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ARTICLE

An Empirical Test of Recruitment Limitation in a Coral Reef Fish

Peter Doherty* and Tony Fowler†

A long-term, large-scale empirical test of the recruitment limitation hypothesis was done by sampling fish populations from the southern Great Barrier Reef after having monitored their recruitment histories for 9 years. After adjustment for demographic differences, recruitment patterns explained over 90 percent of the spatial variation in abundance of a common damselfish among seven coral reefs. The age structures from individual reefs also preserved major temporal variations in the recruitment signal over at least 10 years. Abundance and demography of this small fish at these spatial and temporal scales can be explained almost entirely as variable recruitment interacting with density-independent mortality.

The most common strategy of reproduction among marine animals involves broadcasting propagules (eggs or larvae) into the sea where the developing offspring may seek food and gain protection from benthic predators. In a dynamic ocean, many larvae will be dispersed by currents to new locations, with some destinations being more favorable than others for completion of the next phase of the life cycle. This alternation between different developmental states that live in different habitats is an example of a complex life cycle (*1*). Spawning adults with this type of life cycle cannot anticipate the conditions that their offspring will encounter during and after the larval stage. Consequently, their reproduction is characterized by high risk and almost total mortality of propagules. Many taxa compensate for these losses by producing large numbers of zygotes, investing little in each; perennials may also spread their risk through repeated spawning episodes.

The combination of high fecundity and small variations in larval success can result in large variations in replenishment of the next generation (*2*), which can impact significantly on the dynamics, demography, and genetic structure of populations and the composition of communities. The "recruitment problem"—the variable and often inadequate supply of juveniles—has been known to fisheries scientists since the turn of the century (*3*): It is evident first in the bioeconomic consequences of fluctuating yields caused by variable year-class strength (defined here as the number of juveniles added to a population through seasonal reproduction), and second, in the collapses of stocks where overfishing occurred because the management regime did not make sufficient allowance for the possibility of repeated recruitment failure (*4*).

The hallmark of a recruitment-limited system is that abundance varies as some function of the colonization rate rather than being modified by internal processes, such as competition and predation, to some predictable carrying capacity. This disequilibrium means that input levels can determine the productivity of a system and its resilience to disturbance (*5*). It is therefore a condition with significant economic and other practical consequences.

Recruitment Limitation Ideas in Marine Ecology

Although there have been regular reports since the 1920s of abnormal recruitments affecting various marine invertebrate stocks (*6*), the marine (and theoretical) ecological literature, as distinct from the fisheries literature, generally ignored the recruitment problem and concentrated instead on post-recruitment processes affecting the abundance of juveniles and adults. To some extent, this emphasis arose from the greater difficulty and expense of studying the early life history stages (*7*), but it was also sustained by the apparent adequacy of ecological models that did not contain a term for recruitment. In retrospect, it appears that many of these models were developed or tested (unknowingly) from situations of relatively high recruitment. The lack of robustness in these models has been apparent as a greater variety of organisms has been examined, showing that recruitment levels can be limiting for a wide range of taxa in at least some part of their domain (*8*).

Among the recent examples are an influential series of papers by Roughgarden and his colleagues (*9*) describing the dynamic links between populations of barnacles inhabiting northern Californian shorelines and the offshore pool of propagules. These papers demonstrate unequivocally that any description of the population dynamics of these sessile intertidal animals is incomplete without data on larval supply and that understanding this supply requires knowledge of both biology and physical oceanography. Wind, topography, and oceanic boundary currents interact with spawnings and larval biology to control cross-shelf larval transport and introduce chaos into recruitment. For a variety of reasons, some sites will be chronically starved of replenishment, while most sites will experience at least occasional years of recruitment failure. Similar mechanisms have been shown to affect fish and invertebrate dispersal on other continental shelves (*10*), indicating a general phenomenon.

As shown by reanalyses of historical data (*11*), evidence of recruitment limitation in some barnacle populations does not revoke the evidence of deterministic processes in others, but it expands the paradigm. The modern pluralism provides for a continuum across time, space, and taxonomy between situations dominated by pre- or postdispersal processes (*12*). The revised paradigm admits both equilibrial and nonequilibrial concepts and has restructured the way marine ecologists think about populations.

For sessile or sedentary organisms with complex life cycles, propagule dispersal breaks the nexus at local scales between reproduction and recruitment; hence, local populations are "open" (replenished from other sources) subunits within a network of habitat patches linked by dispersal (*13*). The genetic unit is therefore a "metapopulation" that does not need consistent dynamics throughout all of its parts; connectivity among parts of the network is an emergent property of great importance, and poor connectivity is more likely to result in recruitment limitation at local scales. This expanded paradigm is especially germane to marine populations, but it can be adapted to other organisms with complex life cycles and dispersive offspring, including plants and insects.

Application to Coral Reef Fishes

Coral reef fishes share several characteristics with benthic marine invertebrate faunas, namely, a sedentary spawning stage, a

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dispersive pelagic larval stage, and a metapopulation structure forced by the patchiness of the coral reef environment (*14*). This fauna, dominated by small forms with brilliant color and extravagant behavior, is still regarded by many as emblematic of stable resource-limited assemblages, although there have been claims for nonequilibrial alternatives (*15*). The equilibrium hypothesis draws part of its support from the spectacular diversity of this fauna (*16*) and the strong emphasis in the theoretical literature on competition as a major diversifying force. However, this approach confuses issues that belong to evolutionary (diversity) and ecological (population dynamics) time.

The recruitment limitation hypothesis predicts patterns of abundance in space or time among replicate situations that vary mainly in the level of recruitment. It is strictly an argument about patterns expected within habitats for a given species over ecological time. If the hypothesis is valid, differential recruitment among similar places (defined by similar turnover) should result in patterns of abundance that can be predicted from the recruitment statistics. Similarly, differential recruitment over time to an unchanging habitat should result in the pattern of initial abundance being fixed in the age structure of the population. In contrast, the equilibrial alternative predicts that any spatial and temporal vagaries in replenishment should be smoothed out by density-dependent processes as individuals compete for the limiting resource, usually assumed to be living space on the reef.

Doherty proposed that populations of territorial damselfishes in the One Tree Lagoon, southern Great Barrier Reef, were recruitment-limited on the basis of an ability to predict local abundance among parts of the lagoon from recruitment data (*17*) and on the failure of experimental manipulations of juveniles to produce compensatory mortality even at transplant densities well above any observed in the natural populations (*18*). Critics countered that recruitment rates in the One Tree Lagoon may be atypically low and that the experiments were not long enough to reveal density-dependent bottlenecks in later life, such as limited entry to the adult breeding stock (*19*). We address both points in this article.

A Large-Scale, Long-Term Study

In 1981, standardized recruitment surveys were extended to six other coral reef lagoons within 70 km of One Tree (Fig. 1). In this region of the Great Barrier Reef, fish recruitment is seasonal with most colonization occurring between November and February. Consequently, all lagoons were surveyed in April of every year since 1981 to provide quantitative indices of year-class strength for a clutch of species with sedentary conspicuous juveniles.

The sampling protocol consisted of exhaustive visual censuses by a pair of divers on five large patch reefs (mean surface area, 89.4 m^2; SE = 1.8; n = 315) chosen haphazardly from the windward edge of each lagoon. For each patch, counting continued until a stable total was achieved for each species, the surface area of the patch was measured, and all counts were later transformed to estimates of density (all measured as fish per 100 m^2).

In 1989, after nine year-classes of recruitment had been monitored, 10 large patch reefs were sampled from each of the seven lagoons. Each patch was encircled by a fine meshed barrier net and poisoned with the ichthyocide Rotenone. This was done in September, right before the start of the spawning season, when fish from the most recent recruitment season would have been about 10 months old. Throughout the collection, the surface was patrolled to collect

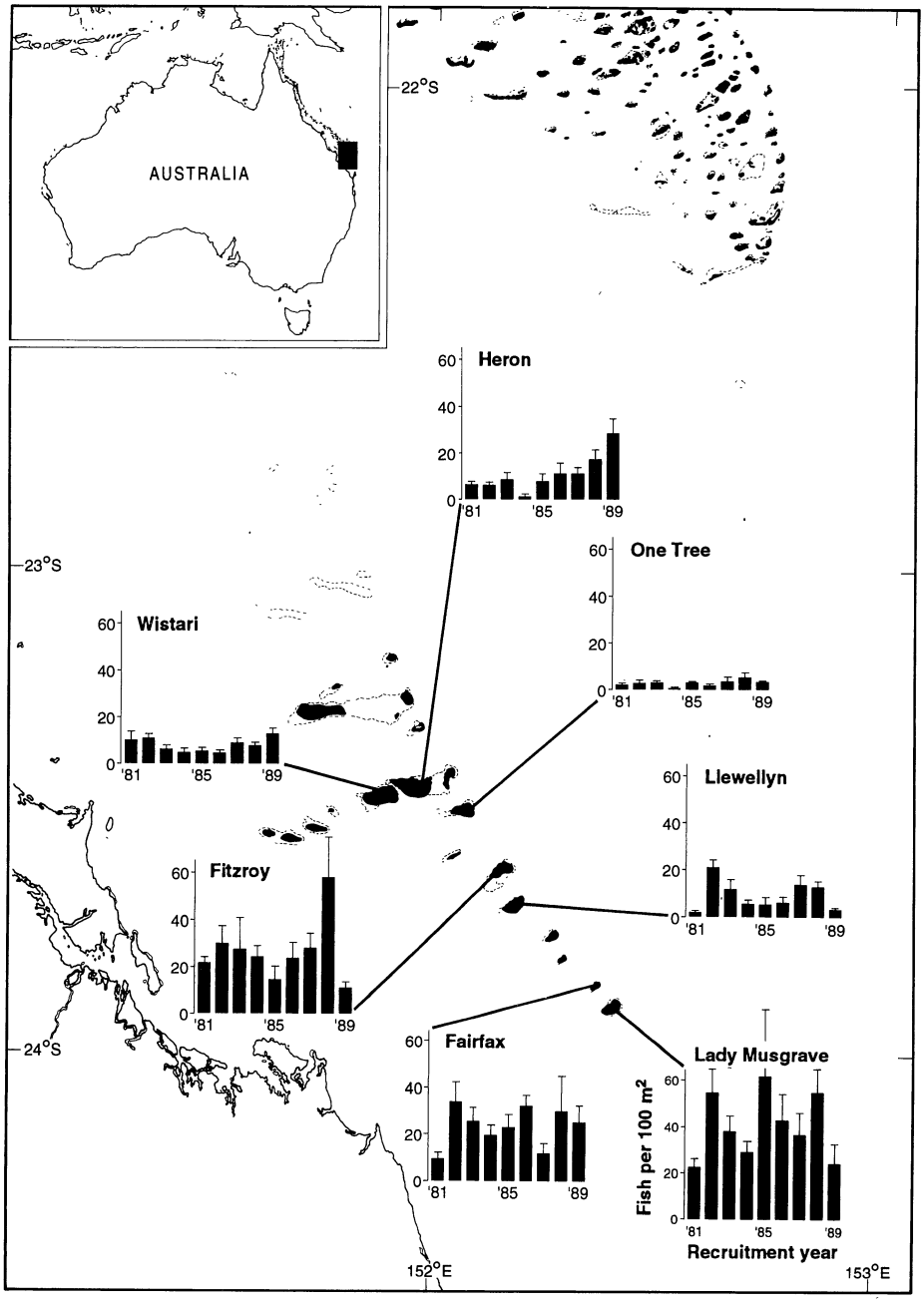

Fig. 1. Map of the Capricorn-Bunker Group from the southern Great Barrier Reef showing the location of reefs used in this study and nine year-classes of recruitment density for *Pomacentrus moluccensis* (error bars indicate 1 SE). In addition to local spawnings, this recruitment may have come from reefs to the north (shown at the top of the figure) as the dominant current flows are poleward.

floaters and prevent predation by birds. Dead fish were collected exhaustively by at least four divers, who searched the bottom for at least 2 hours.

The purpose of the collections was to determine the ages of the fish to correlate their initial and final abundances over time. The need to validate these estimates of age defined the choice of species. To date, we have shown that two damselfishes from this region form readable annuli in their otoliths (ear bones) (*20*). Of this pair, we concentrated on *Pomacentrus moluccensis* because its more variable recruitment pattern among reefs (Fig. 1) provides the most powerful test of the recruitment limitation hypothesis.

This species is a small, common damselfish that settles into live coral colonies and thereafter has a sedentary life-style. As a diurnal planktivore, its juveniles swim above the surface of the reef, where their bright yellow color makes them conspicuous. The combination of seasonal recruitment and fast early growth ensures a clear separation by size of the first- and second-year cohorts, so that there was little confusion about which individuals should be assigned to the most recently recruited year-class.

Spatial and Temporal Outcomes

By using year-classes as replicates, we detected three statistically significant levels of recruitment among the seven lagoons (Table 1): (i) One Tree and three other coral reefs (Wistari, Llewellyn, and Heron) fell into a low recruitment group; (ii) two reefs (Fairfax and Fitzroy) fell into an intermediate group; and (iii) Lady Musgrave received more recruitment than all other reefs (Student–Newman-Kuels tests, $P < 0.05$). Although the rankings of individual reefs changed slightly over the years, recruitment was respectively lowest and highest in the One Tree (mean, 2.8 recruits per 100 m^2) and Lady Musgrave (mean, 40.4 recruits per 100 m^2) lagoons in 7 of the 9 years. Thus, we can evaluate the long-term consequences of more than an order-of-magnitude variation in natural replenishment rates and test whether recruitment limitation is restricted only to those populations with the lowest colonization rates (like One Tree).

Hydrodynamics is the most likely explanation of the consistent differences in recruitment detected among the seven lagoons. Two of the reefs (Fitzroy and Lady Musgrave) have permanent passes connecting their lagoons with the surrounding sea. The others are impounded to varying degrees at some stage in the tidal cycle (*21*). The different residence times of water in the seven lagoons are reflected in their different turbidities and proportions of live coral. Differential flushing may affect the recruitment of *P. moluccensis* either directly through variations in larval supply related to access or indirectly through habitat selection as this species settles from the plankton into live coral.

The historical record of average recruitment was a good predictor of the mean number of *P. moluccensis* recovered by the poison stations (Fig. 2). With one exception, the seven lagoons were ranked as in the recruitment study: The four reefs with low recruitment fell into one group that returned lower catches than a second group containing the other three reefs. The exception was Lady Musgrave, which received significantly greater recruitment but did not yield higher catches than Fitzroy and Fairfax.

Treating the problem as a regression analysis (*22*), we identified Lady Musgrave as a significant outlier ($P = 0.02$) by a least squares regression fitted to the data. Nonetheless, this model explained 84% of the spatial variation in catch among lagoons ($n = 7$, $P = 0.002$). Curiously, this regression had a positive, albeit statistically nonsignificant ($P = 0.09$), intercept ($c = 11.3$), which interpreted literally means that some fish are expected without recruitment. Although this result and the unexplained variance in the regression might be dismissed as sampling error, aging of the collections resulted in a significant improvement in explanatory power.

The ages of individual fish were determined from duplicate readings of annuli seen in thick sections (300 μm) cut close to the primordium of one sagitta. Because more than 2000 *P. moluccensis* were collected from the seven reefs, it was not feasible to section all of them. Thus, we processed complete collections from haphazardly chosen patch reefs until the aggregate sample from each lagoon exceeded 150 individuals. On Lady Musgrave, this total was surpassed after processing just four patch reefs, whereas on One Tree, it was necessary to process 18 samples (*23*), given the low levels of recruitment.

In Fig. 3, the age structure of the sample from Lady Musgrave is compared with its historical recruitment record. This reef had

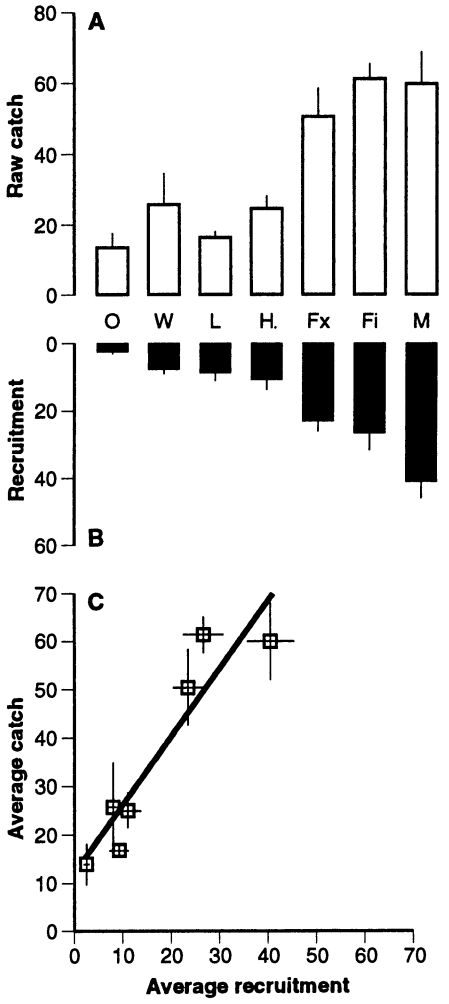

Fig. 2. (**A**) Average density of *P. moluccensis* on 10 patch reefs in seven lagoons; O, One Tree; W, Wistari; L, Llewellyn; H, Heron; Fx, Fairfax; Fi, Fitzroy; M, Lady Musgrave. (**B**) Average densities of recruitment (1981–89) in the seven lagoons. (**C**) Least squares regression of average catch versus average recruitment. All density units are fish per 100 m^2, and all error bars are 1 SE.

Table 1. Summary statistics of the study. All density units are fish per 100 m^2; all estimates of variation are standard errors based on the above sample sizes; no error has been calculated for the adjusted catch because different numbers of patch reefs were used from different lagoons.

Lagoon	Reef area* (m^2)	Recruitment density†	Raw catch density‡	Proportion >9 years old (%)	Adjusted catch§
One Tree	85.1 ± 6.2	2.8 ± 0.4	13.6 ± 3.9	32.8	8.6
Wistari	81.9 ± 4.6	7.9 ± 1.0	25.4 ± 8.8	34.0	16.0
Llewellyn	84.7 ± 3.4	9.0 ± 2.0	16.9 ± 1.4	4.2	15.7
Heron	95.6 ± 5.4	10.9 ± 2.6	24.9 ± 3.4	9.7	22.5
Fairfax	98.6 ± 4.9	23.1 ± 2.9	50.4 ± 7.8	11.7	49.4
Fitzroy	90.9 ± 4.7	26.5 ± 4.4	61.4 ± 3.8	2.8	55.1
Lady Musgrave	88.9 ± 4.0	40.4 ± 4.7	60.1 ± 8.2	1.3	58.8

*Mean surface area of 45 patch reefs (five replicates by 9 years) monitored in each lagoon. †Mean of nine year-classes (April 1981–89) of *P. moluccensis*. ‡Mean density of *P. moluccensis* removed from 10 patch reefs in September 1989. §Adjusted catch density for fish recruited from the 1981–89 year-classes.

highest recruitment and should have the clearest evidence of compensatory mortality if such processes are important. Instead, the first four age classes in the sample reflect their initial strengths and indicate a constant reduction to 24 to 29% of their initial abundance, despite a twofold difference among the original inputs. This result implies that a constant fraction (~75%) of each cohort was lost between April and September of the first year of life in the benthic habitat but that once past this stage, mortality was negligible for the next 3 years.

On the same basis, Fig. 3C indicates increased mortality between the fourth and fifth years, which may coincide with major reproductive activity (24). Beyond this age, there is another inflection in the mortality schedule with ~5% of each cohort left after 8 and 9 years, respectively. Although Fig. 3 is not a conventional survivorship curve in that it is not based on the decline of a single cohort, the high degree of order in this plot suggests a consistent, albeit nonlinear, mortality schedule. The constant proportional decline of the four most recent year-classes provides the best evidence that this mortality is independent of settlement density.

The age structure from Lady Musgrave also revealed the presence of two individuals that had been recruited before the period of monitoring began in 1981 (Fig. 3A). These individuals were 12 and 13 years old. On other reefs, the proportion of such old fish was found to be much greater. For example, on One Tree (Fig. 4A), the reef with lowest recruitment, some fish were >17 years old, and >30% of the total sample consisted of fish recruited before the period of monitoring.

The age structure from One Tree Lagoon is also remarkable for its bimodality. Contrary to an expectation of declining abundance with age, 12% of this population in 1989 was contributed by 10-year-old fish recruited during 1979. Although this was before the start of the expanded monitoring effort, populations at One Tree have been under surveillance since the mid-1970s. These longer records confirm that 1979 was an exceptional year for recruitment of a wide range of damselfish species, including *P. moluccensis* (25). They also show that the 1980 year-class was of below average strength, which is exactly the pattern preserved in the age structure from this reef after a decade of postsettlement mortality.

The age structure at nearby Wistari Reef (Fig. 4B) contained a similar excess of 10-year-old fish in September 1989, implicating some large-scale phenomenon in the formation or delivery of the exceptional year-class of 1979. The Wistari Reef example is clear proof of the effect that fluctuating year-class size can have on abundance: 20% of that population in 1989 was composed of individuals recruited during a single year-class out of the 14 represented in the age structure. Few examples from the literature on temperate fish show more extreme influences of recruitment on demography.

Although it is possible that a regional phenomenon was responsible for the strong 1979 year-class, we cannot prove that it stretched as far south as the Lady Musgrave Lagoon. The higher turnover in that system means that all evidence of the 1979 year-class had been purged from the population by 1989 (Fig. 3).

Differences among the seven reefs in the proportion of fish older than 9 years (Table 1) mean that the regression analysis of the raw data is biased. At one extreme, populations from the two lagoons with lowest recruitment (One Tree and Wistari) each contained >30% of fish that predated the monitoring program. At the other extreme, Lady Musgrave, which received the highest recruitment, contained relatively few fish older than 5 years. Both types of departure had the same effect, namely to lower the slope and increase the intercept of the relation based on the uncorrected data.

Elimination of this bias, by truncating all of the age structures to 9 years, improved the overall fit of the linear regression (n = 7, P = 0.0008, R^2 = 0.89) and relocated the intercept closer to the origin (c = 6.0, P = 0.24) (Fig. 5). Despite the better fit, examination of the residuals still identified

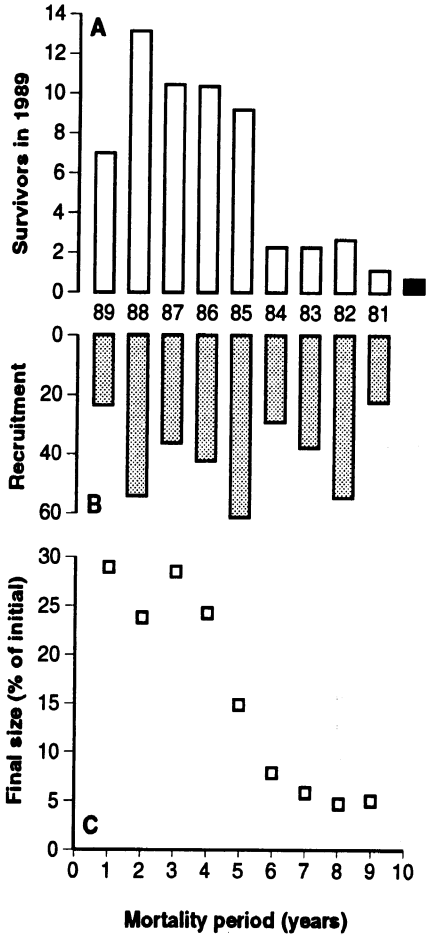

Fig. 3. (**A**) Density (fish per 100 m^2) by age group of 154 fish from Lady Musgrave; bottom axis identifies the originating year-classes; shaded bar indicates two fish (12 and 13 years old) that predated the recruitment surveys. (**B**) Recruitment densities from Lady Musgrave, 1981–89. (**C**) Final cohort size (relative to initial size) plotted against elapsed time.

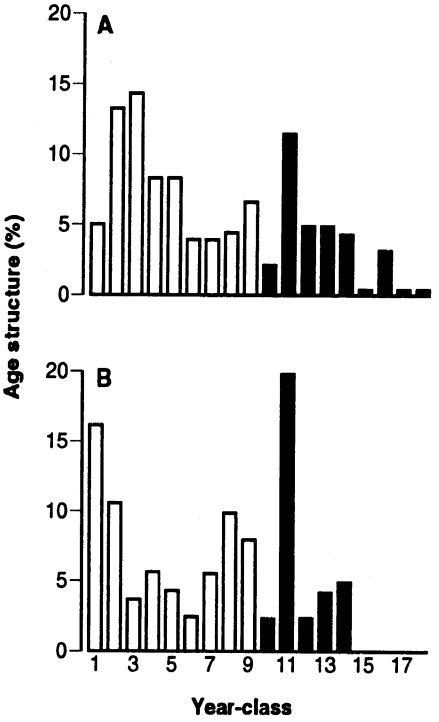

Fig. 4. Age structure for (**A**) 183 fish from One Tree and (**B**) 162 fish from Wistari; shaded bars indicate fish that predated the recruitment surveys.

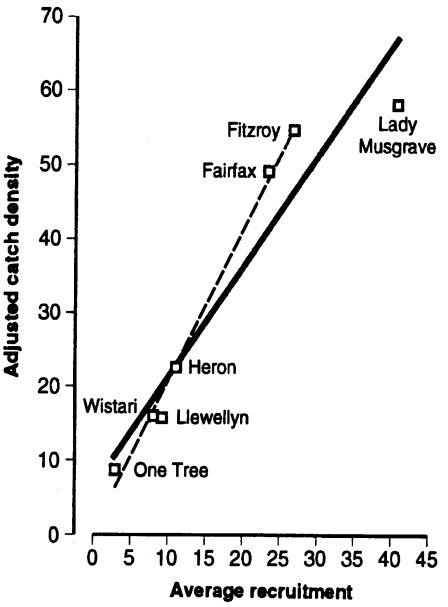

Fig. 5. Adjusted catch densities (survivors from the 1981–89 year-classes) versus average size of the originating year-classes (both in fish per 100 m^2). Solid line, least squares regression on all data; dashed line, same without Lady Musgrave.

Lady Musgrave as a significant outlier from the rest of the data ($P = 0.002$) with lower abundance than expected from the observed level of recruitment. Figure 3 suggests that this is because this population contained relatively few fish older than 5 years, a bias that could not be removed except by truncating all of the age structures more severely (26).

It is simply not possible to trace the recruitment signal through any system beyond the average extinction time for cohorts, and in that regard, the regression analysis was confounded by the more rapid turnover of fish on Lady Musgrave. When the data were reanalyzed without this reef, the remaining six reefs showed a very high correlation between catch and recruitment ($n = 6$, $P < 0.0001$, $R^2 = 0.99$) and a linear relation that passed close to the origin ($c = 0.09$, $P = 0.96$) (Fig. 5).

The proportion of older fish in the seven populations was broadly the inverse of abundance (Table 1), although this factor was not statistically significant when regressed against either settlement densities ($n = 7$, $P = 0.16$, $R^2 = 0.23$) or adult densities ($n = 7$, $P = 0.09$, $R^2 = 0.37$). Despite the correspondence, there is no evidence that extinction time is a compensatory response to increasing recruitment (27). We suggest that the hydrodynamic differences among the lagoons affect the colonization rates of both prey and predators in a similar way and that differential predation causes the demographic differences observed in the prey populations.

Concluding Remarks

Shulman and Ogden (28) suggested that stochastic variations in predation will swamp variations in recruitment within systems with high turnover. Although this is likely for all species at small scales corresponding to the home ranges of predators, our data suggest that mortality is fairly consistent at the larger scale of whole coral reefs, which often provide the logical unit for management of human activities. In contrast, replenishment will vary at this scale because year-class formation is controlled by large-scale events like climate, whereas larval transport is controlled by short-term weather (29).

We conclude that the abundance of *P. moluccensis* on the reefs covered by our study is simply the nonequilibrial balance of variable recruitment interacting with density-independent mortality. Given the similar early life histories of most reef fishes, there is no reason why this conclusion should not apply equally to exploited species, which highlights the importance that the monitoring of recruitment dynamics has for the effective management of reef fisheries. Where recruitment limitation is demonstrated, the degree of connectivity to potential sources of larval supply is an important determinant of how a local area will recover from disturbance (including fishing pressure). Furthermore, there is potential under conditions of recruitment limitation to boost the productivity of reefs through artificial enhancement of juvenile abundance. With such practical outcomes possible, it is important to establish the generality of this condition. Given the evidence even within the Great Barrier Reef of strong regional variation in levels of natural recruitment (30), there is a need for more long-term monitoring of recruitment at large scales and a need to repeat our experiment in regions receiving higher levels of recruitment.

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