A quantitative framework to evaluate the attraction–production controversy

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Osenberg, C. W., St. Mary, C. M., Wilson, J. A., and Lindberg, W. J. 2002. A quantitative framework to evaluate the attraction–production controversy. – ICES Journal of Marine Science, 59: 000–000.

Artificial reefs have been proposed as a tool to mitigate impacts on natural reefs, augment natural fish production, and divert detrimental harvesting activities from sensitive natural habitats. The efficacy of this strategy depends on the extent to which artificial reefs contribute to new production or simply redistribute fish during or after settlement. Small coral reef fishes are ideal study subjects because redistribution is most likely during the larval stage, given limited dispersal of benthic stages. We develop a model that incorporates the simultaneous effects of habitat augmentation, competition among reefs for larval settlers, and post-settlement density-dependence, and propose two experimental approaches for evaluating the effects of artificial reefs on local production of natural reefs. One is based on small-scale studies using replicated patch reefs, the other on unreplicated studies using larger reefs and the Before-After-Control-Impact Paired Series (BACIPS) design. Using field data for six fish species, we estimated spatial and temporal variance and thus statistical power of both designs. Power varied among species, but in most cases was sufficiently high to detect local reductions in density of 10–40% with modest levels of replication (6–20 patch reefs or sampling dates).

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Keywords: artificial reefs, BACIPS (Before-After-Control-Impact Paired Series) design, density-dependence, marine ornamentals, reef fish, settlement, statistical power.

Received ??; accepted 14 December 2001.

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Introduction

Artificial reefs may harbour high densities of fish and often resemble natural reefs (e.g. Bohnsack and Sutherland, 1985; Bortone *et al.*, 1994; Tupper and Hunte, 1998). Therefore, they might represent an effective management tool for increasing fish productivity while also redirecting harmful human activities away from sensitive, natural reefs (Ambrose, 1994; Beets and Hixon, 1994; Sosa-Cordero *et al.*, 1998). Despite considerable effort, however, we still lack the scientific data necessary to evaluate this conjecture (Seaman, 1997; Lindberg, 1997; Wilson *et al.*, 2001).

The uncertainty surrounding the value of artificial reefs as a fisheries management tool has arisen for at least four reasons. First, marine systems are notoriously variable and fish dynamics are affected by many factors. This has often led to debates about which factor (of the many) drives variation in fish abundance (Doherty and Fowler, 1994; Caley *et al.*, 1996). Instead of continued debate, we need a more pluralistic approach that recognizes the simultaneous influence of multiple processes, quantifies their relative importance, and delineates the conditions under which different results may be obtained (Schmitt *et al.*, 1999; Walters and Korman, 1999). Second, many artificial reefs have been deployed without any predefined scientific programme to study their effects (but see Lindberg and Loftin, 1998). As a result, studies are often post-hoc and offer only limited insights. Third, many investigations conducted so far have focused almost exclusively on the artificial reefs (e.g. their construction and attributes of the associated

fishes), rather than on how nearby natural reefs may have been affected (Bohnsack *et al.*, 1994; Caley and St. John, 1996; Tupper and Hunte, 1998). Finally, it has been argued that artificial reefs may not be the cure-all, nor the production tool, that advocates envision. Instead, they may simply affect distribution, by attracting fish from natural reefs and concentrating them upon artificial ones. If artificial reefs also attract anglers, the fishing industry, or other predators, then mortality rates may increase and actually cause long-term net declines in fish stocks (Samples and Sproul, 1985; Bohnsack, 1989). If true, then resources currently spent on artificial reef programme may be misdirected, if not harmful, to natural reef systems.

Here we develop an explicit conceptual approach to evaluate the attraction–production controversy. We present a mathematical model to explore the effects of multiple processes on reef fish dynamics, and propose two empirical study designs to quantify the effects of artificial reefs, and thus test the attraction and production hypotheses. We evaluate the feasibility of these designs by conducting statistical power analyses based on field estimates of spatial and temporal variability in reef fish density. In developing this framework, we refer to marine ornamentals, small, typically tropical, fishes that are harvested for the aquarium trade. Focus on these species may facilitate the development of a more cogent conceptual framework and the resolution of the attraction–production debate because they are site-attached and distances moved by post-settlers may be on the order of metres or tens of metres, instead of kilometres or hundreds of kilometres. Thus, artificial reefs are most likely to attract these small fish through settlement-redirection rather than migration of older life stages. In addition, there is a wealth of observational and experimental data on the ecology and dynamics of small reef fishes.

Conceptual approach

The attraction–production controversy and the importance of density-dependence have played central roles in the debate about the efficacy of artificial reefs (Bohnsack, 1989; Lindberg, 1997). The basic problem is often viewed as two mutually exclusive scenarios. Artificial reefs either increase production (e.g. because they provide new habitat in an otherwise saturated benthic environment) or they simply redistribute fish biomass without augmenting production (i.e. the artificial reef attracts fishes, but these fishes would have settled, survived, and grown at comparable rates on natural habitats in its absence).

Much of this debate is tied up in the parallel debate about the role of larval supply versus density-dependence in driving fish dynamics in general (Hixon, 1998; Tupper and Hunte, 1998; Schmitt *et al.*, 1999). There is little value in arguing about whether artificial reefs attract versus produce fish biomass – they probably do both (Bohnsack, 1989; Lindberg, 1997; Pickering and Whitmarsh, 1997). For example, attraction and production probably interact (via density-dependence) to drive the dynamics of an artificial-natural reef complex (Wilson *et al.*, 2001). The immediate effect of attraction is to reduce the density of settlers or benthic juveniles and adults on natural reefs. Reduced density could easily lead to greater settlement or greater per capita rates of production (via increased growth, survival, or reproduction). The strength of density-dependence will determine how much the production of the natural reef sub-population compensates following the redirection of fish to the artificial habitat (Wilson *et al.*, 2001). Thus, the challenge lies in devising an effective, and pluralistic, conceptual framework that allows us to quantify the net production of a system, partition that production to the respective habitats (natural and artificial), and evaluate how much harvesting the aggregate system can likely sustain.

Consider a natural reef characterized by some amount of fish production. Now assume that an artificial reef set is deployed near enough to potentially influence the biota associated with the natural reef, and we measure the reef-wide production on both. Further imagine that the artificial reef could vary in size. The attraction-only versus production-only hypotheses make divergent predictions about the response of these systems (Figure 1; cf. Bohnsack, 1989). If the artificial reef only attracts fishes (either by redirecting settlement or by attracting previously settled fish), is of comparable quality, and there is no density-dependence, then the production associated with the natural reef will decline as the size of the artificial reef increases. The net effect on the total production associated with both reefs will be negligible. If the artificial reef is of lower quality (supports an inherently lower aerial production rate) than the natural reef, then the maximum production associated with the artificial reef will always be less than the maximum on the natural reef. Consequently, total production will decline as the area of the artificial reef increases. If the artificial reef is of higher quality, then the total production will increase with area.

Under the production hypothesis, the natural reef will be unaffected by the artificial reef. The production associated with the artificial reef, however, will increase as its area increases and it "captures" larvae from the water column that never would have settled or recruited otherwise (Polovina and Sakai, 1989). This assumes that the population is limited by available habitat. The net effect is an ever-increasing total production.

These two scenarios represent extremes, with most real systems probably lying in between. Importantly,
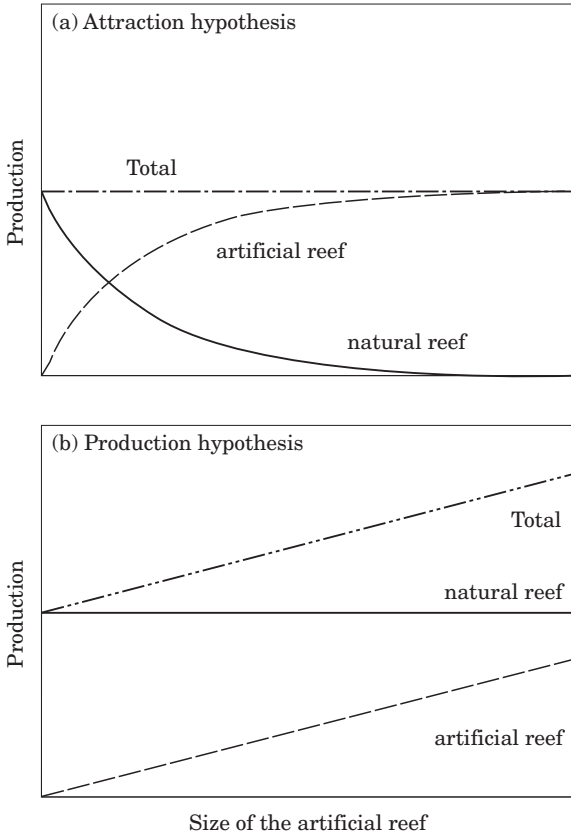
Figure 1. Schematic representation of the relationship between reef fish production and the size of an artificial reef as envisioned by (a) the attraction hypothesis and (b) the production hypothesis.

both scenarios require modification to be more pluralistic. For example, the production hypothesis assumes that larvae are not limiting, but habitat is. As a result the production curve increases without bound. However, multiple processes can simultaneously limit fish production (Chesson, 1998; Hixon, 1998; Schmitt *et al.*, 1999), and real systems may be limited both by habitat and larval supply. Similarly, the attraction hypothesis ignores effects of density-dependence. Instead of there being one possible production curve for the natural reef, there are many, depending on the strength (and form) of density-dependence.

The essential questions to be addressed are: (1) how is the natural reef ecosystem affected by the deployment of artificial reefs (largely the attraction side of the problem coupled with effects of density-dependence), and (2) how much production arises from the artificial reef (which may either compensate for reductions on natural habitat or represent entirely new production). The latter issue has been the focus of most studies comparing natural versus artificial reefs or various designs among artificial reefs (Bohnsack *et al.*, 1994; Bortone *et al.*, 1994; Chua

and Chou, 1994; Carr and Hixon, 1997). In effect, these studies often address the question of how well the artificial reef mimics a natural reef, rather than the attraction–production issue. Instead, the kind of study required is similar to a field assessment of an environmental impact, where the impact is the deployment of artificial reefs.

A population dynamics model

In developing a mathematical model that provides an explicit framework for the interactions among important processes affecting reef populations (settlement, density dependence, and competition among habitats for settlers via redirection), we make the following assumptions: (1) larval supply to a local site is independent of local larval production; (2) once settled, fish do not move between natural and artificial reefs; (3) the life history is split in three phases – larval, benthic juvenile, and benthic adult; (4) for simplicity, density-dependence acts only during the juvenile stage; and (5) density-dependence takes the form of a modified Beverton–Holt function, as indicated by experimental studies of reef fishes (Steele, 1997; Schmitt *et al.*, 1999; Shima, 1999). These assumptions lead to the following model:

$$A_{R,t+1} = (1-\mu)A_{R,t} + aS_R/[1+aS_R/(p_R b - (1-\mu)A_{R,t})] \quad (1)$$

where A_R is the abundance of adults on reef type R (indexed as nat for natural or art for artificial reef), μ is the natural mortality rate of adults (assumed similar between the two reef types, although this can easily be modified to reflect differences in harvesting rates, for example), S_R is the abundance of settlers, a is the density-independent mortality of benthic juveniles (i.e. the fraction that survive from settlement to maturation in the absence of density dependence), b is the maximum population density that can be supported (and controls the strength of density-dependence), and p_R is the absolute reef area. Thus, the two terms represent the survival of adults and the recruitment of previously settled larval into the adult stage. The recruitment function is density-dependent, with the maximum recruitment being constrained by the number of surviving adults. We further assume that the natural reef has an area of 1 ($p_{nat}=1$), and look at the effects of varying the area of the artificial reef ($p_{art}=p$). The total abundance of fish on a reef complex is just the sum of the abundances on the two reef types:

$$A_{tot,t} = A_{nat,t} + A_{art,t} \quad (2)$$

Note that attraction, or competition between natural and artificial reefs for fish, is restricted to the larval

stage. For example, a competent larval fish that encounters an artificial reef and settles is not available to settle elsewhere. We assume that the total number of settlers (S_{tot}) is allocated to the two habitats in proportion to their respective areas (i.e. 1 and p). Thus,

$$S_{nat} = S_{tot}/(1+p) \text{ and } S_{art} = S_{tot} \cdot p/(1+p). \quad (3)$$

Total settlement is modelled in two different ways. The simplest, derived from the attraction hypothesis, is that the total number of settlers is constant and unaffected by the artificial reef or its size. In a more realistic scenario, larger reef complexes receive more settlement because they intercept a greater fraction of the larval pool, and that depletion of the larval pool leads to lower settlement at down-current sites. In the absence of a detailed understanding of these processes, we take a simple approach and assume that total settlement can be approximated by a situation in which there is unidirectional flow over a square combined reef area (1+p). In this case, total settlement can be shown to be:

$$S_{tot} = L \, (1 - e^{-c\sqrt{(1+p)}}) \cdot \sqrt{(1+p)} \quad (4)$$

where L is the larval concentration in the water column (before any depletion) and c is the settlement rate (given occurrence above suitable substrate). Total settlement is then partitioned between the reefs in proportion to their relative areas using (3): i.e. all reef habitat is influenced to the same degree by depletion of larvae that have settled to other portions of the reef complex. This simple model displays plausible behaviour, with settlement increasing with larval concentration and settlement rate, and settlement increasing with reef area but at a decelerating rate.

We then solve (1) at equilibrium. The resulting quadratic has two possible solutions, both of which are positive, but only the smaller of which is biologically plausible. That solution yields equilibrium adult population sizes for each reef type:

$$A_R^* = \{ -\mu b p_R - a S_R + [(\mu b p_R + a S_R)^2 + 4 a S_R b p_R \mu \cdot (\mu - 1)]^{0.5} \} / [2\mu \cdot (\mu - 1)] \quad (5)$$

Simulations show that the equilibrium is stable, owing both to the openness of the system (Warner and Hughes, 1988) and to the density-dependence incorporated in the Beverton–Holt recruitment function (Getz and Haight, 1989). Equation (5) combined with (3) can be used to examine the effects of artificial reefs on the two subpopulations (A_{nat} and A_{art}) and on the total local population ($A_{nat} + A_{art}$). To the extent that local larval production is proportional to adult abundance, these solutions also provide estimates of the local export of larvae to the regional system.
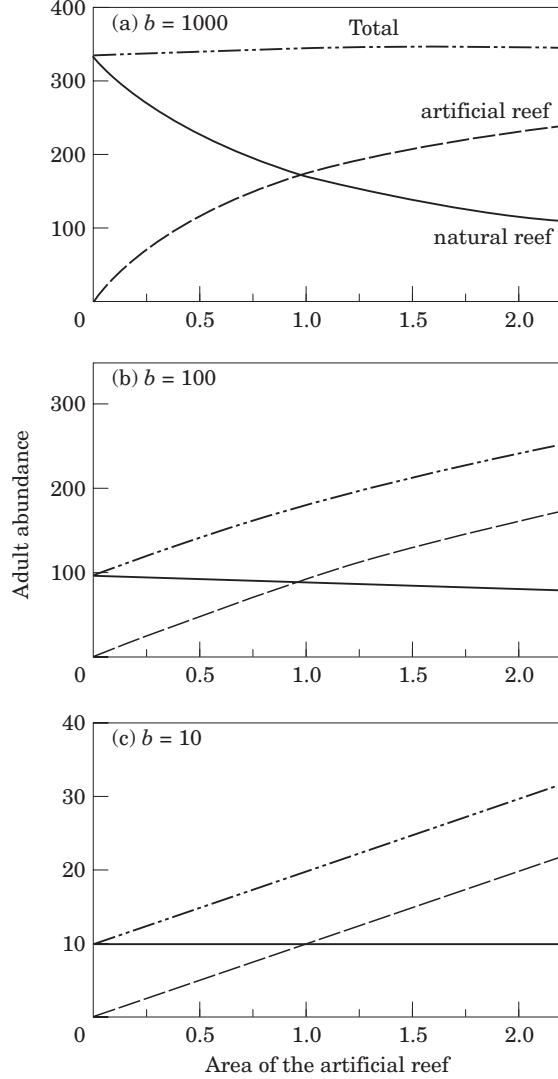

Figure 2. The relationship between artificial reef size and fish abundance on artificial and natural reefs predicted from the model ($S_{total} = 50$, $a = 0.7$, and $\mu = 0.1$) assuming settlement is constant for (a) weak density dependence, (b) moderate density dependence, and (c) strong density dependence.

Several factors strongly affect the equilibrium abundances predicted by the model, with the general pattern influenced by the relative strength of larval limitation versus habitat limitation (i.e. density-dependence) and the degree of competition among reefs for larvae. First, consider the case when S_{tot} is held constant. If density-dependence is weak (i.e. b is large), then there is little potential for new production (Figure 2a). As density-dependence is increased (b is reduced), total production increases with artificial reef size even though settlement is held constant (Figure 2a–c). The redirection of larvae leads to competitive release on the natural reef, which
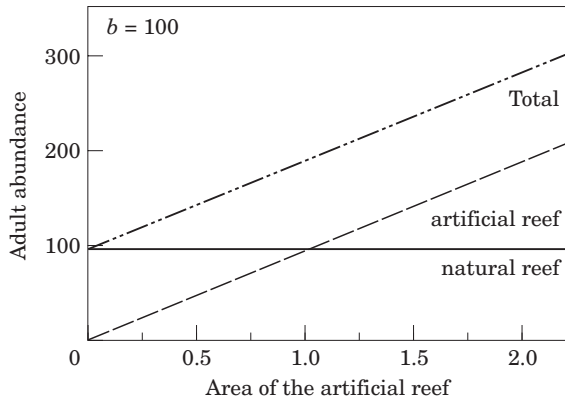
Figure 3. The relationship between artificial reef size and fish abundance on artificial and natural reefs predicted from the model assuming variable settlement (S_{total} modelled as in (4); $b=100$, $a=0.7$, and $\mu=0.1$, $L=100$, and $c=0.5$).

can be sufficiently strong to prevent declines in adult abundance even though fewer larvae settle locally. Thus, even when attraction is strong, we can obtain a pattern identical to the production scenario (Figure 1b). The full spectrum of the attraction–production dichotomy can be obtained simply by changing the strength of density-dependence.

This "redirection" scenario (with larval settlement held constant) is rather extreme, however. If instead, we use (4), then the effect of the artificial reef on the natural reef is lessened, and the entire complex attracts more settlers than the natural reef alone. Thus, more new production is expected, and the attraction–production continuum can also be recreated by keeping density-dependence constant, but varying the way in which reefs compete for larvae (Figure 3). Thus, the attraction–production dichotomy represents end-points of a continuum that can be recreated by varying either density-dependence or competition for larvae among reefs. Increasing settlement intensity by increasing larval concentration (L) or settlement rate (c) in (4) should change these relationships in much the same way as does increasing density-dependence.

Empirical approaches

This framework suggests a new way to evaluate the attraction–production controversy: by comparing natural reefs influenced by nearby artificial reefs with natural reefs that are similar but lack nearby artificial reefs (Alevizon and Gorham, 1989). The reason for examining artificial reefs stems not from their own inherent productivity, but from what can be learned by comparison with associated natural reefs: to what extent does the presence of an artificial reef compensate for production lost from nearby natural reefs? We know of no study

that has quantitatively compared production (or fish abundance) of replicate natural reefs with and without nearby artificial reefs and partitioned the total production between them. This is critical to quantitative evaluation of the attraction–production issue, and requires a specific and novel type of field study.

The simplest approach would be to conduct an experiment with two treatments: (1) natural reefs and (2) natural reefs with "adjacent" artificial reefs. More complex designs might involve varying the size of the artificial reefs or their proximity to a natural reef, but for simplicity we ignore these options. There are two basic designs for conducting this type of study: (1) a standard, replicated experiment; or (2) an unreplicated assessment. These two approaches would be likely to differ in spatial scale.

The response variables measured should be settlement, survival, growth, and movement of biota on both reef types. Together, these variables contribute to production. However, because, in the model presented here, density-dependence affects survival and attraction arises via settlement redirection (both of which affect abundance), we will continue to use fish abundance as a surrogate of production.

Replicated field experiments

By necessity, a replicated experimental study would occur on a limited spatial scale, with natural and artificial reefs probably on the order of several to tens of square metres in area (Carr and Hixon, 1997; Shima, 1999; Wilson and Osenberg, 2001). The design would rely on classic components such as replication, controls, and random assignment of treatments. Half of the natural reefs would receive artificial reefs in their vicinity, whereas the other half would be controls. The number of replicate reefs and the spatial variation among replicate reefs limits the power of such designs.

Unreplicated assessments

Many artificial reef projects involve a single, large reef structure. Because these reefs are not replicated and placement is not selected at random among candidate sites, a different approach is required. The constraints of this situation are identical to those faced in most assessments of environmental impacts. We therefore propose the application of the Before-After-Control-Impact Paired Series (BACIPS) assessment design (Stewart-Oaten *et al.*, 1986; Schmitt and Osenberg, 1996).

In a BACIPS design, at least two natural reefs are required, a Control site and an Impact site. Both sites need to be sampled at least several times prior to deployment of the artificial reef at the Impact site.

Each sampling date provides an estimate of the spatial difference between sites. After deployment, simultaneous sampling continues, yielding a time series of differences from the Before and After periods. These two time-series are then compared statistically to assess whether there has been an impact and to estimate the magnitude of the effect (Stewart-Oaten *et al.*, 1986; Stewart-Oaten, 1996a). It is important that samples be sufficiently dispersed in time so that the time-series of differences exhibits little serial correlation (Stewart-Oaten *et al.*, 1986; Osenberg *et al.*, 1994). In a BACIPS design, the number of sampling dates and the variance of the differences through time limit statistical power.

Statistical power

The two experimental designs will not help resolve underlying controversy unless they provide sufficiently precise estimates of the effects. Because fish densities exhibit considerable spatial and temporal variability, the level of replication or sampling intensity needed to achieve high statistical power may be prohibitive. Statistical power is the probability that the null hypothesis of no effect will be rejected when it is, in fact, false. Although the utility of null hypothesis tests has been questioned and arguments in favour of estimation put forward (Stewart-Oaten, 1996b; Osenberg *et al.*, 1999), power can also be related to the size of a confidence interval associated with an estimate of a treatment effect.

Power (equal to $1 - \beta$, where β is the Type II error rate) is a function of sample size, variance among replicates, the Type I error rate (α), and the effect size (i.e. the true difference between the two groups being compared). We set $\alpha = 0.05$, $\beta = 0.25$, and defined effect size as the percentage reduction in density on natural reefs with artificial reefs compared to natural reefs without associated artificial reefs. We then used power tables from Gill (1978) to show the relationship between effect size, variance, and sample size (Figure 4). Variances were based on $\log_{10}$ transformed density estimates, as often recommended in BACIPS studies. This has the advantage of putting different variables in a common currency (variance of logs yields a measure of variability on a relative, or percentage, basis).

The nature of variance and replicates depends on design. In the classic experimental design, the variance of interest is the spatial variation at a point in time among replicate reefs, and sample size is the total number of natural patch reefs (combined across both treatment groups). A BACIPS design focuses on the variance in the differences between the two study sites over time and the total number of sampling dates in the Before and After periods (Osenberg *et al.*, 1994).
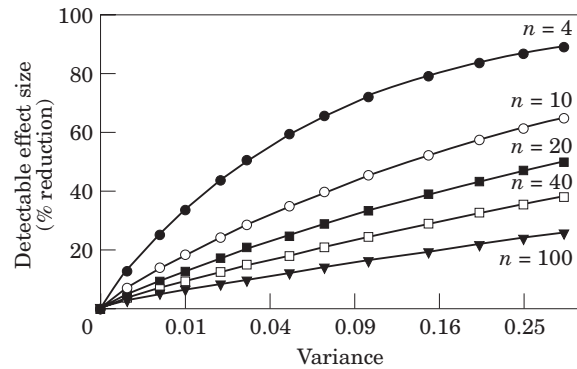

Figure 4. Detectable effect size given a fixed level of spatial and/or temporal variance (axis square-root transformed) for sample sizes of 4, 10, 20, 40, and 100 (number of reefs in a replicated experiment or number of sampling dates in a BACIPS design).

Variation estimated from field studies

Estimates of fish density and settlement were available from five studies of seven small reef-associated fishes collected in the marine ornamental industry: *Parablennius marmoreus* (Poey, 1876), *Serranus subligarius* (Cope, 1870), *Dascyllus trimaculatus* (Rüppell, 1829), *Gobiosoma prochilos* (Böhlke and Robins, 1968), *G. evelynae* (Böhlke and Robins, 1968), *Thalassoma bifasciatum* (Bloch, 1791), and *Thalassoma hardwicke* (Bennett, 1828). In four studies, the data were from natural reefs, whereas Lindberg and Loftin (1998) studied artificial reefs constructed of concrete cubes. All studies provided estimates of spatial as well as temporal variance. For two species, sampling was conducted at two spatial scales. In most cases, multiple estimates of variance were available. We report the average of these estimates (after discarding variances based on small sample sizes). For some fish with specific settlement requirements, density could be expressed as both number per reef area and number per area of settlement habitat. For all analyses, densities were $\log_{10}$ transformed before estimating variance. These analyses are intended as crude guides to the feasibility of conducting the proposed field studies, and therefore detailed descriptions of the analyses are not provided.

Spatial and temporal variances were of similar magnitude, with means variances within studies ranging from 0.01 to 0.30 (Table 1). Interestingly, expressing densities per unit of preferred substrate (e.g. live coral for *Gobiosoma* or anemones for *Dascyllus*) reduced spatial variance by $\sim 50\%$ compared to densities expressed per total area. Spatial variation within a species did not show a consistent relationship as the spatial scale increased. Data were available for both settlers and older age classes, although variances did not vary consistently between these groups. Across all

Table 1. Estimates of spatial (RA: per unit reef area; PS: per unit of preferred substrate) and temporal variance in fish density (after $\log_{10}$ transformation), as well as typical distances between sampling sites (SS), for different life stages (S: settlers; J: juveniles; A: adults) of ornamental fish species (n.a.: not available; data sources: C+W – Caselle and Warner, 1996; L+L – Lindberg and Loftin, 1998; S+H – Schmitt and Holbrook, 1999; S – Shima, 1999; W+O – Wilson and Osenberg, 2001).

Species and source	Life stage	Spatial V		Temporal V	SS (km)[a]
		RA	PS		
Dascyllus trimaculatus (S+H)	J+A	0.19	0.10	0.04	0.1; 1–10
Gobiosoma prochilos and *G. evelynae*, pooled					
(W+O)	J+A	0.07	0.03	0.09	0.1
	S	0.04	0.02	0.04	0.1
Parablennius marmoreus (L+L)	J+A	0.08	n.a.	0.06	0.2; 4–28
Serranus subligarius (L+L)	J+A	0.06	n.a.	0.09	0.2; 4–28
Thalassoma bifasciatum (C+W)	S[b]	0.14	n.a.	n.a.	0.1
	S[c]	0.30	n.a.	0.17	10
Thalassoma hardwicke (S)	S[b]	0.08	n.a.	n.a.	0.004–0.1
	S[c]	0.01	n.a.	0.09	3–7

[a]If scales differ for spatial and temporal variance, two values are given, respectively.
[b]Within site variance.
[c]Among-site variance.

species and scales, variance averaged approximately 0.09. Excluding *T. bifasciatum*, the most variable species, reduces this average by ∼25%.

Most species exhibited variances between approximately 0.03 and 0.09, indicating that effects on the order of 20–40% could be detected with total sample sizes of between 10 and 20 reefs, equally divided between experimental and control sites, or sampling dates equally divided between Before and After (Figure 4). For *Gobiosoma* or *T. hardwicke*, effects as small as 10–20% might be detected using such modest sampling effort. Effects on the order of 50% should require even lower samples sizes of 4–8 reefs or dates. These results suggest that the proposed field studies are not only feasible, but have a high likelihood of documenting biologically significant reductions in fish density on natural reefs (or increases on artificial-natural reef complexes) if they exist.

Conclusion

Controversy surrounding the attraction and production hypotheses will not be resolved without integrative approaches that recognize the effects of several processes and employ a variety of techniques and new conceptual approaches. Historically, the two hypotheses have been seen as two distinct options, rather than end-points on a continuum. Where a particular system lies along the continuum will depend on several factors, including reef sizes, their proximity, the strength of density-dependence, rate of larval supply, and the extent to which the artificial reef and natural reefs compete for larvae. Mathematical models can be instructive by making clear underlying assumptions, and highlighting interactions between these factors. New empirical approaches can complement these models by providing field tests designed to quantify the effects of artificial reefs on local production. The results of these studies should lead to more informed decisions regarding the use of artificial reefs in environmental management.

Acknowledgements

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