

Quantifying the effects of multiple processes on local abundance: a cohort approach for open populations

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Abstract

A challenge for species with demographically open populations is to evaluate the relative importance of various processes that together set local abundance. We developed a cohort-based framework for quantifying the influence of an external supply of colonists and subsequent density-independent and density-dependent mortality on local abundance. Two complementary approaches – based on limitation and elasticity – revealed the nature of interactions and nonlinearities among these processes. Data for an Indo-Pacific reef fish were used to document the settler–survivor relationship and to quantify natural variation in settlement. Limitation by density-dependence was two-fold and 20-fold greater than by supply or density-independent mortality, respectively. Elasticity analyses showed that adult abundance was 40% more sensitive to small proportionate changes in supply than in density-dependence. These techniques provide a way to compare across systems, which could enhance our ability to draw general conclusions regarding the processes that shape local abundance of species with open populations.

Keywords

Abundance, density-dependence, elasticity analyses, recruitment limitation, reef fish, relative importance

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INTRODUCTION

It is widely appreciated that multiple factors contribute to ecological patterns, and evaluating their relative importance poses a major challenge to ecologists. One constraint has been a paucity of operational frameworks that allow the contributions of multiple processes to be estimated and compared within and across systems (Underwood & Petraitis 1993; Osenberg & Mittelbach 1996). The current state of our understanding of processes that determine local abundance of benthic marine organisms cogently illustrates the need for such frameworks, especially for species with demographically open populations. For most benthic marine fishes and invertebrates, early developmental stages disperse widely in the plankton whereas older reef-associated stages are relatively sedentary. A long-standing and still-debated issue for such species concerns the relative contribution to local abundance of three processes: the external input of colonists (“larval supply”), subsequent losses that are independent of density and losses that are density-dependent (Doherty 1991; Jones 1991a; Forrester 1995; Caley *et al.* 1996; Sponaugle & Cowen 1996; Steele 1997a; Chesson 1998; Schmitt & Holbrook 1999a).

“Recruitment limitation” in reef organisms has been used to describe the situation where local abundance is less than the maximum possible due to an under-supply of colonists (Doherty 1981, 1991; Olafsson *et al.* 1994; Hixon 1998). A common empirical “test” of recruitment limitation involves a cohort approach based on the premise that in the absence of local density-dependent interactions, the relationship between the number of settlers and the number of subsequent survivors will be linear (Connell 1985; Robertson 1992; Doherty & Fowler 1994; Caselle 1999; Schmitt & Holbrook 1999a). This approach works only if single processes act in isolation: e.g. local abundance is only recruitment limited at low settler densities, and only affected by density-dependent mortality after local resources become saturated. This contrasts with the findings of recent studies, which have shown that the dynamics of reef fishes probably are affected simultaneously by several processes (e.g. Jones 1991a; Forrester 1995; Steele 1997a, b; Caselle 1999; Schmitt & Holbrook 1999a). Thus, we require an approach that can quantify the influence of multiple processes.

We elaborate a conceptual framework to quantify the relative effects of processes that affect local abundance.

Included are two related approaches to examine the factors that influence adult density: one (termed Limitation) quantifies the degree to which particular processes constrain adult density (Osenberg & Mittelbach 1996), and the other (termed Elasticity) quantifies the relative sensitivity of adult density to small proportionate changes in rates of key processes (Caswell 1989). We illustrate the application of both approaches using data from an Indo-Pacific damselfish and highlight the need to deal explicitly with variability in settlement rates.

METHODS

The framework

Settler–adult relationships. We take a cohort approach to provide a quantitative framework for open populations. Thus, we begin by describing the relationship between the input of colonists (supply or settlement) and subsequent abundance of these individuals at an older stage. We use a general three-parameter recruitment model (Shepherd 1982):

$$A = aS/[1 + (a/b) S^d] \quad (1)$$

where A is the density of older stages (which for simplicity we refer to as “adults”) produced by a settler density S , and a , b and d are fitted parameters (e.g. based on data from experimental manipulations of S and subsequent measurement of adult density). d controls the shape of the recruitment function. When $d = 0$, the relationship is linear and all losses are density-independent. When $0 < d < 1$, the relationship is a decelerating curve in which adult density increases but without limit as settlement increases (i.e. density-dependence occurs but is weak). When $d > 1$, density-dependence is strong and the recruitment function is hump-shaped; although adult density initially increases with increasing density of settlers, density-dependence eventually produces over-compensation at high settler densities and adult density declines. Finally, when $d = 1$, the relationship is a saturating function and adult density approaches an asymptote as settler density increases. In this last case, Eqn 1 simplifies to a two-parameter model:

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

where a is the density-independent survivorship and b is the maximum (i.e. asymptotic) adult density. Because our data fit this latter pattern (see Results) and because other studies also have documented asymptotic recruitment functions (Jones 1991a, b; Steele 1997b), we use Eqn 2 to develop the next phase of our approach.

Quantifying effects of multiple processes. There is no single solution to quantifying the effects of ecological processes

(Osenberg *et al.* 1999). Here, we develop two approaches that quantify how much the system is affected by particular processes but that differ in the scale of comparison. In one approach (Limitation) we estimate how much each process constrains adult density by using Eqn 2 to quantify how much adult density increases given *complete removal* of the constraint. The other approach (Elasticity) quantifies how much adult density responds to *small* (i.e. infinitesimal) relative changes in model parameters. The concept of limitation is probably most useful to empiricists, whereas elasticity may be more valuable in a theoretical context (where infinitesimal changes can be reasonably discussed). We use Eqn 2 and the parameterized model for a damselfish (see below) to illustrate the application of both approaches.

Limitation. To estimate the amount that each process limits adult abundance, we “remove” limitation imposed by one process and compare the resulting adult density with that observed under ambient conditions. Thus, four adult densities are required (Table 1): the ambient density (A_{AMB}), which is based on field observation, and three densities estimated from the fitted model (Eqn 2), including A_S (adult density in the absence of settlement limitation), A_{DI} (adult density in the absence of density-independent mortality), and A_{DD} (adult density in the absence of density-dependent mortality). For example, Settlement Limitation is the difference between the adult density under ambient settlement and the adult density that would arise if settlement was unlimited (i.e. essentially infinite). Figure 1 illustrates our approach graphically. Limitation can be expressed either as an absolute change ($A_{\text{without limitation}} - A_{AMB}$) or a relative change [$(A_{\text{without limitation}} - A_{AMB})/A_{AMB}$] (note that when $A_{AMB} = 0$, relative change is undefined).

Elasticity. Limitation emphasizes the response of adult density to removal of specific constraints. Alternatively, we could perform more classic sensitivity analyses and evaluate how much adult density changes in response to small perturbations in the input variable (settlement, S) or model parameters (density-independent survivorship, a , maximum adult density, b). Sensitivity analyses, however, are problematic when parameters are measured on different scales. To facilitate comparison among variables having different units, elasticities, which quantify proportionate and not absolute changes, are often preferred (Caswell 1989). In our framework, elasticities, e , quantify the percentage change in adult density (A) that results from, and is expressed relative to, a small percentage change in a , b or S . For example, $e_S = 1$ indicates that a small percentage change in settlement (S) yields an equivalent percentage change in adult density (A); $e_S < 1$

Table 1 Equations for Limitation (absolute and relative) and Elasticity based on the settler-survivor function (Eqn 2): $A = aS/[1 + (a/b)S]$, where A is sub-adult density, a is density-independent survivorship, b is the asymptotic density of sub-adults and S is settler density. Note for elasticities based on Eqn 2, proportionate changes in a and S have the same effect on sub-adult density (A) because a and S always appear as a product in Eqn 2; as a result, $e_a = e_S = e_{aS}$

Limitation	Absolute	Relative (%)
Supply limitation (L_S)	$A_S - A_{AMB}$	$[(A_S - A_{AMB})/A_{AMB}] \times 100$
Density-independent limitation (L_{DI})	$A_{DI} - A_{AMB}$	$[(A_{DI} - A_{AMB})/A_{AMB}] \times 100$
Density-dependent limitation (L_{DD})	$A_{DD} - A_{AMB}$	$[(A_{DD} - A_{AMB})/A_{AMB}] \times 100$

Where:

$A_{AMB} = aS/[1 + (a/b)S]$
 $A_S = b$ (found by letting $S \rightarrow \infty$)
 $A_{DI} = S/(1 + S/b)$ (found by setting $a = 1$)
 $A_{DD} = aS$ (found by letting $b \rightarrow \infty$)

Elasticity	
For adjusted settlement ($\partial \ln A / \partial \ln aS$):	$e_{aS} = 1/[1 + (a/b)S]$
For density-dependence ($\partial \ln A / \partial \ln b$):	$e_b = (aS/b)/[1 + (aS/b)]$

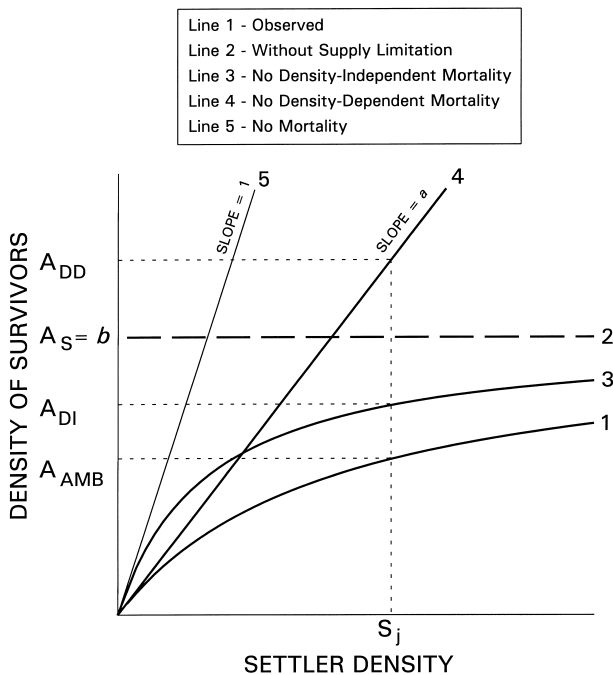


Figure 1 Graphical representation of Limitation. Line 1 represents an observed relationship between adult density and initial settler density (for comparison, line 5 represents no postsettlement mortality). S_j is the ambient settlement rate of a system, which yields an adult density of A_{AMB} . Allowing settlement to be unlimited in Eqn 2 (letting $S \rightarrow \infty$) results in a new adult density A_S , which is the saturation density b (line 2); Supply Limitation (L_S) is the difference between lines 1 and 2 ($L_S = A_S - A_{AMB}$). Removing limitation due to density-independent mortality in our model (setting $a = 1$) results in an adult density of A_{DI} (line 3); Density-Independent Limitation (L_{DI}) is the difference between lines 1 and 3 ($L_{DI} = A_{DI} - A_{AMB}$). Eliminating density-dependent mortality (letting $b \rightarrow \infty$) produces an adult density of A_{DD} (line 4); Density-Dependent Limitation (L_{DD}) is the difference between lines 1 and 4 ($L_{DD} = A_{DD} - A_{AMB}$). See Table 1 for equations.

indicates that there is a less than proportionate change in adult density; and $e_S > 1$ indicates that there is a greater than proportionate change. Mathematically, elasticities are calculated as $\partial \ln A / \partial \ln S$, $\partial \ln A / \partial \ln a$ and $\partial \ln A / \partial \ln b$ [because $\partial \ln A / \partial \ln x = (\partial A / A) / (\partial x / x)$ and therefore quantify proportionate responses as compared to standard sensitivities $\partial A / \partial x$, which quantify absolute responses].

In our model (Eqn 2), proportionate changes in a and S have the same effect on adult density because they always appear together as a product; as a result, their elasticities are identical because, for example, a 10% increase in density-independent survival (a) has the same effect on adult density as a 10% increase in settler density (S). We therefore treat them simultaneously and compare their joint elasticity (e_{aS}) with that associated with the density-dependent term, b (e_b). These two elasticities sum to one ($e_{aS} + e_b = 1$). Table 1 provides the equations for these elasticities based on Eqn 2.

Comparison to field data. Armed with this quantitative framework for Limitation and Elasticity, we now require empirical data to (i) support our use of a particular form of the recruitment function (i.e. Eqn 2); (ii) parameterize the model (i.e. estimate a and b); and (iii) use the framework and fitted parameters to estimate the magnitude of limitation and elasticity for a specific empirical system. Thus, we conducted a field experiment to estimate the recruitment function for a damselfish, and we also estimated ambient settlement rates to assess the relative importance of different processes in this system.

Empirical patterns

Fieldwork was conducted in lagoons of Moorea, French Polynesia ($17^{\circ}30'S:149^{\circ}50'W$), and used a coral reef

damsel fish [the three-spot dascyllus, *Dascyllus trimaculatus* (Ruppell)] as the model organism. This diurnal planktivore has a planktonic larval stage of ~ 22 days; competent larvae settle to sea anemones (*Heteractis magnifica*) where they remain until sexual maturity (~ 9 – 12 months). Sexually mature adults, which can reach 110 mm SL, do not associate closely with anemones.

The settler–sub-adult relationship. We characterized the relationship between settler density and the density of these fish at a specified older stage through a field experiment. Because adults no longer associate with anemones (which precluded following settlers to adulthood), we instead focused on recruitment into a sub-adult stage (6 months after settlement, but still associated with anemones). Settler densities were manipulated among naturally occurring anemones at an inshore section of Moorea's Haapiti lagoon where settlement rates of *D. trimaculatus* were low, presumably because of low current flow and therefore low delivery rates of larvae. Survivorship to 6 months was estimated as a function of initial settler density. One-hundred and thirty-seven isolated anemones, each with an oral surface area of ~ 0.05 m², were measured and individually marked. Resident fish were removed. Immediately following a large settlement pulse, ~ 1400 new settlers were collected from anemones in other lagoon areas, placed in running seawater tanks for 24 h, and then transplanted to the experimental anemones (for details on fish handling, see Schmitt & Holbrook 1996, 1999a, c; Holbrook & Schmitt 1997, 1999). We outplanted ~ 1050 fish. The remaining ~ 350 individuals were returned to lab seawater tanks and held for a week to estimate handling mortality (which was $\sim 2\%$). Anemones were assigned randomly to 11 density treatments: 1, 2, 3, 5, 7, 14, 25, 50, 75, 135 and 315 fish per 0.1 m² surface area of anemone; the numbers of replicates per treatment were: 63, 3, 8, 8, 12, 12, 14, 6, 5, 4 and 2, respectively. There was no statistical difference in average anemone size among the density treatments ($P > 0.9$). We estimated recruitment to the sub-adult stage by counting the number of settlers that survived 6 months.

Estimates of natural settlement levels. The settlement experiment provided data to estimate the recruitment function, i.e. a and b in Eqn 2. To estimate the relative importance of different processes, we needed to also know the natural settlement rate of *D. trimaculatus* and how it varied in time and space. To estimate natural settlement patterns, 10 anemones were transplanted to each of 10 lagoon sites distributed around the perimeter of Moorea. Resident fish were removed just prior to a settlement pulse. The number of settlers per anemone per site was estimated for six settlement pulses between 1996 and 1997 (see Schmitt

& Holbrook 1999c). The entire dataset (600 observations) was used to construct a distribution of settlement rates, which we used along with Eqn 2 and the definitions of limitation and elasticity to quantify the contribution of each process for *D. trimaculatus* in lagoons of Moorea.

RESULTS

The settler–sub-adult relationship. In the field experiment, the density of sub-adults was a nonlinear function of the initial density of settlers (Fig. 2). Fitting the data to a three-parameter nonlinear model (Eqn 1) indicated that sub-adult densities reached an asymptote, and that there was no statistical evidence of overcompensation, at high settler densities ($d = 1.14$; not statistically different from 1). The fraction of settlers that survived 6 months declined exponentially with increasing density of settlement ($r^2 = 0.84$; $F_{1,9} = 47.8$; $P < 0.001$), confirming the presence of strong density-dependent mortality.

The two-parameter saturation model (Eqn 2) matched the data well (Fig. 2; $r^2 = 0.97$), although deviations between the data and model suggest the true asymptote was slightly lower and approached somewhat more quickly than indicated by the model. The model yielded estimates (± 1 SE) of 0.696 (± 0.095) for the density-independent survivorship rate, a , and 9.79 (± 0.45) sub-adults per 0.1 m² anemone for the asymptotic sub-adult density, b . This value for a was quite similar to an independent estimate (0.640 ± 0.067) of density-independent survivorship for naturally settled *D. trimaculatus* at nearby locations (Schmitt & Holbrook 1999a). We conclude that the two-parameter model was an appropriate function to describe the data.

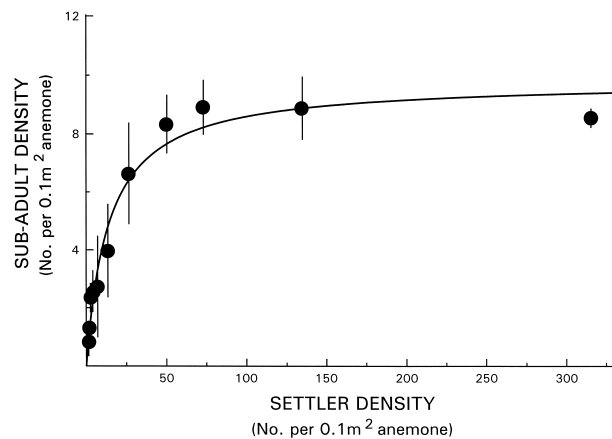


Figure 2 The experimentally estimated settler–sub-adult relationship for *D. trimaculatus*. The mean (± 1 SE) density of sub-adults (no. per 0.1 m² anemone) as a function of initial settler density is given. The fit of the two-parameter saturation model (Eqn 2) to the data is shown ($r^2 = 0.97$; $a = 0.696$, $b = 9.79$ per 0.1 m²).

Limitation. Using estimated values for a and b , we explored the degree to which local populations of *D. trimaculatus* were constrained by larval supply, density-independent mortality, and density-dependent mortality. Limitation depends on settler density (Fig. 3). Supply Limitation is maximal and when expressed as an absolute change, is equal to the saturation density of sub-adults ($L_S = b$) when settler density is 0. As settler density increases, Supply Limitation declines, approaching an asymptote of 0. Obviously, limitation due to both sources of mortality equals 0 when settler density is 0. Limitation by density-independent mortality (L_{DI}) initially increases with increasing settlement, but eventually declines in importance and converges to zero (Fig. 3A). Limitation imposed by density-dependence (L_{DD}) increases monotonically as settlement increases. Settlement Limitation and Density-Dependent Limitation vary in opposite

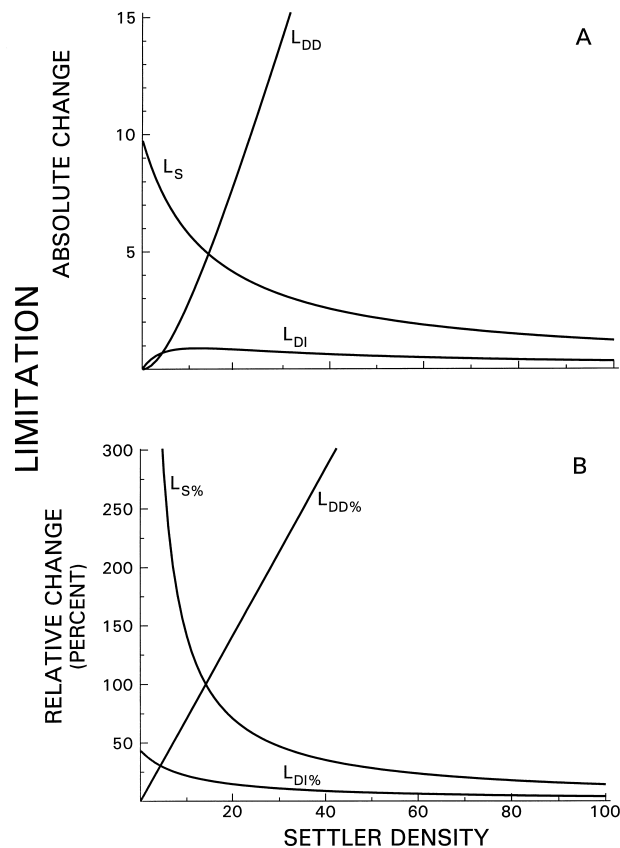


Figure 3 Limitation functions for the empirical estimates of a (density-independent survivorship) and b (saturation density) in Eqn 2 as a function of settler density. Given are the absolute (A) and percent relative (B) change in sub-adult density that results from removing the constraint of a process (see Table 1 and Fig. 1). L_S denotes the Supply Limitation function, L_{DD} is the Density-Dependent Limitation function and L_{DI} is the Density-Independent Limitation function.

directions [when limitation is expressed as a proportionate change (Table 1), Supply Limitation varies inversely with Density-Dependent Limitation: $L_{S\%} = 1/L_{DD\%}$].

For the functional form of our model, Supply Limitation always is greater than Density-Independent Limitation ($L_S > L_{DI}$; Fig. 3). This arises because of interactions between the processes. Saturating the habitat with settlers increases sub-adult density to the maximum (b), whereas the effect of removing all density-independent mortality is constrained to be always $\leq b$ (i.e. due to density-dependence, removal of density-independence can never yield more than b sub-adults, but because of settlement limitation, often yields $< b$).

The relative importance of Density-Dependent Limitation varies with settlement density. Settlement Limitation exceeds Density-Dependent Limitation until $S = b/a$, at which point supply and density-dependence impose equivalent constraints on sub-adult density (Fig. 3). At higher settlement rates ($S > b/a$), Density-Dependent Limitation (L_{DD}) has the strongest influence. In our graphical model (Fig. 1), this crossover between dominance by L_S and L_{DD} is the intersection between Line 2 (supply limitation removed: $A_S = b$) and Line 4 (density-dependence removed: $A_{DD} = aS$). The crossover occurs at $S = b/a$, which corresponds to a sub-adult density that is half of the maximum (i.e. $A = b/2$). Thus, the dominant process is determined by how close the system is to saturation; if A is within 50% of b , density-dependence (L_{DD}) is strongest and if $A < 50\%$ of b , then Supply Limitation (L_S) dominates. Therefore, given our estimates of a and b , our damselfish system should be primarily Supply Limited when settlement is < 14.1 per 0.1 m^2 and primarily Density-Dependence Limited when settlement is > 14.1 per 0.1 m^2 . The relative importance of Density-Independent Limitation and Density-Dependent Limitation switches at an even lower settlement level, i.e. at $S = (b/a) - b$ (Fig. 3). This crossover occurs at the intersection of Line 3 [no density-independent loss: $A_{DI} = S/(1 + S/b)$] and Line 4 (density-dependence removed: $A_{DD} = aS$) in our graphical model (Fig. 1). Based on our fitted recruitment function, this transition from Density-Independent Limitation to Density-Dependent Limitation occurs when settler densities are 4.3 per 0.1 m^2 .

Elasticity. Elasticities showed similar patterns as revealed by the analysis of limitation, although here we focus on only two processes: density-dependence and the combined effects of settlement and density-independent mortality (Fig. 4). Elasticities were always between 0 and 1, indicating that increased settlement or survival (due to relaxation of density-independent or density-dependent mortality) always led to increased sub-adult density that

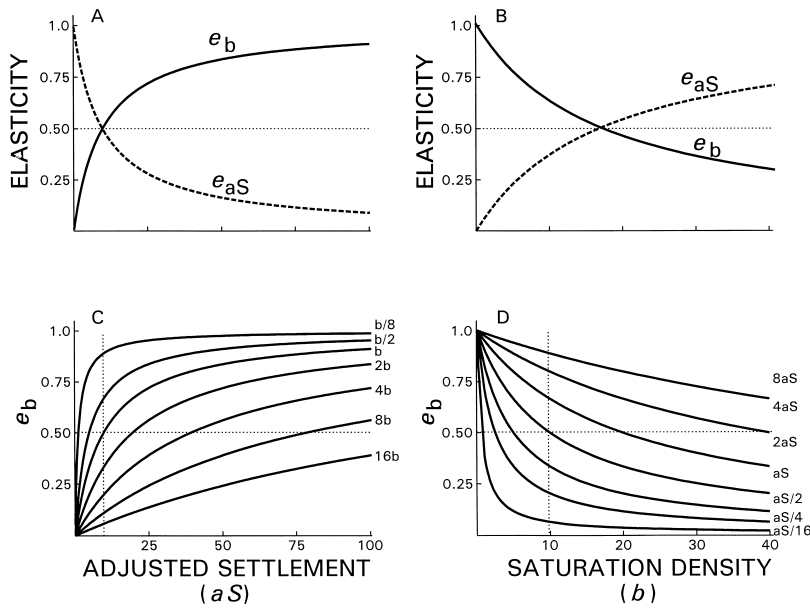


Figure 4 Elasticities of sub-adult density A with respect to settlement adjusted by density-independent loss (e_{aS} ; dashed line) and to sub-adult saturation density (e_b ; solid line) as a function of adjusted settlement density, aS (A) and sub-adult saturation density, b (B). Because the two elasticities sum to 1 (hence $e_b = 1 - e_{aS}$), the functions are symmetrical around 0.5, which is where A is equally sensitive to small proportionate changes in aS and in b ($e_{aS} = e_b$). The lower panels represent elasticities with respect to b (e_b) for systems where the saturation density b (C) or adjusted settlement rate aS (D) were varied systematically about the values observed for *D. trimaculatus* [elasticities with respect to aS are not shown in (C) and (D); e_b and e_{aS} functions cross at 0.5, where the horizontal dashed line intersects each e_b function]. The vertical dashed line in (C) is the adjusted settler density at which $e_b = e_{aS}$ assuming $b = 9.79$. The vertical dashed line in (D) is $b = 9.79$; the curves for various levels of adjusted settler density are based on $a = 0.696$ and $S = 14.1$ (i.e. the settler density at which $e_b = e_{aS}$ given the empirical estimates of a and b).

was proportionately smaller than the proportionate change in the model parameters. The elasticities also varied in opposite directions from one another (recall that $e_{aS} + e_b = 1$). As was also true for the Limitation analysis, the results (Table 1, Fig. 4A, B) emphasize that these processes interact and have nonlinear effects, e.g. the effect of small changes in larval supply (or density-independent mortality) depends upon the strength of density-dependence. Similarly, the relative importance of the two processes shifts as settlement increases. This shift occurs at the same point as in the Limitation analysis: sub-adult density is more sensitive to settlement (discounted by density-independence) when $S < b/a$ and more sensitive to density-dependence when $S > b/a$, again indicating that the dominant process is determined by how close the system is to saturation. In our system this transition should occur when settlement density is 14.1 per 0.1 m^2 (Fig. 4A, B).

We further explored the interactions between processes by calculating the elasticities for systems in which the saturation density (b) or adjusted settlement rate (aS) were varied systematically about the values observed for *D. trimaculatus* at Moorea (Fig. 4C, D). For a given level of settlement (discounted by density-independent survival: aS), changing b effectively moves the system closer to or further away from saturation, which alters the relative contributions of supply (discounted by density-independent loss) and density-dependence. For example, if we use

the observed value of density-independent survivorship (a) and assume a settler density of 14.1 (which together with the observed parameter values, yields $e_{aS} = e_b$), then doubling b (i.e. reducing the strength of density-dependence) results in a system in which effects of supply and density-independent mortality now dominate (i.e. e_b is reduced, so $e_{aS} > e_b$, Fig. 4C). Furthermore the resulting relationships between elasticity and either aS (or b) depend upon the level of b (or aS), demonstrating how the processes interact (Fig. 4C, D, Table 1).

Natural settlement rates – where does the damselfish system lie?

The previous analysis (using estimates of a and b) can reveal the strength of different processes at various settler densities. What it does not reveal is where a specific system actually lies with respect to settlement rates. If this were known, we could then determine the relative importance, for example, of Settlement Limitation vs. Density-Dependent Limitation for the Moorea damselfish system. The average density of settlers across the six settlement events and 10 lagoon sites around the island was 24.1 settlers per 0.1 m^2 . Using this average leads to the conclusion that the removal of Density-Dependent Limitation would lead to an increase in sub-adult density three-fold greater than could be achieved by removing Settlement Limitation and 13-fold greater than could be achieved by eliminating density-dependent mortality, i.e. $L_{DD\%} = 171\%$, $L_{S\%} = 58\%$, $L_{DI\%} = 13\%$. Similarly, the

elasticity associated with density dependence ($e_b = 0.63$) is almost two-fold greater than the elasticity associated with the other terms ($e_{aS} = 0.37$). These conclusions, however, could be misleading because they ignore variability in settlement among anemones (Fig. 5). Because the functions describing limitation and elasticity are nonlinear with respect to settler density (Table 1, Fig. 3 & 4) and because the mean of a nonlinear function is not equal to the function of the mean, we need to consider explicitly variance in settlement.

The supply of larval fish varied substantially through time, among lagoons and among anemones, with settlement on individual anemones ranging from 0 to 463 per 0.1 m² (Fig. 5). These settlement rates range from those that yield complete Settlement Limitation (0 settlers) to those in which there essentially is complete Density-Dependent Limitation (463 settlers). The median was 10.7 per 0.1 m² with the middle 50% of the observations falling between 3.5 and 25.1 settlers per 0.1 m². Although the mean settlement rate exceeded 14.1 (the settler density equal to b/a), suggesting that Density-Dependent Limitation exceeded Supply Limitation, 58% of the individual observations were less than this value. Hence, the production of sub-adults was more limited by supply than by density-dependence on a majority of anemones.

We assessed the average degree of limitation and elasticity in Moorea lagoons based on the distribution (not mean) of 600 settlement observations (obtained across both time and space). We estimated average limitation (on an absolute or relative basis) and average elasticity as:

$$\bar{L} = \frac{\int_0^{\infty} f(S)[g(S) - g_{\text{obs}}(S)]dS}{\int_0^{\infty} f(S)dS} \quad (3a)$$

$$\bar{L}_{\%} = \frac{\int_0^{\infty} f(S)[g(S) - g_{\text{obs}}(S)]dS}{\int_0^{\infty} f(S)g_{\text{obs}}(S)dS} \quad (3b)$$

$$\bar{e} = \frac{\int_0^{\infty} f(S)e(S)dS}{\int_0^{\infty} f(S)dS} \quad (3c)$$

where $f(S)$ is the frequency distribution of settlement densities, $g_{\text{obs}}(S)$ is the ambient recruitment function (i.e. Eqn 2 using the empirical estimates of a and b), $g(S)$ is the function describing sub-adult density in the absence of limitation (i.e. either A_S , A_{DI} , or A_{DD} in Table 1), and $e(S)$ is the elasticity associated with S settlers (and the empirical estimates of a and b). Hence, Eqns 3a and 3b yield the average absolute or relative degree of limitation for the three processes depending on how $g(S)$ is defined. Eqn 3c yields the elasticities (e_{aS} or e_b). If the frequency distribution is broad and spans a strongly nonlinear portion of the limitation functions (Fig. 2), the answer obtained using Eqn 3 will differ markedly from that obtained using the mean settlement rate.

Despite the large variation in settlement rates, we found that Limitation was only mildly affected by the variance, e.g. based on the mean settlement rate, $L_{DD} = 10.6$, $L_S = 3.6$, and $L_{DI} = 0.8$, whereas based on Eqn 3a, $\bar{L}_{DD} = 12.8$, $\bar{L}_S = 5.7$, and $\bar{L}_{DI} = 0.6$. Thus, for the more accurate estimates, Density-Dependent Limitation still was much stronger than Settlement Limitation. Notice that the functions describing limitation (especially L_{DD} and L_{DI}) are not severely nonlinear (Fig. 3).

Average elasticity, by contrast, was greatly affected by the variance. Although the elasticity associated with density-dependence was twice as strong as e_{aS} when based on the mean settlement rate [$e_b(\bar{S}) = 0.63$, $e_{aS}(\bar{S}) = 0.37$],

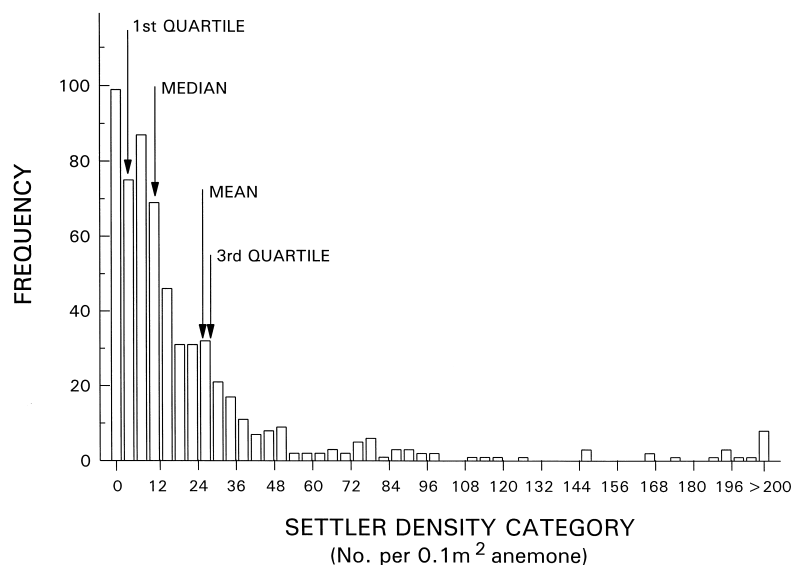


Figure 5 Frequency distribution of 600 settlement observations (across time and space) of *D. trimaculatus* in lagoons of Moorea. The lowest and highest settler densities observed were 0 and 463 per 0.1 m² anemone. Arrows denote the locations of the median settler density (10.7), 1st quartile (3.5) and 3rd quartile (25.1) of the distribution; mean settler density (24.1) is also indicated. Except for the 0 settler density category (which only contains anemones that received no settlers), the bin size of settler density categories is 4.

this pattern was almost reversed when the variance in settlement was taken into account: $\bar{e}_b = 0.42$, $\bar{e}_{aS} = 0.58$. Hence, the elasticity associated with supply (and density-independent mortality) is considerably greater than the elasticity associated with density-dependence. In other words, a small proportionate change in settlement (or a) would yield a 40% larger change in sub-adult density than would the same size change in the saturation density (b). The stronger nonlinearity in elasticities (Fig. 4) compared to limitation (Fig. 3) is responsible for this difference in the effect of variance.

DISCUSSION

Although it is recognized that several processes typically act in concert to shape patterns of abundance for species with demographically open populations, few approaches have been developed that allow the contribution of each process to be quantified. For example, the aim of many experimental studies of reef fishes has been to test for the existence or strength of density-dependence. Instead, we need empirical work and conceptual frameworks to assess the relative effects of multiple processes that simultaneously affect a system's dynamics (e.g. that compare the effects of density-dependence on local abundance to the effects of larval supply and density-independent loss). Here we developed and applied a general procedure for addressing this challenging issue using a model system (the damselfish *D. trimaculatus* in lagoons of Moorea).

As a first step in this approach, the recruitment function must be quantified and the parameters be well estimated. This may require many low density sites to permit good estimation of the density-independent survival (a). It is also critical that there be a sufficiently high range of settlement examined to ensure that adult saturation (or peak) density is well estimated. This is particularly important because we found that the relative strength of different processes depended primarily on how close the system was to saturation. Thus, even for a system that incurs little density-dependence, it would be valuable to know the maximum density of older age-classes. This often may require the use of settler densities that are well above the ambient settler density, and perhaps even well above natural extremes.

The particular saturating recruitment function we found for *D. trimaculatus* is just one of several possibilities, although the Limitation and Elasticity approaches are general and do not depend on the specific form of settler-survivor relationship, nor on the parameters of that relationship. Some analysis detail could change, especially in the case of overcompensation. For example, a hump-shaped curve would alter the manner by which Supply Limitation is estimated. When there is not a

true asymptote, the settler density that produced the peak adult density could be used to quantify Supply Limitation (i.e. evaluate L_s relative to the settler density S that produces the maximum adult density A_{\max} , which may not be the adult density approached as $S \rightarrow \infty$). While there is not sufficient information in the literature to evaluate the prevalence of functionally different relationships between settler density and subsequent adult density, relationships qualitatively similar to that we observed for *D. trimaculatus* have been reported for at least three other species of reef fishes (Jones 1991a, b; Steele 1997b).

Based on the recruitment function, we quantified Limitation and Elasticity. The mathematical expressions and graphical representations for Limitation and Elasticity (Table 1, Figs 2–4) demonstrate nonlinearities in the relationships and the interactions among the processes, thus highlighting one of the advantages of having an explicit quantitative framework. For example, the effect of increasing density-independent survival (a) is small when settlement (S) is high (or maximum sub-adult density, b , is low), because the system is near saturation. However, when settlement is lower (or b is higher), increasing density-independent survival can have a much larger effect—the additional survivors do not greatly intensify density-dependence and they therefore contribute significantly to the older age-class.

The framework becomes a useful analytical tool when quantification of the recruitment function is coupled with estimates of intrinsic settlement rates for a species. However, when settlement is highly variable (as in our system), Limitation and Elasticity need to be assessed by integrating across the range of settler densities (Eqn 3) rather than by using the mean settler density. This is because of the nonlinearities in the limitation and elasticity functions. The integration method for our system yielded qualitatively different results for Limitation and Elasticity, which arose in part because of greater nonlinearity in the elasticity than limitation functions. This result further stresses that Elasticity and Limitation quantify strengths of processes in different ways and therefore address different questions. Limitation was defined as the difference between the realized adult density (from a given settler density) and that predicted when the constraint from a process was completely removed (see also Osenberg & Mittelbach 1996). By contrast, Elasticity quantified proportionate change in sub-adult density (the output) to small (infinitesimal) proportional changes in settlement, density-independent, or density-dependent mortality. Hence, Limitation and Elasticity represent two ends of a spectrum defined by scale of the perturbation applied to a system.

There are at least two caveats regarding our approach. First, just as settler density can vary spatially and

temporally, so too can the strengths of density-independence and density-dependence (Wilson 1998; Caselle 1999). Here, we have assumed that these processes are fixed in their intensity and differ only through the effects of settlement. However, sites (and times) could vary in a and b , and this variation could be correlated with variation in settlement (Wilson 1998). Understanding and incorporating variation in density-dependence and density-independence is an important next step in the application of this conceptual approach.

Second, our approach focuses on cohort dynamics to the exclusion of inter-cohort interactions. Settlement pulses of *D. trimaculatus* occur about twice each lunar month throughout the year (Schmitt & Holbrook 1999b), so multiple cohorts generally co-occur on anemones. If inter-cohort interactions are strong, which appears to be the case for newly settled *D. trimaculatus* (Schmitt & Holbrook 1999a), additional approaches will be required to estimate the strength of these other processes and to extrapolate to longer-term dynamics (e.g. using structured population modelling; DeRoos *et al.* 1992; McCauley *et al.* 1993; also see Caswell 1989; Nisbet *et al.* 1989). In such cases, our experimental approach could be modified to estimate density effects among cohorts or species.

While we have developed and applied a cohort framework in the context of reef fishes, it potentially is a powerful tool for exploring the same issues for other types of organisms whose local populations are demographically open. Extensive movement of early developmental stages among subpopulations is a common feature among marine, aquatic and terrestrial organisms, and understanding the contributions of external input and subsequent patterns of mortality to shaping local abundance remains a substantial challenge. The application of quantitative frameworks to achieve this goal will be necessary to resolve such fundamental issues as the relative importance of the multiple processes that affect local abundance or dynamics, where and how regulation occurs, and the potential for compensation. By quantifying effects of various processes in a range of systems, we can begin to ask how the intensity of these processes (e.g. Density-Dependent vs. Settlement Limitation) varies among organisms that differ in trophic ecology, life history traits, and occupy different types of environments (e.g. by conducting meta-analysis: Osenberg *et al.* 1999). More general theory about the effects of, and interactions among, these processes can emerge from such syntheses.

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BIOSKETCH

The research interests of Russell J. Schmitt, like those of his coauthors, concern factors influencing the abundance, dynamics and regulation of stage-structured, demographically open populations. He also explores consumer–resource interactions and the responses of communities to environmental forcing.

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