Importance of various marine coastal habitats during the life cycle of Spratelloides delicatulus in Con Dao, the oldest MPA in Vietnam

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▶ To cite this version:

HAL Id: hal-03411054

https://hal.umontpellier.fr/hal-03411054

Submitted on 17 Mar 2023

Importance of various marine coastal habitats during the life cycle of *Spratelloides delicatulus* in Con Dao, the oldest MPA in Vietnam

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Abstract

1. Marine protected areas (MPAs) are set up to conserve biodiversity, but their design is not always based on strictly scientific considerations. Ideally, an MPA should protect all key habitats necessary for a marine species to complete its life cycle. The identification of these key habitats is complex, especially during the early life of marine fishes.

2. A widely distributed tropical and important low trophic-level fish species, *Spratelloides delicatulus* (Clupeidae), was used to evaluate the significance of various coastal habitats for its larvae and juveniles in the Con Dao Archipelago MPA in Vietnam. Early stages (larvae and juveniles) were sampled monthly over one year (June 2016 to May 2017) using light traps in three main habitats (seagrass beds, coral reefs and harbour). The species was identified using morphometry and DNA barcoding. Age and growth variables were estimated using otolith daily growth increments.

3. A total of 3,581 fish were caught. The species was not found in captures between January and February, directly linked to the decrease in seawater temperature and was most abundant from April to June. For a subsample of 248 fish (7–38 mm standard length), ages ranged from 7 to 108 days.

4. Captures and back-calculated birthdates using otolith daily increments showed that *S. delicatulus* spawns during the period of high seawater temperature, from March to October. The species colonizes all three habitats during the early stages (0–26 days old), with growth rate lowest on the seagrass beds. Nevertheless, the species occupies seagrass beds exclusively during the older stages.

5. The conservation of seagrass beds in the Con Dao archipelago is essential for protection of juvenile stages of this species but this habitat is presently not included in the MPA patches. Establishment of a continuum of protected areas linking habitats, rather than the existing patches is needed to conserve the complete life cycle of this species in the Con Dao MPA.

KEYWORDS

Clupeidae, conservation, coral reef, growth, otolith, seagrass

1 | INTRODUCTION

Marine protected areas (MPA) are considered effective instruments to help mitigate the loss of marine biodiversity, including restoration of intensively fished stocks (Hiscock, 2008) and protection of particular key habitats (Bailey & Thompson, 2009; Evans, Peckett, & Howell, 2015). In tropical regions, coastal marine habitats such as seagrass beds, coral reefs and mangroves are considered to be nurseries for juvenile stages of many species (Igulu et al., 2014; Minello, Able, Weinstein, & Hays, 2003; Nagelkerken et al., 2000), thus, the protection of these habitats is essential. The Con Dao archipelago houses the oldest MPA in Vietnam, established in 1984 to conserve essential habitats, not for fisheries but for dugong (*Dugon dugong*), blue whales (*Neophon phocaenoides*), Irrawaddy dolphin (*Orcaella brevirostris*), green turtle (*Chelonia mydas*) and hawksbill sea turtle (*Eretmochelys imbricata*). Therefore, this MPA focuses on protecting a few patches of coastal waters (Figure 1) which correspond to separated habitats (mainly coral reefs and a few seagrass beds) where these threatened or endangered species are present. Fishing is still active in the different habitats of this MPA. The roles and functions of the various habitats in fish life cycles are unknown in this area, in particular, the use of habitats by early life stages of various fish species and habitat connectivity during the fish life cycle.

The blue sprat *Spratelloides delicatulus* (Bennett, 1832) is a low-trophic-level fish species, and important prey for many predators such as *Lutjanus vitta*, *Auxis thazard*, *Megalaspis cordyla* and *Scomberoides lysan* (Blaber, Milton, Rawlinson, Tiroba, & Nichols, 1990). It is abundant along the Vietnamese coasts (Le & Vo, 2013) and more generally in the Indo-Pacific Ocean, from Southeast Africa to Southern Japan and Southern Australia (Whitehead, 1985). This species is important in live-bait fisheries in the Solomon Islands, the Maldives and the Laccadive Sea (India) (Pillai et al., 1986; Milton, Blaber, Rawlinson, Hafiz, & Tiroba, 1990). In the recent past, over-exploitation of this species was reported after the introduction of mechanized vessels in the pole and line tuna fishery, with demand exceeding the stock capacity (Pillai et al., 1986). Although the IUCN status of this species is least concern (LC), research on its life history and ecology is needed in the current context of its exploitation (Santos et al., 2017). In Vietnam, *S. delicatulus* is exploited in most coastal waters, including the Con Dao MPA, because it is one of the six species included in the production of fish sauce (Chabanaud, 1924; Pham, 1964). It also has a great value as 'pickled anchovy' and is used as bait for tuna fishing. It is a short-lived species, with a lifespan which does not exceed more than 5–6 months (Milton, Blaber, & Rawlinson, 1991). During its short life, it is found in various different marine coastal habitats such as coral reefs, lagoons and seagrass beds (Milton et al., 1991). *S. delicatulus* becomes sexually mature at 60–65 days old and then grows slowly (Milton et al., 1990; Milton et al., 1991; Milton, Blaber, & Rawlinson, 1993). Some studies have reported variation in age and growth of *S. delicatulus* in coral reefs and coastal lagoon habitats in the Pacific and Indian Oceans (Milton et al., 1990; Milton et al., 1991; Milton et al., 1993). Although this species is abundant in seagrass beds (Milton et al., 1991), it is not known if these habitats are optimal for growth. In addition, there is very limited information on early stages and the life cycle of this species (Milton et al., 1990; Milton et al., 1991; Milton et al., 1993). *S. delicatulus* smaller than 15 mm have not been studied (Conand, 1985; Dalzell, Sharma, & Prakash, 1987; Milton et al., 1991; Milton et al., 1993; Milton, Blaber, & Rawlinson, 1995; Milton, Rawlinson, & Blaber, 1996;

FIGURE 1 Map of the Con Dao MPA showing the five sampling sites in Con Son Bay: seagrass 1 (dark green dot), seagrass 2 (light green dot), coral reef 1 (dark blue dot), coral reef 2 (light blue dot) and harbour (orange dot)
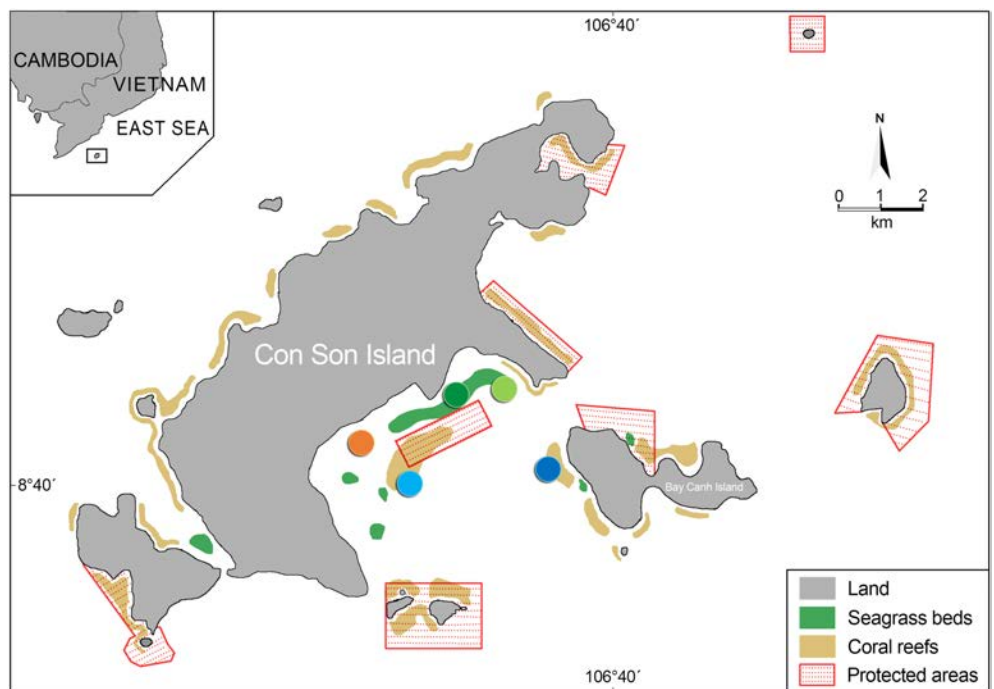
Mohan & Kunhikoya, 1985) because the identification of Clupeiformes larvae is challenging with uncertain morphology which changes rapidly during early stages (Ko et al., 2013; Victor, Hanner, Shivji, Hyde, & Caldow, 2009). In this context, a better understanding of spatial and growth dynamics of *S. delicatulus* is needed to clarify the importance of the various habitats during its life cycle, and specifically at the beginning of its life.

DNA barcoding is becoming more widely used as a tool for identifying larval fishes rapidly and efficiently, replacing conventional morphological methods (Collet et al., 2017; Ko et al., 2013). The present study identified early stages of *S. delicatulus* from very diverse ichthyoplankton samples using DNA barcoding coupled with morphometry, to determine its pattern of habitat occupation using spatial and temporal sampling. The study sought to provide information about the life history of this species in the Con Dao MPA as well as: (a) determine the distribution of *S. delicatulus* in different habitats (seagrass beds, coral reefs and a harbour) during early stages using monthly sampling with light traps; (b) estimate the ages and variable growth across habitats by analysing otolith growth increments; (c) discuss the colonization and survival of *S. delicatulus* in the various habitats; and (d) provide recommendations on key habitats for conservation. This is the first study in the Con Dao MPA to improve the conservation of an important low-trophic-level and prey fish species, targeted by specific fisheries.

2 | MATERIALS AND METHODS

Early life *S. delicatulus* were caught in three different marine coastal habitats in the Con Dao Archipelago: seagrass beds, coral reefs and a harbour. Two sites were chosen in seagrass beds and coral reefs, and one in the only harbour closely connected to the seagrass and coral reef sites (Figure 1): seagrass 1 (8°41′05.9″ N 106°37′52.1″ E), seagrass 2 (8°41′11.7″ N 106°38′34.0″ E), coral reef 1 (8°39′55.0″ N 106°39′33.1″ E), coral reef 2 (8°40′10.7″ N 106°37′13.4″ E) and harbour (8°40′36.6″ N 106°36′19.3″ E). All of these sites were in Con Son Bay. Fish were collected monthly for one year at the new moons, from June 2016 to May 2017, except for August 2016 owing to the loss of collection equipment at sea. The samples were taken using four 5 L light traps at each site during the whole night. Because fish are sensitive to different light wavelengths depending on the species or ontogenetic stage (Bowmaker, 1995; Fitzpatrick, McLean, & Harvey, 2013), two types of light traps were used at each sampling site: two with two LED lights (3 W), and two others with four LED lights (3 W) to attract different fishes. Three Panasonic 3,400 mAh Li-ion batteries were used for each light trap to ensure that the lights worked all night. The light traps were set at 3–5 m deep from 6:00 p.m. to 4:00 a.m. (10 h). The contents of each light trap were collected early in the morning. Fish were killed by placing on ice and then stored preserved in 1 L containers filled with 99% ethanol. While the light traps were in place, the environmental parameters (temperature, salinity) were recorded from the sea surface to the bottom using a Castaway CTD probe (four times at each sampling site).

Fish from each light trap were sorted in the laboratory by morphology as described by Leis and Carson-Ewart (2004). The samples from each light trap that were identified as *Spratelloides* spp. were sorted according to morphotypes. At least one specimen of each morphotype was selected for DNA barcoding using a 650 bp fragment of the mitochondrial cytochrome *c* oxidase I gene (COI), which was considered relevant for identification at the lowest taxonomic level (Ko et al., 2013). DNA was extracted from muscle tissue using the NucleoMag 96 Tissue kit (Macherey-Nagel). A fragment of approximately 650 bp of the mitochondrial DNA COI gene was amplified using the primers FishF1 and FishF2 in combination with FishR1 (Ward, Zemlak, Innes, Last, & Hebert, 2005). The 25 ml PCR reaction mixtures comprised 7.5 µl of ultrapure water, 12.5 µl 2X Tools Taq PCR Master Mix, 1 µl of each primer (1 mM), and 3 µl of DNA template. The amplification consisted of an initial step of 3 min at 92 °C followed by 35 cycles of 45 s at 92 °C, 45 s at 52 °C and 1 min at 72 °C, finishing with 5 min at 72 °C, and then held at 8 °C. After purification of the PCR products based on paramagnetic beads technology with the CleanPCR kit (Proteigene, Saint-Marcel, France), Sanger sequencing was performed using the BigDye Terminator v3.1 Cycle Sequencing Kit (Life Technologies, Carlsbad, CA). Electrophoregrams were obtained on an ABI3500 XL apparatus (Life Technologies, Carlsbad, CA). The species was then identified using the Identification Engine of BOLD (http://www.boldsystems.org). Once a set of specimens has been identified by DNA barcode as *S. delicatulus* (BIN BOLD:AAE9133), specimens were re-examined to find key characteristics for distinguishing species with similar morphologies. These key characteristics were used to identify *S. delicatulus* among the specimens that had not been DNA barcoded.

To estimate the effect that habitat had on the life history traits, the fish age and growth rates were calculated and compared between habitats. Up to 20 individuals were subsampled from each habitat and each month based on the following criteria: (a) sizes ranging from the smallest to the largest fish in the samples; and (b) at least five individuals for each stage unless there were fewer than five individuals for a given stage, habitat and month, when all individuals were selected. For each individual, the standard length (SL) was measured (using image processing), and the sagittal otoliths (sagittae) were extracted to estimate the age. Both otoliths were embedded in thermoplastic resin (Crystalbond 509®) on the sagittal plane. The left otolith was used to estimate the age and, if it was missing or damaged, the right one was then used. Opaque daily increments (D-zone, Kalish et al., 1995) were counted manually from the core to the edge: two counts were done by one reader at two different times, first from the core to the edge and inversely. The maximum radius and increment radius were measured from the core to the edge. For larger otoliths that were difficult to interpret, the otoliths were polished in the sagittal plane with 2,400 grit sandpaper and then with aqueous aluminium powder (1 µm) on a polishing cloth, to see the increments more clearly. The ages were estimated directly from the number of daily growth increments. The individual date of hatching was back-calculated by subtracting the age from the date of capture.

The otolith growth was estimated using the relationship between the otolith radius at a given age and the age. The mean increment at each age was calculated and otolith dimensions at a given age (radius and increments) were compared using ANOVA. The relationships between fish length and age were fitted by the von Bertalanffy growth model which has been used previously to describe growth of *S. delicatulus* (Milton et al., 1991):

$$SL = SL_\infty(1 - \exp(-K(t - t_0)))\qquad(1)$$

where SL is the standard length (mm), SL_∞ is the asymptotic length (mm), K is the growth coefficient, t is the age and t_0 is the predicted age at which SL is zero. The parameters of the growth model were estimated by non-linear least-squares fitting using the Statistica 6® software and the accuracy of the model was assessed using the coefficients of determination. The von Bertalanffy parameters SL_∞ and K from the least squares equations at each site were used to calculate the growth rate (dSL/dt) at $SL_\infty/2$.

The equation is of the form:

$$dSL/dt = K * SL_\infty/2\qquad(2)$$

where SL_∞ is the asymptotic length and K is the growth coefficient.

3 | RESULTS

The seawater temperatures in 2016 and 2017 showed two periods: a slightly lower seawater temperature from November 2016 to February 2017 (north-east monsoon), (25–28 °C), and a higher seawater temperature from June to October 2016 (south-west monsoon) and March to April 2017 (29–31 °C). The mean temperatures did not vary much among the five sampling sites across the months (28.7 °C ± 0.06). The salinity was similar among the five sample sites (32.7 ± 0.5). A total of 160 individuals were identified genetically as *S. delicatulus* (BIN BOLD:AAE9133) in order to then recognize a total of 3,581 individuals of *S. delicatulus* morphologically among the total sample. The highest number of *S. delicatulus* was collected at the harbour site in July 2016 (956 specimens), and the second highest was collected at seagrass 1 site in June 2016 (825 specimens). No specimens were found in January 2017 and February 2017 (Figure 2). At the two seagrass sites, the standard lengths were similar (7.8–37.9 mm for seagrass 1 site and 7.7–37.3 mm for seagrass 2 site), but the age ranges were different (8–108 days for seagrass 1 site and 7–65 days for seagrass 2 site). For the other sites, the standard lengths were smaller (7.1–22.6 mm) and the maximum age was 26 days (Table 1).

3.1 | Otolith increments and hatching date

The daily growth increments were clearly visible on all 248 otoliths with radius from 27.9 to 609.2 μm and 7–108 increments. For the

seagrass 1 site, there were 8–108 increments and for the seagrass 2 site there were 7–65 increments. The maximum number of daily growth increments was lower for the coral reef and harbour sites with 9–26 for the coral reef 1 site, 9–22 for the coral reef 2 site and 7–24 for the harbour site (Table 1).

Of the 248 *S. delicatulus* subsampled, the hatching dates were from March to October (Figure 3). There was a peak in March 2017 (n = 44). The hatching dates were irregularly distributed across the other months, with no clear peaks and none between November and February. There were differences in hatching dates between the five sites. For the seagrass sites, there was one long hatching period, from early February to late October in 2016, and again in February 2017. For the coral reef sites, there were more than two hatching periods. For the harbour site, there was a peak hatching period in June 2016, but with hatching in other months in lower numbers (Figure 3). There was a clear relationship between the decrease of temperatures at each site and an absence of births in the coldest period (Figure 3).

3.2 | Otolith and individual growth

Up to the tenth day, the otolith radius did not differ significantly among the five sampling sites (p > 0.05, Table 2). From 15 days old, there were significant differences among otolith radii for the different sites (p < 0.05). At 25 days old, when fish were found only in the seagrass beds, there was no difference in otolith radius. After 25 days old the otolith radius of samples were significantly different among the seagrass beds (Table 2). The otolith growth increments showed a similar pattern to the otolith radii. Up to 10 days, the otolith growth rate increased from 3.8 ± 1.3 to 8.4 ± 2.5 μm day^{-1} for all sites. After the tenth day, the otolith growth rates varied among sites. For the coral reef sites, the otolith growth rate increased strongly to a maximum of 14.5 ± 1.1 μm day^{-1} (day 18). The otolith growth rate increased from 1 to 10 days old at all sites, and then varied significantly among the five sites (Figure 4). It was highest for the coral reef sites, but the maximum age was only 26 and 22 days old (258.21 and 191.37 μm radius). For the harbour site the otolith growth rate was similar to that of coral reef sites; it was non-significantly slower. For seagrass beds, it was different between the two hatching periods. For individuals hatched during the dry season at seagrass 1, the otoliths grew more slowly than for the other sites after 12 days, and significantly slower from 31 days old (344.0 μm radius). Otoliths of fish hatched during the rainy season had similar growth among all sites (Figure 4). At seagrass 2, ages from dry season births grew strongly and were older (maximum 65 days old), while the samples hatched in rainy season had younger-age individuals (<15 days old).

The von Bertalanffy model provided a good fit to length-at-age data with a high coefficient of determination (all combined data, i.e. all sites mixed, R^2 = 0.95, Table 3). The growth model predicted that *S. delicatulus* grew rapidly from 7 to 30 days old (7–25 mm SL) in the five sampling sites, and that the growth was slower after 60 days old, when they remained in seagrass beds (Figure 5). For each sampling site, the von Bertalanffy model provided a less good least squared adjustment
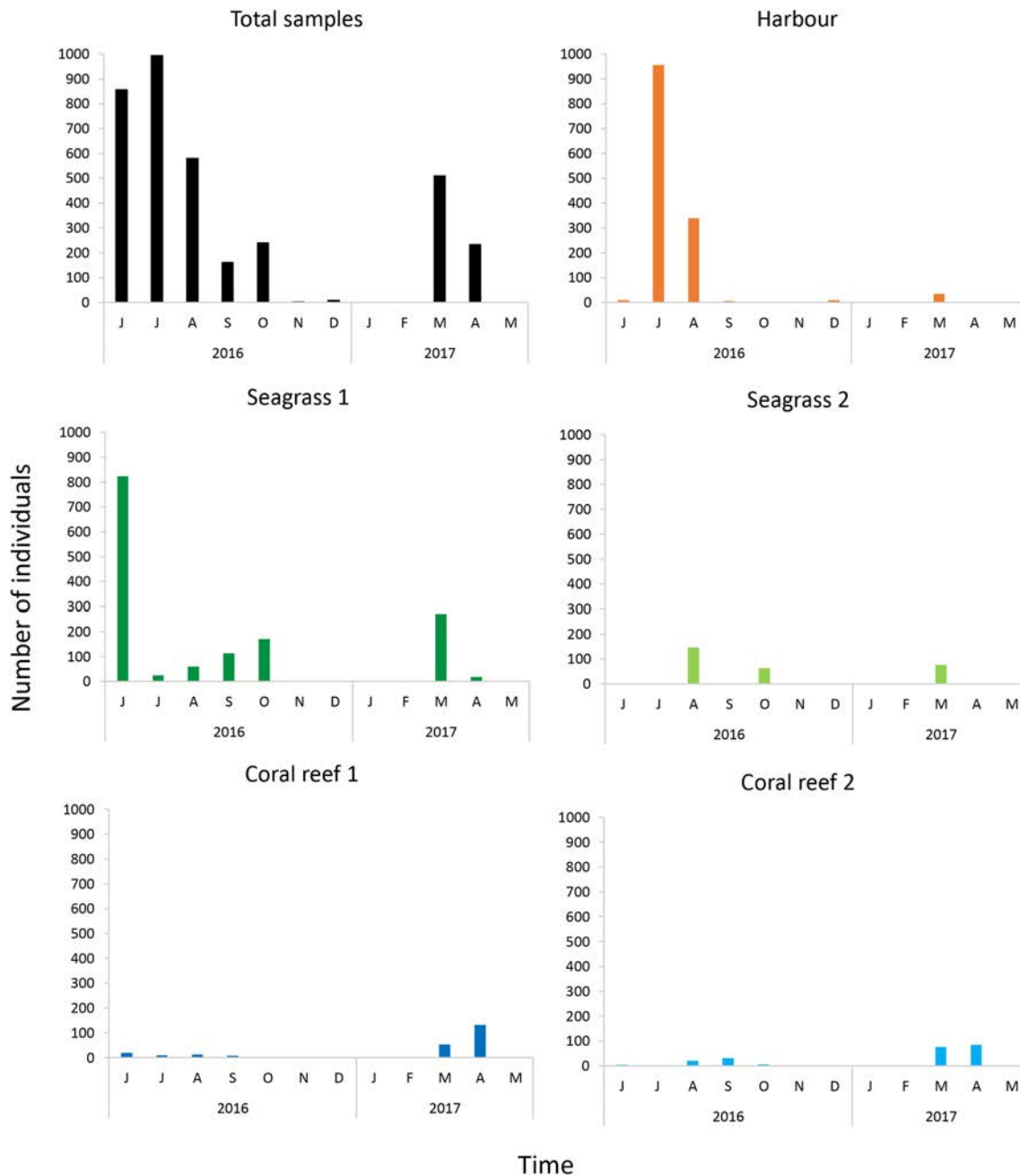
FIGURE 2 *Spratelloides delicatulus* caught each month by light-traps between June 2016 and May 2017 at the five sites in Con Son Bay (total number of fish caught = 3,581)

(R^2 between 0.71 and 0.91, Table 3). The estimation of the asymptotic size SL_∞ was less significant at each site (Table 3). The estimated growth coefficient (K) was different between the sampling sites: coral reef 2 showed the highest K, and the harbour the lowest K (Table 3).

4 | DISCUSSION

4.1 | Demography

The spatial and temporal variability in the abundance of early life history stages implies a complex set of interacting processes operating across various scales to produce the observed patterns: density and reproductive period, physical dispersal processes, migratory behaviour (e.g. vertical migration), predator/prey mediated survival, available habitats for settlement, post- settlement survival and larval condition (Robert & Sponaugle, 2009). During the one-year sampling, this species was found continuously from June to December 2016 and then from March to April 2017 (end of the sampling), but fish were not observed in January and February 2017. This absence could be explained by an active avoidance of the light traps or non-attraction to the light. There are two main currents in Con Son Bay during the year: the northward current from offshore to the inshore during the south-west monsoon (April to October) and the reverse current during

TABLE 1 Size and age of *Spratelloides delicatulus* young of year for the five sites of the Con Son Bay

Site	n	Standard length (mm)		Age (days)	
		Mean ± SD	Range	Mean ± SD	Range
Seagrass 1	92	20.4^a ± 8.6	7.8–37.9	39.4^a ± 29.0	8–108
Seagrass 2	28	16.2^b ± 9.4	7.7–37.3	21.4^b ± 17.5	7–65
Coral reef 1	40	14.5^{bc} ± 3.3	7.1–22.6	17.7^b ± 4.4	9–26
Coral reef 2	18	13.7^{bc} ± 3.4	7.6–18.8	15.0^b ± 4.5	9–22
Harbour	70	12.0^c ± 2.0	7.5–16.8	14.2^b ± 4.1	7–24

Means with different letters in superscript are significantly different (one-way ANOVA, $P < 0.05$).
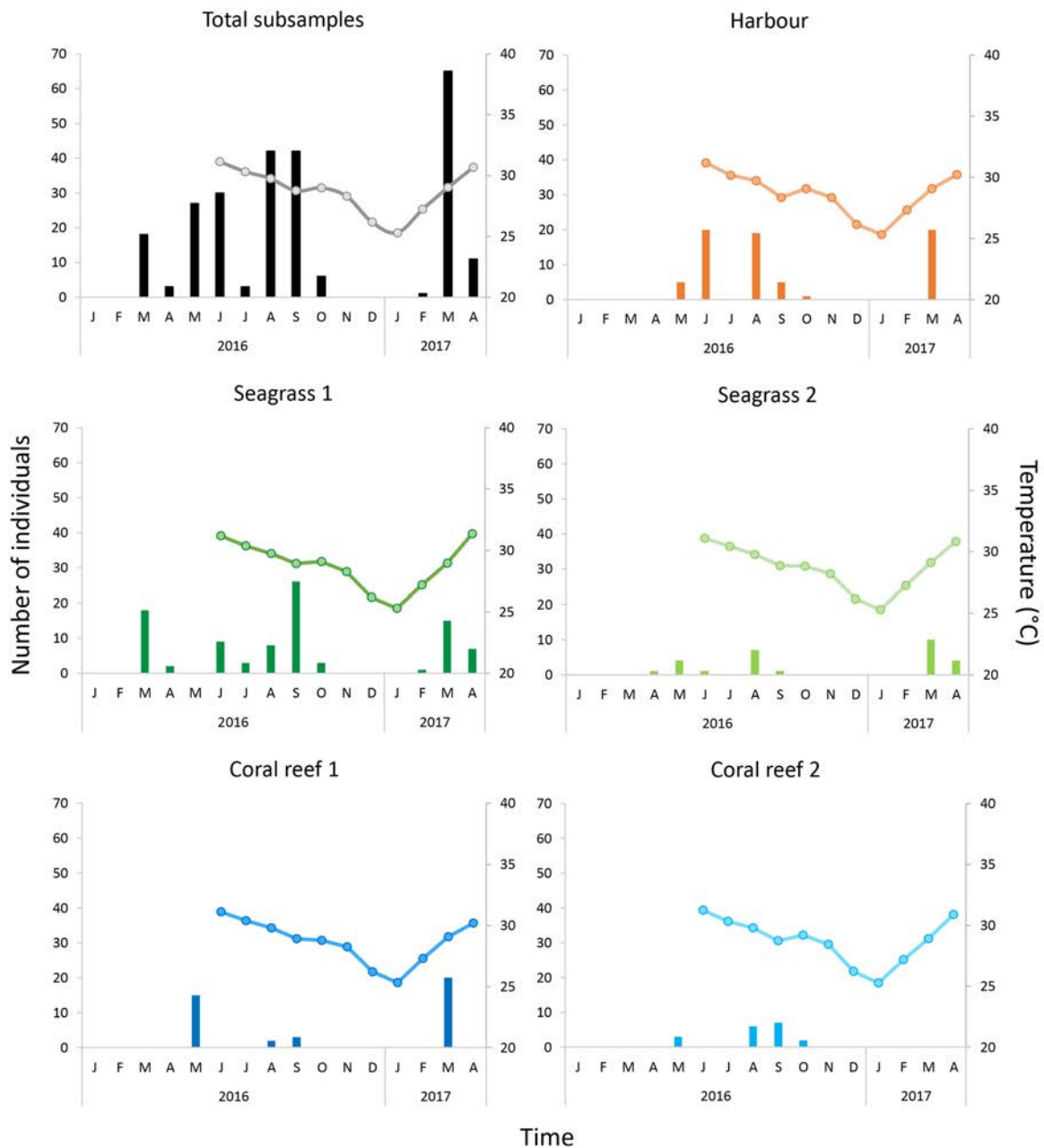

FIGURE 3 Temporal distribution of *Spratelloides delicatulus* hatching dates back-calculated from otolith readings (histograms) and mean of sea surface water temperature (points and line) for the five sites in Con Son Bay

6

TABLE 2 *Spratelloides delicatulus* otolith radius and growth increment as a function of age for the five sites in Con Son Bay

Age (day)	Mean otolith radius (μm)					P_1	Mean growth increment (μm)					P_2
	G1	G2	R1	R2	H		G1	G2	R1	R2	H	
5	22.7[a]	22.6[a]	22.1[a]	21.5[a]	20.2[a]	0.09	5.3[a]	5.6[a]	5.6[a]	5.5[a]	5.0[a]	0.48
10	57.5[a]	67.1[a]	60.8[a]	61.2[a]	56.7[a]	0.13	7.7[a]	9.5[b]	8.9[ab]	8.9[ab]	8.3[ab]	0.00
15	93.6[a]	117.1[b]	107.7[b]	115.6[b]	99.8[ab]	0.00	7.6[a]	9.4[b]	10.7[b]	11.5[b]	9.6[b]	0.00
20	124.7[a]	162.9[b]	169.6[b]	174.7[b]	151.2[ab]	0.01	7.54[a]	9.89[ab]	12.15[b]	13.17[b]	10.47[b]	0.00
25	164.0[a]	196.4[a]	–	–	–	0.12	8.3[a]	9.0[a]	–	–	–	0.57
30	203.5[a]	247.1[a]	–	–	–	0.11	8.4[a]	9.8[a]	–	–	–	0.33
35	220.6[a]	298.8[b]	–	–	–	0.00	7.7[a]	10.1[b]	–	–	–	0.04
40	229.5[a]	349.4[b]	–	–	–	0.00	6.4[a]	9.5[b]	–	–	–	0.00
45	251.7[a]	397.0[b]	–	–	–	0.00	6.6[a]	9.7[b]	–	–	–	0.00
50	285.3[a]	439.3[b]	–	–	–	0.00	6.6[a]	10.4[b]	–	–	–	0.00
55	318.5[a]	491.6[b]	–	–	–	0.00	6.7[a]	10.7[b]	–	–	–	0.00

G1, Seagrass 1 site; G2, seagrass 2 site; R1, coral reef 1 site; R2, coral reef 2 site; H, harbour site; P_1, P-value of ANOVA test for otolith radius between habitats; P_2, P-value of ANOVA test for otolith growth increment between habitats. Means with different letters in superscript are significantly different (one-way ANOVA, $P < 0.05$).
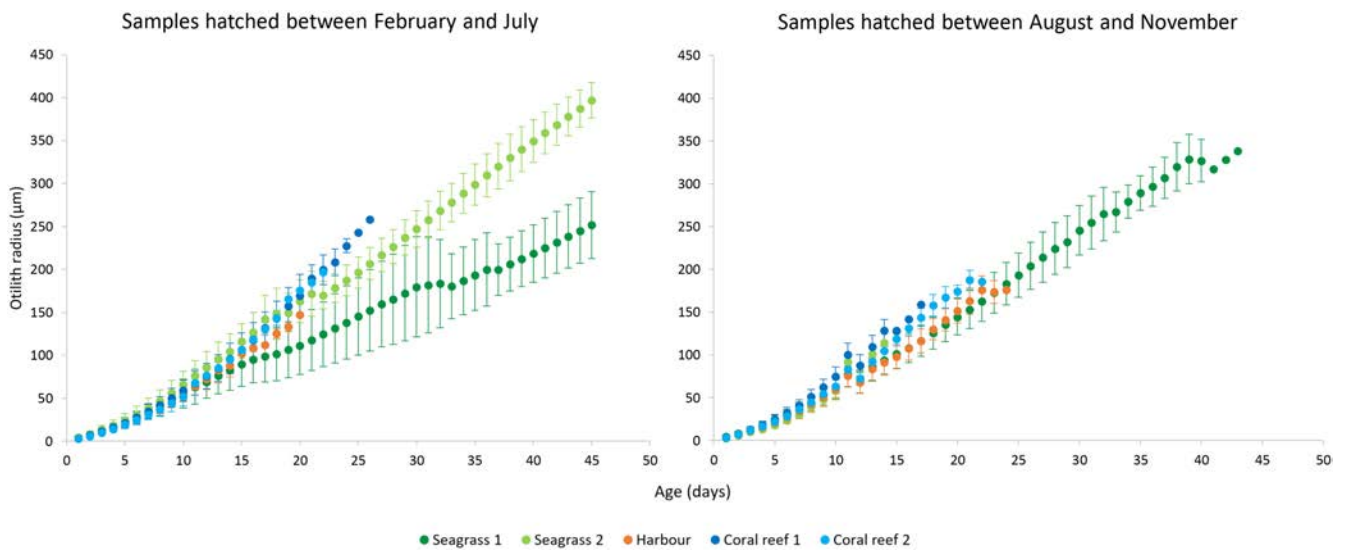

FIGURE 4 Mean otolith radius of *Spratelloides delicatulus* from 1 to 45 days old for the five sites, distributed during the two hatching periods (dry season from February to July, and rainy season from August to November) at Con Son Bay

TABLE 3 Parameter estimates and coefficient of determination R^2 for the von Bertalanffy model of *Spratelloides delicatulus* from five sites in Con Son Bay

Sites	SL_∞ (mm)	P-value	K (year^{-1})	P-value	Growth rate (mm year^{-1})	R^2
Seagrass 1	58.8	0.71	3.4	0.78	101	0.81
Seagrass 2	2085.3	0.99	0.2	0.99	156	0.87
Coral reef 1	107.4	0.89	2.3	0.91	123	0.79
Coral reef 2	22.9	0.01	28.9	0.31	332	0.91
Harbour	522.1	0.99	0.3	0.99	65	0.71
All sites	38.3	0.00	8.1	0.00	155	0.95

FIGURE 5 Von Bertalanffy growth model for *Spratelloides delicatulus* (total subsample) in Con Son Bay
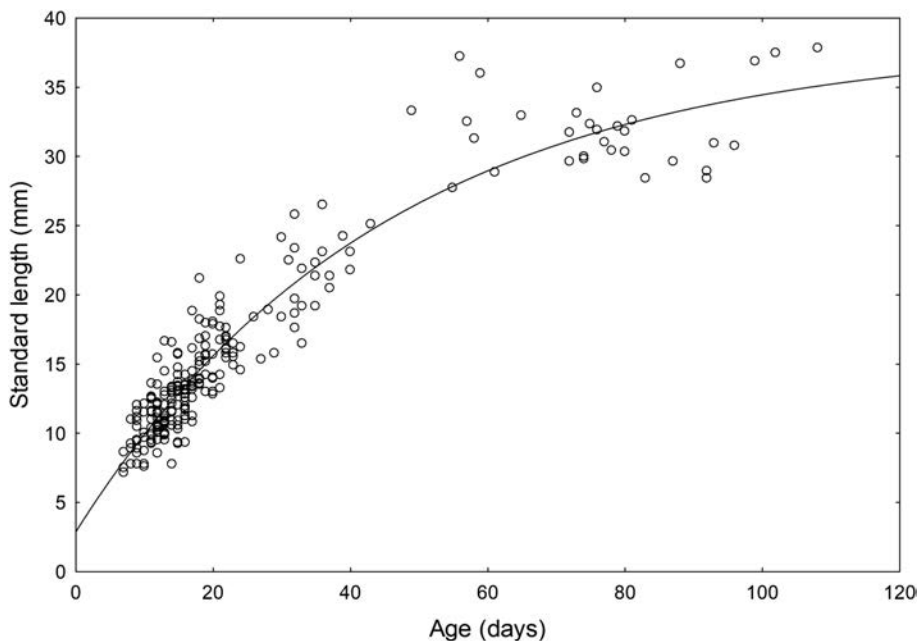
the north-east monsoon (November to March) (Doan & Nguyen, 2009). The density of plankton samples collected by every light trap was very low during the north-east monsoon in Con Dao. A supposition could be that *S. delicatulus* larvae were carried away by these offshore currents and so did not occur at sampling sites during the north-east monsoon. Lecomte and Dodson (2004) reported migration of the rainbow smelt (*Osmerus mordax*) larvae through the water column to maximize landward transport and minimize seaward transport in the St Lawrence Estuary. Some other studies have found that clupeid larvae can also migrate through the water column (Blaxter & Holliday, 1963). Although it is possible that vertical migration by *S. delicatulus* larvae may help them to adapt to surface currents, the hypothesis for the explanation of the pattern of captures in the Con Dao Archipelago is still untested.

Using otolith daily growth increments, the hatching dates were estimated from March to October 2016 and March to April 2017, with a very small number in February 2017, indicating that there was no spawning from November 2016 to February 2017. Milton and Blaber (1991) showed that *S. delicatulus* also has a protracted spawning season during the year in the tropical Indo-Pacific. Birthdates calculated in Con Dao confirmed that the spawning period of this species is not continuous. The absence of larval hatching corresponded closely with the lowest water temperatures in this area (Figure 3), as has also been observed in Tulagi by Milton and Blaber (1991). The reproduction would therefore seem to be temperature-dependent, occurring at higher temperatures (Figure 3), which could explain the absence of fish in the capture at the end or beginning of the year. Differences in the timing of reproduction may be linked to the ocean currents and the productivity of the environment. In the Solomon Islands, *S. delicatulus* spawn in lagoons fringed by coral reefs where the currents are negligible (Milton &

Blaber, 1991) whereas the currents in the Con Dao Archipelago are strong and seasonal (Doan & Nguyen, 2009). Most coastal marine fishes spawn buoyant eggs that drift in the surface currents (Lobel & Robinson, 1986). Therefore, the spawning grounds chosen by fish species must ensure that larvae are recruited in the best areas (Lobel & Robinson, 1983). For example, some fishes have spawning peaks that match the period when the prevailing currents are weakest, probably to avoid eggs and larvae drifting (Johannes, 1978; Lobel & Robinson, 1983; Lobel & Robinson, 1986; Watson & Leis, 1974). *S. delicatulus* does not reproduce in Con Dao during the north-east monsoon, and the offshore dispersion of eggs and larvae by the northward current is therefore reduced.

The highest abundance of *S. delicatulus* was at the harbour site in July 2016 (956 individuals captured), almost one-third of the total capture. The second highest abundance was at the seagrass 1 site in June 2016 (825 individuals) and the lowest overall abundance was at the coral reef sites. The high abundance in the harbour could be due to the characteristics of this specific habitat and town lights, which may attract some fish species (Doherty, 1987; Leis & Rennis, 1983). Blaxter and Holliday (1963) reported that most clupeids are attracted by artificial lights, such as *Sardinops caerulea* in Eastern Pacific, *Clupea pallasii* in the Pacific and *Clupeonella* spp. in the Caspian Sea. However, this does not explain the high abundance observed in the seagrass beds. Surface currents are major factors affecting the spatial distribution of the young of the year (Harrison et al., 2012; Robert & Sponaugle, 2009). In Con Dao, as suggested earlier, the reproductive activity of the species seems to be linked to temperature and seasonal currents. These currents may also play an important role in the spatial distribution of *S. delicatulus*, as shown by the relationship between abundance at the sampling sites and the distance of these sites from the shore. The closest sites to the shore (harbour and seagrass 1) had

the highest abundances, while the two coral reef sites had the lowest. The larvae could have been carried passively by the northward currents to reach locations close to the coast (harbour and seagrass beds). However, the abundance at the coral reef 2 site was the lowest even though this site is closer to the shore than coral reef 1. The explanation could be that the coral reef 2 is in a bay of Bay Canh Island where water currents are weaker. Hydrodynamics could explain the distribution of early stages of *S. delicatulus* between the various habitats (Eckman, 1987), but without a fine-scale map of the currents of Con Dao and a larger-scale sampling campaign, this assumption is difficult to test.

4.2 | Individual growth

For marine fishes, a change of habitat is often associated with behavioural and/or ontogenic changes or even metamorphosis and modification of the growth rates (Linkowski, 1991; Ré & Gonçalves, 1993; Tomás & Panfili, 2000). The growth rates of *S. delicatulus* otoliths were the same in the various habitats (seagrass beds, harbour and coral reefs) until the tenth day of life. After 10 days old there was a shift in the otolith growth between sampling sites, and the differences increased until around 26 days old. After this, the fishes were only caught in seagrass beds. For the samples hatched during the dry season, the otolith growth of samples in seagrass 1 was lower than the other seagrass after 26 days old. It underlined a probable difference in environmental factors in this habitat, inducing different growth of *S. delicatulus*.

The growth of *S. delicatulus* was rapid up to two months old and then slower in Con Son Bay, as observed in the Solomon Islands, the Maldives and Australia (Milton et al., 1991; Milton et al., 1993). *S. delicatulus* possibly grew slowly after two months to use energy for sexual maturity and reproduction, as the species is mature at 60–65 days old (Milton et al., 1991; Milton et al., 1993; Milton & Blaber, 1991). The asymptotic size of *S. delicatulus* in Con Dao was much lower than that observed at the barrier reef in Townsville (Australia), while the growth coefficient was similar (Milton et al., 1991). An absence of the oldest and biggest individuals in light traps in Con Dao could explain low asymptotic size. *S. delicatulus* spread very early to the different habitats in Con Son Bay; the growth rates were different in each habitat, the coral reefs allowing higher growth rates than other habitats. Fish growth depends on numerous factors, such as genotype, food availability, food consumption, condition, predation pressure, competition and abiotic variables such as water temperature and salinity (Baltz, Fleeger, Rakocinski, & McCall, 1998; Boeuf & Payan, 2001; Connell, 1998; McCormick, 1998). Milton et al., (1991) concluded that there was a significant negative relationship between the growth rate of *S. delicatulus* and water temperature at large-scale distribution. At the Townsville spot on the Great Barrier Reef, because of a wide temperature range (21–30 °C) during the year, the growth was also faster (Milton et al., 1991). Temperature was identical between the different habitats in Con Dao but *S. delicatulus* growth was slightly different.

There were also differences even for similar habitats, for example between the two seagrass sites and between the two coral reef sites in Con Dao. One important factor that can affect the growth rates of young of the year, and that differs between habitats, is probably the food abundance (Grol, Dorenbosch, Kokkelmans, & Nagelkerken, 2008; Sponaugle, 2009). *Spratelloides* spp. feed mainly on zooplankton (Milton, Blaber, & Rawlinson, 1990). Coral reefs are extremely diverse in terms of living organisms such as zooplankton and could supply more food for early growth of *S. delicatulus* than other habitats, inducing higher otolith growth rates (Grol et al., 2008). Previous studies have shown that the growth rate of *S. delicatulus* early stages was higher near a barrier reef (0.83–1.75 mm day^{-1}) than in a coastal lagoon (0.63–0.74 mm day^{-1}) in Solomon Islands, Maldives and Australia (Milton et al., 1991). Other factors could cause differences in the growth of *S. delicatulus* in various coastal habitats, but they could not be highlighted.

4.3 | Life cycle and implications for conservation

S. delicatulus found in Con Son Bay grow in two phases: first, a planktonic larval stage in seagrass, coral reef and harbour habitats, and second, after 26 days, a pelagic stage only on seagrass beds. Larvae were distributed widely in seagrass, coral reefs and harbour habitats over the whole reproduction period. The strategy of colonizing different habitats at very young stages could be associated with the food supply and survival, which would, therefore, be more diverse, giving the best chances for the early growth and survival. Despite the high growth rates at the coral reef sites, there was no individual older than 26 days caught at these sites. Habitat selection by fish during their life cycle is based on feeding strategy, growth rates, ontogeny, behaviour and predator avoidance (Dahlgren & Eggleston, 2000; Werner & Hall, 1988; Werner, Mittelbach, Hall, & Gilliam, 1983). Although the coral reefs provide a better food supply (Grol et al., 2008), there is a higher predation risk than in other habitats (Chittaro, Usseglio, & Sale, 2005; Major, 1978; Shulman, 1985). In the northern Great Barrier Reef, slower-growing larvae of *S. delicatulus* were associated with more stress than faster growing fish because of the predation (Villacorta, 2011). The fast growth at the larval stage can help them to speed through the high-vulnerability phase on the coral reefs (Froese, 1990). Fish can also shift between habitats to make a compromise between mortality risks and growth rates (Dytham & Simpson, 2007; Grol et al., 2008). Owing to the relatively short distance (less than 3 kilometres) between habitats in the sampling area (Figure 1), the early juveniles of *S. delicatulus* (older than 26 days) could actively migrate to seagrass beds to reduce mortality risks. Similarly, *Haemulon flavolineatum* (Haemulidae) juveniles were found at higher densities in seagrass beds, despite higher growth rates on coral reefs (Grol et al., 2008). In addition to movement strategies of fish larvae in coral reef sites, there were probably also high mortality rates of *S. delicatulus* at these sites for this species with a short life cycle. There could have been a high

predation pressure that occurred at coral reef sites during the sampling period, which resulted in a high mortality rate of *S. delicatulus* larvae. In the Solomon Islands, *Spratelloides* spp. are also recorded as important prey in coral reef fish communities (Blaber et al., 1990). The present results on early life history of *S. delicatulus* in Con Dao demonstrate that seagrass beds are nursery areas for *S. delicatulus* after the larval stage.

Coral reef fishes are very diverse and are the basis of a major fishery in the Con Dao Archipelago (Nguyen & Nguyen, 1997). Thus, protection and conservation of *S. delicatulus*, a low-trophic-level species, is very important for respecting the trophic network and fishery management, and for ichthyophageous species living in the same environments. Improving its conservation will maintain sustainable ecological processes, and resources to ensure the continued fishing of high-value targeted predator species such as *Lutjanus vitta*, *Auxis thazard*, *Megalaspis cordyla* and *Scomberoides lysan*. Connectivity, linking local *S. delicatulus* populations through the dispersal of larval and juvenile stages has important implications for habitat conservation, the persistence of metapopulations and resilience from environmental pressures (Almany et al., 2009; Sale et al., 2005).

The present study has shown that different coastal habitats (seagrass, coral reef, harbour) play different roles in the life cycle of this key pelagic fish species in the Con Dao MPA. Seagrass beds are the key habitats for juvenile growth of *S. delicatulus* in this MPA. Currently, there is only a very small area of seagrass bed that is protected in this MPA, which is based on separate patches of protected zones (Figure 1). For example, in Agatti island (India), *S. delicatulus* populations declined because the seagrass beds were reduced (Arthur, Lal, Alcoverro, & Madhusudan, 2013). Thus, more protection of seagrass beds in Con Dao is needed to conserve *S. delicatulus* and, probably, similar species. In addition, owing to the current fragmentation of the Con Dao MPA, many coral reefs are not protected in the Con Son Bay (Figure 1), whereas coral reefs are also key habitats for early stages of *S. delicatulus*. Establishing a network of continuous areas linking habitats, without patches, could improve the conservation of *S. delicatulus* not only in Con Dao, but also elsewhere in the tropical Indo-Pacific.

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