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NEWS AND VIEWS

PERSPECTIVE

Where are they now? The fates of two genetic lineages in an introduced Hawaiian reef fish

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Humans, both wittingly and unwittingly, have been transporting marine organisms beyond their native ranges for centuries (Ruiz *et al.* 1997). A central challenge of invasion biology is to identify the factors that determine whether introduced species fail to become established, become benign members of a community, or spread so far and reach such densities as to be considered invasive. Organismal features such as physiological tolerance, niche breadth and fecundity are critical, but by themselves are inaccurate predictors of the fates of introduced species (Sakai *et al.* 2001). The size, age distribution, and genetic makeup of founder populations are also important, but because they are usually unknown they are most often viewed as sources of uncertainty. For marine species with planktonic larvae, the challenge is even greater because the consequences of a planktonic phase for dispersal and population viability are not well understood. In this issue, Gaither *et al.* (2010a) present a remarkable account of the introduction of a reef fish for which the number and genetic makeup of the founders are known. Between 1956 and 1961, the Division of Fish and Game for the Territory of Hawaii introduced 12 non-indigenous fish species into Hawaiian waters to establish commercial and sport fisheries. The introduction of *Lutjanus kasmira*, the bluestriped snapper, was the most successful (Fig. 1). There were two releases of fish from French Polynesia. In 1958, 2431 fish from the Marquesas Islands were released on Oahu, followed in 1961 with an additional 728 fish from the Society Islands. The blue striped snapper rapidly spread to the other Hawaiian Islands, reaching the northwestern end of the archipelago by 1992. The choice of the Marquesas as one of two sources for the introduction was fortuitous. Gaither *et al.* (2010b) found that the Marquesas population is genetically distinct from all other Indo-Pacific populations of *L. kasmira*. Mitochondrial cytochrome *b* sequences of fish from the Marquesas belong to a separate lineage that diverged from others in the species roughly half a Ma. Allele frequencies for several nuclear loci are also distinct. This provided Gaither *et al.* (2010a) with an extraordinary opportunity to examine what became of the mixed genetic heritage of Hawaiian blue striped snappers after 50 years.

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Fig. 1 The bluestriped snapper, *Lutjanus kasmira*, introduced to Hawaii 50 years ago and now an abundant reef fish expanded from a small founder population with minimal changes in the diversity or frequencies of mitochondrial and nuclear genetic markers.

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The bluestriped snapper is now one of the most abundant reef fish in Hawaii, but at first there were just a few thousand juveniles. It is conceivable that Allee effects could have eliminated such a small population; individuals could have become too dispersed to find mates, or their larvae could have been carried off to unsuitable habitats. Although there are few documented examples of Allee effects in marine fish (Gascoigne & Lipcius 2004), the risk of extinction for populations that are severely reduced in size has been a growing concern among fisheries and conservation biologists (Reynolds *et al.* 2005). One finding that suggests small populations of marine fish are vulnerable to extinction is that estimates of genetically effective population size are often several orders of magnitude less than estimates of census size (Hauser & Carvalho 2008). This suggests that either marine fish populations undergo large fluctuations in size, or they are subject to 'sweepstakes reproduction', in which a few individuals have very high reproductive success while the rest of the population has very little (Hedgecock 1994). Sweepstakes reproduction is believed to result from the combination of high fecundity and planktonic larval dispersal that is common in marine species. In theory, the vagaries of ocean currents carry most larvae to unsuitable habitats while the larvae that are successful are the progeny of a small number of highly fecund individuals that chanced to spawn under favourable

oceanographic conditions. In a small population this extreme form of demographic stochasticity could result in very few or even no individuals reproducing successfully. If sweepstakes reproduction had occurred during the establishment of Hawaiian bluestriped snappers, the resulting genetic bottleneck would be detectable as a pronounced reduction in genetic diversity relative to the founder population. However, there is no evidence of such a bottleneck. Among 385 fish from the Hawaiian Islands, 142 mitochondrial DNA haplotypes from the Marquesas and 30 haplotypes from the Society Islands were found, which demonstrates that a minimum of 172 female and one male founder left descendants. This is reflected in a statistical analysis that indicated most of the diversity from the founders in both mitochondrial and nuclear markers has been retained. Thus, the initial establishment of the population cannot be attributed to just a few individuals, but rather to many founders from both introductions that were successful at reproducing and leaving descendants. Several factors could have helped the bluestriped snappers avoid a severe genetic bottleneck. The first relates to the age distribution of the founder population. Age, size and fecundity are highly correlated in fish, and in established populations reproductive success can be strongly skewed towards a few old and highly fecund females. This would not be the case for the founders of the Hawaiian bluestriped snappers, which were all collected as juveniles and thus likely to have a relatively narrow variance in reproductive success. Second, bluestriped snappers reach maturity after just 1 or 2 years, which would allow rapid population growth and shorten the duration of any genetic bottleneck that had occurred. Third, shoaling behaviour and mass spawning could have prevented the founder population from becoming too thinly dispersed, favouring high reproductive success and reducing its variance. And fourth, bluestriped snappers were deliberately introduced to fill an open niche in the Hawaiian reef fish assemblage, which had few potential competitors and lacked native snappers in the genus *Lutjanus*. The depauperate fauna of Hawaii has been an important factor in the establishment of many other introduced species, both aquatic and terrestrial.

From its start, the Hawaiian population of bluestriped snappers was more genetically diverse than either source population and retained most of this diversity as it expanded and spread throughout the archipelago. Thus it does not present the 'genetic paradox' of an invasive species that is successful despite reduced genetic diversity in its founder population (Frankham 2005). It is even possible that the starting mixture of two genetically divergent stocks contributed to its success, as appears to have been the case for introductions of invasive green crabs in the genus *Carcinus* (Darling *et al.* 2008). However, regardless of whether genetic diversity favoured their establishment, it is remarkable that in present day Hawaiian populations of bluestriped snappers the relative proportions of mtDNA haplotypes and nuclear alleles from Marquesas and Society Islands are very close to the ratio of the numbers of founders from each source (Gaither *et al.* 2010a). This is a striking and perhaps unexpected finding because there are mechanisms that would appear likely to produce large shifts in these ratios, such as differences in the condition of the fish from the two introductions because of differences in handling, differences in adaptation or acclimation associated with the source populations, or temporal differences in environmental conditions at the times of release. The constancy in the ratios of genetic markers from the initial introduction to the present suggests that the early phases of population establishment were not as stochastic as might have been expected, but followed a similar trajectory for both releases.

A well-documented introduction of a marine species can provide a singular test of our ability to explain the success of a non-indigenous species when we have knowledge of factors that are usually cited as sources of unpredictability. The case of the bluestriped snapper is informative not so much for what happened, but for what didn't happen. No severe bottlenecks occurred, and neither of the two initial stocks outraced the other as they spread and became established. This suggests that chance played a smaller role than might have been expected, and that the outcome may have even been predictable.

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