



Regional genetic structure of sandfish *Holothuria (Metriatyla) scabra* populations across the Philippine archipelago

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ABSTRACT

The sandfish, *Holothuria (Metriatyla) scabra* Jaeger, 1833 is a commercially-valuable tropical sea cucumber species which is overexploited throughout much of its distributional range, the Philippine archipelago included. The need for management interventions to sustain the fishery is recognized. However, the lack of knowledge on the genetic structure of natural populations needs to be addressed to guide management initiatives. The present study examined genetic diversity and spatial patterns of genetic structure of sandfish populations across the Philippine archipelago. Population genetic analysis using 11 microsatellite markers revealed weak yet significant regional genetic structure among 15 *H. scabra* populations across the Philippine archipelago ($F_{ST} = 0.016$; $P < 0.0001$). Six genetic groups broadly concordant with marine biogeographic regions were identified. Genetic connectivity was strongest among populations situated in the center of the archipelago (internal seas; $F_{ST} = 0.002$, $P > 0.05$). Peripheral locations exhibited limited gene flow (Philippine Sea, South China Sea, Sulu Sea and Celebes Sea; mean $F_{ST} = 0.023$, $P < 0.0001$), with significant genetic relatedness further suggesting relative isolation or high levels of self-recruitment. Excluding the two most divergent Sulu Sea populations, there was a significant signal of isolation-by-distance for the rest of the Philippine populations, suggesting that geographic distance between coastal habitats coupled with oceanographic circulation largely influence genetic structure. There was no signature of genetic bottlenecks for any population, although effective population sizes (N_e) were larger for central populations compared to peripheral populations. This study provides information on genetic stocks which has important implications to genetic resource management of Philippine sandfish populations to support sustainability of the fishery.

1. Introduction

The global decline in marine fisheries (Watson and Pauly, 2001) warrants improved management practices to restore fisheries resources, promote recovery (Worm et al., 2009) and move towards longer-term sustainability (Pauly et al., 2002). The identification of management units (MUs, *sensu* Moritz, 1994) is fundamental for management of natural populations (Palsboll et al., 2007). Genetic criteria are primarily used for delineation of MUs (Hauser and Seeb, 2008; Laikre et al., 2010), with the detection of genetic structure among populations as the minimum prerequisite (Moritz, 1994; Reiss et al., 2009). However, further demonstration of low levels of contemporary migration is recommended to infer demographic independence between management units (Paetkau et al., 1997; Palsboll et al., 2007).

Sea cucumbers are soft-bodied marine echinoderms (Class Holothuroidea) which have been harvested in the Indo-Pacific region for at least 400 years (Akamine, 2001; Kinch et al., 2008; Máñez and

Ferse, 2010). Sea cucumber fisheries in the tropics are multi-species (Purcell et al., 2013), with an estimated 60 species having commercial value (Purcell et al., 2012). Traded in processed, dried form known as *trepang* or *beche-de-mer*, the value and demand for sea cucumbers continues to increase rapidly, driven by Asian markets where it is consumed as a luxury seafood commodity (Ferdouse, 2004; Purcell, 2014). Despite the boom-bust cycle typical of individual sea cucumber fisheries, capture production has continued to increase since the 1950s due to serial exploitation (Anderson et al., 2011). This is seen in the rapid geographic expansion from the Indo-Pacific region to a global fishery now covering 90% of the world's tropical coastlines (Eriksson et al., 2015), expansion of fishing effort further offshore as nearshore stocks became depleted, a shift to exploitation of high-abundance yet low-value species as high-value species became scarce (Anderson et al., 2011), and reduction in size of harvested sea cucumbers (Uthicke and Benzie, 2001a). The relative ease with which sea cucumbers can be collected, coupled with slow population recovery rates due to their long

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generation time (Conand, 2001), low recruitment and individual growth (Uthicke et al., 2004) predispose natural populations to over-fishing and local extirpation. Recent assessments indicate global sea cucumber fisheries as characterized by pandemic overfishing (Purcell et al., 2010; Toral-Granda et al., 2008), particularly in the Indo-Pacific region (Purcell et al., 2013). In the Philippines, capture production of sea cucumbers declined from a peak of 3000–4000 metric tons from 1984 to 1992, to 600–800 metric tons from 1998 to 2006 (Choo, 2008a). Such declines in sea cucumber resources have clear implications not only on livelihoods and economies in coastal communities, but on productivity and ecosystem function as well (Schneider et al., 2013; Uthicke and Benzie, 2001a; Wolkenhauer et al., 2010).

The sandfish, *Holothuria (Metriatyla) scabra* Jaeger, 1833, is one of the most valuable aquaculture species of tropical sea cucumber (Robinson et al., 2013), commanding the highest price for *beche-de-mer* in Asian markets (Purcell et al., 2012). Widely distributed throughout the tropical Indo-West Pacific (Hamel et al., 2001), sandfish are deposit feeders inhabiting low-energy environments, particularly intertidal sea grass beds near mangrove areas. Like most sea cucumber species, sandfish juveniles and adults are generally site-attached and slow-moving (Hamel et al., 2001; Purcell and Kirby, 2006). These life history characteristics which make collection of the species easily accessible, coupled with their high commercial value, render sandfish populations particularly vulnerable to overexploitation and collapse. Catch depletion has been reported in New Caledonia, India, and Malaysia (Hamel et al., 2001). Stock depletion and local extirpation has been reported in Egypt (Hasan, 2005), parts of Indonesia, Thailand, Vietnam and Malaysia (Choo, 2008b), Milne Bay in Papua New Guinea (Skewes et al., 2002), some parts of the Solomon Islands (Friedman et al., 2011), and the Philippines (Choo, 2008a; Trinidad-Roa, 1987). In response, management initiatives have been instituted in several locations, with moratoriums in place for fisheries in Palau, Papua New Guinea, Solomon Islands and Moreton Bay, Australia (Kinch et al., 2008). In the Philippines, existing policies regulate the number of collectors, and sets size limits on individuals for transport and trade for sea cucumbers in general (BFAR Administrative Circular No. 248, 2013). Fisheries regulatory measures alone however, may be incapable of restoring populations as recovery has been shown to be slow (Friedman et al., 2011; Skewes et al., 2002; Uthicke et al., 2004). *Holothuria scabra* is currently listed as an endangered species in the IUCN Red List of Threatened Species (Hamel et al., 2013).

Aside from implementing fishery regulations to manage natural populations, the use of hatchery-produced juveniles to manage fisheries, i.e. aquaculture-based enhancement has been identified as a viable prospect in rebuilding wild stock (Bell and Nash, 2005; Bell et al., 2008a; Taylor et al., 2017). Such an approach is particularly applicable to *H. scabra*, as it is the most commonly cultured tropical sea cucumber species (Purcell et al., 2012; Raison, 2008). Developments in hatchery technology to increase efficiency of production (Duy et al., 2017, 2015), and improve sea ranching strategies by identifying habitat requirements (Altamirano et al., 2017; Hair et al., 2016) or appropriate release techniques and grow-out practices (Rougier et al., 2013) represent continued advancements supporting the potential for aquaculture of *H. scabra* to subsidize capture production, and maintain fisheries resources through restocking of natural populations, stock enhancement, or as a byproduct of sea ranching (Bell et al., 2008b). However, aquaculture-based restocking and stock enhancement may pose significant genetic risks which might affect the productivity, fitness and evolutionary potential of natural populations (Lorenzen et al., 2010; Ward, 2006). These include the potential reduction in genetic diversity of hatchery-produced juveniles resulting from a small number of broodstock (Eeckhaut et al., 2012; Hold et al., 2013), disruption of neutral and adaptive genetic structure, potential for outbreeding depression resulting from restocking wild populations with individuals from genetically differentiated stocks, and potential negative effects of interaction between introduced and natural populations (Hindar et al.,

1991).

Genetic resource management is an important component towards a responsible approach to marine stock enhancement and restoration (Blankenship and Leber, 1995; Lorenzen et al., 2010), and relies on the identification of spatial population structure (Ward, 2006). Prior studies on *H. scabra* populations reveal genetic differentiation across the southern Pacific (Nowland et al., 2017; Uthicke and Benzie, 2001b; Uthicke and Purcell, 2004). However, fine-scale genetic structure at scales of tens of kilometers has also been reported (Uthicke and Benzie, 2001b; Uthicke and Purcell, 2004) indicating the influence of local geomorphology, coupled with oceanographic circulation, to restrict dispersal potential even at small spatial scales. No information on genetic structure is currently available for *H. scabra* populations across the Philippine archipelago.

In the Philippines, the deployment of low-cost ocean nursery systems for rearing of hatchery-produced juveniles in a community-managed setting (Juinio-Meñez et al., 2012a,b) can serve as viable spawning populations and source of juveniles for recruitment to wild populations (Juinio-Meñez et al., 2013). Communal sandfish sea ranching was proposed as a model that could be adopted for a developing-country setting, to harmonize the need for restoration and enhancement of depleted wild populations, while providing economic returns for small fishers (Juinio-Meñez et al., 2012a). However, before aquaculture-based restoration efforts commence in earnest, and to guide other spatially-explicit management initiatives, it is essential to determine the genetic structure of natural populations of sandfish across the Philippine archipelago. Thus, it is the aim of this study to examine the genetic diversity and genetic structure of sandfish populations at broad spatial scales across the Philippine archipelago. In particular, we examine spatial patterns of genetic diversity, genetic differentiation, gene flow and estimated effective population sizes for sandfish populations collected from representative marine biogeographic regions across the archipelago using microsatellite markers. Characterizing genetic diversity, inferring spatial patterns of population connectivity, and identifying putative management units among natural populations is a priority to provide baseline genetic data to guide management and conservation initiatives for sandfish populations in the Philippines.

2. Materials and methods

2.1. Sample collection

Holothuria scabra samples were collected from natural populations at 15 locations representing all six marine biogeographic regions across the Philippine archipelago: South China Sea (MAS), Sulu Sea (ELN, COR), Philippine Sea (STA, SOR, GUI), Celebes Sea (DAV, GEN, TWI), and internal seas (Sibuyan Sea, Visayan Sea, Panay Gulf, Bohol Sea; ROM, CON, TIG, CEB, BOH, DUM) over a two-year period from 2011 through 2013. (Fig. 1, Table 1). Non-lethal sampling was performed, with a small piece of tissue biopsied from the body wall and preserved in 96% ethanol. Apart from voucher specimens and those collected by fishermen for trade, all other individuals were returned to their collection locations after tissue biopsy. Specimens and tissue samples are maintained at the Marine Science Institute, University of the Philippines. Total genomic DNA was extracted from tissue samples using a Chelex-proteinase K method (Yue and Orban, 2005). Extracted DNA was quantified using a Nanodrop™ 2000 spectrophotometer (Thermo Scientific).

2.2. Microsatellite genotyping

Microsatellite genotyping was performed using markers developed for *H. scabra* (Fitch et al., 2013). Of eighteen loci available, five loci were not consistently amplified across samples (*Hsc1*, *Hsc4*, *Hsc12*, *Hsc14*, *Hsc54*) and were not used for further genotyping. The remaining

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