

LETTER

Rethinking ecological inference: density dependence in reef fishes

Abstract

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We use a meta-analysis of density dependence in reef fishes to evaluate how ecologists approach detection, inference, and estimation. We compared two groups of studies: those that detected effects of density on survival and those that did not. Distinctions between these groups have spawned heated debate about the processes that affect fish dynamics. Per capita effects of density were similar between the two groups, although total effects (and hence ambient density) were greater in studies that detected density effects. The majority of the variation in effects of density was not resolved by the classification of studies based on the authors' conclusions. These results suggest (1) that standard inferences based on null hypothesis tests may miss important sources of variation in effects and give rise to unnecessary debate; and (2) that estimation of effect sizes and model parameters (including their uncertainty) is a powerful alternative to detection of ecological processes.

Keywords

Estimation, meta-analysis, null hypothesis tests, *P*-values, recruitment, survival.

Ecology Letters (2002) 5: 715–721

INTRODUCTION

Ecologists make inferences about processes based upon tests of hypotheses and the application of statistical tools to the resulting data. Investigators asking similar questions in similar systems often reach conflicting conclusions. These differences in inference can give rise to heated debate that frequently results in the call for pluralistic approaches and the study of 'relative importance' (e.g. Quinn & Dunham 1983; Schmitt *et al.* 1999; Bohannan & Lenski 2000; Doherty 2002). Given the wide range of ecological dynamics, heterogeneity of responses is not surprising (e.g. Turchin & Taylor 1992). Indeed, heterogeneity may yield insights about how environmental or organismal traits influence key processes (e.g. Gurevitch *et al.* 1992; McCauley *et al.* 1999; Osenberg *et al.* 1999). These insights may be central to the development of more general theory (e.g. Sæther *et al.* 2002). Of course, this conclusion presumes that the differences are real and not the result of misleading inferential approaches.

One such debate, arising from conflicting conclusions, has occurred in marine reef fish ecology. Like many marine organisms, reef fish have an early planktonic dispersal stage followed by a more sedentary benthic stage (separated by a process called 'settlement'). Thus, the local dynamics of

these populations are influenced by three key processes: planktonic larval supply and both density-independent and density-dependent losses from the reef-based population. Empirical studies of reef fish have reported mixed results about post-settlement density dependence: it was detected (and presumed strong) in some cases (e.g. Schmitt *et al.* 1999) but not detected (and presumed weak or absent) in others (e.g. Doherty & Fowler 1994); see the Appendix for additional studies. These disparate conclusions have led to debate about when (or even if) regulatory processes operate in the life cycle of reef fish (e.g. Doherty & Fowler 1994; Hixon & Webster 2002).

Several possible hypotheses might reconcile these two sets of contradictory results. (1) Survival is independent of density until a critical resource is saturated (and density-dependent and potentially compensatory thereafter): Victor (1986), Barrowman & Myers (2000). Thus, studies yielding 'no effect' (vs. 'an effect') of density occur below (vs. above) the density at which resources are saturated (Fig. 1a). (2) Per capita effects of density differ between the two sets of systems despite similar ambient density, and larger effects are more easily detected (Fig. 1b). (3) Per capita effects of density are of similar magnitude, but the two sets of systems occur at different ambient densities and effects of density

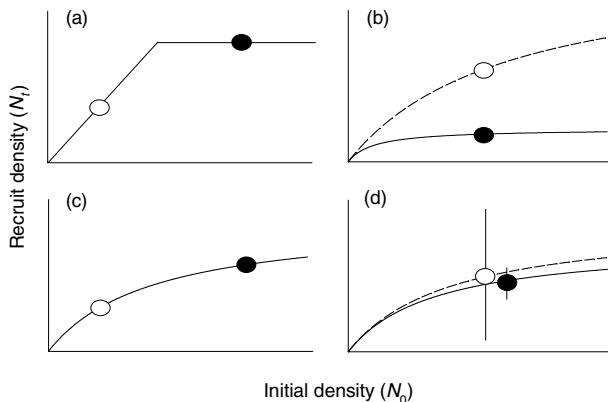


Figure 1 Recruitment relationships corresponding to four hypotheses intended to resolve the conflict between studies that did (vs. did not) detect density-dependent survival. A linear recruitment function results from the absence of an effect of density on survival. Density-dependent survival causes the recruitment functions to decelerate; stronger density dependence (all else equal) results in lower numbers of recruits (and more rapid approach to an asymptote). (a) Hypothesis 1. Victor's (1986) hypothesis in which survival is density-independent up to a threshold and compensatory thereafter (see also Barrowman & Myers 2000). (b) Hypothesis 2. The strength of density dependence (β) is weaker for systems in which density dependence was not detected and stronger in systems where it was detected. (c) Hypothesis 3. Per capita effects were similar, but ambient density (and hence the study's density gradient) was higher in systems where density dependence was detected. (d) Hypothesis 4. The strength of density dependence was the same (as was ambient density), but there was lower variance in survival (and hence recruitment) in systems where density dependence was detected. In all panels, open symbols (\circ , and/or dashed lines) correspond to systems in which density dependence was not detected; closed symbols (\bullet , and solid lines) correspond to those in which density dependence was detected.

are more easily detected in systems at high density (Fig. 1c). (4) Effects of density are similar, as are ambient densities, but other factors vary, making effects of density harder to detect in more variable systems (Fig. 1d). Note that for hypotheses 2–4, statistical power is critical in determining whether density dependence is detected or not.

Each hypothesis offers a plausible resolution of the putative controversy – but which one best explains the empirical results? Unfortunately, these scenarios cannot be distinguished based on discussions in the literature, because (1) most inferences have been derived from P -values and null hypothesis tests, which provide little information about the strength of processes (Yoccoz 1991; Stewart-Oaten 1996; Johnson 1999; Osenberg *et al.* 1999); and (2) few studies have attempted to estimate per capita and total effects, relying instead on *detection* of density dependence. Meta-analysis can yield insight into this debate (and others)

by comparing the strength of density dependence across studies using a common model of the underlying process (Liermann & Hilborn 1997; Osenberg *et al.* 1999). Here, using data from empirical studies of marine reef fish published during the past three decades, we conduct a meta-analysis on the strength of density dependence to explore patterns in two sets of studies: those in which the authors concluded that density dependence was operating, and those in which the authors concluded it was not. Specifically, we evaluate the four hypotheses in Fig. 1 and then discuss how ecologists approach detection, inference, and estimation.

METHODS

Schmitt *et al.* (1999) quantified the strength of density dependence using a Beverton–Holt recruitment function that described the relationship between initial cohort size and the number that survive to a later life stage; as initial cohort size increased, recruitment (i.e. number of survivors) approached an asymptote. They asserted that the inverse of this asymptote estimated the strength of density dependence. Empirical studies support the use of the Beverton–Holt function (e.g. Steele 1997; Doherty 2002; Shima & Osenberg 2003); however, the asymptote is a function of density dependence as well as other factors. We therefore reformulated the discrete-time Beverton–Holt model used by Schmitt *et al.* (1999) in continuous time so that estimates of density dependence were not confounded with variation in study duration and density-independent factors (see Osenberg *et al.* 1997, 1999). We sought a general non-linear model that included the linear model as a special case (i.e. where per capita mortality rates are independent of density). There are an infinite number of non-linear models, but if we choose any of these, Taylor expand the density-dependent portion, and retain only the first term, we obtain a model expressing the instantaneous mortality rate of fish in a single-aged cohort:

$$(1/N)dN/dt = -\alpha - \beta N \quad (1)$$

where N is the cohort density, α is the density-independent mortality rate, and β is the density-dependent mortality rate (measured as the per capita effect). Equation 1 can be integrated to yield:

$$N_t = \frac{e^{-\alpha t} N_0}{1 + \frac{\beta(1-e^{-\alpha t})N_0}{\alpha}} \quad (2)$$

This function starts at $(0, 0)$, rises monotonically at a decelerating rate, and asymptotes to $N_t = \alpha e^{-\alpha t}/\beta(1 - e^{-\alpha t})$ as $N_0 \rightarrow \infty$ (as in Fig. 1b–d). Note that the density of recruits (N_t) is a function of the initial cohort density (N_0) and the time period over which mortality accrued (t), in addition to the strength of density-dependent (β) and density-independent (α) mortality. In the data

analyses below, time (t) is fixed within a study but varies among studies. Explicit recognition of dependence on t allows effects of different time intervals to be factored out, thereby permitting comparison of density dependence among studies. In addition, within-study variation in N_0 (but not t) permits us to estimate α and β for each study.

We obtained studies of post-settlement survival of reef fishes by searching 22 different journals (Appendix) published between 1970 and 2001, yielding 617 journal-years. This was supplemented by an electronic search. Some papers reported results from several species, locales or years. We used all relevant comparisons that could be used to estimate α and β in eqn 2. We excluded studies where predators were experimentally reduced, because predators are believed to be a major source of density dependence (Hixon & Carr 1997; Holbrook & Schmitt 2002) and including such studies could bias the results. We also excluded four studies where patterns of survival indicated that eqn 2 was inappropriate (e.g. they showed 'Ricker'-type behaviour) and two papers that gave density in units that could not be converted to areal units. The final data base consisted of 71 studies presented in 28 papers (Appendix).

We obtained N_t , N_0 , and t for each study using data provided by the authors or by digitizing data from their figures. Ambient initial density for each study was based on the author's assessment (for experiments) or by averaging reported initial densities (for observational studies). Densities were converted to a m^{-2} basis so that all studies were compared using the same units. We estimated α and β (and their variances) for each study using non-linear regression (SAS v8.02, NLIN procedure, method = Marquardt, with alpha constrained to be ≥ 0). We varied the search grid until all solutions converged and ensured that final estimates represented the best solutions. We used MetaWin (Rosenberg *et al.* 2000) to analyse estimates of β using (1) random effects models to examine the entire data set, and (2) mixed-effects models to compare effects between groups of studies. We used β and βN as our measures of effect size, corresponding to the per capita and total cohort effects on survival, and weighted each estimate by the reciprocal of its variance (i.e. the sum of the within-study variance, obtained through non-linear regression, and among-study variance, estimated by MetaWin). We obtained 95% confidence limits using both parametric (CI_p) and bias-corrected bootstrapping (CI_b) methods (Rosenberg *et al.* 2000). Because many reports of ambient density lacked error estimates, we ignored error in this term and assumed all error in βN was due to error in β – this assumption does not bias estimates, but does slightly underestimate CIs. We determined the overall effect of density on survival, assessed its heterogeneity, and then compared the effect of density for two classes of studies: those in which the authors concluded

there was density-dependent survival with those in which the authors concluded there was no effect of density.

RESULTS

Overall, there was a significant effect of density on post-settlement survival: $\beta = 1.30 \times 10^{-4} m^2 fish^{-1} day^{-1}$ (CI_p : 9.0×10^{-5} to 1.7×10^{-4} ; CI_b : 7×10^{-5} to 2.3×10^{-4}), $\beta N = 3.19 \times 10^{-3} day^{-1}$ (CI_p : 2.59×10^{-3} to 3.80×10^{-3} ; CI_b : 1.92×10^{-3} to 4.8×10^{-3}). More importantly, effects were significantly heterogeneous (see Rosenberg *et al.* (2000): $Q_{\text{total}} = 939$, $P \ll 0.0001$, for β ; $Q_{\text{total}} = 560$, $P \ll 0.0001$, for βN), indicating substantial variability in the effects of density among studies. However, there were no consistent differences in the per capita strength of density dependence (β) between studies in which investigators concluded survival was vs. was not density-dependent (Fig. 2a). Indeed, studies in which the authors concluded there was *no* evidence for density dependence actually provide strong evidence for density dependence. In contrast, total effects of density (βN) did differ between the two classes of studies: those inferring density dependence had cohort effects that were *c.* 10-fold greater than those not inferring density dependence (Fig. 2b) due to a comparable disparity in ambient density (Fig. 2c).

When the authors' conclusions were entered as a categorical variable in the analysis, the effects of density (β or βN) remained significantly heterogeneous ($Q_{\text{within group}} = 939$, $P < 0.0001$ for β and $Q_{\text{within group}} = 506$, $P < 0.0001$ for βN), suggesting that categorizing studies by authors' inferences did little to resolve biologically important variation in results (Fig. 3). Instead, other features of the systems (such as life history, habitat type, predator density, interspecific competitor density, etc.) may explain this variation. This will require further investigation using a similar quantitative approach.

DISCUSSION

Our findings provide a new perspective on the disparate results obtained for reef fishes and offer a general lesson about ecological inference. The reason that authors differed in finding significant effects of density is *not* due to differences in the per capita effects of conspecifics (hypotheses 1 and 2), but rather is due to differences in the ambient densities of the systems studied, which led to differences in the total effect of conspecifics (hypothesis 3). Our results also support the idea that statistical power constrained the detection of density dependence, but not as represented in hypothesis 4 (Fig. 1d), which assumed that survival is inherently more variable in some systems. Instead, the ability to detect density dependence was greater when densities were higher (hypothesis 3: Fig. 1c). Density

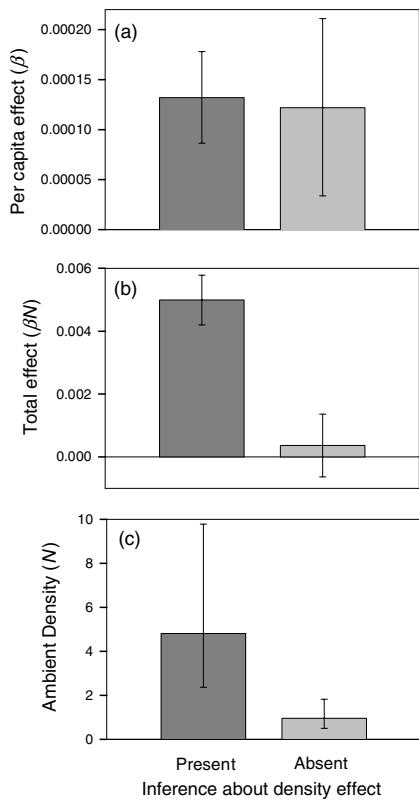


Figure 2 Strength of density dependence and ambient density in studies in which the authors concluded that survival declined with density vs. studies in which the author concluded survival was unaffected by density. (a) Per capita effects (β), given in units of m^2 fish $^{-1}$ day $^{-1}$. (b) Total cohort effects (βN), given in units of day $^{-1}$. (c) Ambient density, given in units of fish m^{-2} . Ambient densities were back-transformed following log-transformation for summarization. Parametric 95% confidence intervals are shown. Bias-corrected boot-strapped confidence intervals were also estimated for panel A: 7×10^{-5} to 2.7×10^{-4} and 3×10^{-5} to 2.8×10^{-4} ; and panel B: 3.2×10^{-3} to 7.4×10^{-3} and -3×10^{-4} to 1.2×10^{-3} , for present and absent, respectively.

dependence in systems typically at low density eluded detection, despite comparable per capita effects.

The similarity in β between groups (Fig. 2a) and the disparity in βN and ambient density (Fig. 2b,c), coupled with the large heterogeneity in effects within groups (e.g. Fig. 3) suggests that future efforts should focus on: (1) why these systems exist at different densities, not why these systems incur different intensities of per capita effects (they do not); and (2) what causes variation in the strength of density dependence. The answers to these questions cannot be inferred from the authors' conclusions.

At the heart of our results is the distinction between null hypothesis tests and estimation of effects. P -values derived from null hypothesis tests remain the most common way in which investigators summarize their results and derive

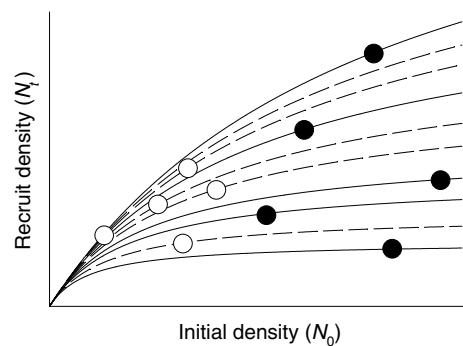


Figure 3 A schematic of the results indicating that on average there was no difference in per capita effects (β) on survival between studies in which the authors did (●) or did not (○) detect density dependence, but that these systems did have different average ambient densities and considerable heterogeneity in density dependence. The five different recruitment functions for each group represent the heterogeneity in β . Therefore the major source of variation was not resolved based on the authors' conclusions. The average recruitment function for each group corresponds to Fig. 1(C) (hypothesis 3).

inferences from their data. Interestingly, P -values are also commonly used to synthesize the literature and evaluate controversies (e.g. how often a process does vs. does not operate, as in Connell's (1983) and Sih *et al.*'s (1985) classic reviews of competition and predation). Unfortunately, even some quantitative forms of meta-analysis (e.g. Gurevitch *et al.* 1992) are based on effect sizes closely tied to test statistics and P -values (Osenberg *et al.* 1997).

Estimation of effects is a more powerful approach (see Hilborn & Mangel 1997; Burnham & Anderson 1998), especially when combined with among-system comparisons using mixed-model meta-analyses (Gurevitch & Hedges 1999; Osenberg *et al.* 1999) or Bayesian approaches (Ellison 1996; Liermann & Hilborn 1997). Our results provide an example of how different insights can be gained by this approach, in which synthesis is tied directly to models of underlying dynamics, and field data are used to estimate associated parameters instead of focusing only on the detection of processes (see also Turchin & Hanski 2001).

ACKNOWLEDGEMENTS

This work was conducted as part of the Competition Theory Working Group (organized by W. Wilson and P. Abrams), supported by the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (DEB-0072909) and the University of California. Additional support was provided through several awards from the National Science Foundation and the National Sea Grant Program. We also thank B. Bolker, J. Wilson, and W. Wilson for helpful discussion, M. Mangel and two anonymous

referees for comments, and B. Chockely and J. Wilson for invaluable assistance with the literature search and data base.

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Editor, E. McCauley

Manuscript received 19 June 2002

First decision made 20 July 2002

Manuscript accepted 7 August 2002

Appendix Studies and parameter estimates for meta-analysis of density-dependent survival in reef fish†.

| Paper | Study | Species | Con-clusion‡ | Ambient density (N) (fish $^{-1}$ m $^{-2}$) | Per capita effect (β) (m 2 fish $^{-1}$ day $^{-1}$) | Variance (β) | Citation |
|--------------------------|--|------------------------------------|--------------|--|---|----------------------|---|
| Anderson, 1994 | Fig. 4 | <i>Brachyistius frenatus</i> | DD | 0.324 | 1.98E-01 | 6.10E-04 | Mar. Ecol. Prog. Ser. 113 : 279-290 |
| Anderson, 2001 | Fig. 3 | <i>Brachyistius frenatus</i> | DD | 0.324 | 3.06E-02 | 3.97E-05 | Ecology 82 : 245-257 |
| Beukers & Jones, 1997 | Fig 1.a: fish/preferring substr | <i>Pomacentrus moluccensis</i> | DD | 9.84 | 4.60E-04 | 3.72E-08 | Oecologia 114 : 50-59 |
| Brooks, 1999 | PhD | <i>Gillichthys mirabilis</i> | DI | 50 | 3.70E-04 | 2.36E-07 | Dissertation, University of California, Santa Barbara |
| Brooks, 1999 | PhD | <i>Leptocottus armatus</i> | DD | 37.5 | 1.21E-03 | 9.00E-08 | Dissertation, University of California, Santa Barbara |
| Casselle, 1999 | Fig. 4 | <i>Thalassoma bifasciatum</i> | DI | 0.11 | -1.57E-03 | 3.07E-05 | Ecol. Monog. 69 : 177-194 |
| Casselle, 1999 | Fig. 7 | <i>Thalassoma bifasciatum</i> | DD | 0.516 | 3.48E-02 | 2.84E-05 | Ecol. Monog. 69 : 177-194 |
| Casselle, 1999 | Fig. 8 | <i>Thalassoma bifasciatum</i> | DD | 15.7 | 1.63E-03 | 4.83E-07 | Ecol. Monog. 69 : 177-194 |
| Casselle, 1999 | Fig. 2 | <i>Thalassoma bifasciatum</i> | DI | 0.11 | -9.66E-04 | 4.04E-04 | Ecol. Monog. 69 : 177-194 |
| Casselle, 1999 | Fig. 3 | <i>Thalassoma bifasciatum</i> | DD | 0.11 | 6.43E-02 | 9.78E-02 | Ecol. Monog. 69 : 177-194 |
| Doherty & Fowler 1994 | Fig. 7 | <i>Pomacentrus moluccensis</i> | DI | 1.55 | 2.09E-04 | 9.80E-09 | Bull. Mar. Sci. 54 : 297-313 |
| Doherty & Fowler 1994 | Fig. 7 | <i>Pomacentrus nardi</i> | DI | 0.719 | 2.06E-03 | 9.62E-07 | Bull. Mar. Sci. 54 : 297-313 |
| Doherty, 1982 | <i>P. nardi</i> | | DI | 0.07 | 1.40E-04 | 4.38E-07 | J. Exp. Mar. Bio. Ecol. 65 : 249-261 |
| Forrester & Steele, 2000 | Fig. 2, w/predators | <i>Lythrypnus dalli</i> | DD | 70 | 4.42E-03 | 1.06E-06 | Ecology 81 : 2416-2427 |
| Forrester & Steele, 2000 | Fig. 3A, w/predators | <i>Coryphopterus nicholsii</i> | DI | 10 | 2.38E-03 | 1.19E-04 | Ecology 81 : 2416-2427 |
| Forrester & Steele, 2000 | Fig. 3B, w/predators | <i>Coryphopterus nicholsii</i> | DI | 10 | 5.20E-04 | 2.62E-08 | Ecology 81 : 2416-2427 |
| Forrester & Steele, 2000 | Fig. 3C, w/predators | <i>Coryphopterus nicholsii</i> | DI | 10 | 7.39E-04 | 4.03E-07 | Ecology 81 : 2416-2427 |
| Forrester & Steele, 2000 | Fig. 5, w/predators | <i>Coryphopterus glaucofraenum</i> | DD | 10 | 1.26E-01 | 0.00410 | Ecology 81 : 2416-2427 |
| Forrester, 1990 | w/adults | <i>Dasyatis arianaus</i> | DD | 41.0 | 2.35E-06 | 7.32E-12 | Ecology 71 : 1666-1681 |
| Forrester, 1990 | w/o adults | <i>Dasyatis arianaus</i> | DD | 41.01 | 2.09E-05 | 1.48E-11 | Ecology 71 : 1666-1681 |
| Forrester, 1995 | Fig. 2, artificial reef | <i>Coryphopterus glaucofraenum</i> | DD | 4 | 4.81E-03 | 7.45E-06 | Oecologia 103 : 275-282 |
| Forrester, 1995 | Fig. 2, natural reefs | <i>Coryphopterus glaucofraenum</i> | DD | 4 | 3.00E-03 | 1.17E-06 | Oecologia 103 : 275-282 |
| Hixon & Carr 1997 | All predators present | <i>Chromis cyanus</i> | DD | 2 | 2.51E-02 | 1.60E-05 | Science 277 : 946-949 |
| Jones, 1984 | Fig. 6 | <i>Pseudolabrus vittatus</i> | DD | 0.104 | 2.62E-02 | 2.25E-05 | J. Exp. Mar. Bio. Ecol. 75 : 277-303 |
| Jones, 1987 | Fig. 2, <i>D. arianaus</i> , w/o adults | <i>Dasyatis arianaus</i> | DD | 38.4 | 8.77E-06 | 2.54E-11 | J. Exp. Mar. Bio. Ecol. 114 : 169-182 |
| Jones, 1987 | Fig. 2, <i>D. arianaus</i> , w/adults | <i>Dasyatis arianaus</i> | DD | 38.4 | 2.98E-07 | 8.99E-12 | J. Exp. Mar. Bio. Ecol. 114 : 169-182 |
| Jones, 1987 | Fig. 4, LR data | <i>Pomacentrus amboinensis</i> | DI | 2.26 | 2.80E-04 | 2.81E-09 | J. Exp. Mar. Bio. Ecol. 114 : 169-182 |
| Jones, 1987 | Fig. 3, w/adults | <i>Pomacentrus amboinensis</i> | DI | 1.63 | 2.21E-07 | 4.84E-10 | Ecology 68 : 1534-1547 |
| Jones, 1987 | Fig. 3, w/o adults | <i>Pomacentrus amboinensis</i> | DI | 1.63 | 5.46E-05 | 1.82E-08 | Ecology 68 : 1534-1547 |
| Jones, 1987 | Fig. 6, w/adults | <i>Pomacentrus amboinensis</i> | DI | 1.15 | -4.32E-04 | 1.04E-07 | Ecology 68 : 1534-1547 |
| Jones, 1987 | Fig. 6, w/o adults | <i>Pomacentrus amboinensis</i> | DI | 1.15 | 6.87E-04 | 8.28E-07 | Ecology 68 : 1534-1547 |
| Jones, 1988 | <i>D. arianaus</i> on <i>Porites</i> | <i>Dasyatis arianaus</i> | DD | 5 | 3.00E-04 | 5.48E-09 | J. Exp. Mar. Bio. Ecol. 123 : 115-126 |
| Jones, 1988 | Fig. 2, <i>D. arianaus</i> on <i>Porites</i> | <i>Dasyatis arianaus</i> | DD | 5 | -1.59E-04 | 2.43E-08 | J. Exp. Mar. Bio. Ecol. 123 : 115-126 |
| Jones, 1990 | <i>P. amboinensis</i> | <i>Pomacentrus amboinensis</i> | DD | 0.694 | 1.60E-04 | 4.08E-08 | Ecology 71 : 1691-1698 |
| Letourneau et al. 1998 | Fig. 5 | <i>Epinephelus merra</i> | DD | 2.5 | 1.41E-02 | 1.58E-05 | J. Mar. Biol. Assoc. UK 78 : 307-319 |

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|------------------------------|------------------------|----------------------------------|----|--------------------|-----------|----------|-------------------------------------|
| Robertson, 1992 | Fig. 3A, ref A | <i>Stegastes dorypanicus</i> | DI | 0.792 | 2.38E-03 | 5.86E-04 | Mar. Biol. 114 : 527-537 |
| Robertson, 1992 | Fig. 3B, ref B | <i>Stegastes planifrons</i> | DD | 0.208 | 1.58 | 3.72 | Mar. Biol. 114 : 527-537 |
| Robertson, 1992 | Fig. 3C, ref A | <i>Acanthurus chinungus</i> | DI | 0.547 | 2.23E-02 | 4.45E-03 | Mar. Biol. 114 : 527-537 |
| Robertson, 1992 | Fig. 3D, ref B | <i>Stegastes dorypanicus</i> | DI | 1.19 | 4.77E-02 | 1.02E-03 | Mar. Biol. 114 : 527-537 |
| Robertson, 1992 | Fig. 3E, ref A | <i>Stegastes variabilis</i> | DI | 0.110 | 9.38E-01 | 2.53 | Mar. Biol. 114 : 527-537 |
| Robertson, 1992 | Fig. 3F, ref B | <i>Acanthurus chinungus</i> | DI | 2.06 | 1.27E-01 | 2.63E-03 | Mar. Biol. 114 : 527-537 |
| Robertson, 1992 | Fig. 3G, ref A | <i>Stegastes leucostictus</i> | DI | 0.123 | 5.89E-01 | 5.81E-01 | Mar. Biol. 114 : 527-537 |
| Robertson, 1992 | Fig. 3H, ref B | <i>Stegastes variabilis</i> | DI | 0.246 | -8.67E-02 | 1.17E-01 | Mar. Biol. 114 : 527-537 |
| Robertson, 1992 | Fig. 3I, ref B | <i>Acanthurus coeruleus</i> | DI | 0.034 [†] | -4.17E-02 | 6.64E-02 | Mar. Biol. 114 : 527-537 |
| Robertson, 1992 | Fig. 3J, ref B | <i>Stegastes leucostictus</i> | DI | 0.217 | 1.59E-01 | 3.33E-02 | Mar. Biol. 114 : 527-537 |
| Robertson, 1992 | Fig. 3K, ref A | <i>Abudefduf saxatilis</i> | DI | 0.458 | 4.53E-01 | 5.58E-02 | Mar. Biol. 114 : 527-537 |
| Robertson, 1992 | Fig. 3L, ref B | <i>Acanthurus coeruleus</i> | DI | 0.140 | 1.233 | 7.90E-01 | Mar. Biol. 114 : 527-537 |
| Robertson, 1992 | Fig. 3M, ref A | <i>Stegastes partitus</i> | DI | 0.150 | 3.12E-01 | 7.28E-03 | Mar. Biol. 114 : 527-537 |
| Robertson, 1992 | Fig. 3N, ref A | <i>Acanthurus bahianus</i> | DI | 0.99 | -6.46E-03 | 2.96E-04 | Mar. Biol. 114 : 527-537 |
| Robertson, 1992 | Fig. 3O, ref B | <i>Thalassoma bifasciatum</i> | DI | 0.227 | 1.36 | 1.91 | Mar. Biol. 114 : 527-537 |
| Robertson, 1992 | Fig. 3P, ref B | <i>Stegastes partitus</i> | DI | 1.02 | 3.69E-02 | 1.41E-03 | Mar. Biol. 114 : 527-537 |
| Robertson, 1992 | Fig. 3Q, ref B | <i>Acanthurus bahianus</i> | DI | 0.632 | 8.53E-01 | 3.77E-01 | Mar. Biol. 114 : 527-537 |
| Sano, 1997 | Fig. 4, 1992 | <i>Sagamia genionema</i> | DD | 0.853 | 9.44E-03 | 8.19E-07 | J. Exp. Mar. Bio. Ecol. 214 : 67-84 |
| Sano, 1997 | Fig. 4, 1993 | <i>Sagamia genionema</i> | DI | 1.16 | -2.42E-04 | 1.38E-07 | J. Exp. Mar. Bio. Ecol. 214 : 67-84 |
| Sano, 1997 | Fig. 4, 1994 | <i>Sagamia genionema</i> | DD | 0.998 | 1.32E-02 | 1.12E-06 | J. Exp. Mar. Bio. Ecol. 214 : 67-84 |
| Schmitt & Holbrook, 1999 | Fig. 4, w/older fish | <i>Dasyllis trimaculatus</i> | DD | 64.5 | 1.44E-04 | 1.00E-10 | Ecology 80 : 35-50 |
| Schmitt & Holbrook, 1999 | Fig. 4, w/o older fish | <i>Dasyllis trimaculatus</i> | DD | 64.5 | 1.00E-04 | 5.25E-12 | Ecology 80 : 35-50 |
| Schmitt <i>et al.</i> , 1999 | Fig. 2 | <i>Dasyllis trimaculatus</i> | DD | 241 | 4.71E-05 | 2.50E-11 | Ecol. Lett. 2 : 294-303 |
| Shima, 2001 | Fig. 3 | <i>Thalassoma hardwickii</i> | DD | 0.938 | 1.21E-01 | 4.60E-03 | Oecologia 126 : 58-65 |
| Shima, 2001 | Fig. 4 | <i>Thalassoma hardwickii</i> | DD | 0.938 | 1.40E-02 | 1.92E-05 | Oecologia 126 : 58-65 |
| Shima, 2001 | Fig. 5 | <i>Thalassoma hardwickii</i> | DD | 0.531 | 1.81E-02 | 2.59E-05 | Ecology 82 : 2190-2199 |
| Steele 1997 | <i>C. nicholsii</i> | <i>Corophopterus nicholsii</i> | DD | 20 | 2.29E-03 | 2.28E-07 | Oecologia 112 : 64-74 |
| Steele 1997 | <i>L. dalli</i> | <i>Lethrinus dalli</i> | DD | 100 | 2.00E-03 | 4.08E-08 | Oecologia 112 : 64-74 |
| Stewart & Jones, 2001 | Fig. 5A | Several species | DD | 27.3 | 6.47E-05 | 5.76E-10 | Mar. Biol. 138 : 383-397 |
| Stewart & Jones, 2001 | Fig. 5B | Several species | DI | 5.32 | 3.20E-04 | 8.29E-06 | Mar. Biol. 138 : 383-397 |
| von Herbing & Hunte, 1991 | Fig. 9 | <i>Thalassoma bifasciatum</i> | DD | 1.81 | 6.12E-03 | 2.41E-07 | Mar. Ecol. Prog. Ser. 72 : 49-58 |
| Webster, 2002 | Fig. 4B, w/predators | <i>Neopomacentrus cyanomelas</i> | DI | 4.34 | 1.97E-03 | 2.50E-06 | Oecologia 131 : 52-60 |
| Webster, 2002 | Fig. 4D, w/predators | <i>Pomacentrus amboinensis</i> | DD | 3.14 | 1.30E-02 | 5.48E-06 | Oecologia 131 : 52-60 |
| Webster, 2002 | Fig. 4F, w/predators | All Pomacentrids | DI | 9.82 | -4.76E-04 | 4.80E-08 | Oecologia 131 : 52-60 |
| Wilson & Osenberg, 2002 | Text, expt. | <i>Gobiosoma</i> sp. | DD | 65.8 | 8.66E-02 | 1.55E-04 | Oecologia 130 : 205-215 |
| Wilson & Osenberg, 2002 | Text, obs. | <i>Gobiosoma</i> sp. | DI | 65.8 | 3.67E-04 | 5.42E-07 | Oecologia 130 : 205-215 |

[†]Based on search of papers published between 1970 and 2001 in *American Naturalist*, *American Zoologist*, *Australian Journal of Ecology*, *Australian Journal of Marine and Freshwater Research*, *Bulletin of Marine Science*, *Canadian Journal of Fisheries and Aquatic Sciences*, *Copeia*, *Ecological Applications*, *Ecological Monographs*, *Ecology*, *Ecology Letters*, *Environmental Biology of Fishes*, *Fishery Bulletin*, *Journal of Animal Ecology*, *Journal of Experimental Marine Biology and Ecology*, *Journal of Fish Biology*, *Marine Biology*, *Marine Ecology Progress Series*, *Natur*, *Oecologia*, *Oikos*, *Science* and supplemented with an electronic search using Web of Science and JSTOR.

[‡]DD: detected density dependence; 'DI': failed to detect density dependence.