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Domestication reduces the capacity to escape from predators

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Abstract

Phenotypic plasticity in response to variations in predatory pressure frequently occurs in wild populations, but it may be more evident and critical in species subjected to high exploitation rates and aquaculture. The Chilean scallop *Argopecten purpuratus* is becoming a domesticated species and the production of hatchery-reared scallops (closed environment), has implied the development of successive generations of individuals deprived of several stimuli normally present in their natural habitats (e.g. predators). We compared the escape capacities between wild and cultured *A. purpuratus* and also evaluated the effect of reproductive investment on the escape response capacities. Wild and cultured scallops, at different reproductive stages (maturing, mature and spawned), were stimulated to escape with the predatory sea star *Meyenaster gelatinosus*. We recorded: (1) the time to reaction, (2) the total number of claps, the duration of the clapping response and the clapping rate until exhaustion, (3) the time they spent closed after exhaustion, and (4) the proportion of claps recovered, the duration of the clapping response and the clapping rate after 20 min of recuperation. We found that wild *A. purpuratus* (1) reacted earlier when contacted by their natural predator, (2) escaped faster (greater clapping rates), (3) spent less time with their valves closed when exhausted, and (4) most of their escape capacities (i.e. claps number; clapping time; capacity of recuperation) were less affected by the energetic requirements imposed by gonad maturation and/or spawning than in cultured scallops. We considered that all these aspects of the escape response would make wild scallops less vulnerable to predation than cultured scallops, thus decreasing predation risk. Given the reduction of escape performance in cultured scallops, we suggest that this aspect should be considered for the success of culture-based restocking programs.

Keywords: *Argopecten purpuratus*; Cultured scallops; Escape response; Reproductive cost; Restocking; Wild scallops

1. Introduction

Predation is a major factor causing mortality in wild populations, and consequently species have evolved a varied set of response mechanisms to avoid or decrease predation pressure (Sih, 1987). Passive defensive mechanisms (e.g. morphological traits) as well as active responses (e.g. escape behaviours) often have direct energetic costs (Sih, 1987; Kleinman et al., 1996) and consequently, many animals have evolved flexible mechanisms that may be developed or lost over short periods, depending on the predation risk (Havel, 1987; Legault and Himmelman, 1993; Reimer et al., 1995; Reimer and Tedengren, 1996; Rochette et al., 1998). Morphological, physiological and behavioural responses to predation seem to be attenuated in culture-reared fishes in comparison to wild populations (Huntingford,

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2004). This suggests the important selective pressure of predation, but also suggests that changes in the genetic structure, and in the phenotypic response of individuals to predation, may occur in species subjected to high exploitation rate and aquaculture (Huntingford, 2004).

Comparisons of responses to predators between cultured and wild animals show differences in both juvenile and adult stages in species of different taxa (Haugum et al., 1999; Álvarez and Nicieza, 2003; Lafrance et al., 2003). Hatchery reared juvenile brown trout (*Salmo trutta*) approached dummy predators more frequently than wild juveniles, and this "naiveness" was due to a decreased capacity to detect predation risk (Fernö and Järvi, 1998). Mussels exposed to predator odours developed smaller and thicker shells, stronger byssal attachment and a larger adductor muscle than non-exposed mussels, which made them less vulnerable to predation by sea stars and crabs (Hancock, 1965; Reimer and Tedengren, 1996; Reimer and Harms-Ringdahl, 2001). In the scallops *Pecten maximus* and *Placopecten magellanicus*, weaker shells (i.e. less resistant to mechanical pressure) have been observed in cultured stocks when compared to wild populations (Haugum et al., 1999; Lafrance et al., 2003). Moreover, the intensity of the escape response (i.e. swimming speed) was lower in cultured than in wild juvenile *P. magellanicus* (Lafrance et al., 2003) and mortality due to predation was greater in cultured stocks of *P. maximus* (Haugum et al., 1999).

Differences between cultured and wild populations may also be affected by reproductive status, as investment in reproduction affects the energetic reserves used for fleeing predators in several marine and terrestrial taxa (Koch and Wieser, 1983; Hughes and Rayner, 1993; Brokordt et al., 2000a,b, 2003). Scallops are exceptional among bivalve molluscs in having an excellent swimming capacity, which is exhibited upon detection of predators (Vogel, 1997). Investment in reproduction (i.e. gonad maturation and spawning) markedly reduced the capacity of sub-Arctic (*Chlamys islandica*) and tropical (*Euvola ziczac*) scallops to escape predators (Brokordt et al., 2000a,b). In both species, investment in gonads led to an important decrease in muscle glycogen content and in the metabolic enzymes that support adductor muscle contraction and recuperation during and after the escape response (Brokordt et al., 2000a,b; Brokordt and Guderley, 2004). A similar trend was observed in *Argopecten purpuratus*, which exhibits an important decline of muscle carbohydrates and the enzyme octopine dehydrogenase (implicated in muscle contraction and recuperation), after gonad maturation (Martínez et al., 2000).

Many marine and terrestrial wild populations have declined over the past several decades, largely as a result of fishing or hunting pressure (Brown and Laland, 2001; Fuller, 2002; Letty et al., 2002; Friedman and Finley, 2003). Most restocking programs of wild populations rely on farm- or hatchery-reared stocks (Brown and Laland, 2001; Friedman and Finley, 2003; Huntingford, 2004). However, the mortality rates of hatchery reared individuals after release are very high, mainly due to diseases and predation (Hatcher et al., 1996; Barbeau and McDowell, 1998; Brown and Laland, 2001; Friedman and Finley, 2003). In Chile the scallop *A. purpuratus* is becoming a fully domesticated species, as ~90% of the individuals are kept in suspended cultures along the Chilean coast (Stotz, 1999). Only two natural seabeds remain, and they show low scallop densities and high predator (sea stars and crabs) abundance (Ortiz et al., 2003; Stotz, 1999). Thus, the persistence of *A. purpuratus* populations in Chile will most probably rely on descendants of "domesticated" (cultured) scallops to restore natural beds (Stotz, 1999). Moreover, the settlement of scallop larvae on collectors, which in the past was exclusively dependent on wild populations, is now strongly based on larvae produced in hatcheries. Therefore, these animals are deprived of direct stimuli by natural predators for several consecutive generations.

In the present study, we compared escape response capacities between wild and hatchery cultured *A. purpuratus*, evaluating the effect of gonad maturation and spawning. We discuss the implications of our results for conservation and restoration of wild populations, given the current increase of cultured stocks of several marine species and the reliance of restocking on hatchery-reared individuals.

2. Materials and methods

2.1. Sampling and reproductive conditioning of scallops

Wild *Argopecten purpuratus* were sampled by SCUBA diving from Puerto Aldea, one of the few natural beds that remain in the Chilean coast, located in Tongoy Bay, northern Chile (30° 18′ S, 71° 33′ W) (Fig. 1). Hatchery reared scallops were obtained from a scallop farm (Cultivos San José), also located in Tongoy Bay (30° 16′ S; 71° 35′ W). Adult scallops (75–85 mm in shell height) from both populations were transported to the Central Culture Laboratory at the Universidad