MANAGEMENT AT A DIFFERENT SCALE: MARINE ORNAMENTALS AND LOCAL PROCESSES

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ABSTRACT

In many parts of the world, marine ornamentals, fishes and invertebrates collected and sold in the aquarium trade, comprise an increasingly important fishery. Few management strategies have been devised for these fisheries, yet they may represent the most tractable systems: e.g., the benthic life stages are relatively site attached and easily sampled, and many species are amenable to experimental study. Here, a stochastic population model is developed with which to investigate the efficacy of exploitation strategies designed to manage a marine ornamental fishery. Extensive field studies of the tropical damselfish *Dascyllus trimaculatus* were used to define functions and estimate associated parameters that govern the dynamics of the unexploited population. Sources of uncertainty in the predictions of the model were then evaluated and the responses to different exploitation-control rules simulated. Effects resulting from uncertainty due to variable larval settlement were comparable in magnitude to effects of uncertainty in parameter estimates. In addition, despite resident-facilitated settlement, yields were not a unimodal function of catch rate. Instead, yield typically increased with catch rate. The absence of a dome-shaped yield curve appeared to result from an interaction between facilitated settlement and subsequent density dependence.

Management targets (such as maximum sustainable yield, MSY), although theoretically tractable, have been criticized for their failure to protect exploited stocks (Larkin, 1977; Ludwig et al., 1993; Mangel, 2000). The primary criticism of targets points out that most systems are subject to uncertain natural variation in their dynamics and that this uncertainty can cause some management targets to overestimate badly levels of sustainable exploitation (Lande et al., 1997; Lauck et al., 1998; Roughgarden, 1998). In fact, several different features of traditional fisheries make it difficult to develop management strategies for them. First, these fisheries are often difficult to sample, so stock size or other state variables are not well known. Second, the relationships that describe the deterministic component of the population dynamics are poorly characterized and the associated parameters poorly estimated. This problem is particularly severe for functions that describe the form and intensity of density dependence, because the experimentation needed to assess density dependence is difficult or impossible to conduct on most exploited species. Third, marine systems are subject to uncertainty imposed by natural variation in the strength of important processes, such as oceanographic factors governing the dispersal, growth, and condition of larvae. Indeed, fisheries biologists and marine ecologists alike have noted the inherent variation in population dynamics that larval supply introduces (e.g., Caley et al., 1996).

An important emerging fishery in many parts of the world is the marine ornamental fishery—fishes and invertebrates that are caught for sale in the aquarium trade. In Florida alone, over 300 species of marine ornamental fishes and invertebrates are collected and sold in the marine aquarium trade, contributing ~\$4 million yr^{-1} to the collectors (statistics from the Florida Department of Environmental Protection) and over \$30 million yr^{-1} to the industry

(Donna Lee, Food and Resources Economics, Univ. Florida, pers. comm.). Few management strategies have been devised for these fisheries, yet they may represent a more tractable system for studying exploitation impacts than the classic food fisheries. For example, in the ornamental fishery, collecting occurs on smaller spatial scales than is typical for food fisheries. The population dynamics of target reef fishes and invertebrates also operate on a spatial scale different from that of many food fishes (Lindeman et al., 2000; St. Mary et al., 2000); many coral-reef fishes settle to and spend their entire lives on a single reef or even coral head (see, e.g., Sale, 1980). These small reef fishes also have been the subjects of many experimental studies of density dependence and population dynamics (e.g., Sale, 1991; Hixon and Carr, 1997; Forrester and Steele, 2000). Because of the limited benthic movement of older age classes and the long-distance dispersal of larvae, local populations are typically considered 'open' (Warner and Hughes, 1988). Local benthic population dynamics have been shown in many species to result from variable larval settlement tempered by density-dependent, postsettlement processes (see, e.g., Caley et al., 1996). In some species, larval settlement is facilitated by the presence of older age classes (Sweatman, 1985, 1988; Schmitt and Holbrook, 1996; but see Wilson, 1998, for a counter example). This positive effect of density may have important consequences for population dynamics and consequently for management.

The limited spatial scale of marine ornamental fisheries allows us to accomplish several things that are difficult in more traditional, larger-scale fisheries. The ability to measure recruitment accurately and to perform controlled experiments on recruitment and survivorship allows us to estimate population-dynamic parameters directly from experimental data. We can also estimate the uncertainty in these parameters as well as the uncertainty resulting from natural variation in settlement intensity. Armed with this information, we can then begin (1) to evaluate the relative effects of uncertainty in settlement rates and in parameter estimates and (2) to compare alternate management strategies.

In comparing management strategies, we focus particularly on the facilitation of larval settlement by resident conspecifics. Facilitation may provide a built-in mechanism promoting restrained local exploitation and thus leading to the sustainable exploitation of marine ornamentals at a regional scale. Intermediate catch on a local scale could increase yield because the remaining fishes increase settlement and thus the exploitable stock. In such cases, we may be able to envision management arising from decisions chosen by collectors rather than imposed by a federal regulatory agency (see, e.g., Hilborn et al., 1996). If sustainable strategies actually coincide with optimal short-term behavior, regulatory enforcement will also be less problematic.

Furthermore, uncertainty and facilitation can interact with density-dependent mortality to determine both the population dynamics of exploited marine ornamentals and our predictions of yields. Parameter uncertainty may lead to misestimation of the optimal exploitation strategy, and overexploitation, even when a restrained exploitation strategy would be the optimal behavior from a local collector's point of view. In addition, natural variation may lead to high catch rates through the effect of Jensen's inequality (Ruel and Ayres, 1999), which lowers yields under uncertainty when catch is a saturating function of yield.

Marine ornamentals have not been studied extensively from a management perspective, although some data suggest that collecting can deplete natural stocks by as much as 50% (Tissot and Hallacher, 1999). It is therefore critical to develop and implement management strategies for marine ornamentals. Here, we develop a single-species population-dynamics model, which we parameterize using data from a well-studied Indo-Pa-

cific damselfish, the three-spot humbug, *Dascyllus trimaculatus*—a species that is collected and sold in the marine aquarium trade and is similar in many ways to other marine ornamentals. Importantly, facilitation occurs in this system; presence of resident *D. trimaculatus* increases the settlement of larvae at least at low to intermediate density (Schmitt and Holbrook, 1996). We examine the relative importance of two sources of uncertainty to the predicted dynamics of the system: (1) larval settlement, which is notoriously variable in space and time and is widely believed to drive local dynamics (see, e.g., Caley et al., 1996), and (2) parameter uncertainty, which arises because of error in the estimation of parameters in the population model. We then explore how different exploitation scenarios affect local yield, as well as the export of larvae to the regional stock. In this context, we consider the relationships among facilitation, density dependence, and exploitation strategy. Finally, we look at the interactions between parameter and settlement uncertainty, population dynamics, and exploitation.

THE STUDY SYSTEM AND THE MODELING CONTEXT

Exploitation and management of marine ornamentals differs from traditional fisheries, and our approach differs from many previous approaches. We assume that collections are made from a leased site, where a single collector has exclusive access and can set an exploitation strategy. Most marine ornamentals occur on coral reefs, which are increasingly protected and can be damaged by collecting activities (Jones and Steven, 1997; Jones and Hoegh-Guldberg, 1999). As a result, collecting may become restricted to nonnatural habitats, including artificial reefs or live-rock lease sites (Wilson et al., 2001). Removal of habitat, 'live-rock' (e.g., corals and other living assemblages attached to limestone) is illegal in Florida waters, but collectors can lease sites in soft-bottom habitat and deploy quarry-mined limestone rocks (artificial reefs). Sessile invertebrates settle and grow on these rocks, which are then collected and sold in the aquarium trade. These live-rock sites may also serve as production sites for marine ornamental fishes (Wilson et al., 2001). If coral-reef tracts are protected with marine reserves, then collection of marine ornamentals from live-rock lease sites is likely to become more commonplace. This scenario underlies our modeling efforts and analyses. The consistent and exclusive exploitation of a specific area by a local fisher provides incentive to collect in a sustainable and economically stable manner. This scenario may not be so different from the current exploitation practices of marine-ornamental collectors, at least in its effects on the population dynamics of exploited species. Currently most collectors in the Florida Keys collect marine ornamentals over a relatively small region and look for specific species in a fraction of that area (pers. observ.). With respect to the exploitation of one species, this practice differs from the assumptions of our model and from lease sites only in that a single collector does not have exclusive fishing rights.

We explore alternative exploitation policies for *D. trimaculatus*, a small damselfish that occurs in lagoons and outer reefs throughout most of the Indo-Pacific (Bagnis et al., 1987; Fautin and Allen, 1992). Settlement occurs throughout the year, in biweekly pulses that last several days (Holbrook and Schmitt, 1997; Schmitt and Holbrook, 1999a). Larvae settle almost exclusively to large anemones (Fautin and Allen, 1992), where they reside for approximately 6 mo (i.e., until they reach approximately 60 mm SL). At this point fish become independent of anemones and have few interactions with the younger fish still resident on the anemone. Resident fishes can facilitate (at low density) or inhibit

(at high density) settlement to anemones (Schmitt and Holbrook, 1996, 2000). Postsettlement survival declines with increasing cohort density (Schmitt and Holbrook, 1999b; Schmitt et al., 1999) and with increasing density of older juveniles that reside on the anemone (Schmitt and Holbrook, unpubl. data). For our model, we characterize the benthic population as consisting of settlers (aged 0 to 2 wks, i.e., from the most recent settlement pulse), juveniles (2 wks to 6 mo), and adults (older than 6 mo).

Our model explores the dynamics of the anemone-associated subpopulation (settlers and juveniles). We assume that juveniles are collected for the aquarium trade (settlers are too young to be handled without high mortality, and adults are less desirable because of their size and lack of association with anemones). We use observational and experimental data from studies of *D. trimaculatus* conducted on Moorea, French Polynesia, to guide the development of the model, choose the form of the functions, and estimate the associated parameter values.

We assume that local egg production is uncoupled from settlement of larvae to the local site (the local population is very small compared to the regional stock from which larvae are produced). In these open systems, local exploitation can be intensive and 'sustainable' simply because external supply always replenishes the locally depleted site. As the number of locally exploited sites increases, the regional dynamics (and the supply of larvae) to the local sites become coupled, so sustainability depends on the aggregate effects of all local strategies on the regional dynamics. Here we focus on the local dynamics and discuss some implications for larger regional dynamics.

THE MODEL: FORM AND PARAMETERIZATION

We developed an age-structured population model with open recruitment, based on a one-week time step with larval settlement every 2 wks. All predictions of average population densities, variation in population densities, and exploitation yields are expressed in terms of the fish densities on a 0.05 m^2 area, which corresponds to the typical size of an anemone (Schmitt et al., 1999).

SETTLEMENT TO EMPTY ANEMONES.—The level of new settlement (i.e., the number of settlers per 0.05 m^2 anemone per pulse) to empty anemones during a biweekly settlement pulse, s(0), follows a zero-augmented exponential distribution. This distribution is the standard exponential distribution, described by the parameter λ (mean settlement density equals $1/\lambda$) with an additional chance of complete settlement failure, described by the parameter p(0) (Table 1). Thus the zero-augmented exponential distribution gives settlement s(0) of

s(0) = 0 with probability p(0)

x < s(0) < x + dx (where x > 0) with probability $(1 - p(0)) \lambda e^{-\lambda x} dx$.

The parameters p(0) and λ, and their variation through time, among reefs, and between different anemones, were estimated from data on settlement to 600 anemones without juveniles (10 anemones at 10 sites at 6 different times; Fig, 1A; Schmitt et al., 1999). We fit the p(0) and λ parameters for a particular site and time directly by counting the fraction of anemones without settlers (to estimate p(0)) and taking the reciprocal of the mean settlement on anemones with settlers (to estimate λ), because these are the maximum-likelihood estimators for this distribution.

A two-way ANOVA on settlement across sites and times showed that site, time, and their interaction were all significant sources of variation in settlement. We characterized

Table 1. Parameters and state variables.

Parameters	Definition (and units)	Estimate	95% profile confidence limits
$p(0)$	Probability of no settlement in a given pulse	0.165	
λ	Exponential distribution of settlement density (on empty anemones) (per (no./per 0.05 m^2))	0.0689	
a	Intercept of resident effect on settlement, relative to empty anemones	1.000 (scaled)	0.584, 1.41
b	Initial slope of resident effect on settlement (per (no./0.05 m^2))	0.380	0.255, 0.523
c	Exponential parameter of resident effect on settlement (per (no./per 0.05 m^2))	0.0725	0.0597, 0.0870
α_1	Instantaneous density-independent mortality of fish aged 0 to 1 wk	−0.113	−0.143, −0.0759
β_1	Intracohort density-dependent mortality of fish aged 0 to 1 wk	-1.31×10^{-6}	$-3.96 \times 10^{-10}, -6.35 \times 10^{-5}$
γ_1	The degree of compensation in mortality of fish aged 0 to 1 wk	2.74	1.99, 4.38
α_2	Instantaneous density-independent mortality of fish aged 1 wk to 6 mo	-1.15×10^{-5}	$-2.49 \times 10^{-3}, 9.41 \times 10^{-4}$
β_2	Intracohort density-dependent mortality of fish aged 1 wk to 6 mo	-1.53×10^{-5}	$-4.85 \times 10^{-8}, -6.04 \times 10^{-4}$
γ_2	The degree of compensation in mortality of fish aged 1 wk to 6 mo	2.16	1.11, 3.83
β_{SJ}	Intercohort density-dependent mortality imposed by older juveniles (aged 2 wks to 6 mo) on younger fish	−0.00561	−0.00686, −0.00442

State Variables

S	Density of settlers (no./0.05 m^2)		
J	Density of juveniles (no./0.05 m^2)		
A	Production of adults (no./0.05 m^2/2 wks)		

the variance in log mean settlement density between times within sites (incorporating both the time factor and time-by-site interaction).

To test the effects of temporal and spatial (among-anemone) variability in settlement on variability in juvenile densities, we (1) eliminated all variation in settlement (setting settlement level at every anemone equal to the grand mean), (2) allowed among-anemone variation by choosing from the zero-augmented exponential distribution described above, or (3) allowed both among-anemone and temporal variation by first choosing a mean settlement density from a log-normal distribution using the temporal variance in log mean settlement density described above and then choosing random deviates from the zero-augmented exponential distribution to describe the settlement to each anemone. We used the relationships

$$\lambda = \min(1/\mu, 0.437\, \mu^{-0.768})$$
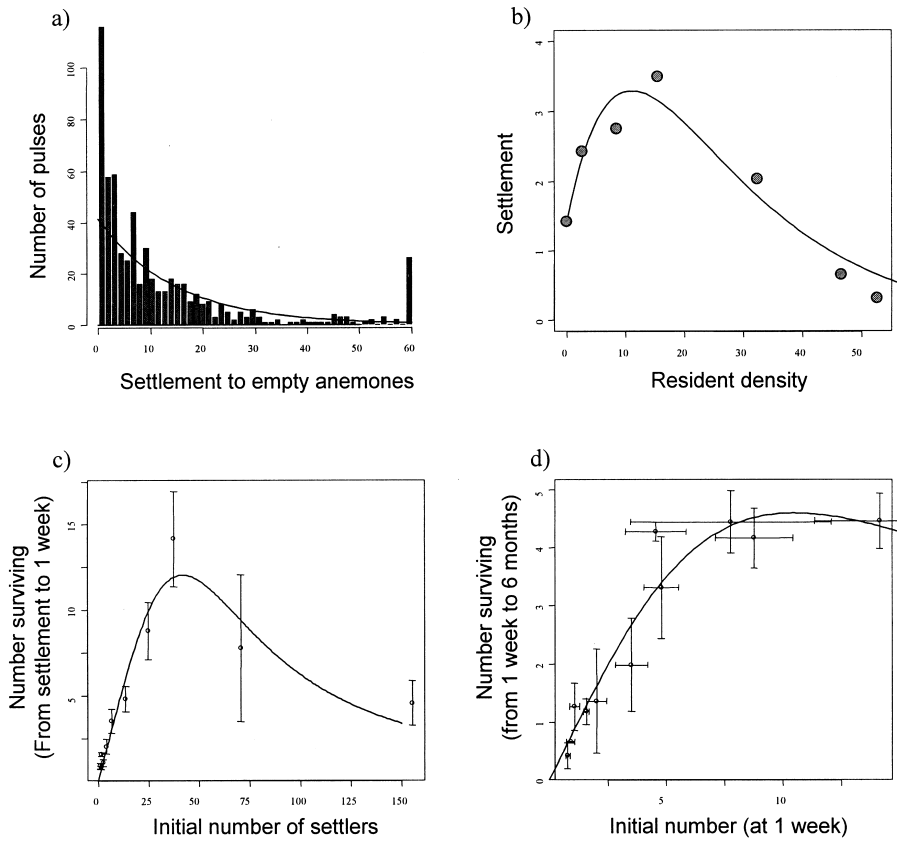$$p(0) = 1 - \mu\lambda,$$

Figure 1. Data used to parameterize the model and submodel fits to the data. A. Settlement to empty anemones: numbers of settlers recruiting to empty anemones (600 data points: 10 anemones measured at 10 sites during 6 distinct recruitment pulses), scaled per 0.05 m^2 area of anemones. The generally exponential shape of the distribution is clear, as is the excess of anemones with zero recruits. B. Facilitation and suppression of settlement by residents. The horizontal axis shows number of previously established settlers on the habitat, the vertical axis shows settlement over the next six days. The line shows the best fit of the modified Ricker equation (described in text). C. Survivorship to one week. Number of settlers surviving to one week (per 0.05 m^2 of anemone surface) as a function of the initial number of settlers. The line shows the best-fit Shepherd function. Error bars represent standard errors about the mean. D. Survivorship from 1 wk to six mo; axes and line as in Fig. 1C. Error bars represent standard errors about the mean.

which were derived from the relationships among p(0), λ, and mean settlement seen in the data, to estimate λ and p(0) from the mean settlement level μ.

SETTLEMENT AS A FUNCTION OF RESIDENT DENSITY.—Given the overall estimated settlement to empty anemones, the model then accounted for facilitation or suppression by resident juveniles by means of a modified Ricker function,

$$s(J) = s(0)((a + bJ)\, e^{-cJ}),$$

where the parameters a, b, and c (defined in Table 1) were fit to data from settlement experiments on anemones with different resident juvenile densities (Fig. 1B, data taken

from fig. 3 of Schmitt and Holbrook, 1996). After fitting, all parameters were scaled to make a = 1 so that the function would represent the relative effect of residents on settlement. This function resembles a Ricker function in having a unimodal shape (at low juvenile densities, increasing juvenile density increases settlement density) and an exponential decline in settlement with increasing juvenile density for high juvenile densities, but the additional parameter, a, allows anemones without juveniles to receive settlers ($s(J) > 0$ for $J = 0$). Parameters were fitted by nonlinear least squares, with standard minimizers (quasi-Newton/BFGS and Nelder-Mead simplex) available in the R programming language (Ihaka and Gentleman, 1996).

SURVIVORSHIP.—Survivorship of new settlers (0–1 wk), older settlers (1–2 wks), and juveniles (2 wks–6 mo) were determined according to a Shepherd function of within- and between-stage densities (Shepherd, 1982; Quinn and Deriso, 1999). Within-stage effects were estimated from data provided by an experimental cohort study described in Schmitt et al. (1999). Between-stage effects were estimated from an unpublished study (Schmitt and Holbrook, unpubl. data). Because the survivorship data were obtained on a variety of time scales (1-wk, 2-wk, and 6-mo survivorship), depending on the data source, we estimated the 'instantaneous' parameters of the Shepherd function. Given the instantaneous decline in settlers (S) due to postsettlement mortality,

$$dS/Sdt = \alpha' + \beta S^{\gamma}$$

(where α', $\beta < 0$ and $\gamma > 0$, Table 1), the survivorship to time τ of a cohort that starts at size S_0 is $S_{\tau} = e^{\alpha'\tau}S_0 / (1 + (\beta/\alpha')(1 - e^{\alpha'\tau})S_0^{\gamma})$.

On the basis of this relationship, we used 1-wk time steps but integrated the effects of changes in population density over the course of the week. The elapsed-time parameter τ varied for fitting parameters to experiments of different durations but was always one week in model runs.

Data from experiments indicated that within-cohort survivorship parameters in the first week differed significantly from those at later times. We therefore used one set of survivorship parameters (estimated directly from 1-wk survivorship data, Fig. 1C) for the 0–1-wk time step and a different set of parameters (estimated indirectly from the survivorship from 1 wk to 6 mo, Fig. 1D) for all individuals older than 1 wk. Parameters for within-stage effects were fitted by nonlinear least squares as described above.

We estimated and incorporated effects of juveniles on settler mortality by decomposing the α' parameter above into a truly density-independent term (α) and one accounting for the effects of juveniles (β_{SJ}):

$$\alpha' = \alpha + \beta_{SJ}J$$

The only data available for estimation of β_{SJ} (defined in Table 1) were from a two-week survivorship experiment that measured cohort survivorship in the presence and absence of juveniles (Schmitt and Holbrook, unpubl. data). We did not estimate all the Shepherd parameters independently for these observations because the data were insufficient to estimate three independent parameters with reasonable accuracy. Instead, we assumed that the density-dependent mortality parameters β and γ remained constant across experiments and fit only the density-independent mortality rate (α) and the effect of juveniles (β_{SJ}) to the new data. We calculated equivalent density-dependent mortality parameters β

and γ for a two-week experiment from our previous fits by extrapolating the survivorship to two weeks for a variety of initial densities using the previously estimated parameters and fitting a Shepherd function to this relationship. We then held these β and γ parameters constant while we fitted the α (density-independent mortality) parameter for anemones without juveniles as well as the additional density-independent mortality caused by juveniles (β_{SJ}) for the anemones with juveniles. We assumed that additional density-independent mortality was a linear function of resident juvenile density.

Juveniles leave the anemones after six months, at which point we consider them to be adults (although maturation actually occurs slightly later). Adults were assumed to have no effects on the settlement and survival of younger individuals because of their shift to another benthic habitat and the lack of coupling between local egg production and larval supply.

UNCERTAINTY IN PARAMETER ESTIMATES.—Along with the best-fitting parameter estimates, the fitting procedure also provided an estimate of the uncertainty in parameters and the correlations between parameters, based on the local curvature (second derivatives) of the goodness-of-fit surface at the location of the best-fit parameters. The parameter variances and correlations can be combined into a variance-covariance matrix. This matrix determines a multivariate normal distribution, centered on the best-fit parameters, that describes the estimated sampling distribution of the parameters. In each case, the parameter uncertainty estimated from local curvature was checked against more exact estimates of parameter uncertainty, the profile confidence limits, which compare the minimum sum of squares obtainable while holding a parameter of interest at a fixed value against the overall minimum sum of squares (Hilborn and Mangel, 1997). If the true sampling distribution of the parameters is multivariate normal, the profile confidence limits will match the uncertainty estimate based on local curvature. The multivariate normal confidence limits agreed reasonably well with the profile confidence limits for all parameters except the within-cohort density-dependence (β) parameter. The true sampling distribution of β appears to be log-normal rather than normal; the parameter uncertainty of log(β) estimated from the curvature matches the profile confidence limits.

ANALYSES AND RESULTS

SOURCES OF VARIATION.—With the best estimates and variance-covariance estimates in hand, we explored the effects of parameter uncertainty by drawing random samples from the multivariate normal sampling distribution for each set of parameters (the effects of older age classes on settlement, 1-wk survivorship, 6-mo survivorship, between-cohort effects on survivorship). We contrasted variation among time-averaged juvenile densities caused by this parameter variation ('parameter variation') with the variation caused by between-anemone sampling variability, and we contrasted temporal variability in settlement rates ('among-anemone variation') with parameters fixed at their best-fit values. We also examined the variation caused by the combination of parameter uncertainty and larval settlement variation ('among-anemone and parametric variation'). For each random resampling of larval settlement rate or parameter values, we sampled the settlement and population dynamics of 150 anemones (corresponding to the approximate spatial scale of a single collector's lease site) over 200 weekly time steps (corresponding to several years).
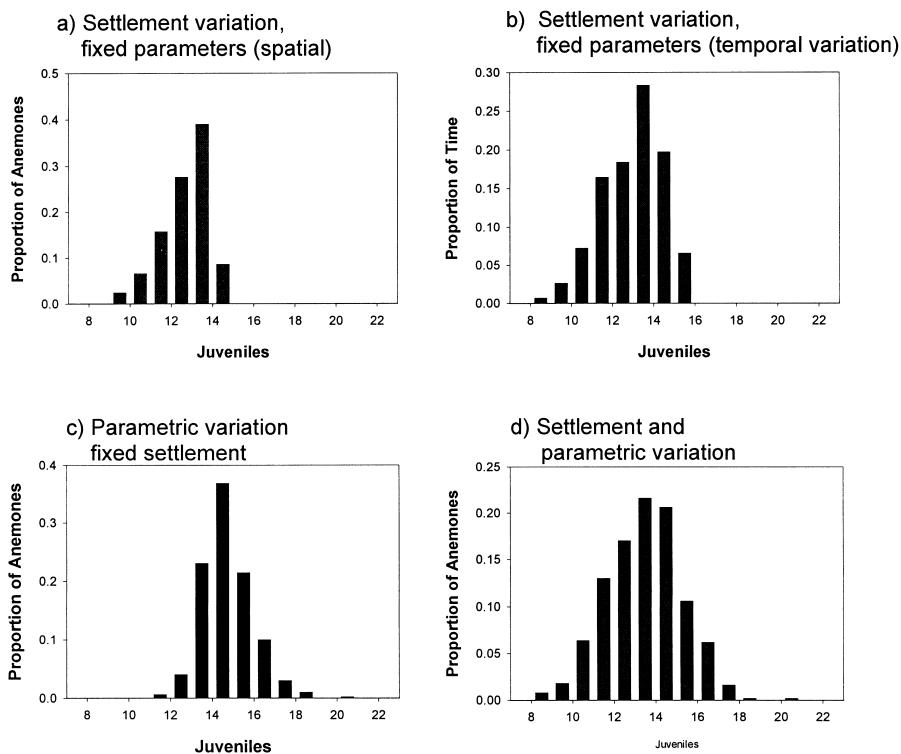
Figure 2. Effects of variation of larval supply and parameter estimates. A. Distribution of juvenile densities for 150 anemones, averaged over 200 weekly time steps after a 50-wk transient period, with the best-fit parameters and larval settlement that varied between anemones. The distribution of larval supply (specified by p(0) and v) was allowed to vary over time, but the same time series of larval supply was used for every anemone. B. Distribution of juvenile densities (time period and transient period as in Fig. 2A), with a different temporal distribution of larval supply allowed for each anemone. C. Distribution of juvenile densities for completely fixed larval settlement densities (supply in every pulse equal to the overall mean larval supply), but with parameters chosen by random sampling from multivariate normal distributions as described in the text. D. Distribution of juvenile densities when both parameters and larval supply vary through time (combining the forms of variation seen in Fig. 2A,C).

The results of our 'factorial experiment' incorporating different combinations of settlement and parameter variation show that, overall, the population dynamics of juvenile *D. trimaculatus* could (hypothetically) be reasonably accurately determined in our system (Fig. 2). With any combination of parameter and settlement uncertainty, juvenile densities were fairly tightly constrained in the neighborhood of 10–16 juveniles per anemone. The strong density dependence in the system and the six-month residence time in the juvenile stage damp the effects of variation in larval supply. Contrary to conventional wisdom, the effects of larval supply do not preclude reasonably accurate estimation of juvenile densities. The effects of variation in parameter values are relatively constrained for at least two reasons: (1) This system is intensively studied, and parameters were estimated with greater confidence than is typically the case. (2) The strength of density dependence tends to limit the effects of variation in other parameters. However, despite the relatively tractable nature of the system and the extensive field studies, the uncertainty

contributed by ignorance of exact parameter values (Fig. 1C) is at least as large as that contributed by settlement variability (Fig. 1A,B). Furthermore, our estimate of parameter uncertainty is probably conservative because we assume that the experimental data we have used provide parameter values that, subject to estimation uncertainty, apply to all times and sites. Even the rough comparisons we were able to make between experiments (e.g., between the 2-wk experiment on between-stage density dependence and the six-month experiment on within-stage survivorship) suggest considerable variation even between controlled experiments. We therefore expect that there is considerable (and as yet unknown) spatial and temporal variability in survivorship parameters, beyond the parametric variation we have already accounted for.

EFFECTS OF EXPLOITATION.—We explored the effects of three forms of exploitation rules—fixed collection rate, fixed escapement, and rotating closure—and we considered varying levels of effort or collection restriction for each exploitation rule. For each exploitation rule, we examined the equilibrium yield and the recruitment rate of juveniles into the adult population (as measures of long-term, large-scale sustainability), as well as the fluctuations around these values for exploitation rates ranging from 0 to 100%. Equilibrium yield was defined as the long-term biweekly collection rate that resulted after the initial transients in the system died out.

1. *Fixed collection rate:* Under this rule, a constant proportion of the juveniles present on an anemone was collected after each 2-wk settlement pulse. [Exploitation parameter: 0 (no collection) to 1 (complete collection).]

2. *Fixed escapement:* A constant number of juveniles was allowed to remain on each anemone. If fewer than the minimum were present, none was collected during that time period. [Exploitation parameter: 0 (complete collection) to 20 (no collection, because observed juvenile densities were always less than 20).]

3. *Rotating closure:* All juveniles on each anemone were collected every *n* time steps. This form of exploitation restriction is (roughly) equivalent to a rotating-closure scheme in more traditional fisheries. [Exploitation parameter: 1 (complete collection at every time step) to 31 (collection once every 62 wks).]

We expected that, despite the openness of recruitment in this system, juvenile facilitation of larval settlement (e.g., Fig. 1B) would result in a dome-shaped yield curve as a function of exploitation rate. In contrast, in open systems where recruitment is independent of juvenile density, we expect yields always to increase with exploitation rate. Subsequent analysis of a simple continuous-time version of our model, without pulsed recruitment, shows that facilitation of settlement by juveniles is balanced by the additional mortality in the settler class caused by higher juvenile densities. Facilitation is necessary but not sufficient to cause dome-shaped yield curves; the specific criteria involve the shape of the mortality function with respect to both juvenile and settler density as well as the shape of the facilitation function.

Contrary to our initial expectations, we did not find an intermediate optimum in exploitation rates for any of the three exploitation strategies, for the best-fit parameters with variable larval settlement (Fig. 3). Our simulations suggest that increasing collection effort generally increases yield. In this open system, individual collectors can afford to collect all individuals as they mature without reducing recruitment to their lease sites, because new pulses continually bring in new larvae. Of course, the complete failure of settlers to recruit to the adult population under this exploitation strategy causes obvious and severe management problems at a larger scale, as we discuss below.
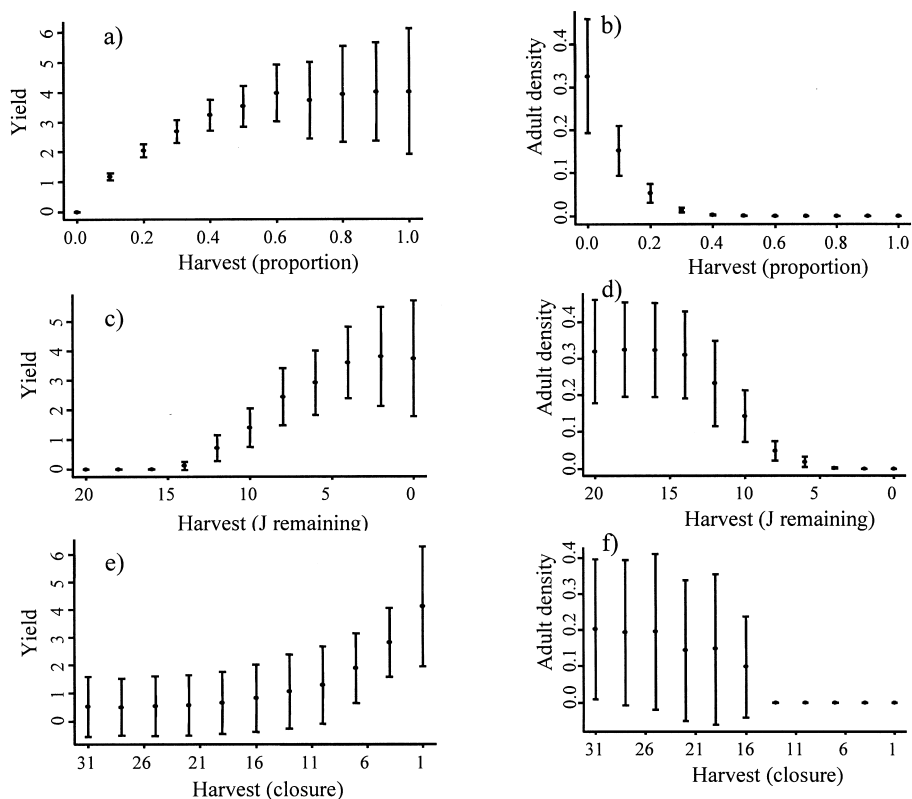
Figure 3. Variation in average yield per anemone (based on the exploitation of 20 anemones) and equilibrium rate of new adult recruitment (per 0.05 m²) as a function of exploitation rate and exploitation rule. Simulations are based on the best-fit parameters with variable larval settlement. Points show time-averaged yield for 200 weekly collections (after a 50-wk transient period), error bars show ± 1 SD over this period. In all cases the horizontal axes run from minimal to maximal exploitation rate; because the exploitation rate is inversely proportional to the exploitation parameter for the fixed-escapement and rotating-closure rules (minimum number left on the anemone and number of weeks in the closure cycle, respectively), these axes run from high to low exploitation rates. A. Yield, fixed exploitation rate. B. Adult recruitment, fixed exploitation rate. C. Yield, fixed escapement. D. Adult recruitment, fixed escapement. E. Yield, rotating closure. F. Adult recruitment, rotating closure.

In some cases (e.g., fixed collection rate with exploitation above 50% or rotating closures with exploitation more frequent than every third pulse; Fig. 3), variability in yield continues to increase even after average yields have more or less reached a plateau. Therefore, a risk-averse collector, one who preferred slightly lower but more constant yields, would choose lower exploitation rates. Unfortunately from the perspective of larger-scale management, small reductions in exploitation rate are insufficient to maintain an adult population. For example, if all anemones are exposed to 40% juvenile collection at every pulse (the level at which yield starts to plateau, Fig. 3A), the number of juveniles that will survive 13 successive collections and recruit to the adult class is negligible (Fig. 3B).

The scenarios presented in Figure 3 ignore uncertainty in parameter estimates, and changes in parameters may greatly influence the exploitation strategy: e.g., for some parameter combinations, the yield-exploitation rate relationship may indeed show the
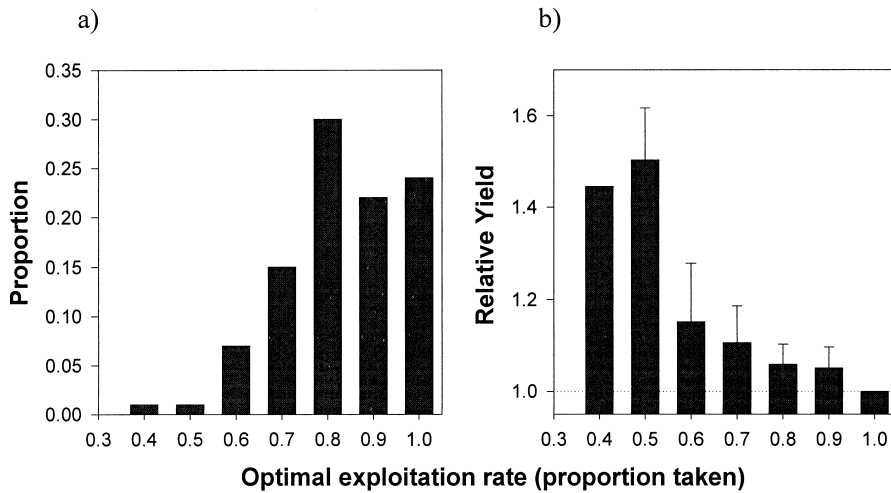
a)   b)

Figure 4. Variation in optimal exploitation rate and relative yield with parameter variation. A. The frequency distribution of optimal exploitation rates (assuming a fixed exploitation strategy) for 150 runs with between-anemone and temporal variation in settlement (as in Fig. 3), each with a different randomly selected set of parameters. B. Relative yield as a function of the optimal exploitation for the same runs. Relative yield is defined as the ratio of the yield at the optimal exploitation rate to the yield at 100% exploitation (e.g., the relative yield = 1.0 when the optimal exploitation rate is 1.0).

expected unimodal shape. Although the best-fit parameters suggest that collectors should always collect at the maximum rate, it is quite possible that intermediate collections are optimal for a broad range of plausible parameter values. We drew random sets of parameters from the multivariate normal sampling distribution. We then calculated the average equilibrium yield and adult recruitment rate for each set using the fixed-collection-rate model and determined the optimal exploitation intensity (the one that maximized average equilibrium yield). We also calculated the ratio of the optimal yield (that obtained at the optimal exploitation intensity) to the yield obtained at 100% exploitation (i.e., the relative yield, a measure of the advantage of collecting at an intermediate optimum as opposed to at the maximal rate).

Of the sets of parameters sampled, most parameter combinations (~75%) yielded an optimal exploitation rate that was less than the maximum (i.e., dome-shaped yield curves are common within the range of possible parameter values estimated from field data). The most common optimum yield occurred at 80% exploitation (Fig. 4A). The relative yield (optimal yield/yield at maximum exploitation) at the optimum was greatest when the optimum exploitation rate was lowest (Fig. 4B). When the optimum exploitation rate was near 50%, the relative yield was approximately 1.5, but high relative yields were very rare (Fig. 5); only 5% of all runs produced relative yields that were more than 1.2. Furthermore, for the majority of these cases, optimal exploitation rates were still high enough essentially to preclude maturation to the adult stage.

We explored why yield was not a strongly dome-shaped function of exploitation intensity by varying both the degree of facilitation (by increasing b, the initial slope of the resident-settlement relationship) and the strength of density dependence (by setting the density-dependent parameters β and/or β_{SJ} to zero) in the proportional exploitation model.
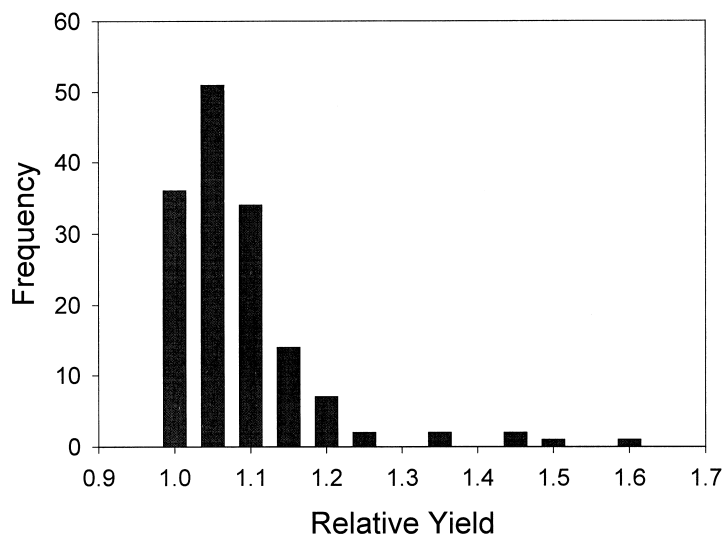
Figure 5. Variation in relative yield with parameter variation. The frequency distribution of relative yields (as defined in Fig. 4) for 150 random-parameter sampling runs.

We also explored the effects of removing variation in settlement. A complete examination of this issue is beyond the scope of the present paper, so we present a brief qualitative overview. Eliminating density dependence produced a small dome in the yield function. Increasing facilitation (even by large amounts) produced little, if any, effect on the yield function, in the presence of density dependence of the strength that is naturally observed in *D. trimaculatus*. Increased facilitation in the absence of density dependence produced a clear intermediate optimal exploitation rate, demonstrating a strong interaction between these processes. Increased facilitation appears to have little effect in the presence of density dependence because the increased settlement is damped out by enhanced mortality. Surprisingly, eliminating variability in larval settlement also produced intermediate exploitation optima (exploitation rate ~60%, fixed exploitation), with a relative yield on the order of 1.2. We are uncertain of the cause of the disparity between the results with constant and those with variable settlement but suppose it involves Jensen's inequality (Ruel and Ayres, 1999).

DISCUSSION

Our goals in the present paper were to begin to explore two fundamental aspects of fisheries management—sources and consequences of uncertainty and the effects of alternative exploitation rules, as they pertain to marine ornamentals. In particular, we were interested in the role of settlement facilitation in creating local collection optima that would encourage individual exploitation restraint and therefore, potentially, lead to regional sustainability. For example, facilitation by juveniles, or preference of collectors for temporally constant yields, might lead to optimal exploitation rates (at the local scale) that were lower than the maximal rate. In that case, it would be in collectors' financial interest to exercise restraint in exploitation, and if optimal rates were low enough, older juveniles would survive to adulthood. This expected pattern of increasing and then de-

creasing yields with increasing effort superficially resembles the basic results from large-scale, closed systems to which MSY-based management strategies have been applied. Although MSY strategies have been criticized because of the instability introduced by uncertainty, among other things, they do suggest that intermediate exploitation rates produce optimal yields. Beyond this superficial similarity, however, we expected that the fundamental differences in the underlying mechanisms would lead to significant differences between the stability and sensitivity of MSY in large-scale closed systems and in small-scale systems. Unfortunately, although we have found intermediate exploitation optima for some parameter estimates, the associated reductions in exploitation were small and rarely (if ever) allowed juveniles to survive to adulthood. Therefore, the facilitation found in this system, at least when combined with the observed density-dependent mortality, does not alleviate the larger-scale danger of overexploitation.

Facilitation did not have the large beneficial effect we expected because density dependence and variability in larval settlement combined to flatten the unimodal curve of yield as a function of exploitation. Although the simulation model allowed us to discover and briefly explore this phenomenon, we do not fully understand it. In the future, we plan to compare the results of the full model with cruder but more tractable differential-equation models that use well-established linearization techniques to approximate the effects of variability on dynamical systems (Nisbet and Gurney, 1982; Hilborn and Mangel, 1997).

The complete suppression of facilitation effects by density dependence and settlement variation is unlikely to apply to all reef fisheries. The strength of density dependence and facilitation and the degree of variation in larval supply will all vary among species, and the interaction among these parameters appears to have a dramatic effect on the optimal exploitation strategy. Species that have a different balance between density-dependent mortality effects within or between stages, settlement facilitation or suppression, and variability in settlement may still show the patterns we expected. We do not yet have enough data on the range of parameters found in reef ornamental systems to rule out the possibility of stable exploitation strategies at optimal rates. Collector interests and larger-scale management objectives may indeed coincide for some systems, allowing management to arise from internal controls rather than external regulation.

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