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## Regulation of local populations of a coral reef fish via joint effects of density- and number-dependent mortality

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**Abstract** Density-dependent mortality can regulate local populations – effectively minimizing the likelihood of local extinctions and unchecked population growth. It is considered particularly important for many marine reef organisms with demographically open populations that lack potential regulatory mechanisms tied to local reproduction. While density-dependent mortality has been documented frequently for reef fishes, few studies have explored how the strength of density-dependence varies with density, or how density-dependence may be modified by numerical effects (i.e., number-dependent mortality). Both issues can have profound effects on spatial patterns of abundance and the regulation of local populations. I address these issues through empirical studies in Moorea, French Polynesia, of the six bar wrasse (*Thalassoma hardwicke*), a reef fish that settles to isolated patch reefs. Per capita mortality rates of newly settled wrasse increased as a function of density and were well approximated by the Beverton-Holt function for both naturally formed and experimentally generated juvenile cohorts. Average instantaneous mortality rates were a decelerating function of initial densities, indicating the per capita strength of density-dependence decreased with density. Results of a factorial manipulation of density and group size indicate that per capita mortality rates were simultaneously density- and number-dependent; fish at higher densities and/or in groups had higher probabilities of disappearing from patch reefs compared with fish that were solitary and/or at lower densities. Mortality rates were ~30% higher for fish at densities of 0.5 fish/m<sup>2</sup> than at 0.25 fish/m<sup>2</sup>. Similarly, mortality rates increased by ~45% when group size was increased from 1 to 2 individuals per patch, even when density was kept constant. These observations suggest that the number of interacting individuals, independent of patch size (i.e., density-

independent effects) can contribute to regulation of local populations. Overall, this work highlights a greater need to consider numerical effects in addition to density effects when exploring sources of population regulation.

**Keywords** Density dependence · Number dependence · Population regulation · Post-settlement mortality · Reef fish

### Introduction

Population regulation arises from one or more feedback mechanisms that modify population growth rates in such a way as to bound temporal fluctuations in abundance (Nicholson 1933; Murdoch 1994; Turchin 1995). Most commonly, local feedback mechanisms take the form of density dependence in either per capita reproductive rates (e.g., Larsson and Forslund 1994; Wauters and Lens 1995; Both 1998) or mortality rates (e.g., Hopper et al. 1996; Bertness et al. 1998; Schmitt and Holbrook 1999a). Because unregulated populations are likely to fluctuate unchecked and eventually go extinct (Dennis and Taper 1994), much research has been devoted to identifying both specific mechanisms (e.g., Hixon and Carr 1997) and generalities (e.g., Connell 1985) associated with the regulation of local populations.

For populations that are demographically open, with local input rates of new individuals decoupled from local reproductive effort (e.g., many reef fish populations), density-dependence in local reproductive rates is unlikely to regulate local populations. Although Warner and Hughes (1989) used simulations to demonstrate how constant inputs (i.e., larval settlement) coupled with only density-independent post-settlement mortality can result in an equilibrium density of an open population, much research has focused on whether density-dependent interactions have a role in bounding fluctuations of such populations. These studies primarily have focused on the nature of per capita mortality after colonization (Jones 1991; Booth and Brosnan 1995; Caley et al. 1996).

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To date, numerous studies have documented density-dependent mortality that potentially is capable of bounding fluctuations in density of local reef fish populations (Jones 1984, 1991; Forrester 1990, 1995; Tupper and Hunte 1994; Tupper and Boutilier 1995; Schmitt and Holbrook 1996, 1999a, b; Hixon and Carr 1997; Sano 1997; Steele 1997; Caselle 1999; Schmitt et al. 1999; Shima 1999a; but see Doherty 1982, 1983; Victor 1986a; and Behrents 1987 for counter examples).

Despite the large number of studies evaluating the existence of density-dependent mortality in reef fishes, there remains a poor understanding of how the quantitative form (i.e., per capita strength) of density dependence varies with density. This is due in part to logistical and statistical difficulties associated with empirical investigations of density-dependent mortality (reviewed in Hassell 1986; Warner and Hughes 1989; Jones 1991; Murdoch 1994). An intensification or relaxation of density dependence, as evidenced by a non-linear relationship between instantaneous mortality rates and density, may alter the strength of regulation and affect spatial patterns of abundance and dynamics of local populations.

In addition, none of the studies exploring density-dependent mortality in reef fishes have attempted to evaluate potential numerical effects on population regulation independent of possible density effects, despite the long appreciated observation that survival rates in many fishes are coupled to group (i.e., school) size (Radakov 1973). Indeed, most experimental designs that have been used to test for density-dependence potentially confound density- and number-dependent effects on mortality. This distinction between 'density' (no./unit-area) and 'number' per se is critical in systems where patch sizes (i.e., unit-areas) and numbers (and hence densities) vary widely. For example, a population may be regulated by per capita mortality rates that are *number-dependent* but fundamentally *density-independent*, provided 'number' and 'patch size' positively co-vary (i.e., larger reefs receive more settlers), and per capita deaths increase with group size.

Here, I explore patterns of post-settlement mortality of the six bar wrasse (*Thalassoma hardwicke*), a common resident of Indo-Pacific coral reefs that settles to isolated reefs in low numbers. I employ experimental and analytical techniques to estimate the functional relationship between density and per capita mortality. This work also incorporates a factorial experiment that isolates the effects due to 'density' from those due to the 'number of individuals locally present', and evaluates the separate and joint effects of each on the regulation of local populations.

## Materials and methods

### The system

Field work was conducted on the island of Moorea, French Polynesia (17°30'S; 145°50'W) from 1996 through 1999. The island is

surrounded by a barrier reef that encloses a series of lagoons ranging from 500–1500 m in width and 0.5–5 m in water depth (see Galzin and Pointier 1985). On Moorea, six bar wrasse (*T. hardwicke*) are found exclusively within these shallow lagoons, and new settlers and juveniles primarily associate with small patch reefs (~3–4 m<sup>2</sup>), which are interspersed with sand or cobble (Shima 1999b).

Six bar wrasse are among the most common labrids on Moorea (Galzin 1987a, b). Adults are diurnal omnivores foraging over large (>1000 m<sup>2</sup>) home ranges (Shima 1999b). Adults spawn pelagic eggs yielding larvae with a planktonic larval duration of approximately 47 days (Victor 1986b). Settlement occurs in pulses (>90% of settlers/month appear during a pulse), over 5 consecutive nights surrounding new moons between January and June (Dufour et al. 1996; J. Shima, personal observations). Individuals settle directly to patch reefs composed of algal turf or live coral, and remain site-attached for approximately 4–6 months (Shima 1999b). This pattern of pulsed monthly settlement and subsequent residence on isolated patch reefs creates distinct populations of juvenile wrasses, each composed of a series of discrete size-cohorts that can be visually distinguished from one another (Shima 1999a).

Newly settled (day-0) individuals remain relatively inactive in masses of algal turf or within interstices of branching corals for 1–3 days while they develop juvenile pigmentation patterns (J. Shima, personal observations). Newly settled fish can be censused and distinguished from 1+day-old fish in careful visual searches (census accuracy verified with quinaldine-assisted collections following visual censuses; aging accuracy verified using post hoc otolith analyses; J. Shima, unpublished data).

### Surveys of natural settlement and post-settlement mortality

Demographic data for cohorts of six bar wrasse were collected from 96 patch reefs spread along the north shore of Moorea. Patch reefs were similar in size (mean area=4.03 m<sup>2</sup>; SD=1.67); depth, and rugosity, and all were composed of mounding coral skeletons (*Porites lobata*), with >80% surface area covered by algal turf (primarily *Spacelaria* spp. and *Polysiphonia* spp.) farmed by the territorial damselfish *Stegastes nigricans*. Each patch reef was isolated from its nearest neighbor by >3 m of reef flat (sand, pavement, or cobble). This distance appears sufficient to provide an effective barrier to successful migration, as no immigrants (i.e., appearances of older juveniles not attributable to prior settlement) were observed on any of the reefs over 6 consecutive months of observation. Six bar wrasse on patch reefs were censused daily during settlement pulses in 1996 and 1997 (5 days centered around new moons during May 1996, May 1997, and June 1997) and every third day during non-pulse periods through September 1996 and 1997. For each census, I conducted thorough searches of all branching corals and algal turf clumps within each patch reef to estimate new settlers (unpigmented 'day-0' fish) that had arrived the previous night. 1+day-old individuals of the same cohort (i.e., fish settling on the previous 1–4 nights) were visually distinguished from day-0 fish based on degree of pigmentation. Individuals from different cohorts (i.e., fish settling 1–4 months before or after the focal cohort) were easily identified based on size differences.

Six bar wrasse exhibit an excellent linear relationship between size and age up to 90 days post-settlement age ( $r^2=0.96$ , Shima 1999a). This strong relationship, coupled with the highly pulsed nature of six bar wrasse settlement, facilitates estimates of settler cohort abundance 90 days after settlement as the number of individuals ~35 mm in length (after Shima 1999a). Individuals from successive cohorts (separated in age by ~30 days) differ in size by ~10 mm and the accuracy of these visual censuses in assigning individuals to correct settlement cohorts was confirmed using post hoc analyses of otoliths (Shima 1999a).

Because none of the 96 patch reefs received any known immigrants (i.e., inputs not attributable to settlement) over 6 months of observation, I consider successful migration of juveniles among

patch reefs to be rare. Hence, losses of individuals from patch reefs, estimated as the difference between the number settling and the number remaining after 90 days, were interpreted as mortality, although some small amount of migration remained possible. Estimates were converted to per capita mortality rates by calculating the fraction of individuals disappearing over 90 days.

Because the fate of an individual fish in this study was binary (it either survived or died), one death contributes more to per capita (fractional) mortality rates at lower than at higher densities. Consequently, estimates of per capita mortality rates based on smaller numbers of settlers will be less precise than those based on larger numbers of settlers. To remedy this in my analyses and to achieve more equal precision in the estimates of per capita mortality rates over a range of settler abundances, I chose to pool individuals from different patch reefs containing similar densities of fish into 'density-categories' (after Schmitt and Holbrook 1999a). Separately for each of three settlement cohorts, I assigned patch reefs to density-categories such that each category contained roughly equivalent numbers of initial settlers (except for a 'solitary settler' category, which was limited to the number of sites receiving a single new individual). These effectively standardized denominator values used to calculate fractional (i.e., per capita) mortality rates, and homogenized precision of these estimates across density.

To explore the effect of density on per capita mortality rates, fractional losses calculated for each density category were regressed against the mean density of new settlers within each category. Because this relationship appeared curvilinear, and reef resources in this system appear to impose a ceiling on recruit abundance (Shima 1999a, b), I used the Beverton-Holt model (Beverton and Holt 1957) to explore the form of the relationship between per capita mortality and density:

$$\text{Per Capita Mortality} = [(1-a) + (aS/b)] / (1+aS/b) \quad (1)$$

where the independent variable  $S$  is the initial settler density. Parameter  $a$  estimates the proportion of fish that survive at very low (effectively 0) densities, and is constrained to values ranging from 0 to 1. Parameter  $b$  (constrained to values greater than 0) estimates the maximum density of fish (i.e., no./m<sup>2</sup>) that survive given excess densities of settlers. Both parameters were estimated through an iterative process (DUD method, NLIN procedure, SAS 1990), 95% confidence intervals for the parameter estimates were used to compare relationships calculated for each settlement event.

#### Experimental test for density-dependence

Estimates of per capita mortality rates from surveys (above) are useful because they utilized natural variation in settlement to explore patterns of density dependence at actual settlement levels in this system. However, because settler densities were not manipulated and assigned at random to patch reefs, these data alone are limited in their ability to attribute a causal relationship between density and per capita mortality rates. This is because settler density is potentially confounded with other natural differences that can also affect survivorship. Hence, I conducted a field experiment to confirm the shape of the density-mortality function.

To estimate patterns of mortality of newly settled wrasse experimentally, I marked 58 natural patch reefs on the north-central shore of Moorea. Patch reefs were of similar morphology and size (mean area=3.5 m<sup>2</sup>, SD=1.80), and composed of algal turf and large mounding corals (*Porites lobata*). Each was isolated from the nearest neighboring patch reef by a minimum of 5 m of sand. Resident six bar wrasse were initially removed from all patch reefs using hand nets. Following a period of heavy settlement in early May 1997, 300 six bar wrasse of less than 5 days post-settlement age were captured with hand nets and randomly assigned to one of five density-treatments ('solitary settler', 1 fish/m<sup>2</sup>, 2 fish/m<sup>2</sup>, 3 fish/m<sup>2</sup>, and 5 fish/m<sup>2</sup>, representing the natural range of densities at settlement). The 'solitary settler' treatment contained 21 individuals transplanted to 21 separate, randomly as-

signed patch reefs (i.e., mean initial density=0.3 fish/m<sup>2</sup>). Replication for the other density treatments was unbalanced to roughly equalize the total numbers of fish per density treatment (~60). All fish in these treatments were transplanted to patch reefs as groups of individuals (ranging from 2 to 22 fish per patch reef) to achieve desired densities for each treatment. Hence, the number of patch reefs used for each density treatment varied (from 21 at the lowest density to 4 at the highest density).

I estimated per capita mortality rates as the fraction of the total fish per treatment lost over 2 weeks. This estimate of per capita mortality was then regressed against the mean initial density experienced by fish in each treatment. As this relationship was curvilinear in form, the Beverton-Holt model (Eq. 1) was used to explore the pattern of density-dependence.

#### Variation in the per capita strength of density dependence

To further ascertain whether per capita effects (i.e., the strength of density-dependence) varied across settler densities for natural cohorts, I estimated the average instantaneous mortality rate of newly settled six bar wrasse (evaluated over a 90 day time-step) as:  $-\ln(R/S)$ , where  $R$  is the mean density (within a density category) of fish 90 days after settlement and  $S$  is the mean initial settler density. The negative sign preceding the natural log is inserted for the benefit of presentation (to reflect larger effects as more positive). I tested the hypothesis that the per capita strength of density dependence varied with settler density by evaluating the deviation-from-linearity (Zar 1996) of the relationship between the instantaneous mortality rate and initial settler density [ $H_0$ :  $-\ln(R/S)$  is linear with respect to  $S$ ]. This analysis requires replication in estimates of instantaneous mortality rates with respect to  $S$ . Consequently, evaluation of variation in the per capita strength of density dependence was possible only for the natural cohorts (the experiment did not yield the required replication). Following this formal analysis, a form of the Beverton-Holt model was fit to the relationship between average instantaneous mortality rate and initial settler density:

$$-\ln(R/S) = -\ln[a/(1+aS/b)] \quad (2)$$

#### Decoupling effects of density and number on post-settlement mortality

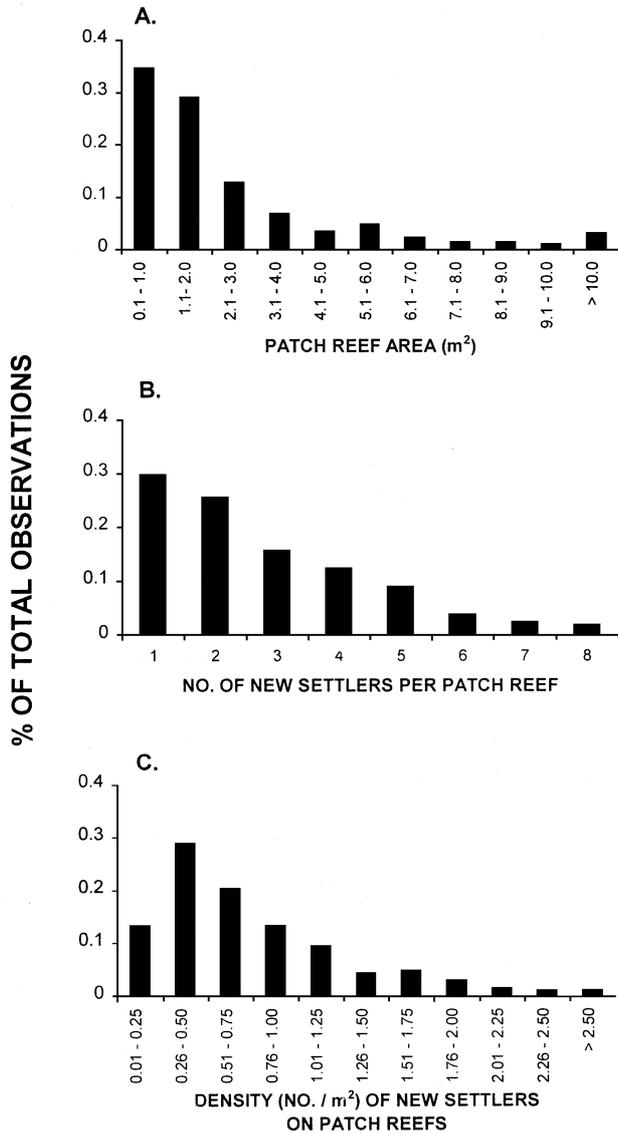
Although per capita mortality rates estimated from surveys and an experiment (above) varied with gradients in density, they were also confounded by variation in concomitant changes in the number of individuals per patch reef. To isolate effects on per capita mortality rates due to density and number, I conducted a factorial experiment in May 1999, to determine whether per capita mortality rates of newly settled wrasse occur primarily as (1) a function of wrasse densities (i.e., density-dependent losses), (2) a function of the number of individuals resident on patch reefs (i.e., number-dependence), or (3) a combination of these two factors. Both the size of patch reefs and the number of wrasse were manipulated to create a two-factor experimental design with two levels for the 'density' factor (0.25 fish/m<sup>2</sup> or 0.5 fish/m<sup>2</sup>) and two crossed levels for the 'number' factor (1 or 2 individuals per patch reef). Selected levels reflect values where mortality rates scaled most strongly with both 'density' and 'number', as measured from surveys and experiments (above). In addition, these values represent the most common levels of settlement observed on natural patch reefs of Moorea (Fig. 1). I selected 150 patch reefs for the experiment, based on (1) appropriateness of their size, (2) isolation from nearest neighbors (>5 m), and (3) similarity in composition, height (measured from reef base to maximum reef height), depth (measured from water surface to maximum reef height), and rugosity. Patch reefs were chosen from five sites that were spread over 5 km along the north shore of Moorea. Within each site, a total of 30 patch reefs were selected using the above criteria, and apportioned among three size categories: 2 m<sup>2</sup> ( $n=10$  reefs), 4 m<sup>2</sup> ( $n=15$

reefs), and 8 m<sup>2</sup> ( $n=5$  reefs). All patch reefs were cleared of resident six bar wrasse.

Newly settled wrasse (<2 weeks old) were collected from other locations, and either 1 or 2 individuals were randomly selected and transplanted to each experimental patch reef to create the density  $\times$  number factorial design. This design incorporated an unbalanced number of reefs per treatment (treatments with 2 individuals/reef utilized half as many reefs as treatments with a single individual/reef), but yielded an equal number of fish (i.e., 50) per treatment. Patch reefs were visually censused 7 days after trans-

plantation of wrasse to estimate per capita (fractional) mortality over 1 week.

Per capita mortality rates were estimated for each patch reef as the fraction of transplanted individuals that were lost over the 7 days of the experiment. Because these values were not continuous, but rather constrained to a trinomial distribution (0%, 50%, or 100%), tests of statistical significance were conducted using logistic ANOVA, which does not require such data to be transformed, or pooled (as above). I used the CATMOD procedure of SAS and tested effects of density, number, density  $\times$  number, and sites (treated as random blocks) against the generalized logit (SAS 1990). For presentation purposes, treatment effects are depicted as fractional survival (based on 10 fish) averaged across five blocks.



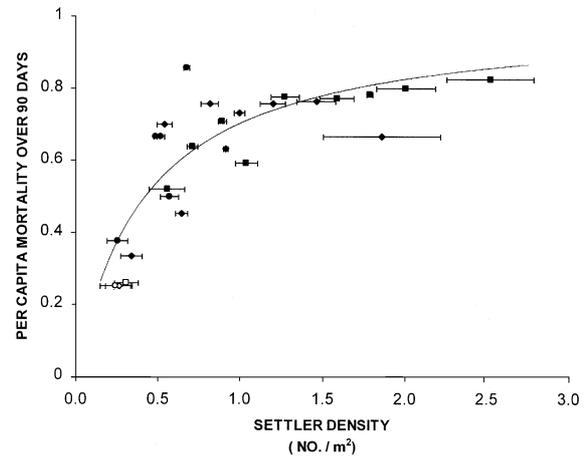
**Fig. 1** Natural distributions of patch reef sizes **A** number of new settlers per patch reef **B** and densities (number per m<sup>2</sup>) of new settlers on patch reefs **C** within the lagoon on the north shore of Moorea. Patch reef sizes were estimated within 12 randomly selected 10 $\times$ 10 m quadrats, each as the area of an ellipse, using measurements of maximum length and maximum perpendicular width as estimated by a weighted fiberglass tape-measure draped along the reef surface. Numbers of new settlers per patch reef were estimated from visual censuses as the number of day-0 fish (unpigmented individuals, after Shima 1999a) observed on 96 patch reefs over each of three settlement pulses. Density distributions were calculated as the number of new settlers per pulse per m<sup>2</sup> patch reef area

## Results

### Patterns of post-settlement mortality

Although the intensity of settlement varied among the three natural settlement pulses, per capita mortality rates increased as a function of initial density in all cases and were well approximated by the Beverton-Holt model, which accounted for 63–88% of the variance (Table 1). As the estimated parameters of this model did not significantly differ among focal settlement cohorts, density-categories were pooled across cohorts and fitted by a single regression (Table 1, Fig. 2). The good fit of the model to the pooled data ( $r^2=0.71$ ) suggests temporal consistency in the relationship between density and per capita mortality rates, at least for the settlement events examined.

Results from the experimental manipulation of settler densities confirmed that per capita mortality rates in-



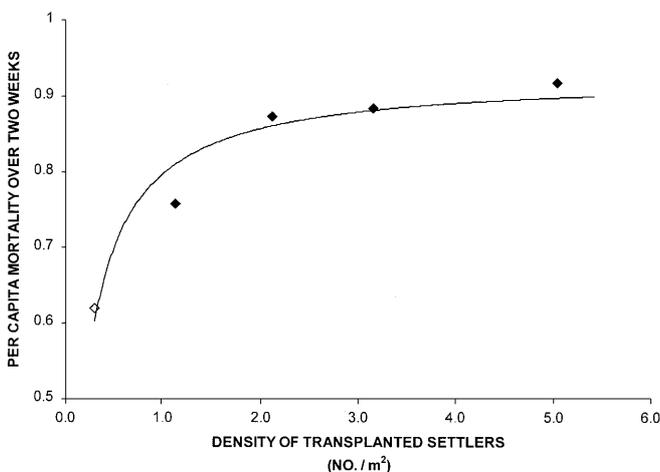
**Fig. 2** Density-dependent mortality of six bar wrasse over 3 months, combined from cohorts settling in May 1996 (squares), May 1997 (circles), and June 1997 (diamonds). Open symbols represent estimates of mortality rates of solitary settlers (i.e., fractional loss of all patch reefs with a single settler). Closed symbols represent the per capita mortality rates of fish settling to reefs in groups of 2 or more individuals, each point is estimated from a collection of patch reefs containing fish at similar densities. Horizontal error bars are  $\pm 1$  SD of the densities over which groupings of fish were pooled. For the Beverton-Holt regression ( $r^2=0.71$ ), estimates of parameters ( $\pm 95\%$  CI) are as follows:  $a=1.00$  (0.59–1.46),  $b=0.42$  (0.26–0.58)

**Table 1** Estimates of Beverton-Holt regression parameters used to explore the shape of the relationship between per capita mortality of six bar wrasse and their density for each of three settlement dates. Given are the parameter estimates ( $\pm 95\%$  CI) and the amount of variance explained ( $r^2$ ) by each non-linear model. Parameter  $a$  esti-

Settlement Date	$n$	$a$	$b$	Explained variance( $r^2$ )
May 1996	10	1.00 (0.49–1.51)	0.53 (0.31–0.75)	0.88
May 1997	6	1.00 (–1.05–3.12)	0.32 (–0.28–0.93)	0.63
June 1997	10	1.00 (0.21–1.84)	0.45 (0.12–0.78)	0.69
3 Cohorts combined	26 (0.59–1.46)	1.00 (0.26–0.58)	0.42	0.71

**Table 2** Test of deviation-from-linearity in the relationship between settler density and instantaneous mortality rate (Fig. 4). Given are the sums of squares (SS) and degrees of freedom ( $df$ ) used to calculate mean square error (MS) for the ‘deviations-from-linearity’ and ‘within groups’ partitions. The  $F$ -ratio of these partitions was used to test  $H_0$ : instantaneous mortality rate is linear with respect to settler density (after Zar 1996)

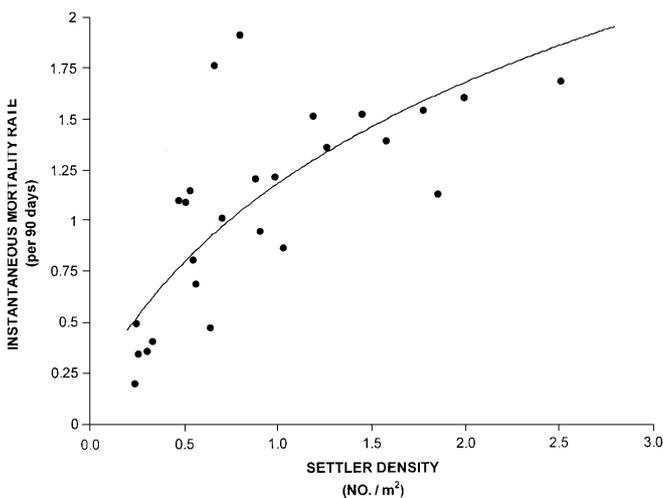
Source of Variation	SS	$df$	MS	Significance
Total	5.91	25		
Among groups	3.83	4		
Linear regression	2.60	1		
Deviations from linearity	1.23	3	0.41	$F=4.1, P<0.025$
Within groups	2.08	21	0.10	



**Fig. 3** Density-dependent mortality of newly settled six bar wrasse over 2 weeks, from an experimental manipulation of densities. The *open diamond* represents an estimate of mortality experienced by solitary settlers, calculated as fractional losses from a collection of 21 patch reefs containing solitary individuals. The *closed diamonds* represent density categories where fractional losses were calculated from collections of patch reefs containing ~60 fish, in groups of 2 or more individuals per patch reef, and at initial densities of 1, 2, 3, or 5 fish/m<sup>2</sup>. For the Beverton-Holt regression ( $r^2=0.98$ ), estimates of parameters ( $\pm 95\%$  CI) are as follows:  $a=0.51$  (0.38–0.65),  $b=0.45$  (0.29–0.61)

creased with density, and suggest that density-dependent losses qualitatively similar to those observed from natural settlers can accrue as rapidly as 2 weeks and result solely from intra-cohort effects. Per capita mortality rates generally increased with density and were well

mates the proportion of fish that survive at very low (effectively 0) densities, and is constrained to values ranging from 0 to 1. Parameter  $b$  (constrained to values greater than 0) estimates the maximum density of fish (i.e., no./m<sup>2</sup>) that survive given excess densities of settlers

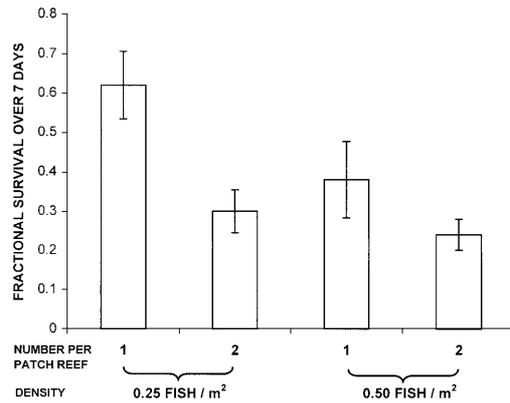


**Fig. 4** Variation in instantaneous mortality rates of six bar wrasse with respect to their densities. Instantaneous mortality rate (per 90 days) was calculated as  $-\ln(R/S)$ , where  $R$  is the density of fish 90 days after settlement and  $S$  is their initial densities (i.e., at settlement). The relationship was fit by the Beverton-Holt model (Eq. 2,  $r^2=0.55$ ) after determination of significant deviation from linearity (Table 2)

approximated by the Beverton-Holt model ( $r^2=0.98$ , Fig. 3). Overall, mortality rates estimated from the experiment were elevated relative to those measured for natural populations, and may represent additional density-independent handling mortality.

#### Variation in the per capita strength of density dependence

Average instantaneous mortality rate increased with density (Fig. 4). If per capita effects were constant across the density gradient, this increase should be linear. However, the observed relationship exhibited a significant deviation-from-linearity (Table 2, Fig. 4). Although the best-fit linear model (instantaneous mortality rate =  $0.54 * \text{settler density} + 0.57$ ) was highly significant ( $P<0.001$ ), it accounted for only 46% of the variation in instantaneous mortality rate, by comparison, the Beverton-Holt model (Fig. 4) explained 55% of this variance, and appeared to better approximate the apparent diminution in instantaneous mortality rates with increasing settler den-



**Fig. 5** Mean fractional survival after 7 days for fish at low densities (0.25 fish/m<sup>2</sup>) and high densities (0.50 fish/m<sup>2</sup>), either as solitary individuals or in groups of two. Statistical tests are based on logistic anova (presented in Table 3) and indicate significant effects of both 'density' and 'number of fish per patch reef' on survival. Mean fractional survival ( $\pm 1$  SE) was calculated here for purposes of presentation, and is based upon 10 fish per treatment, averaged across five blocks

**Table 3** Maximum-likelihood analysis-of-variance of per capita mortality over 7 days of newly settled six bar wrasse as affected by location blocks, density (either 0.25 or 0.50 newly settled wrasse/m<sup>2</sup>), number of newly settled wrasse per patch reef (either 1 or 2), and the interaction between density and number. Results were obtained by fitting generalized logits (log-odds ratios of individual survivorship) using the CATMOD procedure of SAS (SAS 1990). Non-significant Likelihood Ratio indicates a significant model fit

Source of Variation	df	Chi-square	P-value
Intercept	1	11.09	0.0009
Block	4	8.19	0.085
Density of Newly Settled Wrasse	1	4.61	0.032
Number of Newly Settled Wrasse	1	11.10	0.0009
Density $\times$ Number	1	1.29	0.26
Likelihood Ratio	12	11.69	0.47

sities. This deceleration in average instantaneous mortality rates with initial density suggests a relaxation in the intensity of density-dependence at higher levels of settlement.

#### Decoupling effects of density and number on post-settlement mortality

At lower levels of natural settlement, reefs of variable size were colonized by either 1 or 2 individuals, and smaller reefs showed a greater propensity to yield solitary individuals. Hence, solitary settlers on small reefs were at similar densities to fish settling in groups of 2 to reefs twice as large. Despite similarities in density, per capita mortality rates apparently increased from 25% to 35% with the shift from 1 to 2 individuals/reef (Fig. 2) and suggest possible influence of numerical effects on survival. Results from the experimental manipulation of new settlers (Fig. 3) also suggested enhanced survival of

solitary individuals relative to fish inhabiting reefs in groups of 2 or more individuals.

Results from the factorial manipulation indicate both initial density and initial number of fish transplanted to experimental reefs influenced per capita mortality rates over 7 days, and no significant interactions or large block effects were detected (Table 3). Within each density treatment (0.25 or 0.50 fish/m<sup>2</sup>), solitary fish always fared better than fish in groups of two. Similarly, within each number treatment (solitary or group of two individuals), fish at lower densities always survived better than fish at higher densities. Over the range of densities and group sizes investigated (typical values for this species, Fig. 1), doubling the number of fish per reef (solitary vs. a group of two) had a larger effect on survivorship than did doubling density (Fig. 5). This indicates that the number of individuals present is an important component of post-settlement losses that contributes to local population regulation of this species. Increasing densities (from 0.25 fish/m<sup>2</sup> to 0.5 fish/m<sup>2</sup>) reduced survivorship by 33%, while increasing the number of fish per patch reef (from 1 to 2) reduced survivorship by 46%.

#### Discussion

Variation in the per capita strength of density dependence is likely to determine how strongly, and under which conditions, a local population will be regulated by density-dependent interactions. Despite a growing number of studies documenting density-dependent mortality in reef fishes, the quantitative form of density-dependent interactions has received little attention. As a result, we lack a complete understanding of the relative contributions of density-dependent mortality to local population regulation in these systems.

With respect to six bar wrasse, per capita mortality rates were density dependent over all observed levels of natural settlement. Perhaps more importantly, the average instantaneous mortality rate was a decelerating function of initial settler density, indicating an intensification of density-dependence at lower settler densities and a concomitant relaxation in the per capita strength of density dependence with increasing densities. This suggests that six bar wrasse populations are likely to experience stronger regulation (characterized by tighter bounding of fluctuations) at lower settlement densities, with population fluctuations that generally increase with levels of settlement. Because six bar wrasse on Moorea tend to colonize at these lower settlement densities (Fig. 1), the system appears to predominately experience strong regulation.

Evaluating the ubiquity of these results is precluded by the general lack of information on instantaneous mortality rates of reef fishes with respect to their densities. However, these findings call into question the pervasive view that mortality rates are density-independent at low (under-saturated) densities (Connell 1985; Victor 1986a; Forrester 1990; Doherty 1991; Jones 1991; Caley et al.

1996; Steele 1997; Caselle 1999), and suggest instead that strong density-dependent mortality may resound at lower densities for some reef fishes.

Experimental manipulation of settler densities confirmed a causal relationship between density and per capita mortality rates. Furthermore, patterns of mortality that were qualitatively similar to those observed for natural cohorts were apparent over a much shorter period of time (14 days, vs 90 days for natural cohorts) and suggest that strong density-dependence may occur rapidly, and its detection may be missed if older recruits remain the focus of future investigations (reviewed in Jones 1991; Caley et al. 1996). Similar findings have been reported elsewhere (Steele 1997; Caselle 1999; Schmitt and Holbrook 1999a). That the removal of older cohorts from experimental reefs did not affect the qualitative pattern of density dependence suggests intra-cohort effects alone may be responsible for the strong density-dependent mortality observed in natural populations. This interpretation is consistent with behavioral observations of juvenile six bar wrasse (Shima 1999b), which suggest that agonistic interactions occur predominantly among individuals of the same age (i.e., settlement) cohort. Strong intra-cohort interactions have been observed for other sex-changing wrasses (R. Warner, personal communication) and may be important in establishment of dominance hierarchies controlling sex change. While this posturing among individuals of similar age may not constitute a direct source of mortality, it may lead to elevated predation levels resulting from increased visibility and/or decreased vigilance. The apparent relaxation in the intensity of density-dependence with increasing densities may reflect a saturation in the effects of behavioral interactions on local predation rates.

Finally, a factorial experiment that manipulated 'density' and 'number' showed that, for a given density, per capita mortality rates are influenced by the number of individuals within a local population. The experiment also confirmed the simultaneous influence of density on mortality rates, consistent with results from the gradient manipulation of settler density alone. Over the range of densities that exhibited the strongest density dependence (i.e., steepest slope of instantaneous mortality rate vs density, Fig. 4) and for group sizes most commonly experienced by this species (Fig. 1B), post-settlement survival was more strongly affected by increases in group size than by proportionate increases in density. This indicates a potential for numerical effects to strongly contribute to the regulation of six bar wrasse populations, and suggests that number-dependence may need to be explicitly considered as an additional regulatory mechanism for organisms sensitive to group size. In addition, such number-dependence may contribute the observed variation in the per capita strength of density dependence, as numerical effects may be most pronounced at low densities (i.e., when local populations increase from 1 to 2 individuals).

Numerical effects are fast becoming a focal point of new research in evolutionary processes, with recent

studies of frequency- and density-dependent selection (Bennington and Stratton 1998; Nakajima 1998; Newton et al. 1998). Number as an alternative to density plays an acknowledged role in disease transmission (Thrall et al. 1995; Altizer and Augustine 1997), and its importance in animal behavior is evidenced by discussions of frequency-dependent foraging strategies (Church et al. 1996; Marini and Weale 1997; Smithson and Macnair 1997; Allen et al. 1998; Belisle 1998). Ecologists have explored effects of group size on survivorship (e.g., Henschel 1998), and commonly demonstrate both costs and benefits of living in groups (reviewed in Radakov 1973; Bertram 1978). However, population ecologists have traditionally characterized the sizes of populations they study in units of density rather than as frequencies, and perhaps consequently, density-dependent regulatory mechanisms are generally favored over number-dependent ones. Density-dependence is commonly cited as the feedback mechanism that is necessary for the regulation of populations. However, this work illustrates how fluctuations in the number of individuals independent of their densities (i.e., density-independent effects) can provide a feedback mechanism sufficient to influence vital demographic rates and regulate local populations.

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## References

- Allen JA, Raison HE, Weale ME (1998) The influence of density on frequency-dependent selection by wild birds feeding on artificial prey. *Proc R Soc Lond Ser B* 265:1031-1035
- Altizer SM, Augustine DJ (1997) Interactions between frequency-dependent and vertical transmission in host-parasite systems. *Proc R Soc Lond Ser B* 264:807-814
- Behrents KC (1987) The influence of shelter availability on recruitment and early juvenile survivorship of *Lythrypnus dalli* Gilbert (Pisces:Gobiidae). *J Exp Mar Biol Ecol* 107:45-59
- Belisle M (1998) Foraging group size: models and a test with jaegers kleptoparasitizing terns. *Ecology* 79:1922-1938
- Bennington CC, Stratton DA (1998) Field tests of density- and frequency-dependent selection in *Erigeron annuus* (Compositae). *Am J. Bot* 85:540-545

- Bertness MD, Gaines SD, Yeh SM (1998). Making mountains out of barnacles: the dynamics of acorn barnacle hummocking. *Ecology* 79:1382–1394
- Bertram BCR (1978) Living in groups: predator and prey. In: Krebs JR, Davies NB (eds) *Behavioral ecology: an evolutionary approach*. Blackwell, Oxford, pp 64–96
- Beverton RJH, Holt SJ (1957) *On the dynamics of exploited fish populations*. Chapman and Hall, London
- Booth DJ, Brosnan DM (1995) The role of recruitment dynamics in rocky shore and coral reef fish communities. *Adv Ecol Res* 26:309–385
- Both C (1998) Density dependence of clutch size: habitat heterogeneity or individual adjustment? *J Anim Ecol* 67:659–666
- Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA (1996) Recruitment and the local dynamics of open marine populations. *Annu Rev Ecol Syst* 27:477–500
- Caselle JE (1999) Early post settlement mortality in a coral reef fish and its effect on local population size. *Ecol Monogr* 69:177–194
- Church SC, Allen JA, Bradshaw JWS (1996) Frequency-dependent food selection by domestic cats: a comparative study. *Ethology* 102:495–509
- Connell JH (1985) The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *J Exp Mar Biol Ecol* 93:11–45
- Dennis B, Taper B (1994) Density dependence in time series observations of natural populations: estimations and testing. *Ecol Monogr* 64:205–224
- Doherty PJ (1982) Some effects of density on the juveniles of two species of tropical, territorial damselfish. *J Exp Mar Biol Ecol* 65:249–261
- Doherty PJ (1983) Tropical territorial damselfishes: is density limited by aggression or recruitment? *Ecology* 64:176–190
- Doherty PJ (1991) Spatial and temporal patterns of recruitment. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego, pp 261–293
- Dufour V, Riclet E, Lo-Yat A (1996) Colonization of reef fishes at Moorea island, French Polynesia: temporal and spatial variation of the larval flux. *Mar Freshwater Res* 47:413–422
- Forrester GE (1990) Factors influencing the juvenile demography of a coral reef fish. *Ecology* 71:1666–1681
- Forrester GE (1995) Strong density-dependent survival and recruitment regulate the abundance of a coral reef fish. *Oecologia* 103:275–282
- Galzin R (1987a) Structure of fish communities of French Polynesian coral reefs. I. Spatial scales. *Mar Ecol Prog Ser* 41:129–136
- Galzin R (1987b) Structure of French Polynesian coral reefs. II. Temporal scales. *Mar Ecol Prog Ser* 41:137–145
- Galzin R, Pointier JP (1985) Moorea Island, Society archipelago. *Proc 5th Int Coral Reef Sym (Tahiti)* 1:75–101
- Hassell MP (1986) Detecting density dependence. *Trends Ecol Evol* 1:90–93
- Henschel JR (1998) Predation on social and solitary individuals of the spider *Stegodyphus dumicola* (Araneae, Eresidae). *J Arachnol* 26:61–69
- Hopper KR, Crowley PH, Kielman D (1996) Density dependence, hatching synchrony, and within-cohort cannibalism in young dragonfly larvae. *Ecology* 77:191–200
- Hixon MA, Carr MH (1997) Synergistic predation, density dependence, and population regulation in marine fish. *Science* 277:946–949
- Jones GP (1984) Population ecology of the temperate reef fish *Pseudolabrus celidotus* Bloch and Schneider (Pisces: Labridae). II. Factors influencing adult density. *Mar Ecol Prog Ser* 75:277–303
- Jones GP (1991) Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego, pp 294–328
- Larsson K, Forslund P (1994) Population dynamics of the barnacle goose *Branta leucopsis* in the Baltic area: density-dependent effects on reproduction. *J Anim Ecol* 63:954–962
- Marini MA, Weale ME (1997) Density- and frequency-dependent predation of artificial bird nests. *Biol J Linn Soc* 62:195–208
- Murdoch WW (1994) Population regulation in theory and practice. *Ecology* 75:271–87
- Nakajima T (1998) Ecological mechanisms of evolution by natural selection: causal processes generating density-and-frequency dependent fitness. *J Theor Biol* 190:313–331
- Newton MR, Kinkel LL, Leonard KJ (1998) Determinants of density- and frequency-dependent fitness in competing plant pathogens. *Phytopathology* 88:45–51
- Nicholson AJ (1933) The balance of animal populations. *J Anim Ecol* 2:132–178
- Radakov DV (1973) *Schooling in the ecology of fish*. Halsted, New York
- Sano M (1997) Temporal variation in density dependence: recruitment and postrecruitment demography of a temperate zone sand goby. *J Exp Mar Biol Ecol* 214:67–84
- SAS (1990) *SAS/STAT user's guide, version 6, 4th edn*. SAS Institute, Cary, N.C.
- Schmitt RJ, Holbrook SJ (1996) Local-scale patterns of larval settlement in a planktivorous damselfish – do they predict recruitment? *Mar Freshwater Res* 47:449–463
- Schmitt RJ, Holbrook SJ (1999a) Early mortality of juvenile damselfish: implications for assessing the processes that determine patterns of abundance. *Ecology* 80:35–50
- Schmitt RJ, Holbrook SJ (1999b) Settlement and recruitment of three damselfish species: larval delivery and competition for shelter space. *Oecologia* 118:76–86
- Schmitt RJ, Holbrook SJ, Osenberg CW (1999) Quantifying the effects of multiple processes on local abundance: a cohort approach for open populations. *Ecol Lett* 2:294–303
- Shima JS (1999a) Variability in relative importance of determinants of reef fish recruitment. *Ecol Lett* 2:304–310
- Shima JS (1999b) An evaluation of processes that influence variability in abundance of a coral reef fish. Ph.D. Dissertation, University of California, Santa Barbara
- Smithson A, Macnair MR (1997) Density-dependent and frequency-dependent selection by bumblebees *Bombus terrestris* (L.) (Hymenoptera: Apidae). *Biol J Linn Soc* 60:401–417
- Steele MA (1997) Population regulation by post-settlement mortality in two temperate reef fishes. *Oecologia* 112:64–74
- Thrall PH, Biere A, Uyenoyama MK (1995) Frequency-dependent disease transmission and the dynamics of the *Silene-Ustilago* host-pathogen system. *Am Nat* 145:43–62
- Tupper M, Boutilier RW (1995) Effects of conspecific density on settlement, growth and post-settlement survival of a temperate reef fish. *J Exp Mar Biol Ecol* 191:209–222
- Tupper M, Hunte W (1994) Recruitment dynamics of coral reef fishes in Barbados. *Mar Ecol Prog Ser* 108:225–235
- Turchin P (1995) Population regulation: old arguments and a new synthesis. In: Cappuccino N, Price PW (eds) *Population dynamics: new approaches and synthesis*. Academic Press, San Diego, Calif., pp 19–40
- Victor BC (1986a) Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. *Ecol Monogr* 56:1435–1460
- Victor BC (1986b) Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae). *Mar Biol* 90:317–326
- Warner RR, Hughes TP (1989) The population dynamics of reef fishes. *Proc. 6th Int Coral Reef Sym (Townsville)* 2:149–155
- Wauters LA, Lens L (1995) Effects of food availability and density on red squirrel (*Sciurus vulgaris*) reproduction. *Ecology* 76:2460–2469
- Zar JH (1996) *Biostatistical analysis*. Prentice Hall, Upper Saddle River, N.J.