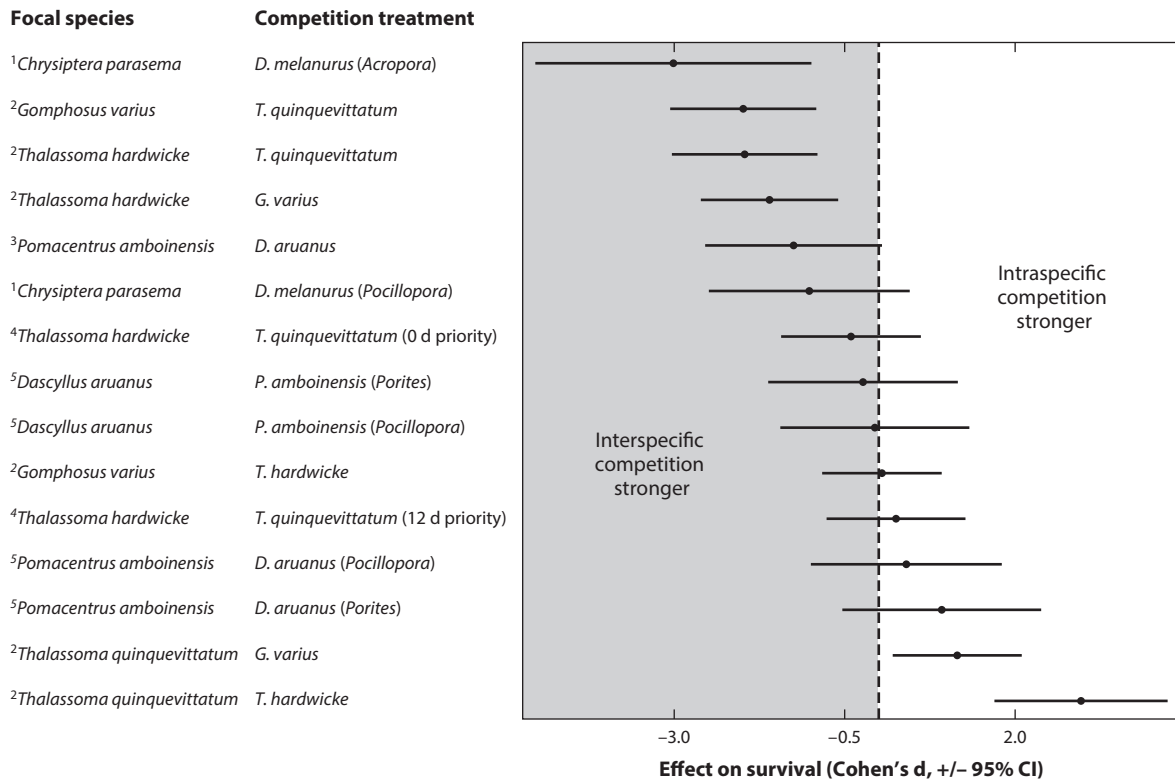


Figure 3

Standardized effect sizes [Cohen's *d*, \pm 95% confidence interval (CI)] of competition on the survival of coral reef fish species. Each effect size estimate indicates the relative strength of intra- and interspecific competition for the focal species. Negative *d* values (shaded area) indicate that the effect of interspecific competition was stronger than that of intraspecific competition. Positive *d* values indicate that the effect of intraspecific competitors was stronger than that of interspecific competitors. Effect sizes were calculated from mean and variance statistics in the following references: (1) Bonin et al. (2009), (2) Geange et al. (2013), (3) Jones (1987b), (4) Geange & Stier (2009), and (5) Jones (1988).

defense of resources. The lack of an effect in resource manipulation experiments may simply indicate that the researcher was not able to identify and manipulate the specific resource that induced competition in a system. Furthermore, resource shortage is often related to quality rather than absolute quantity. As individuals become crowded, the highest-quality parts of the resource become limited well before the resource is completely exploited. Strong competition can therefore occur well below the perceived carrying capacity of the habitat because individuals may aggregate in areas with high-quality resources (Clarke 1989, 1992). Although this makes it more difficult to manipulate resources and detect the degree of resource limitation in natural systems, resource limitation is, by its very definition, a critical component of competition.

6.2. Variation in Habitat Quality

Habitat variability is a good example of how variation in resource quality may obscure the effects of competition (e.g., Wilson & Osenberg 2002, Adam 2011). Wilson & Osenberg (2002) observed highly clumped distributions of *Gobiosoma* cleaning gobies, which created the impression that

increased densities of conspecifics may be beneficial to survival. However, subsequent experiments revealed that competition among the gobies had strong negative effects on settlement and survival once variation in habitat quality had been accounted for. Consistently higher settlement of gobies in high-quality habitat masked the negative effect of competitors. This inspired Shima & Osenberg (2003) to coin the term cryptic density dependence. This concept highlights how other processes that operate in conjunction with competition may sometimes conceal its effects. Experiments that have manipulated both habitat quality and competitor density provide further evidence that habitat can have a strong influence on the detection and strength of competition (Jones 1988, Bonin et al. 2009, Geange 2010, Geange & Stier 2010, Boström-Einarsson et al. 2014). In each of these studies, the separate and interacting effects of habitat and competitor density were isolated, and, in each case, the effect of altering habitat quality on reef fishes was stronger than the effect of changing competitor density. These stronger effects of habitat resulted from a range of different manipulations of quality—from subtle changes, such as switching to a less-preferred species of branching coral (Jones 1988, Bonin et al. 2009), to less subtle changes, such as reducing microhabitat complexity (Geange 2010, Geange & Stier 2010) or decreasing the percentage of live coral available (Boström-Einarsson et al. 2014). The only instance in which the effect of competition was stronger than the effect of altered habitat quality was when the competitor was given a 5-day prior residency advantage (e.g., Geange & Stier 2010). In fact, the effect of reduced habitat quality is sometimes so strong that the effects of competition become experimentally undetectable (Boström-Einarsson et al. 2014), which represents another form of cryptic density dependence. In this type of cryptic density dependence, the process that obscures competition may be increased predation in low-quality habitat, rather than increased juvenile settlement, as is seen in cryptic density dependence in high-quality habitat. Collectively, these studies suggest that the habitat in which competitors interact is an important factor to consider when measuring competition among reef fishes; manipulating habitat can help resolve which resources are limiting.

6.3. Predation

Predation is another factor that can muddy the water when measuring competition, especially when it comes to effects on survival. Although several previous papers have addressed the interaction between competition and predation (e.g., Gurevitch et al. 2000, Hixon & Jones 2005, White et al. 2010), it is important to raise here because competition for refuge space from predators is among the most highly studied types of competition in the reef fish literature. In some of these experiments, it is clear that competition is the ultimate process, with predators serving as the proximate agents of mortality (e.g., Carr et al. 2002, Holbrook & Schmitt 2002). However, when predators are not manipulated or monitored as part of an experiment, it can be difficult to say with certainty whether it is competition, predation, or some combination of these processes that underlies density-dependent mortality. Predators can potentially induce density dependence through an aggregative functional response, although we know very little about how prey densities influence the foraging behavior of coral reef piscivores (but see Stier et al. 2013). Another possibility is that the effects of predation may overshadow the effects of competition (Gurevitch et al. 2000), making it difficult to detect competition in short-term experiments, even when it is occurring (Hixon & Jones 2005). To date, only one long-term experiment has demonstrated that competitive effects on survival actually occur in the absence of predators. Hixon & Jones (2005) manipulated densities of *P. amboinensis* in the presence and absence of predators and found that the mortality of this damselfish became density dependent after 10 months. This effect of density occurred even where predators were excluded, which confirmed that competitors can directly influence the survival of coral reef fish over the long-term. If predator manipulation is not logistically possible in

competition experiments, data on aggression and refuge use among competitors, combined with monitoring of predator distribution and abundance across density treatments, can help researchers test a particular hypothesis about the underlying processes driving experimental results. Clearly, a deeper understanding of the interaction between competition and predation is required, and the manipulation or monitoring of predators is a necessary component of future experiments that set out to measure the effects of competition on reef fish survival.

7. COMPETITION AND COEXISTENCE IN REEF FISH COMMUNITIES

Several mechanisms may enable species to coexist in diverse communities when they are all competing for similar resources. Niche-based models of competition propose that competing species coexist through resource partitioning (Colwell & Fuentes 1975, Diamond 1978). In the presence of interspecific competitors, individuals use a different and/or narrower range of resources than they would if the competing species were absent. As a result, niche overlap is reduced and a diverse community can coexist, with each species specializing in a different portion of the available resources. Species also commonly differ in their competitive abilities. Superior competitors gain disproportionate access to the highest-quality resources and inferior competitors are forced to use less-favorable resources.

The lottery hypothesis (Sale 1977) is an alternative explanation for competitive coexistence. This hypothesis argues that competing species with identical resource requirements can coexist through the chance colonization of vacant space. Coexistence does not come about from resource partitioning but instead results from the stochastic availability of vacant space and the pool of individuals from different species that is present to occupy that space. However, a lottery for space could be ineffective at producing long-term coexistence between species without additional stabilizing mechanisms, such as environmental variation that alternately favors recruits of different species (Chesson & Warner 1981). In long-lived species, favorable recruitment events can be stored in the population age structure and thus prevent any one species from gaining a numerical advantage that would otherwise lead to the competitive exclusion of other species through time (the storage effect; Warner & Chesson 1985). Ironically, the addition of environmentally dependent recruitment fluctuations changes the stochastic lottery hypothesis into the lottery model, in which coexistence depends on some form of niche partitioning that influences the production of recruits from the different species available to settle vacant space.

Although the lottery hypothesis was first developed for coral reef fishes, limited evidence exists for this mechanism of competitive coexistence in this system (Robertson 1995). To date, just two studies (Munday 2004, Pereira et al. 2015) have provided experimental evidence consistent with a competitive lottery in a reef fish assemblage. Munday (2004) showed that two species of coral-dwelling gobies (*Gobiodon histrio* and *Gobiodon erythrospilus*) compete for access to vacant habitat space and have similar habitat preferences and competitive abilities at settlement. By contrast, most other coral reef fishes that compete for limited resources, including other coral-dwelling gobies (Munday et al. 2001), appear to coexist through some form of resource partitioning (e.g., Clarke 1992).

Theory and experimental tests of competition have often assumed that only one mechanism is responsible for the coexistence of competing species (Amarasekare 2003). Nowhere is this more evident than in reef fish ecology, in which niche-based and lottery models have often been viewed as distinct alternatives (Robertson 1995, Munday 2004). However, niche and lottery mechanisms are not mutually exclusive, and both could influence the coexistence of competing species (Chesson 2000, Gravel et al. 2006, Adler et al. 2007). In a recent study on the two goby species mentioned above, Pereira et al. (2015) found that the mechanism of coexistence switches from a lottery at

settlement to a competitive hierarchy and niche partitioning in adults. Juveniles of the two species have similar competitive ability, similar patterns of habitat use, and similar relative abundance, consistent with a lottery at settlement; however, *G. histrio* becomes a superior competitor in larger size classes. As a result, *G. erythrospilus* is forced to use a greater proportion of less-preferred habitat. The fitness loss for *G. erythrospilus* inhabiting alternative habitat is less than that of *G. histrio*, which may explain how *G. erythrospilus* can persist despite the competitive advantage of *G. histrio* in the adult stage. Indeed, our review of the literature has revealed that the strength of competition can vary through time and space, creating windows of opportunity for competing species to stake a claim on their share of available resources through a variety of different mechanisms. Modern competition theory recognizes that both stochastic and stabilizing factors, interacting with other processes such as predation and variation in habitat quality, are likely involved in the coexistence of fishes in diverse coral reef communities.

8. COMPETITION IN A CHANGING WORLD

Climate change and ocean acidification are dramatically changing marine environments and affecting the ecological processes that structure populations and communities of marine species (Harley et al. 2006). The ecological effects of these stressors may be especially severe for coral reefs because of the sensitivity of reef organisms to high temperatures and low seawater pH (Hoegh-Guldberg & Bruno 2010, Rummer et al. 2014). Climate change and ocean acidification could affect competition in coral reef fishes indirectly, through changes in the availability of habitat or other resources, or directly, by altering the competitive ability of individuals.

Coral reefs are being degraded by the combined effects of climate change, severe storms, outbreaks of crown-of-thorns starfish, and poor water quality (Gardner et al. 2003, De'ath et al. 2012). Live coral cover is declining and reef habitat is becoming less structurally complex because of the increased frequency of these disturbances. Loss of coral cover and habitat structural complexity can directly affect reef fish diversity and abundance (Jones et al. 2004, Graham et al. 2006, Pratchett et al. 2008), but how these changes affect competitive interactions within and among species is less certain. Reduced availability of resources, such as preferred habitat, might be expected to intensify the effects of intra- and interspecific competition. This could exacerbate competitive hierarchies, causing dominant competitors to gain a greater share of resources at the expense of subordinate competitors. Alternatively, competitive hierarchies could be weakened, or even reversed, if subordinate competitors perform better than dominant competitors within remaining habitats (Caley & Munday 2003).

Despite the obvious potential for the degradation of coral reef habitat to alter or exacerbate competition among reef fishes, few studies have set out to test whether this occurs. In one of the only such experimental studies conducted to date, Boström-Einarsson et al. (2014) found that reduced habitat quality had such a profound effect on two coral-dwelling fishes (*C. parasema* and *D. melanurus*) that it overwhelmed the effects of both intra- and interspecific competition. In another study, McCormick (2012) observed that mortality of a subordinate competitor, the damselfish *Pomacentrus moluccensis*, was higher on bleached and dead coral than on healthy coral in the presence of a dominant damselfish competitor, *P. amboinensis*. This suggests that habitat degradation intensified the effects of competition on the subordinate species. These two studies show that the effects of habitat loss on competitive interactions can be complex and counterintuitive and that more research is needed before reliable predictions can be made about the effect of habitat degradation on ecological processes in reef fish assemblages.

Climate change and ocean acidification could also have a direct effect on competitive interactions by altering the relative performance of different species in future environments. For

example, if one species has a narrower thermal tolerance range and is living closer to its optimum temperature than a competitor, it may suffer a steeper decline in performance and thus become a less successful competitor. Sorensen et al. (2014) found that the thermal reaction norm of hypoxia tolerance differed between two competing species of coral-dwelling gobies. This suggests that the thermally tolerant species may gain a competitive advantage in the warmer ocean temperatures of the future. Surprisingly, McCormick et al. (2013) demonstrated that ocean acidification can reverse the competitive hierarchy between the damselfishes *P. moluccensis* and *P. amboinensis*, increasing mortality in the species that is currently the competitive dominant (*P. amboinensis*) and reducing mortality in the current subordinate (*P. moluccensis*). In this case, the underlying cause of the switch in competitive dominance appears to be the sensitivity of the two species to neurological impairment caused by elevated levels of dissolved CO₂ (Nilsson et al. 2012). Projected future CO₂ levels have a greater effect on the behavior of *P. amboinensis* than that of *P. moluccensis* (Ferrari et al. 2011), which leads to a reversal in aggression and risk-taking behavior at higher CO₂ levels (McCormick et al. 2013). Such a dramatic shift in the outcome of competitive interactions could have far-reaching implications for the persistence of individual species and the structure of reef fish communities. To date, research on the effects of climate change and ocean acidification in marine ecosystems has tended to focus on individual performance (e.g., growth, survival, calcification) in single species. Future studies will need to place greater emphasis on the function of ecological processes, such as interspecific competition, if broadly applicable predictions are to be made about how these stressors will affect marine ecosystems (Gaylord et al. 2014).

9. CONCLUSIONS

Our review of the literature highlights the wealth of experimental evidence in support of competition as a process that structures populations and communities of coral reef fishes. Intra- and interspecific competitors can alter patterns of distribution, abundance, and resource use and also exert a significant influence on the demographic drivers that regulate populations. Clearly, it is time to move beyond the debates of the past about whether competition occurs and to embrace the pluralistic notion that competition is one of many factors that shape reef communities. Other factors, such as predation, habitat variability, and environmental change, also play a role. The challenge ahead is to better understand the particular conditions under which competition will (or will not) exert a strong influence.

Over the past 40 years, experiments have helped us appreciate the importance of competition for resources in shaping coral reef fish communities. In an era of rapid environmental change and declining resources, continuing to expand our knowledge of this fundamental process has never been more imperative.

FUTURE ISSUES

1. Variation in the strength of competition across gradients in resource quality should be explored. Future experiments that simultaneously manipulate competitor density and resource quality on coral reefs will help to identify the specific resources that limit populations and increase knowledge about how competitive interactions change as resource quality declines. The calculation of effect sizes will aid in comparing the strength of competition across resource gradients within and between studies.

2. Temporal variation in the strength of competition needs to be examined. Most studies have measured variation in the strength of competition spatially; very few have explored variation over time (e.g., Schmitt & Holbrook 2007, Forrester et al. 2008, Hixon et al. 2012). However, it is temporal density dependence that stabilizes populations, and estimates of variation in the strength of competition over time are necessary to truly assess its role in regulating coral reef fish populations.
3. Research on competitive interaction networks should be expanded. Most experimental research on competition among reef fishes has involved measuring pairwise interactions, even though competitors are embedded within a community of interacting species. Experiments that measure variation in the strength of competition among groups of species with similar resource requirements will provide greater insight into mechanisms of competitive coexistence in these diverse communities.
4. Competition research needs to be extended to important functional groups. Competition experiments have almost exclusively been conducted on small-bodied reef fish species: 80% of the experiments reviewed here involved damselfish, wrasse, or gobies. As a result, our current knowledge of competition comes from a limited subset of the coral reef fish community. We still know very little about competition's effects on populations of larger-bodied coral reef herbivores and predators. Although experimental manipulations of the density and resources of larger and more mobile species will be challenging, they are critical for expanding our knowledge of the processes regulating populations of fishes that play such an important role in the health and function of coral reef ecosystems.

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