



**Abstract**—Assessments of the status and ecological linkages of target fish species related to marine habitats are playing important roles in enhancing the effectiveness of marine protected areas (MPAs) and of management in other coastal areas. In this study, we assessed juvenile yield and the abundance of goldlined spinefoot (*Siganus guttatus*) by using local knowledge and visual census in coastal waters of Vietnam. Genetic structure was examined by using DNA analysis of juveniles, collected in seagrass beds and mangroves at major lagoons and estuaries, and of adults, collected from coral reefs. More than 38.6 million juveniles were collected from 8 coastal lagoons and estuaries. The coastal lagoons and estuaries with seagrass beds supported high yield of juveniles, and the nearby MPAs had higher densities of adults. Three distinct genetic groups were identified, with one group found off the central part of the eastern coast from Con Co Island to Quy Nhon Bay, a second group found off the southeastern coast from Nha Trang Bay to the Con Dao Islands, which are located off the southern tip of Vietnam, and a third group found off the southwestern coast at the Phu Quoc Islands in the Gulf of Thailand.

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## Juvenile yield and adult abundance, genetic diversity and structure, and linkages among marine habitats for goldlined spinefoot (*Siganus guttatus*) in the coastal waters of Vietnam

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Results from previous research indicate that more than 210 species of 34 reef fish families have pelagic stages, that larvae disperse away from their spawning area (Green et al., 2015), and that many of them migrate from their settlement habitats of mangroves and seagrass beds in coastal lagoons and estuaries (nursery grounds) to adjacent coral reefs for feeding or shelter (Luo et al., 2009; Honda et al., 2013; Le et al., 2019; Vrdoljak et al., 2021). In an increasing number of studies of marine fish species, strong genetic differentiation among populations from different regions, separated by distances from tens to a few hundred kilometers, has been observed (Hellberg et al., 2002; Jones et al., 2005; Laikre et al., 2005; Planes et al., 2009). These patterns may be influenced by several ecological and behavioral factors, such as the timing of reproduction (Selkoe et al., 2006), larval dispersal ability (Kinlan and Gaines, 2003), homing behavior (Almany et al., 2007), oceanographic patterns (White et al., 2010),

biogeographic barriers (McMillan and Palumbi, 1995), local adaptation (Conover et al., 2006), habitat specialization (Knudsen et al., 2006), and the ecological requirements of each species (Rocha et al., 2002).

Reports from several studies indicate that many reef fish families (Lutjanidae, Haemulidae, Lethrinidae, Scaridae, Siganidae, and others) utilize seagrass beds and mangroves in nearshore and estuarine regions as their nursery grounds (Verweij et al., 2008). Therefore, understanding the degree of connectivity between populations in different geographic areas, or the specific location of genetic breaks, sets the scale at which management strategies for species need to be applied. This information is important in the management of reef fish resources in many coastal areas, especially in marine protected areas (MPAs) (Cowen and Sponaugle, 2009).

Results of studies on the genetic structure of several species of siganids indicate that there are differences in

connectivity among species. In waters of Japan, Iwamoto et al. (2009) reported a higher degree of interpopulation gene flow for bluntnosed spinefish (*Siganus spinus*) than for goldlined spinefoot (*S. guttatus*) between Okinawa Island, Miyako Island, and Ishigaki Island. Magsino and Junio-Meñez (2008) found higher genetic structuring in dusky spinefoot (*S. fuscescens*) than in streamlined spinefoot (*S. argenteus*) along the eastern coasts of the Philippines, and they also observed genetic structure for these 2 species in the South China Sea and South Philippine Sea but no structure for them in the Sulu Sea and Inland Sea. In the South China Sea, high connectivity between populations of reef fish species, including the false pennant bullfish (*Heniochus acuminatus*), the six-barred wrasse (*Thalassoma hardwicke*), and the threespot dascyllus (*Dascyllus trimaculatus*), has been reported from genetic studies, indicating population differences in some areas (Ablan et al., 2002; Chen et al., 2004).

In the coastal waters of Vietnam, results of a genetic study indicate broad connectivity of the goldstripe sardinella (*Sardinella gibbosa*), the giant tiger prawn (*Penaeus monodon*), the threespot dascyllus, the cupped oyster *Crassostrea rivularis*, and the giant clams *Tridacna crocea* and *T. squamosa* between a northern region (from the Cat Ba Islands to Da Nang Bay), a central section (from Quy Nhon Bay to Nha Trang Bay), an area in and around the Con Dao Islands, located off the southern tip of Vietnam, and a region in and around the Phu Quoc Islands, located off the southwestern coast in the Gulf of Thailand, although a weak separation of populations has been found between the Con Dao Islands and Phu Quoc Islands (Dang et al., 2014). Similar patterns have been reported for the ornate spiny lobster (*Panulirus ornatus*) in Southeast Asia (Dao et al., 2015) and for a complex of mullet species, *Mugil cephalus*, in Vietnam (Tran et al., 2017).

The goldlined spinefoot, also known as the *orange-spotted spinefoot* and the *golden rabbitfish*, is 1 of 28 species in the Indo-Pacific family Siganidae. It is widely distributed in shallow-water habitats (including lagoons and river mouths, mangrove swamps, seagrass beds, coral reefs, and sandy and rocky bottoms) to a depth of 6 m in the eastern Indian Ocean and the Indo-West Pacific Ocean (Woodland, 1990; Duray, 1998; Froese and Pauly, 2021). This species is one of the most economically important commercial fishes in tropical and subtropical regions. It has attracted attention from the aquaculture industry in the Indo-Pacific and in the Indian Ocean (Lam, 1974; Randall et al., 1990). Juveniles settle in seagrass beds in lagoons and estuaries during certain periods of the year (Kami and Ikehara, 1976), whereas adults are found in coral reefs (Froese and Pauly, 2021). Because this species has a complex life cycle with linkages to different habitats at different stages, understanding the genetic structure of populations of the goldlined spinefoot is important for developing effective strategies for its proper and sustainable management.

On the western side of the South China Sea, the coastline of Vietnam spans 14° of latitude and extends for 3260 km. The coastal waters support more than 156,000 ha

of mangroves (Do et al., 2005) and 17,000 ha of seagrass beds (Luong et al., 2012), and coral reefs are mainly distributed along the coast and around the adjacent islands over a total area of about 13,400 ha (Nguyen and Vo, 2014; Nguyen et al., 2019). In Vietnam, juvenile goldlined spinefoot have been recruited to seagrass beds and mangrove swamps in the coastal lagoons and estuaries in the central part of the country from Thua Thien Hue Province (which includes Tam Giang–Cau Hai and Lap An Lagoons) to Binh Dinh Province (where Thi Nai Lagoon is located) (Le and Le, 2006). Large numbers have been observed settling during the dark phase of the moon in the summer months from May to August (from day 20 in one month to day 5 in the next month) and sometimes in to September (Le and Le, 2006; Nguyen and Mai, 2018). Adults have been found in the major coral reefs along the coast and around nearshore islands (Nguyen and Mai, 2020). Large schools of juvenile goldlined spinefoot have been caught by purse seine, lift net, stow net, and long trap cage along the coast of Vietnam, including in Thi Nai Lagoon (8.58 million juveniles in 2008) (Nguyen et al., 2010) and in Thu Bon estuary (780 kg, equivalent to 7.02 million juveniles, in 2015) (Nguyen and Mai, 2018). However, data at a larger spatial scale on the distribution of juveniles and broodstocks is lacking, and such information is needed for effective management of this resource in Vietnam.

The aims of this study were as follows: 1) to assess the juvenile yield and adult abundance (broodstock) of goldlined spinefoot; 2) to determine the genetic diversity, structure, and linkages of juvenile goldlined spinefoot collected in coastal estuaries and lagoons and of broodstock collected in coral reefs in coastal waters of Vietnam; and 3) to provide a baseline for future management decisions regarding this species in Vietnam.

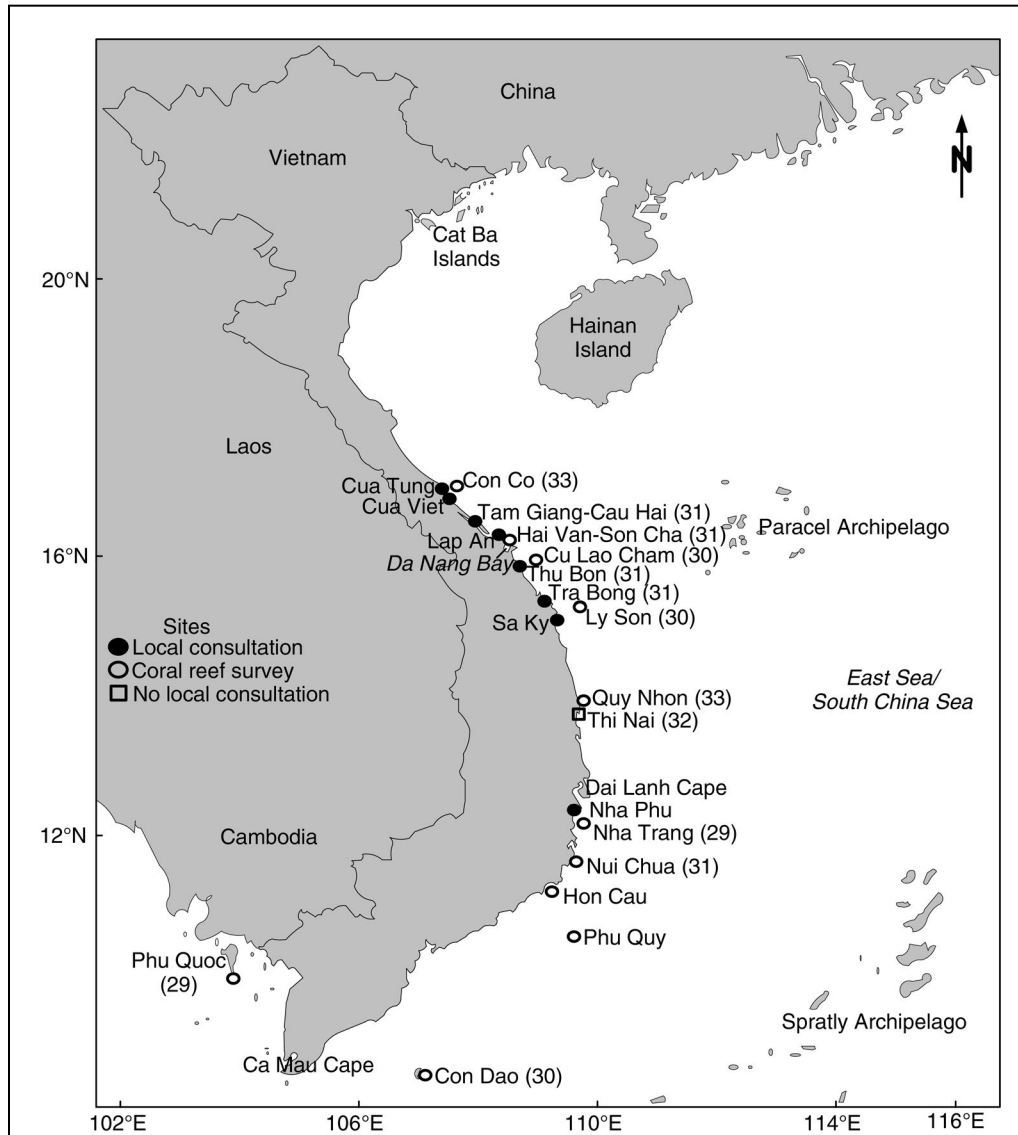
## Materials and methods

### Sampling strategies

**Assessments of juvenile yield** Assessments of the yield of juvenile goldlined spinefoot were conducted through consultations with local communities. The word *juvenile* is used herein for the specimens of goldlined spinefoot, with total lengths (TLs) of 18–45 mm, collected by fishermen for the aquaculture industry. Although there are some limits to accuracy, information and data collected through local consultations, including local ecological knowledge, have been widely used in many countries around the world where accurate scientific data are insufficient (Begossi, 2015; Berkström et al., 2019). Data from local consultations have been considered *semi-quantitative data* for rapid assessments of the status of habitats and related resources that contribute to providing a comprehensive baseline for appropriate planning and sustainable utilization of resources in Latin American countries (Fischer et al., 2015). The local consultations were conducted at 8 fishing communities near major estuaries and lagoons along the coast of Vietnam in November and

December 2019 under a national project. The 8 locations where consultations were conducted are Cua Tung estuary, Cua Viet estuary, Tam Giang–Cau Hai Lagoon, Lap An Lagoon, Thu Bon estuary, Tra Bong estuary, Sa Ky estuary, and Nha Phu Lagoon (Fig. 1).

For each consultation, biological scientists from the Institute of Oceanography, Vietnam Academy of Science and Technology (VAST), together with local authorities selected 10–20 consultants, including experienced fishermen that use different fishing gears, local dealers, and



**Figure 1**

A map of the locations where local consultations regarding goldlined spinefoot (*Siganus guttatus*) (black circles) or coral reef surveys of reef fish taxa (open circles) were conducted along the coast of Vietnam. Yield of juveniles (18–45 mm total length [TL]) was assessed through local consultations at 8 fishing communities near major estuaries or lagoons in November and December 2019. Density of adult (>100 mm TL) goldlined spinefoot was assessed at 11 locations at coral reefs in established or proposed conservation areas during July–September 2020 as part of this study (Con Co Island, Hai Van–Son Cha, the Ly Son Islands, and Nha Trang Bay) or from 2017 through 2021 under support from other projects (the Cu Lao Cham Islands, Quy Nhon Bay, Nui Chua National Park, Hon Cau Island, the Phu Quy Islands, the Con Dao Islands, and the Phu Quoc Islands). For DNA analysis, goldlined spinefoot were sampled from 2017 through 2020: juveniles from 3 locations in an estuary or a lagoon where consultations occurred, as well as from Thi Nai Lagoon, and adults from 9 locations at coral reefs where surveys were conducted. The numerals in parentheses indicate the number of specimens that were collected at each of these 13 sites.

marine aquaculturists, to provide the needed information. Questions were focused on fishing activities for the juvenile yield of goldlined spinefoot and designed to gather the following information: fishing gear and seasons; number of fishing boats; number of fishermen per fishing boat; and catch per unit of effort (CPUE), defined as catch per boat per day or night.

**Assessments of adult abundance** The density of adult goldlined spinefoot was assessed together with those of other groups of reef fishes at 11 widely distributed locations at coral reefs that have been established as MPAs (Con Co Island, the Cu Lao Cham Islands, Ly Son the Islands, Nha Trang Bay, Nui Chua National Park, Hon Cau Island, the Con Dao Islands, and the Phu Quoc Islands) or are being proposed as MPAs (Hai Van–Son Cha and the Phu Quy Islands) or locally managed marine area (Quy Nhon Bay) in Vietnam. The recorded sizes of adult goldlined spinefoot collected on coral reefs were >100 mm TL. Census surveys were conducted at 4 locations—3 sites off the central part of the eastern coast, Con Co Island, Hai Van–Son Cha, and the Ly Son Islands, and 1 site farther south in Nha Trang Bay—during July–September 2020 within the framework of this project and at 7 other locations—2 sites off the central part of the eastern coast in 2017 at the Cu Lao Cham Islands and in Quy Nhon Bay, 3 sites farther south at Nui Chua National Park in 2018, Hon Cau Island in 2020, and the Phu Quy Islands in 2021, 1 site at the Con Dao Islands in 2018, and 1 site at the Phu Quoc Islands in 2019—under support from other projects (Table 1, Fig. 1). At each study site, 2 transects, each 100 m long, were placed haphazardly in 2 reef zones (1 transect on a reef flat and 1 transect on a reef slope) parallel to the shoreline. The depths below low tide level at transects were approximately 2–4 m at reef flats and 5–12 m at reef slopes. Each 100-m transect was divided into 4 replicates (each 20 m long by 5 m wide). Hence, 8 replicate transects were surveyed at each study site.

Along the transect line, the fish observer used scuba gear and swam slowly to count the number of individuals and to estimate the size (TL) of each individual fish from visual estimates using the methods proposed by English et al. (1997) and Hodgson et al. (2006). Fish were identified to species level by using Randall et al. (1990). The survey time at each site was about 50–60 min. The surveys were all carried out during daylight hours between 0900 and 1400 local time. To avoid disturbance from divers, fish surveys were conducted 15 min after the first transect was placed.

**Assessments of genetic diversity and structure** The sequence data used in this study are from fish specimens that were collected from 4 locations at estuaries and lagoons and from 9 locations at coral reefs in the coastal waters of Vietnam from 2017 through 2020 under support from different projects (Fig. 1). Three locations in an estuary or a lagoon, including Tam Giang–Cau Hai Lagoon, Tra Bong estuary, and Thi Nai Lagoon, and 4 locations at coral reefs, including Con Co Island, Hai Van–Son Cha, the Ly Son Islands, and Quy Nhon Bay, were sampled from 2019

through 2020 as part of this study. Thu Bon estuary and the Cu Lao Cham Islands were sampled in 2017 for a study supported by the VAST, and 4 other reef locations, including Nha Trang Bay, Nui Chua National Park, the Con Dao Islands, and the Phu Quoc Islands, were sampled from 2018 through 2019 as part of a study funded by the U.S. Agency for International Development. Because information on occurrence and distribution of juvenile goldlined spinefoot at Nha Phu Lagoon and other lagoons and estuaries off the southern coast was not yet available prior to the designing of sampling for this study, samples were not collected at these locations.

Fish samples were collected by using cast nets and by purchasing specimens at fish landing sites. At each location, 29–33 goldlined spinefoot were collected in estuaries or lagoons (29–105 mm TL) and at coral reefs (202–340 mm TL). A total of 401 individuals (125 juveniles and 276 adults) were sampled.

For each individual, a 1-cm<sup>2</sup> section of the right pectoral fin and a 1-cm<sup>2</sup> section of the upper caudal fin were cut out with fine scissors, washed with water, and immediately fixed in a solution of 95% alcohol in a 2-mL screw-cap tube labeled with species name, code, and preservation solution. Then, these fin samples were cooled and stored frozen at –20°C for further analysis in the laboratory.

Samples of DNA were extracted by using the cetyltrimethylammonium bromide method (Adamkewicz and Harasewych, 1996) and preserved in Tris-EDTA buffer solution (10 mM Tris-HCl, pH 7.2, 1 mM EDTA, pH 8.0) at –20°C. The concentration and purity of the extracted DNA were tested on 1.5% agarose gel and on a spectrophotometer (BioSpec-nano<sup>1</sup>, Shimadzu Corp., Kyoto, Japan). The use of microsatellites or single sequence repeats was referenced from existing studies of molecular biology and population genetics for goldlined spinefoot. In this study, 5 microsatellites used for population genetic analyses of goldlined spinefoot and suggested by Mao et al. (2016) were applied: HLZY-3 (F: TAACGGTTCTATCAGGG and R: TGCTTCGGATTTCAGG at 55°C), HLZY-5 (F: TTCATCACTGCCTGTCCTT and R: AGCGTGTCATTGTTGGT at 62°C), HLZY-12 (F: CGGACCTGCTTGAGT and R: AACCTGTTTGGTGGAA at 47°C), HLZY-13 (F: TGGCAGTGATGAGGTG and R: CATTTGGAATCGCAGT at 57°C), and HLZY-21 (F: CTGACTCCCAACTTCC and R: CAGACCTGTTTCCAATC at 52°C).

Five forward and reverse primer pairs were run through the polymerase chain reaction (PCR) process, in which primers were marked by HEX or FAM fluorescence staining at the 5' end. The PCR amplification was performed with a BOECO Thermal Cycler TC-PRO (Boeckel and Co. GmbH and Co., Hamburg, Germany). The PCR reaction was performed at a total volume of 50 µL, including 10 µL of buffer, 0.2 µL Bioline MyTaq HS Polymerase (Meridian Bioscience, Cincinnati, OH), 0.4 µM of each primer, and 5 ng of the template DNA. The PCR process for microsatellites

<sup>1</sup> Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

**Table 1**

The number of sites at which visual census surveys for adult goldlined spinefoot (*Siganus guttatus*), among other reef fish species, were conducted at each of 11 locations at coral reefs along the coast of Vietnam during 2017–2021. At the time of this study, all locations either had been established or were being proposed as marine protected areas (MPAs) or locally managed marine area. An asterisk (\*) indicates that the location was an established MPA.

Location	No. of sites surveyed	Time of surveys	Sources
Con Co*	10	August 2020	This study
Hai Van–Son Cha	10	July 2020	This study
Cu Lao Cham*	10	July 2017	Nguyen et al. <sup>1</sup>
Ly Son*	10	September 2020	This study
Quy Nhon Bay	24	April 2017	Nguyen <sup>2</sup>
Nha Trang Bay*	10	July 2020	This study
Nui Chua*	10	September 2018	Mai and Nguyen <sup>3</sup>
Hon Cau*	12	August 2020	Hoang et al. <sup>4</sup>
Phu Quy	11	April 2021	Nguyen et al. <sup>5</sup>
Con Dao*	9	June 2018	Mai and Nguyen <sup>3</sup>
Phu Quoc*	10	April 2019	Nguyen <sup>6</sup>

<sup>1</sup> Nguyen, V. L., T. H. Dao, X. D. Mai, T. K. H. Phan, and H. T. Nguyen. 2020. Studies on population connectivity of target fishes among marine habitats in the World Biosphere Reserve of Cu Lao Cham–Hoi An. Final report for the Vietnam Academy of Science and Technology project VAST06.02/17-18, 24 p. [In Vietnamese.] [Available from Inst. Oceanogr., Vietnam Acad. Sci. Tech., 01 Cau Da St., Nha Trang 650000, Vietnam.]

<sup>2</sup> Nguyen, V. L. 2017. Additional assessments and identification of locations with high marine biodiversity in the Quy Nhon Bay. Final report of the project CRSD/BD/3.d.4.1/2016 under the provincial project “Resources in coastal waters for sustainable development (CRSD) in Binh Dinh Province,” 142 p. [In Vietnamese.] [Available from Inst. Oceanogr., Vietnam Acad. Sci. Tech., 01 Cau Da St., Nha Trang 650000, Vietnam.]

<sup>3</sup> Mai, X. D., and L. V. Nguyen. 2021. Status and trends of change of reef fish communities at some locations in the coastal waters of south Vietnam in the period of 2017–2019. Technical report of the project titled, “Study on coral reef resilience in comparative areas in south Vietnam for marine biodiversity conservation in a changing world” (project code: AID-OAA-A-11-0012), 60 p. [In Vietnamese.] [Available from Dep. Mar. Living Resour., Inst. Oceanogr., Vietnam Acad. Sci. Tech., 01 Cau Da St., Nha Trang 650000, Vietnam.]

<sup>4</sup> Hoang, X. B., T. K. H. Phan, K. H. Phan, X. D. Mai, and M. Q. Thai. 2020. Status and trends of change in marine biodiversity and related resources at key sites in the Hon Cau Marine Protected Area. Technical report of the project titled, “Advice on the planning of review, re-zoning, and boundary of Hon Cau Marine Protected Area, Binh Thuan Province,” 57 p. [In Vietnamese.] [Available from Dep. Mar. Living Resour., Inst. Oceanogr., Vietnam Acad. Sci. Tech., 01 Cau Da St., Nha Trang 650000, Vietnam.]

<sup>5</sup> Nguyen, T. H., M. Q. Thai, X. D. Mai, and B. X. Hoang. 2022. Assessments of status of marine biodiversity and related resources in key marine habitats (coral reefs, seagrass beds) in the waters surrounding Phu Quy district. Technical report of the project titled “Advice on the development of the project for the establishment of Phu Quy Marine Protected Area, Binh Thuan Province” (project code: 01-DABTBPQ) 50 p. [In Vietnamese.] [Available from Dep. Mar. Living Resour., Inst. Oceanogr., Vietnam Acad. Sci. Tech., 01 Cau Da St., Nha Trang 650000, Vietnam.]

<sup>6</sup> Nguyen, V. L. 2019. Assessments of marine biodiversity and re-zoning for management of Phu Quoc Marine Protected Area. Final report of provincial project submitted to the Department of Agriculture and Rural Development of Kien Giang Province, 310 p. [In Vietnamese.] [Available from Inst. Oceanogr., Vietnam Acad. Sci. Tech., 01 Cau Da St., Nha Trang 650000, Vietnam.]

or single sequence repeats had six stages. The first stage was the initial denaturation at 95°C for 1 min, followed by 35 cycles of denaturation at 95°C for 15 s, an annealing phase at a suitable temperature for each primer for 15 s, and an extension phase at 72°C for 90 s. Then, the final extension phase began at 72°C for 10 s and ended at 20°C

for 60 s. The PCR products were then run on 1.6% agarose gel/100 mL TBE buffer (0.5×) with 1.0 µL gelled and detected by ultraviolet transilluminator (UVP DigiDoc-It, Analytik Jena GmbH, Jena, Germany) prior to genotyping on an Applied Biosystems 3730XL DNA Analyzer (Thermo Fisher Scientific, Waltham, MA).

## Data storage and analysis

Annual yield of juveniles was calculated as follows: number of boats multiplied by fishing time multiplied by average yield per time unit (CPUE).

The density of fish at each study site was calculated as the mean value of the 8 replicates from the 2 transects on the reef flat and reef slope. To improve the homogeneity of variances, raw data on abundance of adults was  $\log_{10}(x+1)$  transformed prior to the analyses. When the analysis of variance detected significant differences, Tukey's honestly significant difference test was applied in order to separate differences between locations.

The software GeneMarker, vers. 2.7.4 (SoftGenetics, State College, PA), was used to determine the length of alleles. Null alleles were detected by using the software Micro-Checker, vers. 2.2.3 (Van Oosterhout et al., 2004). Genetic variability estimates for each locus, such as those made by using the Hardy–Weinberg equilibrium, number of alleles on each satellite, number of rare alleles, observed heterozygosity, and expected heterozygosity were calculated by using the software GenAlEx 6.1 (Peakall and Smouse, 2006). The statistical significance tests for these indices were revised on the basis of the Bonferroni correction (Rice, 1989).

Evaluation of differences between groups in genetic structure (fixation index [ $F_{ST}$ ] and pairwise  $F_{ST}$ ) was done through analysis of molecular variance with Arlequin, vers. 3.11 (Excoffier et al., 2005). We used the model-based clustering method in the software Structure, vers. 2.3.4 (Pritchard et al., 2000), to elucidate the group structure and visualized results in images by using the program Structure Harvester, vers.0.6.94 (Earl and vonHoldt, 2012). In the model of the software Structure, a Bayesian approach is applied to estimate the probability of correctly assigned genotypes in the data in the number of clusters ( $K$ ). Each value of  $K$  (1–10 clusters) was run for 10 repetitions, and the average log probability of the data,  $L(K)$ , was calculated. The  $L(K)$  plateaued (or continued to increase slightly) when  $K$  approached the true value, and high variance between runs also occurred (Rosenberg et al., 2001). The number of  $K$  groups was then evaluated by using  $\Delta K$ , an ad hoc statistic based on the second order rate of change of  $L(K)$  (Evanno et al., 2005).

## Results

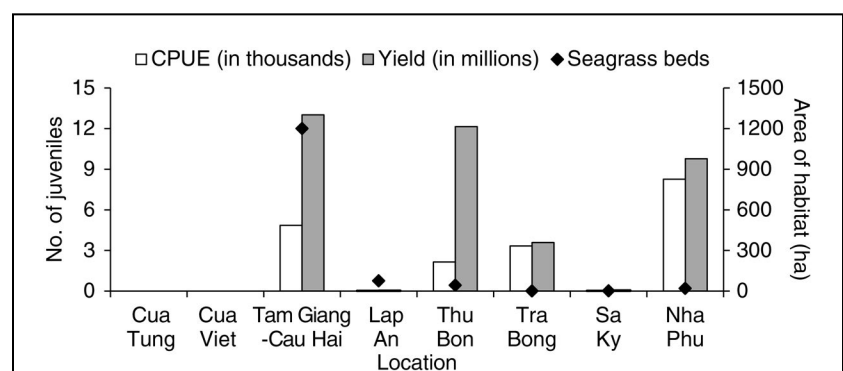
### Juvenile yield

Information for the local consultations at 8 locations in estuaries and lagoons indicates that juvenile goldlined spinefoot were collected only from Tam Giang–Cau Hai Lagoon (in Thua Thien Hue Province) to south-central Vietnam, with 38.61 million juveniles (equivalent

to 4290 kg) collected in 2019. Among the 8 locations, the 3 most important locations, including Tam Giang Cau–Hai Lagoon, Thu Bon estuary, and Nha Phu Lagoon, supported high CPUE (215,000–826,000 juveniles per boat per day) and yield (9.77–13.01 million juveniles). The locations of Lap An Lagoon and Sa Ky estuary supported the lowest CPUE (0.03–0.04 juveniles per boat per day) and yield (<1 million juveniles at each location) (Fig. 2). In general, juvenile goldlined spinefoot were found in lagoons and estuaries that had seagrass beds, with an exception of Tra Bong estuary. However, there was no correlation between the area of seagrass beds and both CPUE and yield of juveniles of this species (Fig. 2). Information from local fishermen indicates that juvenile goldlined spinefoot were also found in the Cua Tung and Cua Viet estuaries (in Quang Tri Province). However, because they occurred in very low numbers, the local fishermen did not make an effort to collect them.

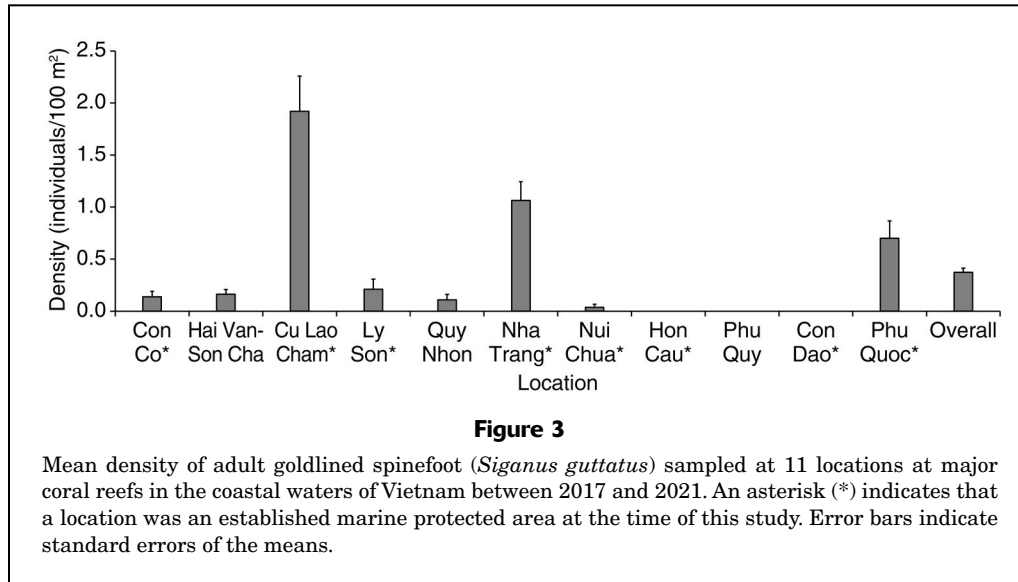
### Abundance of adult stock

Results of an analysis of data from 138 sites at 11 reef locations in the coastal waters of Vietnam that were surveyed during 2017–2021 indicate that the overall mean density of goldlined spinefoot was 0.37 fish/100 m<sup>2</sup> (standard error of the mean [SE] 0.04), with the sites in MPAs supporting a significantly higher mean density (0.51 fish/100 m<sup>2</sup> [SE 0.06]) than that of the sites that were not in MPAs (0.09 fish/100 m<sup>2</sup> [SE 0.03]) (analysis of variance:  $P < 0.001$ ). Among the sites in MPAs, the mean densities in the Cu Lao Cham, Nha Trang Bay, and Phu Quoc MPAs were 3.3–51.2 times higher than and significantly different (analysis of variance:  $P < 0.001$ ) from those in other MPAs (the Con Co, Ly Son, and Nui Chua MPAs) and those in sites not in MPAs (Hai Van–Son Cha and Quy Nhon Bay) (Fig. 3). No goldlined spinefoot were recorded at the Hon Cau MPA, the Phu Quy Islands (proposed MPA),



**Figure 2**

The relationship between catch per unit of effort (CPUE) and yield of juvenile goldlined spinefoot (*Siganus guttatus*) in major estuaries and lagoons along the coast of Vietnam, based on local consultations conducted in 8 fishing communities during November and December 2019. The black diamonds indicate the locations that had seagrass beds and the extent of these habitats.



and the Con Dao MPA. The reef locations that supported higher densities of adult goldlined spinefoot (the Cu Lao Cham and Nha Trang Bay MPAs) than other reef locations are closer geographically to the lagoons and estuaries with higher juvenile yield (Thu Bon estuary and Nha Phu Lagoon). However, sites not in MPAs (Hai Van–Son Cha and Quy Nhon Bay) supported much lower densities than MPA sites despite their proximity to Tam Giang–Cau Hai and Thi Nai Lagoons, which had very high juvenile yield for collections made in this study (Fig. 3).

**Genetic diversity and structure**

Results of analysis of sequence data for 347 samples from 401 specimens collected from 13 locations indicate that the total number of alleles of 5 microsatellites was 110, of which 32 alleles were private (Table 2). Among the 5 microsatellites, HLZY-12 had the highest alleles per locus (36), followed by 25, 22, 18, and 9 alleles per locus for HLZY-13, HLZY-5, HLZY-21, and HLZY-3, respectively. The population of goldlined spinefoot in the Phu Quoc Islands appears to be the most diverse, given that samples from specimens caught at that location had the highest number of alleles (73) compared with the numbers of alleles for samples from specimens collected at the other locations (41–57). The samples from fish caught at Phu Quoc Islands also had the highest number of private alleles (20). The values of observed heterozygosity and expected heterozygosity of each single sequence repeat varied slightly between locations, ranging from 0.33 to 1.00 and from 0.49 to 0.92, respectively (Fig. 4). In general, there was no deviation from the Hardy–Weinberg equilibrium in sequence data for most locations, with some exceptions for microsatellite HLZY-3 (Thu Bon estuary, Thi Nai Lagoon, and the Phu Quoc Islands), HLZY-5 (Hai Van–Son Cha, the Cu Lao Cham Islands, Thi Nai Lagoon, Quy Nhon Bay, and Nha Trang Bay), HLZY-12 (the Cu Lao Cham Islands),

HLZY-13 (Con Co Island, the Con Dao Islands, and the Phu Quoc Islands), and HLZY-21 (Hai Van–Son Cha, Tra Bong estuary, and Nui Chua National Park) (Table 3).

**Genetic linkages among marine habitats**

The results of the analyses of molecular variance indicate a significant difference in genetic structure ( $F_{ST}=0.015$ ,  $P<0.05$ ) among genetic groups, a central group (specimens from Con Co Island to Quy Nhon Bay), a southern group (specimens from Nha Trang Bay to the Con Dao Islands), and a southwestern group (specimens from the Phu Quoc Islands), at the sampling locations with a low percentage of genetic variation (1.5%; Table 4). Results from comparison of pairwise  $F_{ST}$  values indicate that genetic differentiation occurred at all locations (at levels of 1.2–6.5%) and that the difference was significant ( $P<0.05$ ). Generally, results from analyses of molecular variance reveal that there were 2 distinct groups in the genetic structure of collected goldlined spinefoot among the 13 sampling locations: a central group that included specimens from Con Co Island to Quy Nhon Bay and a southern group that included fish caught from Nha Trang Bay south and all the way around to the Phu Quoc Islands on the southwestern coast, with the genetic similarity among locations within each group reaching 99–100%. This genetic similarity indicates that genetic linkages occurred only within each group.

The results from Bayesian analysis (done with the software Structure) indicate that  $\Delta K$  ranged from 0.018305 to 0.774668 when  $K$  was set from 1 to 8. The clearest peak in  $\Delta K$  occurred when  $K$  was set to 3, with a value of 0.774668, indicating that 3 distinct genetic clusters (assigned the colors of green, red and blue in visualizations) existed in goldlined spinefoot among the sampling locations (Fig. 5). The central group included specimens from Con Co Island to Quy Nhon Bay, with most fish having the majority of their genome assigned to the green cluster (Fig. 5). The southern

**Table 2**

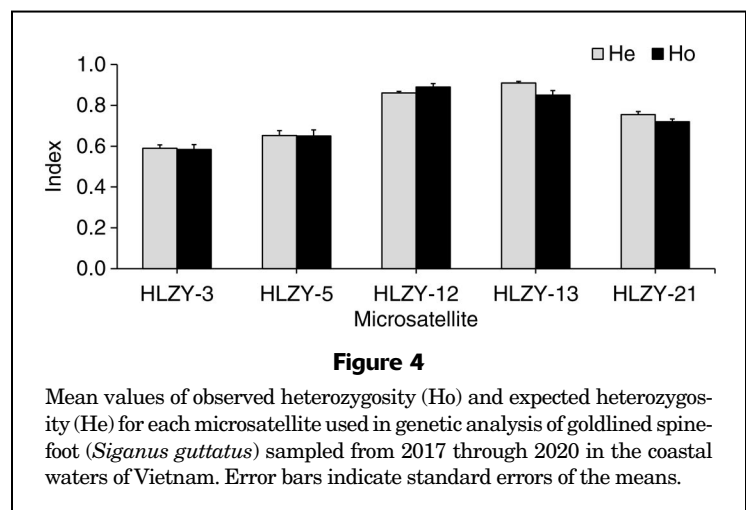
Total number of alleles and private alleles for each microsatellite found in sequence data from goldlined spinefoot (*Siganus guttatus*) sampled from 2017 through 2020 in the coastal waters of Vietnam. Sites where fish were collected include the following locations at estuaries, lagoons, or coral reefs: Con Co Island (CCO), Tam Giang–Cau Hai Lagoon (TAG), Hai Van–Son Cha (HVS), Thu Bon estuary (THB), the Cu Lao Cham Islands (CLC), Tra Bong estuary (TBO), the Ly Son Islands (LSO), Thi Nai Lagoon (TNA), Quy Nhon Bay (QNH), Nha Trang Bay (NTR), Nui Chua National Park (NCH), the Con Dao Islands (CDA), and the Phu Quoc Islands (PQU).

Sampling location	Microsatellite					Total
	HLZY-3	HLZY-5	HLZY-12	HLZY-13	HLZY-21	
<b>Alleles</b>						
CCO	4	5	12	12	8	41
TAG	6	7	15	14	6	48
HVS	4	6	14	17	8	49
THB	5	9	12	15	8	49
CLC	4	7	14	16	10	51
TBO	4	7	11	16	9	47
LSO	4	7	13	16	10	50
TNA	5	8	16	14	9	52
QNH	5	11	15	15	11	57
NTR	3	7	14	15	9	48
NCH	5	6	11	15	11	48
CDA	5	6	11	16	9	47
PQU	7	14	22	16	14	73
Total	9	22	36	25	18	110
<b>Private alleles</b>						
THB			1			1
CLC		2				2
LSO					1	1
QNH	1	4	3			8
PQU	2	3	6	6	3	20
Total	3	9	10	6	4	32

group was composed of individuals caught at locations from Nha Trang Bay to the Con Dao Islands, forming the red cluster (Fig. 5). The southwestern group, consisting of specimens caught off the Phu Quoc Islands, formed the blue cluster (Fig. 5).

## Discussion

The results of this study indicate that the central coast of Vietnam supported the highest yield of juvenile goldlined spinefoot in 2019, with higher yield recorded at Tam Giang–Cau Hai Lagoon, Thu Bon estuary, Thi Nai Lagoon, and Nha Phu Lagoon compared to that at the other estuaries and lagoons. This greater level of yield may be related to the presence and structure of seagrass beds (Nagelkerken, 2009; Nguyen et al., 2015). In this study, CPUE had no correlation with areas of seagrass beds; therefore, differences in the composition of seagrass species may contribute to marked differences in the total yield of juvenile goldlined spinefoot among the lagoons and estuaries.

**Figure 4**

Mean values of observed heterozygosity (Ho) and expected heterozygosity (He) for each microsatellite used in genetic analysis of goldlined spinefoot (*Siganus guttatus*) sampled from 2017 through 2020 in the coastal waters of Vietnam. Error bars indicate standard errors of the means.

Higher densities of adult goldlined spinefoot were mainly found during coral reef surveys at the locations that have been established as MPAs rather than at locations where MPAs do not exist. This finding is consistent with those of other studies in which higher densities or



**Table 3**

*P*-values from tests for deviation from the Hardy–Weinberg equilibrium (HWE), by location for each microsatellite found in sequence data from goldlined spinefoot (*Siganus guttatus*) sampled from 2017 through 2020 in the coastal waters of Vietnam. An asterisk (\*) indicates a significant difference ( $P < 0.05$ ) from HWE. Sites where fish were collected include the following locations at estuaries, lagoons, or coral reefs: Con Co Island (CCO), Tam Giang–Cau Hai Lagoon (TAG), Hai Van–Son Cha (HVS), Thu Bon estuary (THB), the Cu Lao Cham Islands (CLC), Tra Bong estuary (TBO), the Ly Son Islands (LSO), Thi Nai Lagoon (TNA), Quy Nhon Bay (QNH), Nha Trang Bay (NTR), Nui Chua National Park (NCH), the Con Dao Islands (CDA), and the Phu Quoc Islands (PQU).

Sampling location	Microsatellite				
	HLZY-3	HLZY-5	HLZY-12	HLZY-13	HLZY-21
CCO	0.45	0.81	0.82	0.02*	0.36
TAG	0.59	0.63	0.89	0.22	0.26
HVS	0.91	0.03*	0.60	0.79	0.02*
THB	0.02*	1.00	0.74	0.16	0.21
CLC	0.27	0.00*	0.00*	1.00	0.56
TBO	0.95	0.48	0.49	0.14	0.00*
LSO	0.95	1.00	0.68	0.33	0.33
TNA	0.01*	0.01*	0.53	0.72	1.00
QNH	0.99	0.00*	0.30	0.96	0.61
NTR	0.99	0.00*	0.45	0.24	0.23
NCH	0.62	0.99	0.35	0.11	0.02*
CDA	0.99	0.73	0.54	0.01*	0.09
PQU	0.00*	0.84	0.74	0.00*	0.55

**Table 4**

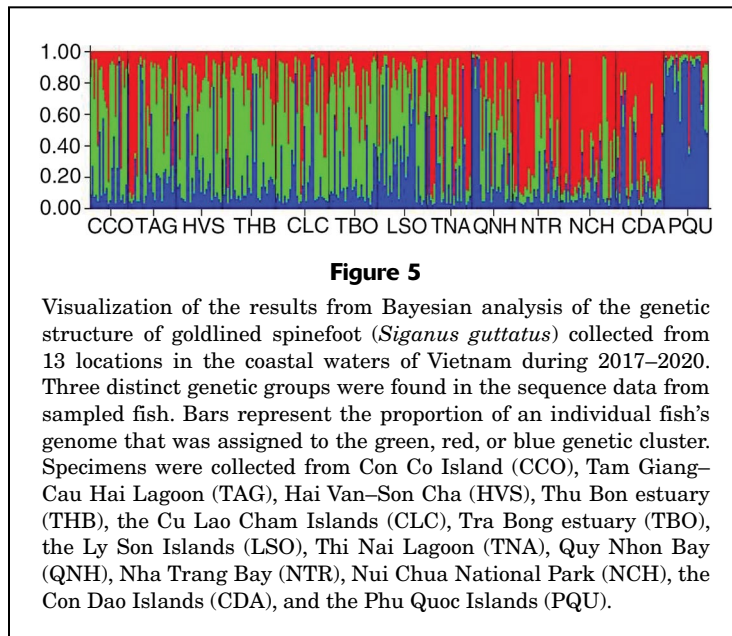
Summary of results from analyses of molecular variance that indicate differences in genetic variation among and within distinct genetic groups of goldlined spinefoot (*Siganus guttatus*). Sequence data used in analyses are from specimens collected in the coastal waters of Vietnam during 2017–2020. The fixation index was 0.015.

Source of variation	df	Sum of squares	Mean of squares	Estimate of variation	Percentage of variation (%)
Among populations	2	23.756	11.878	0.060	1.5
Within populations	344	705.852	2.051	0.114	98.5
Total	693	1362.108		1.997	100.0

abundances and higher levels of biomass of target species were recorded inside MPAs as opposed to outside MPAs (Russ and Alcala, 2003; Maliao et al., 2009). However, the overall densities of goldlined spinefoot in MPAs were very low (with a mean of 0.51 fish/100 m<sup>2</sup>), and these populations may take a long time to recover to a high level of abundance. An effort to protect and conserve broodstocks at some MPAs with higher densities of goldlined spinefoot, especially at the Cu Lao Cham, Nha Trang Bay, and Phu Quoc MPAs, is an important measure that can be used by resource managers in the short term, and conservation at other MPAs can be useful in the longer term as well,

because MPAs play an key role in enhancing local fisheries outside MPAs through either net movement or net export of larvae from MPAs (Russ, 2002).

The differentiation in population genetics of goldlined spinefoot between the central and southern groups is consistent with results of some previous studies, indicating that an oceanographic boundary limits the genetic dispersal between the areas where these groups were found. Ablan et al. (2002) studied the genetic structure of threespot dascyllus and suggested that the South China Sea may be divided into 2 distinct parts on the basis of the differentiation in population genetics with geographical



boundaries located in south-central Vietnam close to Nha Trang Bay. A notable division in the genetic structure of goldlined spinefoot found in this study at the Phu Quoc Islands is in accordance with findings of the previously mentioned studies (Ablan et al., 2002; Dang et al., 2014). In addition, the results from recent studies based on analyses of communities of reef-building corals also indicate a separation in the distribution between the central and the southern groups, with a geographical boundary located at Dai Lanh Cape (at about 13°N) near the city of Tuy Hoa, and between the southern and southwestern groups at Ca Mau Cape (at about 8°N) at the southernmost tip of Vietnam (Vo, 2014; Vo and Nguyen, 2022).

The discharge of the Mekong River (Dang et al., 2014), which acts as an oceanographic barrier to the dispersal of marine planktonic larvae, could be one explanation for the separation of reef fish communities between the southwestern group in the Gulf of Thailand and the central and southern groups in the South China Sea. The recent results from oceanographic modeling indicate that a weak current flowed from the Gulf of Thailand (at the Phu Quoc Islands) to the Con Dao Islands, compared to a strong current from the Java Sea through the Karimata Strait, in Malaysia, up to the mouth of the Gulf of Thailand and over to the Con Dao Islands during the southwest monsoon (July–September), and that a weak current flowed from the Con Dao Islands to the Phu Quoc Islands, compared to a strong current from the Luzon Strait, between Taiwan and the Philippines, east to Hainan Island, in China, and down along the coast of Vietnam through the Con Dao Islands, to Malaysia and the Karimata Strait during the northeast monsoon (January–March) (Li et al., 2019). These currents may limit the larval dispersal of goldlined spinefoot and other marine organisms. Our findings on the separation of the 3 genetic groups are similar to the findings of distinct populations of this species sampled in

Japan off Okinawa Island, Miyako Island, and Ishigaki Island on a geographical scale of about 100–2000 km (Iwamoto et al., 2009).

The spatial genetic structure found in our study for this species in the coastal waters of Vietnam could be related to differences in biological characteristics (Froukh and Kochzius, 2007). Larvae of goldlined spinefoot are in the pelagic stage, which lasts for about 24 d (Juario et al., 1985; Sheaves, 1995; Nabhitabhata and Ikeda, 2014). This factor may be the one that limits the dispersal of this species because larval dispersal of goldlined spinefoot is mainly driven by currents or tides (Kanashiro et al., 1999) and by seawater temperature (Collins and Nelson, 1993). The numbers of alleles for groups of goldlined spinefoot were similar between sampling locations, with the exception that the numbers for groups based on analysis of samples taken from specimens collected at the Phu Quoc Islands are twice as high as those for groups in other locations. This result indicates that there is distinguishable genetic diversity in this species at the Phu Quoc Islands. Therefore,

the Phu Quoc Islands may be considered another functional location because of the differentiation in population genetics of this species. The differences in characteristics mentioned for goldlined spinefoot at the Phu Quoc Islands may play important roles in the creation of the differentiation in population genetics among distinct groups.

## Conclusions

The coastal lagoons and estuaries in Vietnam with seagrass beds (especially, Tam Giang–Cau Hai Lagoon, Nha Phu Lagoon, and Thu Bon estuary) supported high yield of juvenile goldlined spinefoot, and the nearby MPAs (the Cu Lao Cham and Nha Trang Bay MPAs) had higher densities of adults of this species. There were 3 distinct genetic groups, with the central group including specimens from Con Co Island to Quy Nhon Bay, the southern group including individuals collected from Nha Trang Bay to the Con Dao Islands, and the southwestern group including fish from the Phu Quoc Islands in the Gulf of Thailand. Establishment of MPA networks on the basis of both ecological and social interconnectivity among crucial marine habitats, such as coral reefs, seagrass beds, and mangroves, is important because such efforts could help ensure that as many genetic units as possible are maintained for the overall resilience of fisheries. Creating networks of MPAs can further enhance the effectiveness of MPAs in protecting spawners in coral reefs and in increasing the survivorship of recruits in seagrass beds and mangroves in coastal lagoons and estuaries.

## Resumen

Las evaluaciones del estado de las especies objetivo de la pesca y sus vínculos ecológicos con los hábitats marinos

están desempeñando un papel importante en mejorar la efectividad de las áreas marinas protegidas (AMP) y el manejo de otras zonas costeras. En este estudio, evaluamos el rendimiento de juveniles y la abundancia del sigano rayas doradas (*Siganus guttatus*) utilizando el conocimiento local y censos visuales en aguas costeras de Vietnam. La estructura genética se examinó mediante análisis de ADN de juveniles, colectados en pastos marinos y manglares en las principales lagunas y estuarios, y de adultos colectados en arrecifes de coral. Se colectados más de 38.6 millones de juveniles en 8 lagunas costeras y estuarios. Las lagunas costeras y los estuarios con pastos marinos albergaban un alto volumen de juveniles, y las AMP cercanas presentaban mayores densidades de adultos. Se identificaron tres grupos genéticos distintos: un grupo en la parte central de la costa oriental, desde la isla de Con Co hasta la bahía de Quy Nhon; un segundo grupo en la costa sudoriental, desde la bahía de Nha Trang hasta las islas Con Dao, situadas en el extremo sur de Vietnam; y un tercer grupo en la costa sudoccidental, en las islas Phu Quoc, en el golfo de Tailandia.

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