

60 YEARS OF CORAL REEF FISH ECOLOGY: PAST, PRESENT, FUTURE

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ABSTRACT

Revisiting the past 60 yrs of studies of the ecology of fishes on coral reefs reveals successive decadal trends that highlight many lasting contributions relevant to fisheries biology, conservation biology, and ecology in general. The *Bulletin of Marine Science* was founded in 1951, about the same time SCUBA was first used to study reef fishes, so the 1950s was a decade of initial subtidal exploration by early pioneers. Detailed natural-history investigations of the use of space, food, and time by reef fishes developed in the 1960s, including studies based from undersea habitats late that decade. The 1970s saw the first comprehensive observational studies of reef-fish communities, as well as initial breakthroughs in behavioral ecology, especially regarding cleaning symbiosis, mating systems, and sex reversal. In community ecology, the conventional wisdom—that interspecific competition structured reef-fish assemblages via equilibrium dynamics and resource partitioning—was called into question by the “lottery hypothesis,” which posited that coexistence of ecologically similar species was fostered by nonequilibrium dynamics. The 1980s, in turn, were dominated by debate regarding the relative importance of larval supply vs post-settlement interactions in determining the local abundance and diversity of reef fishes. The “recruitment limitation hypothesis” asserted that larval settlement was so low that subsequent population dynamics were not only unpredictable, but also density-independent. Population and community studies during the 1990s thus focused largely on detecting demographic density dependence in reef-fish populations and identifying the mechanisms underlying this ultimate source of population regulation. From the 1980s to the present, studies of behavioral ecology and interactions between fishes and other reef organisms continued to flourish. Late in the 20th century, it became clear that coral reefs and their fish inhabitants were increasingly threatened, and conservation biology of reef fishes developed as a substantial new subdiscipline. The 2000s comprised the “connectivity” decade as new means of tracking patterns of larval dispersal developed. Knowledge of how larval dispersal connects local populations and/or results in self-recruitment that replenishes a local population is essential for understanding metapopulation dynamics and implementing effective fisheries management and conservation efforts. There is currently a major shift toward conservation biology among many reef-fish ecologists, including studies of the effects of and solutions for overfishing, habitat degradation, invasive species, ocean warming and acidification, and other human-caused environmental challenges. Marine reserves and protected areas are now well documented to be particularly effective at fostering both ecological resilience in general and fisheries sustainability on coral reefs. Future research must necessarily be conservation-based if there are to be any reasonably undisturbed reef-fish communities for coming generations of ecologists to study. I personally believe that those of us who have observed the demise of coral reefs first-hand have two major responsibilities: first, conduct basic or applied research indirectly or directly relevant to conservation of reef fishes, and second, speak out as both citizens and scientists to bear witness to these losses, which are largely unseen by the public, and assist managers and policymakers in saving our remaining reefs.

Fishes are perhaps the most conspicuous and certainly among the most fascinating mobile species on coral reefs. Their local diversity (often 100s of species) and especially their global richness (some 8000 species, Bellwood et al. 2011) can be overwhelming, and the variety manifested in their morphology, behavior, and ecology is truly awe-inspiring. Studies of reef fishes have contributed immensely to the general sciences of ecology, behavior, fisheries biology, and conservation biology by serving as model species (review volumes¹ by Sale 1991, 2002). These contributions are due to the fact that reef fishes are among the most observable and diverse assemblages of vertebrates on the planet, and are ideal for controlled field experiments, as well as long-term observations. General ecological concepts that developed from studies of reef fishes and reviewed here include the lottery hypothesis, the storage effect, the recruitment limitation hypothesis, the size-advantage model, diffuse predation, synergistic predation, and cryptic density dependence, among others.

Importantly, reef fishes account for about 10% of the global fisheries catch and are the major source of protein for many island nations (review by Polunin and Roberts 1996, and papers therein). Unfortunately, the rich cornucopia of reef fishes is now threatened by a broad variety of deleterious human activities, making conservation biology the latest focus of research efforts (reviews by Birkeland 1997, and papers therein; Côté and Reynolds 2006, and papers therein; Helfman 2007).

This is a historical overview of the ecology of fishes on coral reefs over the past 60 yrs, with a brief predictive glimpse of the future. This review is not comprehensive, but rather focuses on what I perceive to be some the most exciting discoveries, advances, and issues in behavioral, population, and community ecology of reef fishes over the decades. For brevity, I exclude important related topics, such as physiological ecology, ethology and behavior *per se*, evolution, zoogeography, and fisheries ecology. My perspective is that of an American population, community, and conservation ecologist who has worked only in the Atlantic and Pacific Oceans, so my expertise and experience are incomplete, especially regarding non-English literature. From the 1970s onward, there has been an explosion of field studies of coral reef fishes, so I cite exemplary publications among a rich scientific literature that I believe should be explored much more thoroughly by all practitioners, young and old. If nothing else, I hope that the publications cited herein provide a useful entry to the literature on reef-fish ecology—published mostly in major journals through 2010—for those new to the field.

As we revisit past decades, it seems clear that reef-fish ecology is a healthy discipline, portions of which have undergone phases typical of many sciences: early development, mid-life controversy, later-life consensus, and importantly, constant evolution. With a touch of nostalgia, I have named most decades for the concepts that were prominent in reef-fish population and community ecology at the time.

1950S: THE EARLY EXPLORATION DECADE

Although many indigenous cultures have vast traditional ecological knowledge of coral reef fishes (Johannes 1978a, 1981), and western natural history studies extend back to the time of Darwin, there were very few peer-reviewed publications regarding

¹ Note that individual chapters in books referenced here, as well as individual papers in proceedings, are not cited herein. Please refer to the cited volumes for individual contributions.

reef fish ecology before the use of SCUBA became widespread (early reviews by Ehrlich 1975, Sale 1980a). A classic ecological investigation predating the 1950s was Al-Hussaini's (1947) pioneering study of food habits of Red Sea fishes. Typical of marine journals of the time, during the entire 1950s there were only three bonafide ecological studies of coral reef fishes published in the *Bulletin of Marine Science of the Gulf and Caribbean* (which was founded in 1951):² a survey of shorefishes from Puerto Rico (Erdman 1956), a review of the ecology of ciguatera fish poisoning (Randall 1958), and a life-history study of a squirrelfish (McKenney 1959).

Invented by Jacques Cousteau and Emile Gagnan in the early 1940s, SCUBA allowed scientists to fulfill the dream of studying reef fishes unconstrained in situ. However, it took a few brave souls within the marine science community to get the proverbial ball rolling. One of the first underwater reef-fish ecologists in the United States was Conrad Limbaugh, who introduced scientific SCUBA diving to UCLA in 1949 and to Scripps Institution of Oceanography in 1950 (Price 2008). Limbaugh conducted some of the first investigations of cleaning symbiosis among coral reef fishes, mostly published posthumously following his untimely death in 1960 (Limbaugh 1961, Limbaugh et al. 1961). Also pioneering the behavioral ecology of reef fishes were Winn and Bardach's (1957) descriptions of intersexual behavior of parrotfishes, Bardach's (1958) tagging study of reef-fish movements, Winn and Bardach's (1959) and Bardach et al.'s (1959) investigations of feeding behavior of moray eels, and Randall and Randall's (1960) field descriptions of mimicry in various species.

The first major studies of the community and ecosystem ecology of reef fishes were also conducted during the 1950s, precursors of research that would proliferate during the coming decades. These studies included Odum and Odum's (1955) assessment of energy flow through a Pacific coral reef food web, Bardach's (1959) estimates of the standing crop of fishes on a Bermuda reef, Hiatt and Strasburg's (1960) documentation of food-web structure and resource partitioning (differential use of food and space among species) of reef fishes of the Marshall Islands, and Randall and Brock's (1960) descriptions of diet and habitat of Pacific groupers and snappers. The decade ended with the study of reef-fish ecology gaining steady momentum.

1960s: THE NATURAL HISTORY DECADE

It was during the 1960s that natural history studies of coral reef fishes began to flourish, which provided the essential foundation for future ecological studies. This was the early heyday of a pioneering undersea fish ecologist I consider to be one the four cornerstones of the discipline during the 20th century: Jack Randall (Greenfield 2001, Fig. 1A). Though much of Randall's career has focused on taxonomy, he conducted among the first detailed studies of the ecology of reef fishes in both the Pacific and the Caribbean during the late 1950s and early 1960s. This work included use of exclusion cages to demonstrate intensive grazing by herbivores (Randall 1961), use of artificial reefs to show that reef-based species create grazing halos around reefs in seagrass beds (Randall 1963, 1965), a comprehensive study of food habits that is still regularly cited (Randall 1967), and a classic book on Caribbean reef fishes that includes much ecological information (Randall 1968, and subsequent editions). In

² The *Bulletin of Marine Science of the Gulf and Caribbean* changed its name in 1965 (volume 25) to *Bulletin of Marine Science*.

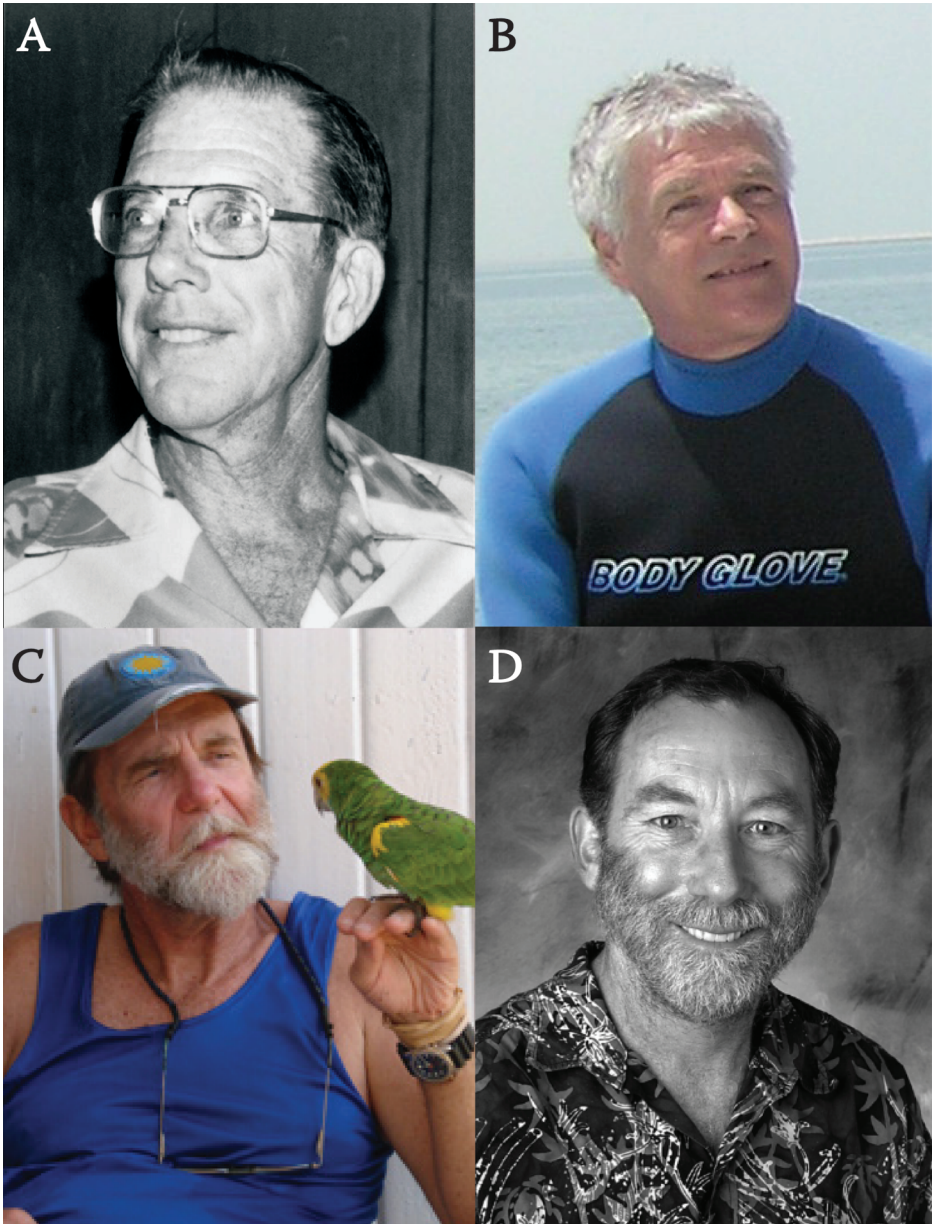


Figure 1. The author's choice of the four foundational cornerstones of 20th century coral reef fish ecology: (A) John E (Jack) Randall, (B) Peter F Sale, (C) D Ross Robertson, and (D) Robert R (Bob) Warner.

the Pacific, Ted Hobson began his long career studying the ecology of predatory reef fishes (Hobson 1963, 1965), later conducting exhaustive studies of reef-fish diets and day-night transitions in Hawaii (Hobson 1972, 1974), as well as fish-zooplankton interactions in the Marshall Islands (Hobson and Chess 1978).

It was also during the 1960s that manned undersea habitats were in vogue. The most relevant to studies of reef fishes were the two Tektite expeditions at Lameshur

Bay, St. John, US Virgin Islands, during 1969 and 1970 (Collette and Earle 1972). Among a variety of studies were those that described day-night transitions in fish communities (Collette and Talbot 1972, previously pioneered by Starck and Davis 1966), and documented spatial partitioning among reef fishes (Smith and Tyler 1972, previously pioneered by Gosline 1965). By the end of the 1960s, the science of reef-fish ecology was heading toward explosive growth.

1970s: THE LOTTERY DECADE

COMMUNITY ECOLOGY.—Studies by Smith and Tyler (1972) exemplified the general direction of community ecology at the time: field observations of between-species differences in resource use (space, food, and by extension, time) and attribution of those differences to niche diversification due to interspecific competition (Schoener 1974). The ultimate question driving such studies was how so many similar species can co-exist in the same habitat without a dominant competitor excluding most other species. Given the immense species richness of reef fishes within most any ecological guild, documenting resource partitioning became a major thrust of reef-fish studies in the 1970s (reviews by Ross 1986, Ebeling and Hixon in Sale 1991).

As the decade progressed, a pioneer I believe to be the second foundational pillar of reef-fish ecology emerged as a creative leader in the field: Peter Sale (Fig. 1B). Sale's (1974, 1977, 1978, 1980b) studies of territorial damselfishes on the Great Barrier Reef suggested that these species indeed compete, but that they are often more ecological equivalents than they are niche diversifiers. Sale's "lottery hypothesis" posited that random mortality events combined with random gain and loss of living space means that no single species has a competitive advantage. Thus, the unpredictability of local dynamics and spatial patterns maintains local species richness. At the time a source of major controversy, the lottery hypothesis stimulated intensive research on the population and community ecology of reef fishes in general. Compendia of studies included special issues of *Environmental Biology of Fishes* (Helfman 1978) and the *Bulletin of Marine Science* (Emery and Thresher 1980).

BEHAVIORAL ECOLOGY.—The 1970s saw major advancements in understanding reproductive ecology and cleaning symbiosis of reef fishes. Many studies focused on sex reversal in the context of mating systems and sexual selection, with detailed investigations of male-dominated harem species (e.g., Robertson 1972, Warner 1975, Warner et al. 1975, Fricke and Fricke 1977, see also Shapiro 1979, 1980). A common pattern among wrasses and parrotfishes is that the loss of the dominant male stimulates the largest female in the harem to change sex, although there are fascinating variations and alternate reproductive strategies. Much of the work published on reef-fish reproductive ecology during the decade was later reviewed in Thresher's (1984) book. Ross Robertson and Bob Warner, among the first to describe these patterns, were to go on to become who I believe to be the third and fourth cornerstones of the discipline during the 20th century, as evidenced by their many papers cited throughout this review (Fig. 1C,D).

Following Limbaugh's (1961) and Youngbluth's (1968) early explorations, multiple studies led by George Losey deepened understanding of cleaning symbioses (e.g., Losey 1972, 1979, Losey and Margules 1974). One prominent finding was that host

fish are attracted to cleaning stations as much by tactile simulation as by parasite removal.

Studies of territoriality (defense of resources within specific areas) also expanded during the 1970s (reviews by Reese and Lighter 1978, Grant 1997), including such topics as "serial territories" (Myrberg and Thresher 1974) and schooling as a mechanism of successfully invading territories (Robertson et al. 1976).

The growth of reef-fish ecology during the 1970s was reflected in the appearance and proliferation of new outlets for publications. The *Environmental Biology of Fishes* was founded in 1976 and has frequently published papers about coral reef fishes. Another growing source of reef-fish literature was the *Proceedings of the International Coral Reef Symposium*, published about every 4 yrs following each symposium. By the end of the 1970s, the ecology of fishes on coral reefs was clearly recognized as a bonafide subdiscipline and source of novel concepts within the broader science of ecology.

1980s: THE RECRUITMENT DECADE

POPULATION AND COMMUNITY ECOLOGY.—Before debate regarding the lottery hypothesis could subside (e.g., Anderson et al. 1981, Chesson and Warner 1981, Ogden and Ebersole 1981, Robertson et al. 1981, Greenfield and Greenfield 1982, Sale 1982, 1988, Sale and Williams 1982, Gladfelter and Johnson 1983, Abrams 1984, Robertson 1984, Chesson 1985, Ebersole 1985, Findley and Findley 1985, Bouchon-Navaro 1986, Robertson and Gaines 1986, Roberts 1987, Clarke 1988), a new idea emerged that shook the conventional wisdom of reef-fish ecology still further. In a seminal paper, Peter Doherty (1981) suggested that competition may not be pervasive as an organizing process in reef-fish population and community structure. Rather, larval mortality may be so high, and subsequent settlement (transition from pelagic to reef habitats) so low, that local populations of juveniles and adults never reach sizes where competition and other density-dependent processes come into play substantially. The key prediction of this "recruitment limitation hypothesis" was that reef-fish dynamics are density-independent (i.e., that settlement, mortality, growth, and reproduction do not vary as a function of local population size). A variety of observational studies at the time were consistent with this hypothesis (e.g., Doherty 1983, Victor 1983, 1986b, reviews by Doherty and Williams 1988, Mapstone and Fowler 1988, Doherty in Sale 1990, Doherty in Sale 2002), setting the stage for controversy that ultimately persisted through the decade (e.g., Shulman et al. 1983, Shulman and Ogden 1987, Robertson 1988, Warner and Hughes 1988) and beyond.

Ultimately, and despite debate among reef-fish scientists, both the lottery hypothesis and the recruitment-limitation hypothesis eventually found relevance in non-fish systems, including marine invertebrates (e.g., Gaines and Roughgarden 1985, Hughes 1990) and terrestrial plants (e.g., Tilman 1997, Clark et al. 1998). One slant on competitive lotteries was Warner and Chesson's (1985) "storage effect," where persistence of populations and coexistence of competing species is fostered by long-lived adults that outlive periods of poor recruitment. The storage effect was another concept based largely on reef-fish studies that ultimately contributed to the ecology of other systems (e.g., Cáceres 1997). In any case, *recruitment* clearly became the bandwagon word of the decade (reviews by Sale 1990, Kaufman et al. 1992, Booth and Brosnan 1995).

Importantly, the new focus on recruitment fostered a long-neglected area of study: the ecology of reef-fish larvae (Richards and Lindeman 1987). Identification guides to larvae appeared (e.g., Leis and Rennis 1983, Leis and Trnski 1989). Explanations of the adaptive significance of larval dispersal were debated (e.g., Johannes 1978b, Barlow 1981, Doherty et al. 1985, Shapiro et al. 1988, Lobel 1989). Measuring pelagic larval durations by counting daily growth rings on otoliths (ear stones) became widespread (e.g., Brothers et al. 1983, Victor 1986a, Wellington and Victor 1989). Distributional studies of larvae at sea intensified (e.g., Leis 1983, 1986, Leis and Goldman 1987). Exploration of factors affecting settlement and recruitment began in earnest (e.g., Shulman 1985a, Sweatman 1983, 1985, 1988, McFarland et al. 1985, Jones 1987), including studies of linkages between cycles of spawning and subsequent recruitment (e.g., Robertson et al. 1988, 1990, Robertson 1990).

Of particular interest was the role of habitat structure and shelter in the recruitment process and the subsequent structure of communities of reef fishes (e.g., Shulman et al. 1983, Bell and Galzin 1984, Kaufman and Ebersole 1984, Sale et al. 1984, Shulman 1985b). It was found that when the relationship between corals and fishes was strong, coral mortality and damage to reefs adversely affected the distribution and abundance of fishes (e.g., Reese 1981, Harmelin-Vivien and Bouchon-Navaro 1983, Kaufman 1983, Sano et al. 1984, Wellington and Victor 1985, but see Walsh 1983). As the decade progressed, it was clear that overfishing was also a growing threat to populations of coral reef fishes (e.g., Russ and Alcala 1989), leading to the first scientific studies of marine reserves as conservation and management tools on coral reefs (e.g., Russ 1989).

It was during the 1980s that field studies of reciprocal effects between herbivorous reef fishes and reef benthos came to maturity. Topics included: effects of herbivores on local species diversity and community structure of macroalgae (e.g., Hay 1981, Hay et al. 1983, Hixon and Brostoff 1983, Lewis 1986, see also Hixon and Brostoff 1996), effects of algal defenses on herbivores (e.g., Littler et al. 1983, Hay et al. 1987, 1988, Paul and Hay 1986, Paul 1987), competition between fishes and urchins (e.g., Williams 1981, Sammarco and Williams 1982, Hay and Taylor 1985), interspecific interactions among herbivorous fishes (e.g., Robertson and Polunin 1981), indirect effects of herbivory on corals (e.g., Wellington 1982), and the relative effects of fishes vs invertebrate grazers (e.g., Carpenter 1986, Morrison 1988), among others. Such studies would continue into the following decades (review by Hay 1997).

A fascinating finding during this decade was that the excrement of reef fishes not only feeds other fishes (Bailey and Robertson 1982, Robertson 1982), but also fertilizes the reef (Meyer et al. 1983, Meyer and Schultz 1985a,b), helping to explain the high productivity of coral reefs in nutrient-poor waters. Building on prior food-habits studies, Polovina (1984) constructed one of the first food-web models of a coral reef (see also Longhurst and Pauly 1987).

BEHAVIORAL ECOLOGY.—The 1980s saw continued advances in understanding the reproductive ecology of reef fishes, including inter-oceanic variation in egg size (e.g., Thresher 1982), sexual selection (e.g., Warner 1984), territoriality and mating systems (e.g., Robertson 1981, Warner 1988b, Clifton 1989), and the mechanisms of sex reversal (e.g., Shapiro 1980, Ross et al. 1983), including a high-profile debate regarding the popular size-advantage model of sex reversal (Warner 1988a, Shapiro 1989). The decade closed with a symposium on butterflyfishes that compiled the state of knowl-

edge on the behavioral ecology and all other biological and ecological aspects of this prominent family of reef fishes (Motta 1989).

1990s: THE DENSITY DEPENDENCE DECADE

The 1990s started with the first comprehensive edited volume on the ecology of fishes on coral reefs (Sale 1991), which broadly reviewed the state of the discipline through the 1980s and stimulated much research during the 1990s and beyond (see also Montgomery 1990). Especially evident during this decade were advances in field methods, including larval collectors of various designs (Choat et al. 1993, Shenker et al. 1993, Dufour et al. 1996), physical tags for smaller reef fishes (Buckley et al. 1994, Beukers et al. 1995, Frederick 1997, Malone et al. 1999), and acoustic telemetry tags for larger species (Holland et al. 1996).

POPULATION AND COMMUNITY ECOLOGY.—Debate over recruitment limitation reached its peak then subsided during the 1990s. The most extreme form of the recruitment limitation hypothesis (Doherty 1998) denied the existence of any form of demographic density dependence (per capita death rate increasing and/or birth rate—growth, fecundity, etc.—decreasing as population size increases), even though the concept originally focused only on competition (Doherty 1981). However, density dependence can also be caused by predation and, in any case, is necessary by definition for any population to be regulated, i.e., to persist over many generations while undergoing bounded fluctuations and return tendency from both low and high levels (review by Hixon et al. 2002). Geoff Jones (1990) was among the first to show that low rates of larval settlement manifest recruitment limitation, whereas higher rates result in density-dependent dynamics. Despite this and other early demonstrations of density dependence in recruitment (Stimson 1990) and mortality (Jones 1987, 1988, Forrester 1990), controversy persisted. Following publication of Doherty and Fowler's (1994a,b) reportedly definitive empirical demonstration of recruitment limitation in Great Barrier Reef damselfish, Caley et al. (1996) published a broad-based critique of the presumed evidence for recruitment limitation. A symposium on the controversy was convened in Australia in 1995, the proceedings of which were published in a special issue of the *Australian Journal of Ecology*, which included a broad variety of relevant empirical and theoretical papers (Caley 1998).

Importantly, the debate over recruitment limitation stimulated numerous field studies that not only examined the recruitment process more closely, but also tested for the presence of density dependence and its underlying mechanisms. Focus on spatial and temporal patterns of recruitment and subsequent population and community structure continued (e.g., Meekan et al. 1993, Fowler et al. 1992, Tupper and Hunte 1994, Caselle and Warner 1996, Ault and Johnson 1998), including new mechanistic studies of habitat selection at settlement (e.g., Sweatman and St. John 1990, Booth 1992, Wellington 1992, Tolimieri 1995), ramifications of variation in life-history traits and condition of settling larvae (e.g., Victor 1991, Sponaugle and Cowen 1997, McCormick 1998, Booth and Hixon 1999), and assessment of the relative importance of multiple factors (e.g., Booth 1995, Danilowicz 1997, Robertson et al. 1999, Shima, 1999). Predation as a source of early post-settlement mortality, density dependence, and community organization was increasingly investigated (e.g., Shpigel and Fishelson 1991, Kingsford 1992, Caley 1993, Carr and Hixon 1995,

Connell 1996, 1998, Beets 1997, Hixon and Carr 1997, Caselle 1999), and the first explorations of the ecological effects of parasites on reef fishes were completed (Adlard and Lester 1994). Related studies examined the role of reef structure as a source of prey refuges (e.g., Hixon and Beets 1993, Caley and St. John 1996, Eggleston et al. 1997, Beukers and Jones 1998), as well as competition for refuges and other living space (e.g., Robertson 1995, 1996, Schmitt and Holbrook 1999a,b). Eventually, a solid majority of studies demonstrated that local reef-fish dynamics are in fact often density-dependent, and that the source of local regulation is typically predation on new recruits, either directly or via competition for prey refuges (reviews by Hixon and Webster in Sale 2002, Osenberg et al. 2002). Importantly, density dependence often involves the diffuse and synergistic effects of multiple species (e.g., Hixon and Carr 1997, Carr et al. 2002). The emerging consensus was that, although competitive lotteries (Munday 2004a), recruitment limitation (Doherty et al. 2004), and even inverse density dependence (White et al. 2010) do indeed occur in reef fishes, direct density dependence is nonetheless evident in most cases (Hixon and Jones 2005), as is necessarily true for long-term persistence (Hixon et al. 2002, but see Sale and Tolimieri 2000).

Larval ecology also continued to evolve during the 1990s, including the fascinating finding that settlement-stage larvae have substantial swimming abilities and thus may undergo greater habitat selection than previously imagined (Leis and Carson-Ewart 1997, Stobutzki 1997, Stobutzki and Bellwood 1997, recent reviews by Fisher 2005, Fisher et al. 2005). Aided by new methodologies, detailed studies of larval dispersal first became practical. The distributions of larvae around islands suggested that larval retention was more common than previously assumed (Cowen and Castro 1994, Cowen et al. 2000). Jones et al. (1999) and Swearer et al. (1999) were the first to document self-recruitment: larvae settling near the same reef from which they were spawned. Population genetics revealed patterns of gene flow that indicated geographic patterns of larval dispersal (Doherty et al. 1995, Shulman and Bermingham 1995, Planes et al. 1996).

BEHAVIORAL ECOLOGY.—Behavioral ecology, especially as it relates to reproduction, continued to develop during the 1990s, as evidenced by a special issue of the *Bulletin of Marine Science* on the reproductive ecology of damselfishes (Sikkel and Petersen 1995) and one of the first books focusing exclusively on the behavior of coral reef fishes (Deloach and Humann 1999). A variety of studies focused on courtship and parental care (e.g., Knapp and Kovach 1991, Knapp and Warner 1991), sexual selection (e.g., Warner and Schultz 1992), mating site determination (e.g., Warner 1990a,b), mating systems (e.g., Petersen 1992), colonial nesting (e.g., Tyler 1995), cleaning and territoriality (e.g., Arnal and Côté 1998), spawning aggregations (e.g., Domeier and Colin 1997, recent review by Claydon 2004), and the relationship between cycles of spawning and settlement (e.g., Robertson et al. 1990, Hunt von Herbing and Hunte 1991). Controversy regarding whether cleaner fishes actually do remove parasites from their reef-fish hosts was settled: they do (Grutter 1999).

CONSERVATION BIOLOGY.—Overfishing on coral reefs became increasingly evident during the 1990s (Roberts 1995). Particularly ominous were, first, extirpation of grouper spawning aggregations (reviews by Domeier and Colin 1997, Claydon 2004, Sadovy and Domeier 2005), and second, the developing live reef fish trade, where practices generally harmful to all reef life are used to capture fish live for high-end

Asian restaurants (review by Sadovy 2005). For the first time, there was discussion of the possibility of reef fish species being driven globally extinct by human activities (Roberts and Hawkins 1999). Studies of and calls for fully-protected marine reserves as tools for conserving and managing reef fishes began to proliferate (e.g., Roberts and Polunin 1991, Polunin and Roberts 1993, Tupper and Juanes 1999, McClanahan and Kaunda-Arara 1996, Russ and Alcala 1996a,b, Roberts 1997, Beets and Friedlander 1998, Johannes 1998, Kramer and Chapman 1999). By the turn of the century, it was clear that the conservation biology of coral reef fishes was a necessary and growing discipline.

2000s: THE CONNECTIVITY DECADE

At the turn of the millennium, heralded by a second comprehensive edited volume on the ecology of reef fishes (Sale 2002), further technological breakthroughs emerged for determining patterns of larval dispersal, including the locations of spawning and settlement, and sometimes the path between. New approaches developed in oceanographic modeling relevant to larval dispersal (e.g., Cowen et al. 2000, 2006, James et al. 2002, Paris et al. 2007), larval behavioral modeling (e.g., Armsworth 2000, 2001, Armsworth et al. 2001, Irisson et al. 2004), otolith microchemistry (e.g., Thorrold and Shuttleworth 2000, Compana and Thorrold 2001), otolith tagging (e.g., Thorrold et al. 2006), and genetic markers (e.g., Christie 2010, Hedgecock 2010). The spatial resolution of modeling and sampling also increased progressively, providing means of attaining holistic understanding of reef-fish population structure at scales ranging from local populations on single reefs to metapopulations: groups of local populations linked by larval dispersal (Mora and Sale 2002, Kritzer and Sale 2004, 2006, and papers therein). Reviews of larval connectivity became extremely numerous, including individual monographs (e.g., Cowen and Sponaugle 2009) and overviews (e.g., Thorrold 2006), as well as special issues of the *Bulletin of Marine Science* (Warner and Cowen 2002, and papers therein), *Oceanography* (Cowen et al. 2007, and papers therein), and *Coral Reefs* (Jones et al. 2009, and papers therein).

Empirical studies of connectivity demonstrated both substantial dispersal between widely separated populations (e.g., Christie et al. 2010a) and larval retention resulting in local self-recruitment (e.g., Taylor and Hellberg 2003, Paris and Cowen 2004, Jones et al. 2005, Almany et al. 2007a, Planes et al. 2009, Christie et al. 2010b). Particularly insightful were combinations of oceanographic modeling with field data (e.g., Paris et al. 2002, Paris and Cowen 2004, Christie et al. 2010a, Salas et al. 2010), including documentation of larval distributions at multiple scales (e.g., Sponaugle et al. 2003, 2005) and in situ observations of larval behavior (reviews by Montgomery et al. 2001, Leis and McCormick in Sale 2002, Leis 2002, 2006). A fascinating finding was Buston et al.'s (2009) evidence that reef fishes may settle (and thus, presumably disperse) in kin groups, tentatively corroborating a hypothesis proposed by Avise and Shapiro (1986, but see Kolm et al. 2005).

Although *connectivity* has been the buzzword of the new millennium, other aspects of reef-fish ecology continued to thrive. Advances included population models specifically relevant to reef fishes (e.g., Armsworth 2002), as well as detailed field studies of intraspecific competition (e.g., Schmitt and Holbrook 2000, Webster and Hixon 2000, Buston 2003), interspecific competition (e.g., Munday et al. 2001), predation (e.g., Stewart and Jones 2001, Steele and Forrester 2002, Webster 2002,

Almany and Webster 2004, 2006, Doherty et al. 2004, Bshary et al. 2006, Almany et al. 2007b), parasitism (e.g., Cribb et al. 2000, Finley and Forrester 2003, Forrester and Finley 2006), corallivory (reviews by Cole et al. 2008, Rotjan and Lewis 2008), and herbivory (e.g., Choat et al. 2002, 2004, Ceccarelli et al. 2005, Fox and Bellwood 2007, Burkepile and Hay 2008). There was extraordinary effort examining factors that affect and determine global and regional patterns of species diversity (Bellwood and Hughes 2001, Findley and Findley 2001, Karlson 2002, Bellwood et al. 2005, Connolly et al. 2005, Sandin et al. 2008a, Bellmaker 2009, Burgess et al. 2010, Mellin et al. 2010a). Also revealing were studies that examined indirect effects, including trophic cascades (Webster and Almany 2002, Dulvy et al. 2004, Holbrook and Schmitt 2004, McCormick and Meekan 2007, Stallings 2008, Schmitt et al. 2009, Madin et al. 2010, O'Leary and McClanahan 2010). There were also advances in understanding priority effects (e.g., Almany 2003, 2004c, Geange and Stier 2009), post-settlement movements (e.g., Dahlgren and Eggleston 2000, Booth 2002, Overholtzer-McLeod 2005, Chateau and Wantiez 2007, Turgeon et al. 2010), and various combinations of processes and mechanisms (e.g., Almany 2004a,b, Aburto-Oropeza et al. 2007, Figueira et al. 2008, Stier and Osenberg 2010).

Density dependence continued to receive extensive attention (e.g., Forrester and Steele 2000, 2004, Carr et al. 2002, Holbrook and Schmitt 2002, Shima 2001a,b, 2002, Brunton and Booth 2003, Webster 2004, Overholtzer-McLeod 2004, 2006, Hixon and Jones 2005, Sandin and Pacala 2005, Steele and Forrester 2005, Anderson et al. 2007, White and Warner 2007, Forrester et al. 2008, Samhuri et al. 2009, White et al. 2010). Novel findings included the first demonstration of truly regulating temporal density dependence (Webster 2003, see also Schmitt and Holbrook 2007), and the derivative concept of "cryptic density dependence" (Shima and Osenberg 2003, Shima et al. 2008).

Additional novel areas of research involved long-term, broad-scale population dynamics (e.g., Cheal et al. 2007), hierarchical patterns of diversity (e.g., Belmaker et al. 2008, MacNeil et al. 2009), and the role of physical disturbance in community structure (e.g., Syms and Jones 2000, Halford et al. 2004, Beruman and Pratchett 2006, Wilson et al. 2009), including nuclear explosions (Planes et al. 2005). There were also advances in understanding the physiological basis of settlement success, including larval condition and parental effects (e.g., Searcy and Sponaugle 2001, Bergenius et al. 2002, Booth and Alquezar 2002, Hoey and McCormick 2004, McCormick 2006, Gagliano et al. 2007, Johnson 2008, Johnson and Hixon 2010). Particularly insightful were studies of the evolutionary basis of parental effects (e.g., Johnson et al. 2010).

BEHAVIORAL ECOLOGY.—The first decade of the 2000s saw extraordinary advancements in understanding cleaning symbiosis in reef fishes and its ecological effects (Bshary and Grutter 2002a,b, Bshary and Schäffer 2002, Grutter et al. 2003, Grutter 2004, Grutter and Bshary 2004, Sikkell et al. 2004, Stummer et al. 2004, Soares et al. 2008, Burton-Chellew 2009, Cheney et al. 2009, Adam 2010, Bshary and Bshary 2010, Oates et al. 2010, reviews by Côté 2000, Floeter et al. 2007). New explorations of the role of senses in behavior revealed that ultraviolet coloration serves in communication among reef fishes (Losey 2003), that reef fishes produce and make use of chemical alarm cues (Larson and McCormick 2005, McCormick and Larson 2008), and that settling larvae are attracted to sounds generated by reef invertebrates (Simpson et al. 2008). New approaches also explored links among

behavioral, population, and community ecology, including interactions among foraging, predation risk, and growth (Meekan et al. 2010), as well as relationships among overfishing top predators, shifts in prey foraging behavior, and trophic cascades (Madin et al. 2010). Finally, advances continued in more traditional subjects of reef-fish behavioral ecology, including egg cannibalism (e.g., Manica 2004), mating systems (e.g., Harding et al. 2003), day-night transitions (e.g., Rickett and Genin 2005), territoriality (e.g., Sikkell and Kramer 2006), courtship and predation risk (e.g., Figueira and Lyman 2007), factors affecting sex reversal (e.g., Clifton and Rogers 2008), social hierarchies (e.g., Wong et al. 2008), and mimicry (e.g., Cheney and Marshall 2009). All told, the new millennium has seen the greatest advances in reef-fish ecology ever, with the sheer number of publications likely soon to eclipse the entirety of the 20th century.

THE FUTURE: CONSERVATION OR EXTINCTION

As our knowledge of the ecology of reef fishes increases exponentially, the worldwide deterioration of coral reefs is also accelerating, clearly to the detriment of reef fishes. The demise of reefs is caused by both local and global human activities (recent reviews by Carpenter et al. 2008, Knowlton and Jackson 2008, Sandin et al. 2008b, Wilkinson 2008). Locally, where humans occur at high densities near reefs, dredging, siltation, pollution, eutrophication, and overfishing take their relentless and cumulative toll. Globally, carbon emissions from burning fossil fuels and deforestation result in widespread bleaching of corals and associated emergent diseases, driven largely by ocean warming, as well as decalcification due to ocean acidification. Introductions of exotic reef fishes are increasing (Semmens et al. 2004). The recent invasion of Atlantic coral reefs by Pacific lionfish, *Pterois volitans* (Linnaeus, 1758), is a particular cause for concern, as these voracious predators overconsume small native reef fishes (Albins and Hixon 2008, 2011, Sutherland et al. 2010).

It is now more obvious than ever that some coral reef fishes are genuinely threatened with global, as well as regional, extinction (Hawkins et al. 2000, Roberts et al. 2002, Dulvy et al. 2003, Munday 2004b, Jones et al. 2004, see also Hutchings 2001, Mellin et al. 2010b). Dozens of species are listed on the International Union for the Conservation of Nature (IUCN) Red List (<http://www.iucn.org>). The humphead or Napoleon wrasse, *Cheilinus undulatus* Rüppell, 1835, taken mostly by the live reef-fish trade (Sadovy et al. 2003), and all seahorses (*Hippocampus* spp.), taken by the aquarium and curio trades (Foster and Vincent 2004), are listed by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) as species in which trade must be controlled “to avoid use incompatible with their survival” (<http://www.cites.org>).

APPLIED ECOLOGY.—As the state of coral reefs worsens due to multiple and synergistic human activities, reef ecologists are increasingly shifting their focus to conservation biology, documenting the declines and their causes, as well as seeking solutions (Birkeland 1997, Côté and Reynolds 2006, and papers therein). If there is a theme for the coming decades, it may be “conservation or extinction.”

Overfishing has historically been the primary threat to reef fishes, and combined with habitat loss, has resulted in severe declines in abundance (global and regional reviews by Friedlander and DeMartini 2002, Robbins et al. 2006, Newton et al.

2007, Tittensor et al. 2007, DeMartini et al. 2008, Wilson et al. 2008, Cinner et al. 2009, Paddock et al. 2009, Stallings 2009). Ocean climate disruption may overtake overfishing as the leading assault on reef fishes. The effects of climate change are accelerating and threaten to catch both corals and fishes in the double bind of coral bleaching and ocean acidification (Hoegh-Guldberg et al. 2007). Pratchett et al. (2008) recently reviewed many studies demonstrating that coral bleaching has indirect negative effects on resident fishes caused by the loss of live coral cover and reef topographic complexity, which in turn reduces food and shelter for fishes. Newer studies have shown that such habitat loss leaves reef fishes more susceptible to predation (Coker et al. 2009), and interacts with overfishing to reduce the abundance of both small and large fish (Wilson et al. 2010). Although ocean acidification mostly affects calcification rates of corals and other invertebrates and algae (Kroeker et al. 2010), increasing acidity also has direct negative physiological effects on reef fishes. Acidification has recently been shown to affect the olfactory system of clownfish, thereby impairing the homing ability of settling larvae (Munday et al. 2009), and disrupting their ability to detect and evade predators (Dixson et al. 2010, Munday et al. 2010, see also Ishimatsu et al. 2008). Reef fishes also suffer reduced respiratory capacity at predicted future ocean temperatures (Nilsson et al. 2009), although they have some capacity to acclimate (Donelson et al. 2010). Indeed, warming ocean temperatures may allow tropical reef fishes to expand their ranges into presently temperate regions (Figueira and Booth 2010).

How can coral reef fishes and their habitats survive the multiple local and global deleterious effects of human activities? The answer lies in fostering "ecological resilience," the ability of an ecosystem to withstand perturbations without shifting to a drastically different stable state that is both undesirable and difficult, if not impossible, to reverse from a human perspective (Walker and Salt 2006). Importantly, relatively intact coral reef ecosystems are demonstrably more resilient than relatively degraded reefs (e.g., Nyström et al. 2000, 2008, Hughes et al. 2005, 2010, Raymundo et al. 2009). Intact food webs of coral reef fishes provide at least two major resilience mechanisms. First, they supply multiple redundant herbivorous species that help prevent phase shifts from coral to macroalgal dominance (e.g., Bellwood et al. 2004, Mumby et al. 2006, 2007, Hughes et al. 2007, Ledlie et al. 2007). Second, they provide multiple species of predators and competitors that are the sources of density dependence required to regulate fish populations and foster their persistence (e.g., Hixon and Carr 1997, Carr et al. 2002).

Given that intact ecosystems are relatively resilient, the most promising ecosystem-based management tools for conserving reefs and their inhabitants are substantial, fully-protected marine reserves (e.g., McClanahan and Arthur 2001, Russ and Alcala 2004, McClanahan and Graham 2005, Hughes et al. 2006, Helfman 2007, McClanahan et al. 2007, Game et al. 2008, 2009, Graham et al. 2008, Russ et al. 2008, Cinner et al. 2009, McLeod et al. 2009). Studies of marine reserves and protected areas on coral reefs are far too numerous to list exhaustively here, but entries to the literature can be found in special issues of the *Bulletin of Marine Science* (Conover et al. 2000), *Ecological Applications* (Lubchenco et al. 2003), and *Conservation Biology* (Lundquist et al. 2005). In addition to fostering ecological resilience in general, reserves have been documented to benefit adjacent coral reef fisheries via spillover of adult fishes (e.g., McClanahan and Mangi 2000, Roberts et al. 2001, Russ et al. 2003, 2004, Abesamis and Russ 2005, Williams et al. 2009). Most recently and importantly,

networks of reserves that have successfully replenished fisheries have been shown to seed fished areas with larvae spawned within the reserves (Christie et al. 2010b). Unfortunately, the number and size of coral reef marine reserves and protected areas are presently and woefully inadequate (Mora et al. 2006). Nonetheless, Australia, Palau, the United States, and some other nations have recently taken the lead in placing large portions of their reefs off-limits to directly deleterious human activities.

BASIC ECOLOGY.—In addition to conservation biology per se, the basic ecology of reef fishes has important roles in saving coral reefs. These roles range from reef fishes as model systems for experimental studies relevant to fisheries and conservation, to elucidation of the complexity and wonders of nature, thereby fostering public interest in conserving reefs.

There are ample areas for future research, three of which I mention here. First, there is growing need for holistic, cross-scale studies that link local demographic processes of reef fishes with broad-scale patterns of larval connectivity. Such studies will be most valuable if conducted over multiple generations of fish, providing mechanistic understanding of the processes that drive and regulate population dynamics at multiple scales of time and space. Second, nested hierarchical studies that connect individual, population, community, and ecosystem ecology will provide holistic understanding of reef fishes in all contexts. Third, understanding the mechanisms that structure populations and communities of reef fishes will benefit from knowledge of “meta-interactions” (direct and indirect interactions among interactions), extending far beyond standard food and interaction webs that focus on predation and competition only. Especially valuable will be more detailed studies of poorly known interactions, including parasitism, disease, amensalism, commensalism, and mutualism.

As ecological studies of reef fishes become more sophisticated, I believe that it is imperative to keep in mind the importance of new knowledge regarding the basic natural history of our study organisms (Dayton 2003). Coral reef fishes—their behavior, populations, and communities—are so very complex that reef-fish ecology will never lack novel study topics.

CONCLUSIONS

Given the ominous future facing coral reefs and their inhabitants, there are increasing calls for marine scientists, as direct witnesses of ongoing declines, to more actively educate the public, managers, and policymakers about a looming disaster that is largely out-of-sight and out-of-mind to most of humanity (Hixon et al. 2001). The reality is that humans can change their behavior once properly motivated (Nisbet et al. 2010), and reef-fish ecologists can play a pivotal role in saving coral reefs by engaging more fully with society as educators, policy advisors, and citizen advocates. Otherwise, scientists may well be relegated to the pitiful role of being caring yet ineffective bystanders at the hospice of terminally ill coral reefs (Hixon 2009). The stakes are high and the probability of success may be low, but I see no better way for marine scientists to serve society than by fighting the good fight to save coral reefs and their amazing inhabitants.

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