

Effects of density-dependent mortality on the relationship between recruitment and larval settlement

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ABSTRACT: Criteria for recruitment limitation or regulation of open populations suggest that such regulation can only occur when population age structure (or recruitment) directly reflects previous settlement events, i.e., when mortality of settlers is density-independent. A simple mathematical model is used to relate recruitment density to settlement density when mortality is density-dependent. The results indicate that recruitment may still reflect settlement despite density-dependent mortality of settlers, especially when settlement densities are low. The conditions under which recruitment reflects settlement, or populations are recruitment limited, are much broader than originally assumed, and can be calculated from field data.

INTRODUCTION

Marine ecologists are currently in the process of constructing a new paradigm synthesizing the roles of larval settlement and post-settlement processes in structuring communities of organisms with open populations. A growing body of theory (Roughgarden et al. 1985, Roughgarden & Iwasa 1986, Warner & Hughes 1989) and data (e.g. sessile invertebrates: Gaines et al. 1985, Gaines & Roughgarden 1985, Davis 1987, Raimondi 1988, Hughes 1989, Sutherland 1989; others: reviewed in Connell 1985; reef fish: reviewed in Doherty & Williams 1988) indicates that larval settlement can generate significant spatial and temporal variation in the size of open populations, their dynamics, and community structure.

A number of criteria have been proposed for distinguishing populations regulated by larval settlement, [i.e., recruitment-limited (Doherty 1983) or recruitment-regulated (Hughes 1989) populations] from those regulated by post-settlement interactions such as inter- or intraspecific competition. One criterion for recruitment regulation is that mortality of newly settled larvae be density-independent, or, equivalently, population age structure be a direct reflection of previous settlement events (Victor 1986, Jones 1987, Doherty & Williams 1988, Mapstone & Fowler 1988). It is suggested that any density-dependent mortality will destroy the direct relationship between larval settlement and

recruitment (Connell 1985, Victor 1986). However, most field studies of larval settlement and pre-recruitment mortality have so far failed to detect density-dependent effects (Davis 1988, Sutherland 1989, others reviewed in Connell 1985, Doherty & Williams 1988), and thus provide no information on the relationship between settlement and recruitment, and therefore recruitment limitation, when pre-recruitment mortality is density-dependent. In this paper I use a simple mathematical model to examine the effects of varying density-dependent mortality on the relationship between settlement and recruitment.

FORMULATION OF THE MODEL

The mathematical model stems from the definitions of settlement and recruitment for sessile invertebrates. A larva is considered to have settled at the moment it irreversibly attaches to the substrate; a settler is considered to be a recruit once it has survived some arbitrary length of time after settlement (Keough & Downes 1982). Thus, the number of recruits is a function of the number of settlers and some probability of survival:

$$\# \text{ Recruits} = (\# \text{ Settlers}) \times (\text{Survival probability}). \quad (1)$$

The survival probability is defined as a function of the number or density of settlers in a cohort; mortality due

to interactions between age classes is ignored. I assume [as, apparently, does Connell (1985)] a simple linear model relating density of settlers and their mortality:

$$\text{Percent mortality} = B(x/A) + DI \quad (2)$$

where x is the number of settlers, A is the area over which they settled, B is the slope of the percent mortality vs settler density regression (equivalent to the strength of density-dependent mortality), and DI is density-independent mortality in form of percent (the Y-intercept of the percent mortality vs settler density regression). Note that this model holds only for $B \geq 0$; inverse density-dependence ($B < 0$) will be considered later. Note also that this regression holds only within a cohort or age class, and is unrelated to the cross-generation regression methods for detecting density-dependent mortality examined by Maelzer (1970) and St. Amant (1970). Fig. 1 illustrates the changing shape of the mortality curve as density-dependence varies. When density-dependent mortality is absent, $B = 0$ and percent mortality is constant and equal to DI (Fig. 1, Line a). As the slope B increases, the effect of settler density on percent mortality also increases (Fig. 1, Lines b and c).

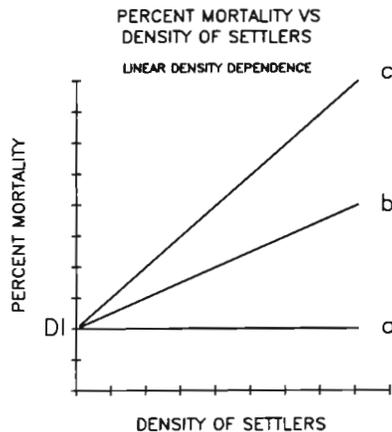


Fig. 1. Mortality as a function of settlement density for various strengths of density-dependent mortality. (a) $B = 0$; (b, c) $B > 0$. DI : Percent mortality due to density-independent factors

Substitution of Eqn (2) into Eqn (1) yields a function relating the number of settlers to the number of recruits under the assumption of linear density-dependent mortality:

$$\text{Survival probability} = 1 - (\% \text{Mortality}/100) \quad (3a)$$

$$= 1 - (Bx/100A) - (DI/100). \quad (3b)$$

$$\# \text{ Recruits} = [1 - (Bx/100A) - (DI/100)]x \quad (4a)$$

where x again represents the number of settlers. Numbers of recruits and settlers can be converted into

densities by dividing both sides of this equation by the constant A . Simplifying,

$$\# \text{ Recruits} = -(Bx^2/100A) + [1 - (DI/100)]x. \quad (4b)$$

This equation describes a parabola (Fig. 2, Line b) when $B > 0$ (some density-dependent mortality) and a straight line (Fig. 2, Line a) when density-dependent mortality is absent ($B = 0$). When mortality is density-independent, the density of recruits is directly proportional to the density of settlers (Fig. 2, Line a).

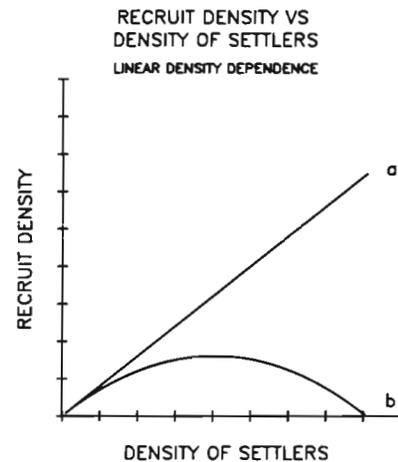


Fig. 2. Recruit density as a function of settlement density with and without density-dependent mortality. (a) $B = 0$; (b) $B > 0$

Effects of density-dependent mortality

When mortality of settlers exhibits some density-dependence, the density of recruits will only reflect the density of settlers over the range of settler densities for which the slope of the parabola is positive. This interval includes all densities less than the maximum of Eqn (4b). Maxima are found by solving the first derivative of the equation for $dy/dx = 0$, then showing that this point corresponds to a negative second derivative. Taking the derivative of Eqn (4b) yields

$$dy/dx = -(2Bx/100A) + [1 - (DI/100)]. \quad (5)$$

The second derivative of Eqn (4b) is

$$d^2y/dx^2 = -2B/100A \quad (6)$$

which is always negative when $B > 0$ (density-dependent mortality occurs). Solving Eqn (5) for $dy/dx = 0$ thus yields the maximum point for the parabola,

$$dy/dx = 0 = -(2Bx/100A) + [1 - (DI/100)], \quad (7)$$

rearranging terms and simplifying produces the final equation

$$x/A = (100 - DI)/2B. \quad (8a)$$

The number and density of recruits is a maximum when

$$\text{Density of settlers} = (100 - DI)/2B, \quad (8b)$$

and the density of recruits will accurately reflect the density of settlers over the interval

$$0 \leq \text{Density of settlers} < (100 - DI)/2B. \quad (9)$$

This result indicates that for any value of $B > 0$, over some range of settlement density, recruitment will increase with settlement. Given an observed level of density-dependent and independent mortality, Eqn (8b) can be used to calculate the range of settlement densities for which recruitment reflects settlement. Conversely, using the same equation, the level of density-dependent mortality at which the direct relationship between recruitment and settlement breaks down can be calculated for a given value of settlement density. Table 1 gives maximum values for strength of density-dependent mortality (B), calculated from Eqn (8b), for various combinations of settlement density and density-independent mortality. These B values represent the strongest density-dependent mortality for which recruitment will directly reflect settlement. At low settlement densities the direct relationship between settlement and recruitment begins to break down only at very high values of B , i.e., when strong density-dependent mortality occurs. B values decrease precipitously with increasing settlement, increases in DI yield decreases of much smaller magnitude (Table 1, Fig. 3).

Density-dependent mortality with thresholds

The above model assumes B and DI are constant over the full range of settlement densities. The occurrence of

Table 1 Values of B , calculated from Eqn (8b), for various levels of settlement density and density-independent mortality (DI). B represents the strongest density-dependent mortality for which recruitment directly reflects settlement (rounded to 4 decimal places)

DI	Settlement density					
	5	10	20	40	80	160
0	10.0	5.0	2.5	1.25	0.625	0.3125
10	9.0	4.5	2.25	1.125	0.5625	0.2812
20	8.0	4.0	2.0	1.0	0.5	0.25
30	7.0	3.5	1.75	0.875	0.4375	0.2188
40	6.0	3.0	1.5	0.75	0.375	0.1875
50	5.0	2.5	1.25	0.625	0.3125	0.1562
60	4.0	2.0	1.0	0.5	0.25	0.125
70	3.0	1.5	0.75	0.375	0.1875	0.0938
80	2.0	1.0	0.5	0.25	0.125	0.0625
90	1.0	0.5	0.25	0.125	0.0625	0.0312
100	0.0	0.0	0.0	0.0	0.0	0.0

$\ln [B+1]$ AS A FUNCTION OF SETTLEMENT DENSITY AND DENSITY-INDEPENDENT MORTALITY

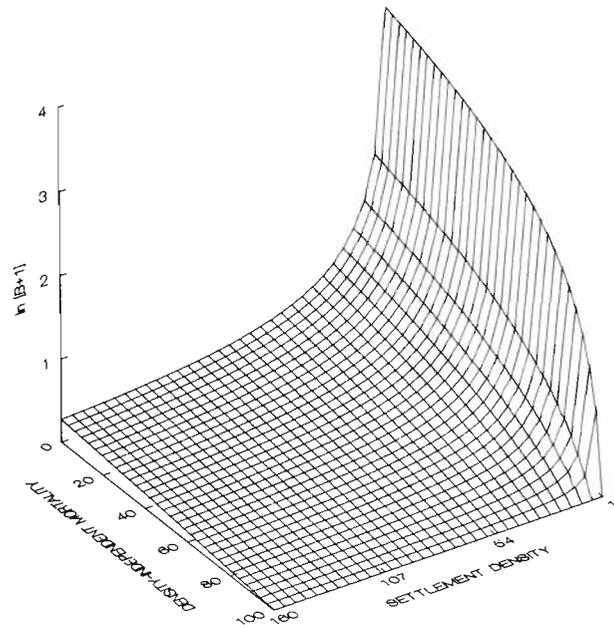


Fig. 3. Plot of $\ln(B + 1)$ as a function of settlement density and density-independent mortality. B represents the strongest density-dependent mortality for which recruitment will directly reflect settlement, and is calculated from Eqn (8b)

density-dependent mortality is likely to vary with settlement density, e.g. mortality may be purely density-independent until an upper threshold in settlement density is reached, at which point mortality is both density-dependent and independent (Connell 1985, Gaines & Roughgarden 1985). Threshold models of density-dependent mortality can be represented by

$$\text{Percent mortality} = B(x/A) + C \quad (10)$$

where x is the number of settlers, A is the area over which they settled, B is the slope of the percent mortality vs settler density regression, and C is the Y-intercept of the regression. Eqn (2), for which $C = DI$, is a special case of this general model. When $C < DI$, the general model has 2 thresholds (Table 2); when Eqn (10) $< DI$, mortality is purely density-independent, when Eqn (10) $> 100\%$, mortality equals 100% . These 2 thresholds occur at settlement densities $< (DI - C)/B$ (Case 1, Table 2) and $> (100 - C)/B$ (Case 3, Table 2), respectively. Between the thresholds, mortality is density-dependent and given by Eqn (10). For the general model the density of recruits will accurately reflect the density of settlers over the interval

$$0 \leq \text{Density of Settlers} < (100 - C)/2B. \quad (11)$$

Table 2. Thresholds for the general linear density-dependence model (Eqn 10). B: slope of percent mortality vs settler density regression; x: no. settlers; A: area over which larvae settle; C: Y-intercept of percent mortality vs settler density regression; DI: percent mortality due to density-independent factors

Case	% Mortality	When?	Settlement density
1	DI	$B(x/A)+C < DI$	$< (DI-C)/B$
2	$B(x/A)+C$	$DI \leq B(x/A)+C \leq 100 \%$	
3	100	$B(x/A)+C > 100 \%$	$> (100-C)/B$

Effects of increased time after settlement on mortality parameters

Eqn 4b relates settlement density to density of individuals at any time after settlement. As time after settlement increases, however, there may be a decrease in the correlation between settlement and recruitment (e.g. Sutherland 1989), or, a decrease in the settlement density at which the direct relationship between settlement and recruitment begins to break down. This results from increases in DI, and possibly B, with time. The probability of density-independent mortality of an individual over a given time span is equal to the sum of the instantaneous probabilities of density-independent mortality for that span. These instantaneous probabilities are not constant; however, they are never less than zero. Therefore, their sum, and thus DI, can only increase with increasing time after settlement. It is not clear if a similar argument can be made for instantaneous probabilities of density-dependent mortality and B. Any increase in DI (if not offset by a decrease in B) and/or B over time will decrease the range of settlement densities over which settlement and recruitment are directly related.

Inverse density-dependent mortality

Mortality of settlers will exhibit inverse density-dependence when group interactions (including, but not necessarily limited to, social interactions) increase survival (e.g. Buss 1981, Keough 1984, Bertness 1989). When inverse density-dependence occurs, the slope B

of the percent mortality vs settler density regression is negative [for examples, see Connell (1985)], and

$$\text{Percent mortality} = -|B|(x/A) + C \quad (12)$$

where x is the number of settlers, A is the area over which they settle, and C is the Y-intercept of the percent mortality vs settler density regression. This mortality model has 2 thresholds (Fig. 4, Table 3); when Eqn (12) > 100 %, mortality equals 100 %, when Eqn (12) < DI, mortality equals DI. These 2 thresholds occur at settlement densities < (C - 100)/|B| (Case 1, Table 3) and > (C - DI)/|B| (Case 3, Table 3), respectively. Between these 2 points, percent mortality varies with density by Eqn (12) (Case 2, Table 3). The relationship between recruitment and settlement is

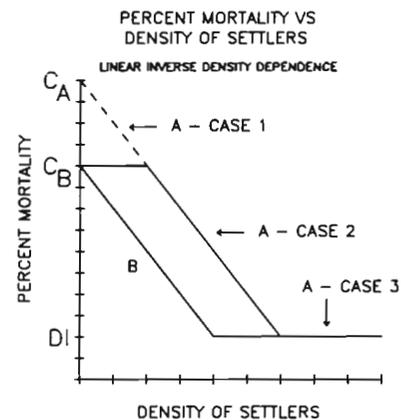


Fig. 4. Mortality as a function of settlement density for inverse density-dependent mortality. CA, CB = Y-intercepts for Lines A, B, respectively. DI: percent mortality due to density-independent factors. (A) Inverse density-dependent mortality with 2 thresholds, occurs whenever C > 100 %. Dashed line represents region for which Eqn (12) > 100 %. (B) Inverse density-dependent mortality with 1 threshold, occurs whenever C ≤ 100 %. 'Case' refers to cases listed in Table 3

straightforward for Cases 1 and 3. For Case 1, there is no recruitment, and for Case 3, mortality is purely density-independent, so recruitment is directly proportional to settlement. To find the form of the recruitment-settlement relationship for Case 2, the steps set out previously are used.

Table 3. Thresholds for the linear inverse density-dependence model (Eqn 12). B: slope of percent mortality vs settler density regression; x: no. settlers; A: area over which larvae settle; C: Y-intercept of percent mortality vs settler density regression; DI: percent mortality due to density-independent factors

Case	% Mortality	When?	Settlement density
1	100	$- B (x/A)+C > 100 \%$	$< (C-100)/ B $
2	$- B (x/A)+C$	$DI \leq - B (x/A)+C \leq 100 \%$	
3	DI	$- B (x/A)+C < DI$	$> (C-DI)/ B $

$$\text{Survival probability} = 1 - (-|B|x/100A) - C/(100) \quad (13)$$

yields,

$$\# \text{ Recruits} = |B|x^2/100A + [1 - (C/100)]x. \quad (14)$$

This equation describes a parabola whenever $B < 0$. Unlike the density-dependence model, however, this parabola is concave up;

$$dy/dx = 2|B|x/100A + [1 - (C/100)] \quad (15)$$

and,

$$d^2y/dx^2 = 2|B|/100A \quad (16)$$

which is always positive. Thus, $dy/dx = 0$ is the minimum of Eqn (14). Whenever settlement density is greater than the density at which $dy/dx = 0$, recruitment will directly reflect settlement. Solving Eqn (15) for zero,

$$dy/dx = 0 = 2|B|x/100A + [1 - (C/100)], \quad (17)$$

rearranging terms and simplifying,

$$\text{Density of settlers} = (C - 100)/2|B|. \quad (18)$$

Note that, when $C > 100$, this density is less than the threshold density for 100% mortality (Case 1, Table 3). Therefore, recruitment accurately reflects settlement whenever

$$\text{Density of settlers} > (C - 100)/|B|. \quad (19)$$

When $C < 100$, Eqns (18) and (19) produce negative densities; when this occurs recruitment will always be an accurate reflection of settlement.

DISCUSSION

Simple linear models of density-dependent mortality produce a parabolic curve relating density of settlers and density of recruits (Fig. 2, Line b). Over the ascending portion of the parabola recruitment and settlement are directly related, and recruit density will mirror density of settlers. As the density of settlers increases out of the ascending portion of the curve, density-dependent mortality leads to the breakdown of the settlement-recruitment correlation. Increasingly dense settlement results in decreasing recruitment; and a given level of recruitment can represent 2 levels of settlement.

These conclusions hold only for the mortality model given in Eqn (2). Other models will produce different functions relating settlement and recruitment. Under weak inverse density-dependent mortality, for example, recruitment will almost always reflect previous settlement. As the strength of this type of mortality

increases, however, low levels of recruitment arise from a wide range of low settlement densities.

These results indicate that density-dependent mortality does not necessarily preclude recruitment limitation of open populations. Because recruitment can reflect previous settlement events over a range of settlement densities and strengths of density-dependent and independent mortality, variations in settlement density can be maintained in the population's age structure despite density-dependent mortality. This will be especially true when settlement density is consistently low, or density-dependent mortality weak.

In an extension of the above, recruit density can often serve as an accurate estimator of previous settlement. Eqn (4b) and the mortality equations given in Tables 2 and 3 can be used to calculate settlement estimates from recruitment data. This result may be of utility in studies of populations and communities of sessile marine invertebrates, where larval settlement is frequently difficult to measure directly. The appropriateness of recruitment estimates for larval settlement will depend on the observed settlement density, density-dependent and independent mortality. The methods used here can be applied by benthic ecologists to calculate the boundary conditions for which observed recruitment estimates settlement. For the linear model of density-dependent mortality examined (Eqn 2), recruitment estimates will be most accurate for organisms exhibiting chronically low settlement densities. In these cases estimates are robust to exceptionally high levels of density-dependent mortality. When settlement density is high, recruitment estimates become inaccurate at much lower levels of density-dependent mortality. For these cases, recruitment estimates of settlement can be improved by decreasing the interval between settlement and sampling of recruits, thus reducing the opportunity for density-dependent and independent mortality to act. When mortality exhibits inverse density-dependence (Eqn 12), recruitment estimates will be unreliable at low settlement densities, but very accurate at high densities.

Extreme care should be taken in the use and interpretation of such estimates. Back-calculation of settlement density from recruitment data requires knowledge of the strength of density-dependent and independent mortality (B and DI) and, more importantly, their variability in space and time. If B and DI exhibit spatial and temporal variability, variation in recruitment may not reflect variation in settlement, but instead variation in pre-recruitment mortality. When such variation exists, studies of spatial and temporal variation in settlement based on recruitment measures may be misleading. A thorough knowledge of the range of settlement densities possible is also required to ensure that some settlement estimates do not in fact represent unusually dense or light settle-

ment and subsequent strong density-dependent or inverse density-dependent mortality (that is, to ensure one-to-one correspondence between a given level of recruitment and previous settlement).

Connell (1985) suggests that recruitment can be used as an estimator of larval settlement, but only when mortality of settlers is density-independent. A number of authors (Victor 1986, Jones 1987, Doherty & Williams 1988, Mapstone & Fowler 1988) contend that an open population can not be recruitment-limited when mortality of newly settled larvae is density-dependent, presumably because density-dependence would destroy the correspondence between population age structure and past settlement events. The results presented here demonstrate that these requirements are too strict; recruit density can serve as an accurate indicator of settlement density, and population age structure may directly reflect past settlement, despite density-dependent mortality of settlers, especially when settlement density is low.

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LITERATURE CITED

- Bertness, M. D. (1989). Intraspecific competition and facilitation in a northern acorn barnacle population. *Ecology* 70: 257–268
- Buss, L. W. (1981). Group living, competition, and the evolution of cooperation in sessile invertebrates. *Science* 213: 1012–1014
- Connell, J. H. (1985). The consequences of variation in initial settlement vs post-settlement mortality in rocky intertidal communities. *J. exp. mar. Biol. Ecol.* 93: 11–45
- Davis, A. R. (1987). Variation in recruitment of the subtidal colonial ascidian *Podoclavella cylindrica* (Quoy & Gaimard): the role of substratum choice and early survival. *J. exp. mar. Biol. Ecol.* 106: 57–71
- Davis, A. R. (1988). Effects of variation in initial settlement on distribution and abundance of *Podoclavella moluccensis* Sluiter. *J. exp. mar. Biol. Ecol.* 117: 157–167
- Doherty, P. J. (1983). Tropical territorial damselfishes: is density limited by aggression or recruitment? *Ecology* 64: 176–190
- Doherty, P. J., Williams, D. McB. (1988). The replenishment of coral reef fish populations. *Oceanogr. mar. biol. A. Rev.* 26: 487–551
- Gaines, S., Brown, S., Roughgarden, J. (1985). Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia* (Berl.) 67: 267–272
- Gaines, S., Roughgarden, J. (1985). Larval settlement rate: A leading determinant of structure in an ecological community of the marine intertidal zone. *Proc. natn. Acad. Sci. U.S.A.* 82: 3707–3711
- Hughes, T. P. (1989). Recruitment limitation, mortality and population regulation in open systems: a case study. *Ecology* (in press)
- Jones, G. P. (1987). Competitive interactions among adults and juveniles in a coral reef fish. *Ecology* 68: 1534–1547
- Keough, M. J. (1984). Kin-recognition and the spatial distribution of larvae of the bryozoan *Bugula neritina*. *Evolution* 38: 142–147
- Keough, M. J., Downes, B. J. (1982). Recruitment of marine invertebrates: The role of active larval choices and early mortality. *Oecologia* (Berl.) 54: 348–352
- Maelzer, D. A. (1970). The regression of $\log N_{n+1}$ on $\log N_n$ as a test of density dependence: An exercise with computer-constructed density-independent populations. *Ecology* 51: 810–822
- Mapstone, B. D., Fowler, A. J. (1988). Recruitment and the structure of assemblages of fish on coral reefs. *Trends Ecol. Evol.* 3: 72–77
- Raimondi, P. T. (1988). Rock type affects settlement, recruitment, and zonation of the barnacle *Chthamalus anisopoma* Pilsbury. *J. exp. mar. Biol. Ecol.* 123: 253–267
- Roughgarden, J., Iwasa, Y. (1986). Dynamics of a metapopulation with space-limited subpopulations. *Theor. Popul. Biol.* 29: 235–261
- Roughgarden, J., Iwasa, Y., Baxter, C. (1985). Demographic theory for an open marine population with space limited recruitment. *Ecology* 66: 54–67
- St. Amant, J. L. S. (1970). The detection of regulation in animal populations. *Ecology* 51: 823–828
- Sutherland, J. P. (1989). Recruitment regulates demographic variation in a tropical intertidal barnacle. *Ecology* (in press)
- Victor, B. C. (1986). Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. *Ecol. Monogr.* 56: 145–160
- Warner, R. R., Hughes, T. P. (1989). The population dynamics of reef fishes. *Proc. 6th int. Coral Reef Symp., Townsville, Australia* (in press)

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