

# Artificial reefs, the attraction-production issue, and density dependence in marine ornamental fishes

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## ABSTRACT

Artificial reefs may provide a useful tool to enhance production of marine ornamentals and to divert detrimental harvesting activities from sensitive natural habitat. The efficacy of this strategy depends, in part, on the extent to which artificial reefs contribute to new production (vs. attract fishes from natural habitat) and therefore benefit harvested populations on a local and regional basis. Here the attraction and production hypotheses and their application to marine ornamentals are presented. Specifically, it is discussed how the strength and timing of density dependence can affect the response of fish population dynamics to artificial reefs. In addition to this discussion, examples of density dependence in marine ornamentals and related reef fishes are provided. Based on this information, a simple conceptual model is presented to clarify the role of density dependence, and this is followed by a discussion on the use of artificial reefs in the management and production of marine ornamentals. Finally, unresolved scientific issues that remain to be addressed are provided.

## INTRODUCTION

The vast majority of marine ornamental fishes sold in the aquarium trade are collected from their natural habitats. Concerns have been raised about the environmental impacts of these wild collections because harvesting may reduce the density of marine ornamentals (via harvesting) and degrade habitat quality (via destructive collecting methods: Jones and Steven, 1997; Jones and Hoegh-Guldberg, 1999). One solution that would greatly reduce the environmental effects of the industry is to increase the use of aquaculture and thus reduce the need for field collections. Although this may be feasible for some species of fishes (e.g., anemone fish in the genus *Amphiprion*, Bloch and Schneider, 1801), the majority (~98%) of all species sold in the aquarium trade cannot yet be produced in aquaculture (Martin Moe of Green Turtle Publications, personal communication). As a result, harvesting of ornamentals from the wild will be required to sustain the marine ornamental industry, at least for the foreseeable future. Therefore, alternative harvesting and management approaches that can facilitate environmentally sound and sustainable exploitation of these marine resources are needed.

One such scenario involves the use of artificial reefs. Artificial reefs are often viewed as a fruitful way to not only increase fish production, but to also redirect harmful human activities away from sensitive, natural reefs (Ambrose, 1994; Beets and Hixon, 1994; Sosa-Cordero *et al.*, 1998; Wilhelmsson *et al.*, 1998). Although the use of artificial reefs is typically focused on commercial and recreational food fishes, they may also prove to be a useful, and as yet unexplored, tool in the management and augmentation of the marine ornamental industry. One vision (spearheaded by Craig A. Watson and the Tropical Aquaculture Laboratory, Ruskin, Florida) is to use specially designed artificial reefs to help facilitate the collection and production of marine ornamentals. For example, companies could lease nearshore areas from a state and then deploy artificial reefs. They could then collect fishes from these artificial reefs rather than from nearby natural reefs, which could be protected from harvesting. This is similar to the way in which 'live-rock' is now produced in Florida (Frakes and Watts, 1995). However, before such a tool can be confidently embraced and successfully implemented, the ways in which artificial reefs can influence natural reef systems need to be evaluated more explicitly (Osenberg *et al.*, 2001).

Artificial reefs have not been discussed previously in the context of enhancing marine ornamentals. They have, however, been discussed and used extensively for other food and recreational fisheries (Beets and Hixon, 1994; Bortone *et al.*, 1994; Chua and Chou, 1994), but even in these contexts, there remains considerable debate and uncertainty about their effectiveness. Before the use of artificial reefs can be embraced, they must be more closely evaluated. This evaluation must include a discussion that focuses on their effects on the population dynamics of natural fish stocks, a topic that received little attention at the Marine Ornamentals'99 Conference in Kona, Hawaii, and which gave rise to this collection of papers. The purpose of this paper is to discuss the conditions that influence the efficacy of artificial reefs as management tools for harvesting marine ornamentals and to introduce some fundamental scientific problems that must be addressed if artificial reefs are to be used as management tools in the future. Specifically, a simple conceptual model is proposed to address some of the controversy surrounding the use of artificial reefs as management tools. The paper concludes with a discussion of how an understanding of population dynamics and basic ecological processes, such as density dependence, can help to determine the net effect of artificial reefs on natural systems and the effect of harvesting on reef fish populations.

#### ATTRACTION VERSUS PRODUCTION

One of the central issues surrounding the effects of artificial reefs is the 'Attraction versus Production' debate (Bohnsack, 1989; Lindberg, 1997). This debate is most easily envisioned, and typically represented, as two opposing viewpoints. The Attraction Hypothesis predicts that artificial reefs simply redistribute fishes without augmenting production (Figure 1a). Although an artificial reef may have high

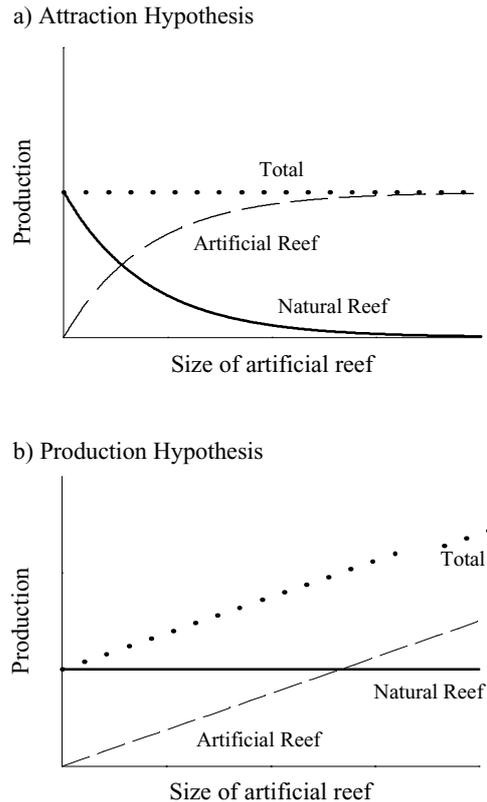


Figure 1. Graphical representation of (a) the Attraction Hypothesis (in which total fish production is constant), and (b) the Production Hypothesis (in which total fish production increases linearly with the addition of new habitat).

densities of fishes, it does so because those fishes have been attracted away from natural reefs. These fishes subsequently survive and grow at comparable rates on artificial reefs as they would have on natural reefs. If artificial reefs only attract fishes from other habitats, then as the size of the artificial reef increases, so will its associated 'production' because more fishes will be pulled from the surrounding natural reef habitat (Figure 1a). Conversely, the production associated with the natural reef habitat will decrease with artificial reef size as more fishes leave the natural habitat for the artificial reef. Therefore, although the spatial distribution of fish production changes, total production associated with the natural and artificial reef complex remains constant.

Fishes can be 'attracted' to artificial reefs at two different life stages – as larvae (via settlement redirection) or as older age classes (via migration). Settlement is the phenomenon when larval fishes leave the pelagic environment and settle to the reef environment (see Keough and Downes, 1982), and it delineates the pelagic

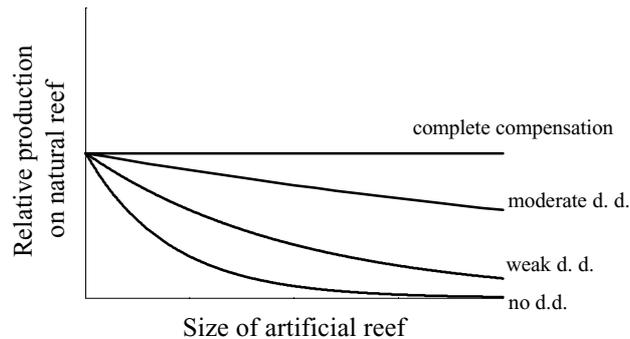
from the benthic life stage. Because marine ornamentals are relatively small and have high site fidelity, migration is likely to play a less important role than for larger reef-dwelling fishes, which can move considerable distances after settlement (but see Frederick, 1997). Therefore, settlement redirection will be concentrated upon, and it will be assumed that migration of settled individuals is relatively minor.

In contrast to the Attraction Hypothesis, the Production Hypothesis in this context predicts that artificial reefs increase fish production by providing new habitat to an otherwise saturated demersal environment. Thus, by providing new habitat in the form of artificial reefs, larvae that would have otherwise never recruited into older age-classes can instead settle and survive on the artificial reefs. Because the artificial reef only produces new fish biomass rather than redistributes it, the production associated with the artificial reefs will increase with increasing artificial reef size, but the production associated with the natural habitat will remain constant. Therefore, there will be a net increase in the production of the overall reef system (Figure 1b).

But what does this mean in terms of harvesting marine ornamentals? If artificial reefs function according to the Production Hypothesis, artificial reefs could be used to enhance the ornamental fishery as well as redirect potentially harmful collections away from natural reefs. As a result, artificial reefs could be embraced as a management tool without any significant detrimental effects to the dynamics of the harvested fishes. However, if artificial reefs function according to the Attraction Hypothesis and only redistribute fish biomass, then no new production is necessarily associated with artificial reefs, and they represent a dangerous management tool. In this case, deploying artificial reefs and attracting fishes away from the natural reef habitat and then targeting these reefs with heavy harvesting for the ornamental industry would likely cause a decline in the overall fishery stock (Samples and Sproul, 1985; Bohnsack, 1989). Thus, it is critical to understand how artificial reefs affect the reef system in order to evaluate their use in management. Unfortunately, there is little data with which to evaluate these hypotheses (Lindberg, 1997; Seaman, 1997), in part because appropriate study designs have not been embraced (Osenberg *et al.*, 2001). Furthermore, artificial reefs probably both produce and attract fish biomass – it is not useful to think of this as an ‘either/or’ issue.

#### EFFECT OF DENSITY DEPENDENCE ON THE RESPONSE OF NATURAL REEFS TO ARTIFICIAL REEFS

Instead of taking a dichotomous approach, as often exemplified by the Attraction–Production debate, an effective conceptual framework is needed. This framework will allow for the quantification of the net production of a system, the partitioning of that production to natural and artificial reef habitats and then the evaluation of how much harvesting the aggregate system can likely sustain. The overall effect of artificial reefs on fish population dynamics will depend, in part, on the degree



*Figure 2.* Graphical representation of how density dependence (d.d.) influences the effect of artificial reefs on the production associated with a natural reef when there is attraction. Not shown are cases when there is overcompensation (i.e., density dependence leading to increased production on the natural reef: the line would lie above those shown) and depensation (i.e., facilitation: the resulting line would lie below those shown).

of attraction as well as the strength of density dependence (Osenberg *et al.*, 2001). This is highlighted by considering a scenario in which attraction occurs, but the strength of density dependence varies. The response of the natural reef to settlement redirection changes as a function of the strength of density dependence (Figure 2).

If fishes are attracted to the artificial reef and thus removed from the natural reef, and there is no density dependence, there will be a decline in the production associated with the natural reef (e.g., Figure 1a). If vital rates do not change with density, then this results in the pure attraction scenario – production on the natural reef would decline as a result of losing fishes to the artificial reef. If, however, certain vital rates (e.g., settlement or per capita survival) increase in response to the initial decline in density, then the production on the natural reef would be greater than expected under the Attraction scenario (Figure 2). The greater the decline in density (and the stronger density dependence is), the greater the compensatory response would be. If the response in the vital rate completely compensates for the decline in density (e.g., if settlement is reduced by 50% in response to the artificial reef, but the survival of the remaining fishes is doubled because of the reduction in density), then the density of older fishes would be unaffected by the artificial reef (Figure 2). If density dependence is extremely strong, there could be ‘overcompensation’ and the production of the natural reef could actually increase in response to the artificial reef. If, conversely, survival or settlement decreases with decreasing density (i.e., exhibit depensation: Liermann and Hilborn, 1997), then the production of the natural reef may be even less than predicted by the pure attraction scenario. So, instead of one possible production curve for the natural reef (as depicted in the Attraction scenario), there may be many, depending on the strength of density dependence (Figure 2). Thus, even when there is Attraction, density dependence could be sufficiently strong to produce a pattern that closely resembles the pure

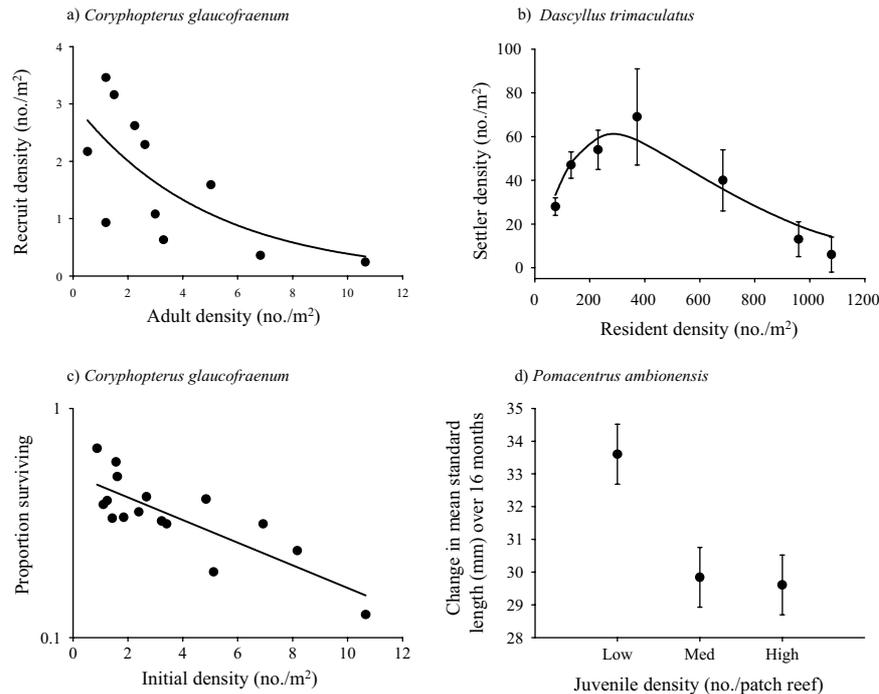
Production Hypothesis (Figure 1b). By changing only the intensity of density dependence, the Attraction and Production endpoints can both be predicted, as well as all points in between (as well as some that are even more extreme) – net production could increase, decrease or stay the same following the deployment of an artificial reef. Thus, the efficacy of artificial reefs as a management tool will depend critically on the strength of density dependence. How then is density dependence produced?

#### DENSITY DEPENDENCE IN MARINE REEF FISHES

Most marine ornamental fishes have a bipartite life cycle (i.e., a dispersive, pelagic larval stage followed by a relatively site-attached, benthic phase) (Sale, 1980; Thresher, 1984). Density dependence can occur at any point in this complex life history, but of interest in this context are the effects of density that arise at settlement and later during the benthic stage – effects in the plankton are less relevant to this discussion. Density dependence is used to refer to a negative (or positive) relationship between vital rates (settlement rates, or per capita post-settlement survival, growth, or reproduction) and density. There are many mechanisms that produce density dependence, including behavioral responses to chemical cues (e.g., in setting settlement levels: Sweatman, 1988; Pawlik *et al.*, 1991), social interactions (e.g., via territoriality or mate-finding: Norman and Jones, 1984; Foster, 1985), competition for food, shelter space or other critical resources (Hixon and Beets, 1993), and numerical and functional responses of predators (Murdoch and Bence, 1987).

To evaluate the importance of these processes to fish dynamics, it is critical to distinguish between local (e.g., at the scale of a reef or < 1 km) and regional (e.g., > 100's of km) dynamics. The local dynamics of a fish population are influenced by factors that influence settlement rate and post-settlement survival. Because eggs and larvae are dispersed via ocean currents (i.e., these local populations are 'open'), the reproduction of adults on a local reef does not have a direct effect on the local dynamics. This local reproduction does, however, contribute to the regional production of larvae and is therefore critical in the sustainability of the overall fishery. Growth of individual fish can have indirect effects on these demographic rates by, for example, changing survival (via effects on size-dependent processes) or by altering reproductive output (e.g., because fecundity often increases with body size).

Although there is considerable debate about the strength of density dependence in marine fishes (e.g., Caley *et al.*, 1996; Steele, 1997; Hixon, 1998), there are abundant data showing that it does operate and that it can occur at various points in a fish's life history. For example, the intensity of settlement (i.e., the number of larval fishes that leave the pelagic environment and enter the reef environment) can be influenced by the number of older fish already present on the reef (Figures 3a,b). In *Coryphopterus glaucofraenum* Gill, a small, short-lived goby



**Figure 3.** Examples of density dependence in marine reef fishes. (a) Effects of resident adult conspecifics on recruitment of the bridled goby, *Coryphopterus glaucofraenum*, in the Bahamas (modified from Forrester, 1995). (b) Effects of resident conspecifics on the settlement of the three-spot humbug, *Dascyllus trimaculatus*, in French Polynesia (modified from Schmitt and Holbrook, 1996). (c) Effects of adult density on survival of adult *Coryphopterus glaucofraenum* in the Bahamas over 2.5 months (modified from Forrester, 1995). (d) Effects of the density of juvenile damselfish, *Pomacentrus ambionensis* (Bleeker, 1868), at One Tree Reef in Australia on their growth over 16 months (low = 4 juveniles, medium = 8 juveniles, high = 12 juveniles, see Jones, 1987 for more details). In (a) the number of recruits was assessed after 2.5 months of cumulative settlement, and in (b) the number of settlers was assessed within 24 h of actual settlement of larvae to the benthic habitat. In both (a) and (b) some post-settlement mortality most likely occurred between initial settlement and subsequent assessment of recruits or settlers. A Ricker Function (settler density =  $0.5767 * [\text{resident density}] * e^{(-0.0035) * [\text{resident density}]}$ ) was fitted to the data in (b).

common in the Caribbean, settlement decreases as the density of resident adults increases (Forrester, 1995). However, studies of other marine fishes have shown no relationship between settlement and resident density (Steele *et al.*, 1998), increasing settlement with increasing adult density (i.e., positive density dependence or ‘facilitation’; Sweatman, 1988), or hump-shaped relationships (Schmitt and Holbrook, 1996: Figure 3b). Hence, not only the strength of density dependence, but also the form of density dependence can vary. Later, the effect of density dependence on harvesting strategies will be discussed.

Similarly, the density of resident fishes can also influence post-settlement survival. Forrester (1995) has shown that the subsequent survival of adult *C. glaucofraenum* decreases as the density of adults increases (Figure 3c). Thus, density dependence can operate simultaneously at different points in the life history of a single species. Density can also reduce growth due to competition for resources (Figure 3d), and decreased growth can reduce reproductive rates because fecundity is usually correlated with fish size. Although growth typically declines (or is not affected) by increasing density, reproductive rates could initially increase with density via social or Allee effects (e.g., yielding depensation: Liermann and Hilborn, 1997) before declining due to the effects of competition. There are, however, little data available on density dependent growth (but see Jones, 1987; Forrester, 1995; Steele, 1998) and even less on density dependent reproduction. There are at least two reasons for this. First, reproductive rates are difficult to measure (but growth is not). Second, and more importantly perhaps, many researchers ignore density dependent reproduction (and growth) in reef fishes given the open nature of these systems – local reproductive output has no direct effect on the subsequent supply of larvae back to the local reef. This local larval production does, however, affect ‘down current’ populations, and in order to understand the dynamics of marine ornamentals over large spatial scales and manage the ornamental fishery as a whole, better information regarding local reproduction and its link to larger scale dynamics is needed.

#### ROLE OF DENSITY DEPENDENCE ON HARVESTING

Besides determining the net effect of artificial reefs on local production (Figure 2), density dependence can also have important implications in terms of harvesting (with or without respect to the use of artificial reefs): e.g., St. Mary *et al.* (2000). To illustrate, consider the example of settlement using data for the three-spot humbug damselfish, *Dascyllus trimaculatus* (Rüppell 1829), in French Polynesia (Figure 3b: see Schmitt and Holbrook, 1996 for more details). In this system, there are two opposing effects of density, which creates the hump-shaped relationship: facilitation at low densities (i.e., residents provide chemical settlement cues for new settlers), and inhibition at high density (i.e., mediated by competition for shelter from predators) (Schmitt and Holbrook, 1996). As a result, the highest settlement occurs at an intermediate density of conspecifics. This is quite different from the pattern observed by Forrester (1995) for *Coryphopterus glaucofraenum* (Figure 3a). All else being equal, the harvesting strategy for these two species should also be quite different, owing to the different forms of density dependence.

#### IMPLICATIONS FOR HARVESTING FISHES

For *C. glaucofraenum*, the greatest yield to a local collector targeting young fish would be obtained by removing all residents, keeping the harvested species at low

local density, and thus maximizing the settlement rate. For *D. trimaculatus*, the best strategy is different: the collector should keep residents at an intermediate density in order to maximize settlement rates (this is a comparable situation to the classic maximum sustained yield problem for closed populations). Hence, a very high harvesting rate can actually reduce yield by greatly reducing resident density and thus subsequent settlement rates.

These scenarios, however, focus on harvesting at a local scale, and ignore the harvesting that arises over much larger scales (involving many collectors in different locales). For example, if *C. glaucofraenum* is depleted to low densities everywhere, then the collecting rate at all locales will crash, owing to the lack of production of larvae on a regional scale. Hence, the collection practices of a single collector may be at odds with that of the entire industry (and the government agencies charged with overseeing marine resources). This is one way in which artificial reefs may help (but not necessarily). If artificial reefs produce fish, without any associated impact on natural reefs, and if the deployment of artificial reefs is accompanied by placement of natural reefs into a no-take reserve, then the local harvesting from the artificial reef may be accomplished without any obvious negative impact to the regional dynamics. If density dependence is sufficiently weak (or attraction sufficiently strong) that the natural reef is negatively affected by the artificial reefs, then this favorable scenario will not hold true.

#### FUTURE SCIENTIFIC NEEDS

The above discussion provides a very brief introduction to a very complex issue. One hope is that it helps highlight the possible role of artificial reefs in the management and harvesting of marine ornamentals. More importantly, it is hoped that this will help stimulate scientific research that can be used to better evaluate this possible management tool. At present, there is insufficient information to lead to a firm conclusion about the efficacy of artificial reefs. Indeed, there are many unresolved issues that prevent us from either embracing or rejecting the use of artificial reefs as a management tool.

For example, the intensity of density dependence, how variable it is (among species and environments), where it operates in the life history, and how it affects the dynamics of reef fishes needs to be known. Although there has been considerable experimental and observational work on these systems, there still is little consensus about its occurrence and even less understanding of the patterns of density dependence among different types of fishes, life stages or environmental conditions. How artificial reefs might modify these processes on natural reefs must be determined. In order to do this, the strength of density dependence operating within the natural reef system must be quantified through experimental manipulations and then how artificial reefs will modify these processes must be determined. In so doing, the effect of artificial reefs on larval behavior during settlement and on the depletion of the larval pool (i.e., via settlement redirection) must also be

understood. Such an understanding will require the integration of larval transport mechanisms, larval behavior, and dispersal rates and distances. By learning more about the basic ecology of this system (i.e., through experimental manipulation, insightful monitoring, and adaptive management), managers and collectors alike can begin to understand what drives particular processes of reef fish systems and develop appropriate management scenarios and harvesting regimes.

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