Aquaculture 452 (2016) 318–325

Contents lists available at ScienceDirect

Aquaculture

journal homepage: www.elsevier.com/locate/aquaculture

Comparison of lines shows selection response in kingfish (*Seriola lalandi*)

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ARTICLE INFO

Article history:
Received 12 June 2015
Received in revised form 7 November 2015
Accepted 10 November 2015
Available online 11 November 2015

Keywords:
Observed selection response
kingfish
Heritability
Domestication selection

ABSTRACT

Recently, aquaculture and captive breeding have commenced for a raft of large fish species, including bluefin tuna (*Thunnus orientalis*), kingfish (*Seriola lalandi*) and giant grouper (*Epinephelus lanceolatus*). With captive breeding, there is often interest to conduct selection and genetic improvement, but these large species present many and substantial challenges to selective breeding. Indeed there are no reports or examples that selection response and forward genetic gain has been achieved for such large and problematic species. These large species, typified by kingfish, are characterized by immense fecundity with ensuing opportunity for intense domestication selection, either adverse or synergistic, that can impact on planned selection response. Moreover, because of size and logistics, typically few broodstock are held and chance sampling of few broodstock individuals has the potential to confound selection response and the repeatability of response.

The main objective here was to assess if forward selection response could be achieved after selection for adult weight of kingfish in sea cages. Selection response was estimated by comparing the performance of F_1 offspring from wild parents with F_2 offspring from selected parents during the larval rearing and adult growout. Pedigree data, from genotyping approximately 1000 individuals using up to 17 DNA microsatellite loci, was added to the larval and adult performance data to resolve the contributions of different sire and dam lineages.

For most traits measured, whether larval survival, incidence of larval deformity, adult weights or adult condition factor, the offspring of selected parents outperformed those from wild parents, whether animals were grown separately in replicate (larval rearing tanks) or communally as adults in tanks. Larval survival was not deliberated selected, yet the dropout of specific parental sire or dam lineages suggest in part genetic differences account for some of the differences between the F_1 and F_2. Observed selection responses for adult weights and condition factor were greater than those predicted from covariances of relatives. Either (synergistic) domestication selection or some type of magnification of line differences under communal rearing may account for these data.

The chance sampling of particularly good or bad broodstock sires or dams did not seem to have been a major contributor to the strain testing results. Whether this means that selection responses are repeatable even when using few broodstock, a situation unavoidable for large marine species, is discussed in terms of how intense deliberate and possible domestication selection could narrow the variances of breeding values of selected broodstock.

Statement of relevance

Can we select large marine species with few broodstock?

1. Introduction

In recent decades there has been a wave of new marine species being domesticated for aquaculture (Duarte et al., 2007), and domestication is often accompanied by interest in some type of genetic improvement (Knibb, 2000; Gjedrem et al., 2012; Lind et al., 2012). Some of the species of recent interest for aquaculture include giant grouper, *Epinephelus lanceolatus* (Pierre et al., 2008), kingfish, *Seriola lalandi* (Whatmore et al., 2013), lutjanids, e. g. *Lutjanus argentimaculatus* (Emata, 2003), Asian sea bass, *Lates calcarifer* (Harvey et al., 1985) and tuna *Thunnus orientalis*, (Sawada et al., 2005). These species share several biological features in common, including a) large size at sexual maturation b) mass spawning during reproduction c) low proportions of broodstock contributing to spawns (Wang et al., 2008; Navarro et al., 2009), d) immense numbers of tiny eggs (Symonds et al., 2014) and larvae with low survival (Woolley et al., 2014).

Research in salmon (e.g. *Salmo salar*) and trout (*Oncorhynchus mykiss*) has pioneered genetic selection models for both within and between family selection (Gjedrem, 2010). However, salmon are readily stripped spawned and controlled pair matings are possible, salmon

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broodstock are relatively plentiful, they produce relatively few eggs with high survival rates. By contrast, many marine fish have proved difficult or impractical to strip spawn, presumably because of their life history trait of being group spawners. This issue was first raised in the 1990s (Gorshkov et al., 1997) for the group and daily spawning marine gilthead seabream, *Sparus aurata*, and subsequently in other species including sole, *Solea solea* (Blonk et al., 2009, 2010).

The difficulties of achieving any spawning and particularly of obtaining successful planned matings in mass mating marine fish are further compounded for the larger species, where offspring for aquaculture are typically produced from large tanks with just few large broodstock individuals. So the salmon genetic model, that considers both within and between family selection, is probably unsuited for the mass or group spawning marine species due to these biological and, likely, logistical, differences (Knibb et al., 1998). Other practical and feasible selection models are needed.

For kingfish genetic improvement in Australia, animals are mass spawned, offspring are communally reared then mass selected for size at harvest. Chosen candidates are then genotyped, pedigrees assigned, and the next generation of mass mating groups, not individuals, allocated to breeding groups in large tanks that avoid the mating of relatives. This selection as applied to kingfish is a variation of "walkback" selection (Doyle and Herbinger, 1994). It is likely this type of breeding design has been, or is being adopted for a range of the newly aquacultured mass spawning marine species (Blonk et al., 2009). However, whether this type of selection as applied to the large marine species has ever yielded selection response or how much, has, to our knowledge, never been demonstrated, an important omission since the magnitude of the selection response achievable is a critical metric for selection programs, including commercial programs, since it can advise on appropriate levels of investments in the genetic programs. Assessment of this metric is the main question and objective addressed by the present report.

Moreover, and importantly with respect to this type of selection as applied to kingfish, there are a variety of reasons, introduced following, why this selection model may not deliver commercially relevant or consistent selection response. The first, and potentially large unknown is the contribution of domestication selection, either adverse or synergistic, to deliberate selection. We have defined domestication selection as the inadvertent or unplanned selection for traits favored for survival, growth and reproduction in captive conditions, with the implication they are genetically different from those analogous traits in the wild. Others have defined domestication selection in rather analogous ways (Doyle, 1983; Vandeputte et al., 2009). The nature of domestication selection could be synergistic or adverse to planned selection, a possible example: shrimp (*Penaeus vannamei*) that survive white spot may be slow growing (Gitterle et al., 2005). Large marine fish typically are highly fecund, able to produce up to millions of eggs per female (Symonds et al., 2014). Literally, it is the "one in a million" fish that not only just survives all the stages of production, including larval rearing, nursery and growth, but also one that thrives under captive culture conditions, resists various diseases and ectoparasites, injury, eats artificial diets, and becomes broodstock for the next generation. Perhaps such selection intensities may be more akin to bacterial genetics, where single gene mutations can be sieved, than to selection response from quantitative shifts of allele frequencies (Cock et al., 2009). In any case, here we attempt to calibrate the role of domestication selection, along with that of planned selection, in kingfish by comparing performance of sire and dam lineages during larval rearing (by assigning pedigrees using genotypes from DNA microsatellite data) and also the selection responses actually observed compared with those predicted from covariance of relatives.

A second concern is the degree to which the random sampling of a small number of families, sires or dams with different breeding values, an aspect almost unavoidable for the large marine species, will impact on the selection response outcomes, or how repeatable they are in different trials. Here we add pedigree data (derived from DNA microsatellite genotypes) to the experimental design in order to assess the variation in performance of different sires and dams lineages, considering the question of whether selection response can be repeatable with only small numbers of broodstock.

2. Methods

2.1. Microsatellite markers and genotyping

Nine microsatellite loci were used to construct the larval pedigree, and 17 were used for the adult fish in this study. A description of the development of six new primers, and evaluation of published primers is given in Whatmore et al. (2013). A further set of eight new primers was developed using methods similar to those described in Whatmore et al. (2013). Genotyping methods were similar to those in Whatmore et al. (2013). Note that most published primers and new candidate primers from transcriptomes were rejected, only a small proportion of primers were deemed highly reliable and repeatable.

2.2. Broodstock parents of the F1 and F2 and tanks

2.2.1. The unselected F1 fish used in the trial

The *unselected* F_1 fish were produced from a single tank containing three male and six female wild parents, ranging between 23 and 34 kg, caught in the local Spencer Gulf. These wild fish are used only to generate *unselected* F_1 offspring for this trial and are not part of, nor related to, the founding breeding nucleus that gave rise to the F_2 fish (see following).

2.2.2. The F_2 fish used in the trial

The F_2 fish are offspring of *selected* F_1 fish that themselves derive from part of a founding nucleus of about 40 wild animals. The breeding pedigree has been managed so there was no inbreeding in the F_2. There were many production runs from various parts of the wild breeding nucleus, and the *selected* F_1 fish in this study derive from three different runs, termed cohorts A, B, and C, in order of their respective ages (cohort A was spawned in 2007, B in January 2010 and C in December 2010). For each of these three cohorts, the F_1 fish were grown through the hatchery, nursery and in sea cages until they reached harvest size of about 3–4 kg, at which time they were selected.

The selection procedure on the F_1 fish from each of the three cohorts was first to sample > 100 random fish and estimate cut off points for the top 10% by weight, and note the minimize length of fish in the top 10%. At harvest, the minimum length was used as a very approximate guide to take fish for actual weighing; fish above the threshold weight were also informally selected to be well conformed (i.e. appear to have an above average condition factor, defined following, and be free of abnormalities/deformities. These procedures resulted in selecting 5–10% of approximately 1500 animals. For cohorts B and C, details (weights, lengths, condition factor) of samples of random unselected fish (>100) and of all selected fish (>100) are available but they were not available for cohort A, so respective values on selection intensities for A were inferred from B, either using information on all random and selected animals from B, or only those few from cohort B that actually spawned (which were only males, see following).

The selected F_1 fish from the three cohorts were mixed then distributed among 3 broodstock tanks, namely, B1, B2 and B5. None of the cohort C males contributed to spawning so are presumed to be young and sexually immature and are set aside from analyses or statistics (there were no cohort C females in the broodstock tanks, presumably they were noted as immature and not put into the breeding tanks). None of the cohort B females present produced offspring and so are also deemed sexually immature and are excluded from further analyses. Apart from those deemed immature, the remaining numbers broodstock that were present as well as the number that spawned are given in Supplementary Fig. 3.