



The Effects of Hypoxia and Anthropogenic Disturbance on the Distribution, Abundance and Recruitment of the Sea Cucumber *Holothuria leucospilota* at the Mouth of a Subtropical Bay, China

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Despite the commercial importance of the sea cucumber *Holothuria leucospilota* increasing in recent years, little is known of its spatial distribution and ecology in the South China Sea. We investigate the distribution, abundance, and recruitment of *H. leucospilota* from 2017 to 2020 at two sites (S1 and S2) in Daya Bay, a typical subtropical bay which is strongly influenced by human activities in the South China Sea. We report hypoxia to drive *H. leucospilota* from deeper into shallower waters with higher DO concentrations at the mouth of Dapeng Cove in Daya Bay (S1), particularly during summer. Population size at S1 decreased by 90% from 2017 levels, before this area was opened to the public in 2018; recruitment was not observed by August (summer) of 2020. In contrast, in summers of 2017 and 2020, *H. leucospilota* abundance at S2, a protected open-water area, increased by 84%, and the proportion of small-sized (recently recruited) sea cucumber in the population increased by 20%. Severe summer hypoxia at S1 could negatively influence *H. leucospilota* spawning and larval settlement, which combined with depletion of broodstock because of fishing pressure and/or hypoxia-induced mortality, could inhibit recruitment. In contrast, higher DO concentrations and abundant broodstock during summer (the breeding season) favoured recruitment of *H. leucospilota* at S2. Overall, hypoxia and anthropogenic disturbance impede recovery of *H. leucospilota* at S1, while at the protected S2, larvae may be released to settle in nearby areas. It is imperative to develop a better understanding of the biology, ecology and conservation of tropical sea cucumbers in China.

Keywords: sea cucumber, summer hypoxia, overexploitation, fishing pressure, recruitment, benthic invertebrates, escape behaviour, mass mortality

INTRODUCTION

The sea cucumber *Holothuria leucospilota* occurs widely in shallow tropical and subtropical Indo-Pacific Ocean waters, where it is usually found on seagrass beds, and sandy and muddy substrata with rubble or coral reefs (Bonham and Held, 1963; Liao, 1997; Purcell et al., 2012; Yu et al., 2013). Being edible, *H. leucospilota* is an important component of traditional subsistence fisheries for some Pacific Island nations (Drumm et al., 1999; Dzeroski and Drumm, 2003; Drumm and Loneragan, 2005; Purcell et al., 2012; Huang et al., 2018). It is also a major source of bioactive substances such as polysaccharides and saponins for biotechnology and medicine, which potentially increase its market value (Yu et al., 2013; Huang et al., 2018).

Holothuria leucospilota plays an important ecological role in nearshore marine systems by moving large amounts of sand, selectively feeding on organically rich components within the sediment, increasing nutrient and dissolved oxygen exchange between water and sediments, and altering sediment biota and carbonate dynamics (Bonham and Held, 1963; Sloan, 1979; Che, 1990; Zamani et al., 2018). Additionally, it is a proposed bioremediator of organic polluted environments; its culture in aquaculture systems mitigates organic pollution and improves environmental quality, rendering it a good candidate for integrated multi-trophic aquaculture (IMTA) systems (Yu et al., 2012, 2013).

Sea cucumbers are considered a delicacy and medicinal food by Chinese and other Asian peoples. Nowadays most tropical sea cucumber species have been overexploited, especially in China, because of increased demand for their product. This overexploitation could indirectly, deleteriously affect marine ecosystems (Purcell et al., 2012; Harith et al., 2018; Huang et al., 2018; Ramírez-González et al., 2020). While *H. leucospilota* is an abundant species in tropical and subtropical waters, and not in danger of extinction like other commercially fished species (e.g., *Stichopus horrens*), it is severely threatened by overexploitation and environmental degradation (Purcell et al., 2012; Harith et al., 2018). Throughout Asia this species is fished in China, Malaysia, Thailand, Indonesia, the Philippines, and Viet Nam, and where it is fished there are few or no regulations pertaining to its harvesting (Purcell et al., 2012). Increased market demand drove the price of dried *H. leucospilota* in the Philippines from USD 1.83 kg⁻¹ in 1998 to USD 4.89 kg⁻¹ in 2000 (Akamine, 2001), and it has acquired more commercial value in recent years [current prices in Guangzhou market range USD 20–40 kg⁻¹ (unpublished data)]. Overfishing and a lack of fishing regulations in Malaysia could put *H. leucospilota* at risk of local extinction (Harith et al., 2018).

The distribution and abundance of *H. leucospilota* is well studied in many countries such as Malaysia, Indonesia, Japan, and the Marshall and Cook islands (Bonham and Held, 1963; Drumm et al., 1999; Dzeroski and Drumm, 2003; Harith et al., 2018; Setyastuti et al., 2018; Tanita and Yamada, 2019). Although this species was reported to be widely distributed in the South China Sea (Liao, 1997; Yu et al., 2013), little is known of its spatial distribution and ecology in these waters. The present study was aimed at investigating the distribution and abundance

of this species, and how environmental and anthropogenic disturbances affect them, in Daya Bay, a typical subtropical bay in the South China Sea. These results will be of value in stock assessment surveys, and sea cucumber sustainable management in China's waters.

MATERIALS AND METHODS

Study Site

Sampling was performed around the mouth of Dapeng Cove, a body of water about 4.5 km (N–S) by 5 km (E–W) (Tang et al., 2003; Wang et al., 2008) in southwest Daya Bay, a semi-enclosed water mass about 15 km wide and 30 km long (about 600 km²) in the South China Sea. Daya Bay is influenced by the East Guangdong upwelling and a thermocline from June to August; water column stratification (temperature and salinity) in this bay begins to develop in June, and is strongest from July to September (Wang et al., 2008). *H. leucospilota* is the most abundant holothurian in Daya Bay (Yu et al., 2013; Huang et al., 2018).

Fish and oyster aquaculture in Dapeng Cove has thrived since the 1990s. In this region fish farms have increased to 30 ha, with an annual production of 450 metric tons, and oyster farms to 200 ha, with an annual production of 1.8 × 10⁴ metric tons. Although mariculture activities within Dapeng Cove contribute greatly to local economy, environmental quality in the bay has deteriorated because of organic and nutrient contamination, and aquaculture waste decomposition, which depletes oxygen and exacerbates problems with hypoxia on the seabed during summer (Yu et al., 2013, 2014, 2017). Thermal pollution from discharged coolant water from two nearby nuclear power plants on the north shore of Dapeng Cove – the Daya Bay Nuclear Power Plant, operating since 1993, and Lingao Nuclear Power Plant, since 2003 – has also profoundly affected the ecology of Dapeng Cove. The thermal plume from these power plants affects water column vertical mixing during winter and stratification in summer. An obvious decline in biomass and richness of benthic taxa has occurred near these power plants between 1991 and 2004 (Tang et al., 2003; Wang et al., 2008). Local fishermen also report that about 30 years prior to mariculture and nuclear power plant development in this region that there were many mangroves, corals, *Sargassum* and sea cucumbers, which have since almost vanished. Large numbers of *H. leucospilota* now occur only around the mouth of this bay in an area that has been closed to the public for more than 10 years, from 2009.

We investigate the abundance and distribution of *H. leucospilota* at two areas – one open to the public (S1) and another that is protected (S2). S1 is located at the mouth of Dapeng Cove (22°34'16"N, 114°32'46"E), about 2.5 km south of the two nuclear power plants. The area around this site was formerly closed and used for sea urchin (*Anthocidaris crassispina*) ranching until 2017, after which these ranching activities were banned by the government and the sea area was opened to public for fisheries and tourism. No regulations were enacted to protect wildlife, and large numbers of sea cucumbers and sea urchins were immediately collected by local fishermen

and tourists, especially during summer 2018 when this area was first opened to the public. S2 is located at breakwaters constructed in the mid-1990s outside a yacht harbour in open water (22°33'36"N, 114°33'12"E). The sea area around S2 has been closed to the public since 2009 in preparation for the 26th Summer Universiade in Shenzhen in 2011, fisheries, SCUBA diving and snorkelling tourism are forbidden (Figure 1).

Distribution and Abundance of *H. leucospilota*

From February 28, 2017 to August 24, 2020, line transects were used to determine the distribution and abundance of *H. leucospilota*. Three permanent 50-m line transects were established at each site (the 50-m length was chosen because the *H. leucospilota* was found to occur mainly within 50 m of the shore in the pilot study). Transect lines began on shore at the water's edge, and ran perpendicular to the shore, spaced about 50 m apart. Surveys along transects were performed on SCUBA at both sites during the day around high tide on February 28 (winter), May 23 (spring), August 26 (summer), and November 21 (autumn) in 2017, and August 24 (summer) in 2020; an additional survey occurred at S1 on November 11, 2019.

All *H. leucospilota* encountered within 1–2 m (distance determined by visibility) either side of the transect line were recorded along 10-m increments (i.e., 0–10, 10–20, 20–30, 30–40, and 40–50 m). Density along each transect and 10-m increment was calculated by dividing the total number of individuals by area surveyed and expressing this as individuals per square meter. Body length of animals in summer was measured (dorsal distance from mouth to anus) to the nearest 1 cm using a standard ruler; individuals were also photographed *in situ* with an Olympus Tough TG4 camera (to verify measurements); substrate type, depth, and distance from shore (DS) were simultaneously recorded.

No hand contact was made with sea cucumbers when measuring them, or their length was measured immediately after removal from the shelter (before they contracted); no sea cucumber along the transect was removed during any survey. In any survey, an area of 100–200 m² per transect and 300–600 m² per site was investigated.

Because *H. leucospilota* is active during the day, does not completely burrow into the sediment, and extends its highly mobile anterior end outward to feed, it is easily observed and surveyed (Massin and Doumen, 1986; Tanita and Yamada, 2019). We believe that any underestimation of its density during surveys (because of possible cryptic behaviour) would have been negligible.

Population Structure of *H. leucospilota*

During summer of 2017, 35 sea cucumbers from S2 (about 50 m outside the transect) were collected, measured (as above), and their wet weight determined (to the nearest 1 g) by portable handheld electronic scale after being drained on sterile gauze for 1 min (to constant weight). All animals were returned to the ocean after measurement. Wet weight and body length relationships were evaluated by linear regression, from

which wet weights of sea cucumbers within transects were subsequently derived.

To evaluate annual changes in reproductive potential, the sizes of sea cucumbers surveyed during the summers of 2017 and 2020 were classified into three groups according to wet weight: small (≤ 90 g), medium (90–180 g), and large (≥ 180 g). This season and these sizes were chosen because the gonad index of *H. leucospilota* is greatest during August in Daya Bay (Huang et al., 2018), and wet weights > 180 g represent mature individuals in the breeding season (Gaudron et al., 2008; Purcell et al., 2012).

Environmental Characteristics

Substratum type, depth, and DS at locations where sea cucumbers occurred were recorded simultaneously. Bottom type at each 10-m increment along each transect was visually classified into sand (<2 mm), rubble (2–63 mm), rock (>63 mm) size fractions, or shell (primarily empty bivalves) (Zhou and Shirley, 1996; Tanita and Yamada, 2019).

Water parameters were monitored along transects at distances of 5, 15, 25, 35, and 45 m from the shore, with seafloor temperature (°C), dissolved oxygen (mg L⁻¹), salinity, and pH measured using an In-Situ smarTROLL Multiparameter Handheld instrument (In-Situ Inc., Fort Collins, CO, United States).

Statistical Analysis

Analyses were performed using IBM SPSS Statistics for Windows, version 19.0 (IBM Corp., Armonk, NY, United States). A linear regression was used to determine relationships between sea cucumber wet weight and body length for summer of 2017. Separate two-way ANOVAs were conducted to assess the effects of sampling time and DS on sea cucumber density within each 10-m increment along each transect, at both sites. Average sea cucumber abundance at each site at different sampling times was analysed by one-way ANOVA, followed by a comparison of mean values using the Student–Newman–Keuls (SNK) test. Differences in average sea cucumber abundance at the two sites on common sampling occasions were analysed by Student's *t*-test. For all data sets, normality was evaluated using the Kolmogorov–Smirnov test, and homogeneity was evaluated by Levene's test. Density data for 10-m increments along each transect were log-transformed [$\log(x + 1)$] to improve normality and homogeneity of variances, but we present results in an untransformed state. Statistical significance is set at $P < 0.05$.

RESULTS

Environmental Characteristics

Water depth varied with DS at both sites (Figure 2). Depth at S1 increased with DS along the transect, while the seabed plateaued at S2 at DS > 15 m. Depths (at high tide) at DS of 5, 15, 25, 35, and 45 m at S1 were about 1.8, 3.0, 3.7, 4.6, and 5.7 m, respectively, while those for S2 were about 1.6, 4.7, 5.2, 5.2, and 5.3 m, respectively.

Four main substratum types occurred along transects (Table 1). At S1 where high numbers of bivalve shells occurred,

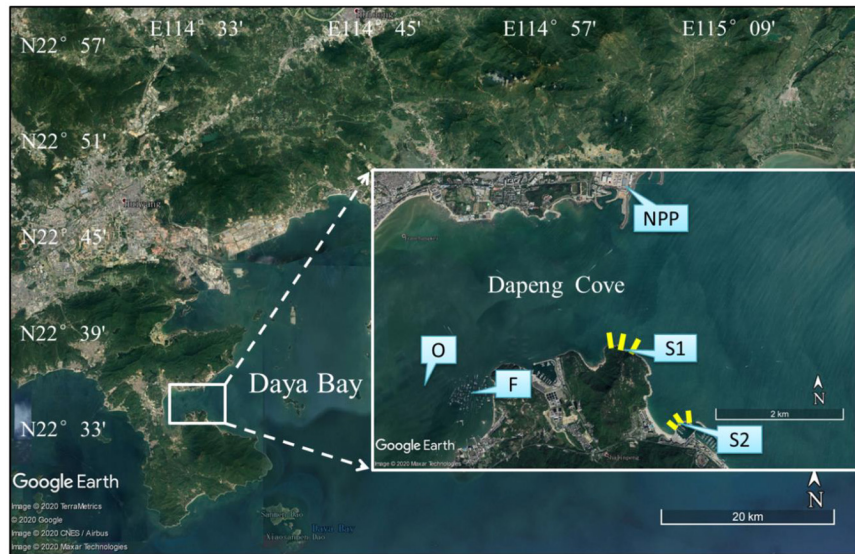


FIGURE 1 | Map of study sites, with inset depicting the open area (S1) at the mouth of Dapeng Cove, and S2, the protected area in open water; yellow bars indicate transect lines. NPP, nuclear power plants; O, oyster farm; F, fish farm.

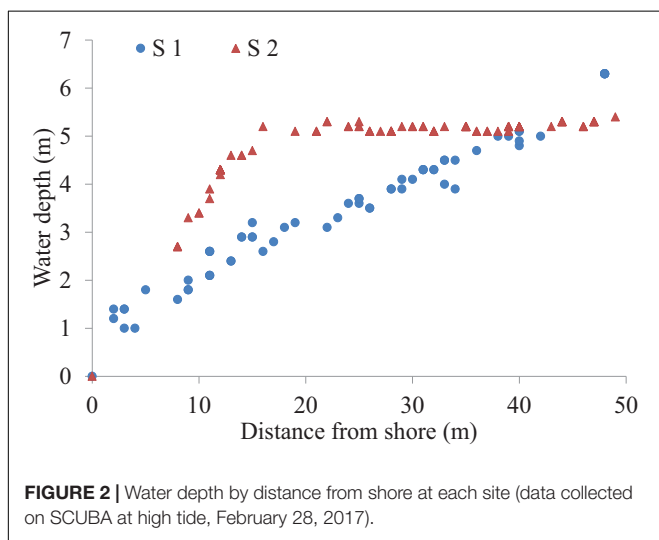


FIGURE 2 | Water depth by distance from shore at each site (data collected on SCUBA at high tide, February 28, 2017).

TABLE 1 | Substratum at 10 m increments along 50 m transects at survey sites S1 and S2.

Distance from shore (m)	S1	S2
0–10	Rock and Shell	Rock
10–20	Sand and Shell	Sand and Rubble
20–30	Sand and Shell	Sand and Rubble
30–40	Sand and Shell	Sand and Rubble
40–50	Sand and Shell	Sand and Rubble

rock and shell substrata characterised the seabed at DS < 10 m; sand and shell substrata prevailed elsewhere. At S2, rock prevailed at DS < 10 m; sand and rubble prevailed elsewhere.

Sample site water parameters are summarised in **Table 2**. Lowest water temperatures at S1 occurred in winter 2017; higher values occurred in summer; temperature decreased with DS in summer, and a thermocline was present at about 4 m depth (from DS 25 to 35 m); values at different DS were similar during other seasons. DO decreased gradually with DS in spring, but dramatically in summer. Hypoxia ($DO < 2.0 \text{ mg L}^{-1}$) (Vaquer-Sunyer and Duarte, 2008) occurred in all near-bottom waters in summer of 2017, with the exception of 5 m DS (2.31 mg L^{-1}). Although hypoxic conditions were not apparent along all S1 transects in summer 2020, DO decreased seaward, with values at 5 and 15 m DS 2–3 × those at 45 m (2.75 mg L^{-1}) DS. At S1, salinity was high and relatively constant with DS on any given sampling event, but values at 5 and 15 m DS were lower than those elsewhere in summer 2020, mainly because of rainfall which preceded sampling; pH was very similar at different DS on any given sampling event, except for summer, when values decreased with DS; pH was low (< 8.00) in summer 2017, but more alkaline (> 8.09) in summer 2020. Similar trends occurred in most cases for water parameters at S2. While the DO at 35 and 45 m DS was low (1.61 and 1.45 mg L^{-1} , respectively), it was 1.6× and 2.3× that at corresponding DS at S1 in summer 2017. Fairly stable water parameters at different DS in winter and autumn indicated strong seasonal vertical water column mixing.

Population Characteristics of *H. leucopilota* Distribution

A two-way ANOVA revealed the distribution of *H. leucopilota* to vary significantly over time and DS at both sites, with an obvious interaction between sampling time and DS at S1 (**Table 3**). The distribution of *H. leucopilota* at S1 is shown in **Figure 3A**. During the 2017 winter, *H. leucopilota* occurred along all 10-m

TABLE 2 | Near-bottom water parameters at survey sites, 2017–2020.

Sampling date	Distance from shore (m)	Water temperature (°C)		DO (mg L ⁻¹)		Salinity		pH	
		S1	S2	S1	S2	S1	S2	S1	S2
Winter 2017	5	16.86	16.74	7.94	7.95	32.10	32.40	8.03	8.03
	15	16.90	16.68	7.94	7.95	32.10	32.40	8.03	8.03
	25	16.90	16.57	7.94	7.94	32.10	32.40	8.03	8.03
	35	16.90	16.59	7.93	7.94	32.10	32.30	8.03	8.02
	45	16.90	16.60	7.93	7.93	32.10	32.30	8.03	8.02
Spring 2017	5	25.88	25.85	6.14	6.29	33.40	32.10	8.24	8.13
	15	25.89	26.02	6.12	6.09	33.30	32.30	8.24	8.13
	25	25.82	26.02	6.09	5.12	33.30	32.40	8.24	8.10
	35	25.82	26.09	5.79	4.95	33.40	33.00	8.22	8.12
	45	25.82	25.67	5.77	4.65	33.50	33.50	8.22	8.12
Summer 2017	5	27.36	29.04	2.31	3.91	34.60	34.10	7.89	8.05
	15	27.23	28.62	1.22	2.48	34.80	34.10	7.89	8.01
	25	26.31	28.54	1.04	2.37	34.50	34.00	7.87	8.00
	35	25.76	28.46	0.99	1.61	34.30	34.00	7.85	7.95
	45	25.77	28.45	0.63	1.45	34.30	34.00	7.83	7.94
Autumn 2017	5	24.48	24.31	5.89	5.79	33.60	33.60	8.12	8.04
	15	24.50	24.30	6.03	5.74	33.60	33.80	8.12	8.03
	25	24.50	24.27	6.08	5.74	33.60	33.40	8.12	8.05
	35	24.49	24.22	6.23	5.72	33.70	33.70	8.12	8.03
	45	24.45	24.21	6.12	5.70	33.70	33.50	8.11	8.03
Autumn 2019	5	25.22	–	6.50	–	34.20	–	8.08	–
	15	25.22	–	6.50	–	34.20	–	8.08	–
	25	25.22	–	6.51	–	34.20	–	8.08	–
	35	25.19	–	6.53	–	34.20	–	8.08	–
	45	25.05	–	6.57	–	34.20	–	8.06	–
Summer 2020	5	30.55	30.50	7.41	7.52	31.00	31.70	8.33	8.36
	15	30.42	29.88	7.05	6.65	31.60	32.30	8.30	8.30
	25	29.74	29.18	5.65	5.59	32.60	32.70	8.20	8.25
	35	28.62	29.13	4.24	5.37	32.70	32.60	8.14	8.24
	45	28.34	28.52	2.75	3.76	32.70	32.60	8.09	8.19

– No data.

increments of transects, with densities at DS 20–30 m (0.23 ± 0.03 ind m^{-2}) and 30–40 m (0.35 ± 0.05 ind m^{-2}) higher than those elsewhere. During spring, comparatively high densities occurred at DS < 30 m, with values at 10–20 m (0.51 ± 0.17 ind m^{-2}) more than $2 \times$ those found at DS 0–10 m or 20–30 m; no or very few individuals occurred at DS > 30 m. During summer, the highest sea cucumber density occurred at DS 0–10 m (0.51 ± 0.02 ind m^{-2}), almost $2 \times$ that from 10 to 20 m (0.24 ± 0.08 ind m^{-2}); no live animal occurred at DS > 30 m, where the water column was stratified and the DO < 1 mg L⁻¹. Although sea cucumbers occurred along all 10-m transect increments in autumn 2017, their densities at DS > 30 m were lower than winter values in that same year. Sea cucumbers also occurred along all 10-m increments along transects in autumn 2019, but densities at DS < 40 m were lower than those at comparable DS in autumn 2017. The density of sea cucumbers at DS of 10–20 m in summer 2020 (0.12 ± 0.03 ind m^{-2}) was less than one-quarter that at this DS in summer of 2017. Unlike summer 2017, when many sea cucumbers gathered at 0–10 m DS, none could be found

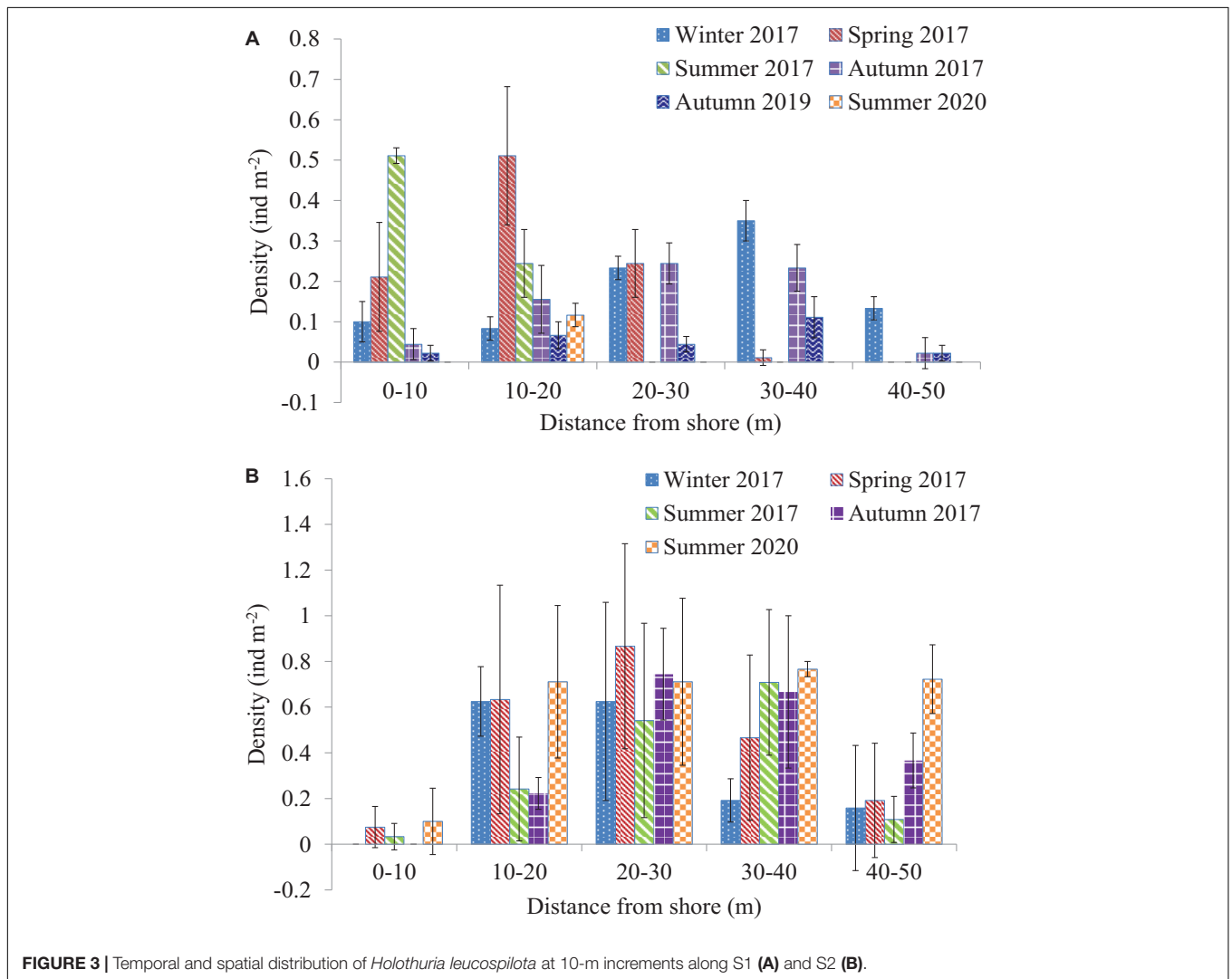
at the same DS in summer 2020. From this we conclude that *H. leucospilota* at S1 tended to aggregate in nearshore shallow areas from winter to summer but dispersed deeper in autumn.

The distribution of *H. leucospilota* at S2 is shown in **Figure 3B**. Sea cucumbers occurred along all 10-m transect increments in spring and summer, but none occurred from 0 to 10 m DS in winter and autumn. For 2017, high densities occurred at 10–20 m and 20–30 m DS in winter and spring, at densities generally $2\text{--}3 \times$ those found at 30–40 m and 40–50 m DS at the same sampling time. Most sea cucumbers aggregated at 20–30 m and 30–40 m DS in summer and autumn, with high densities also occurring at 40–50 m DS in autumn (0.37 ± 0.12 ind m^{-2}). Densities were low at 0–10 m DS (0.10 ± 0.15 ind m^{-2}) in summer 2020, but values were high and generally similar along all other 10-m transect increments at DS > 10 m ($0.71\text{--}0.76$ ind m^{-2}). Unlike 2017, high densities of sea cucumber still occurred at > 40 m DS in summer 2020.

Examples of benthic invertebrates sighted at S1 in summer 2017 are shown in **Figure 4**. Large numbers of decomposing

TABLE 3 | Results of two-way ANOVA on effects of sampling time (time) and distance from shore (distance) on *Holothuria leucospilota* density at 10-m increments along transects.

Source of variation	S1				S2			
	df	Ms	F	P	df	Ms	F	P
Time	5	0.010	25.794	0.000	4	0.019	3.270	0.019
Distance	4	0.009	24.882	0.000	4	0.095	16.775	0.000
Time × distance	20	0.008	20.017	0.000	16	0.008	1.476	0.147
Residual	60	0.000			50	0.006		
Total	90				75			

**FIGURE 3** | Temporal and spatial distribution of *Holothuria leucospilota* at 10-m increments along S1 (A) and S2 (B).

Charybdis japonica and *Portunus pelagicus* crabs (Figures 4A,B), and tests of the sea urchin *Echinocardium* spp. and shells of the bivalve *Asaphis violascens* (Figures 4C,D) were observed from 30 to 50 m DS. No survived sea cucumber remained at DS > 20 m, and three *H. leucospilota* corpses with expelled Cuvierian tubules were observed from 20 to 40 m DS (Figures 4E,F). These decaying corpses indicate severe hypoxia to anoxia had occurred at DS > 30 m before sampling in summer. In contrast,

sea cucumbers from 0 to 10 m DS had normal postures and continued to feed on surface sediments (Figures 4G,H). Few sea cucumbers occurred in 2020 summer sampling; no mass mortality of benthic invertebrates was observed along any 10-m transect increment.

No *H. leucospilota* corpses or other dead benthic invertebrates occurred along S2 transects in summer 2017. All observed sea cucumbers were extending their anterior ends to feed on surface

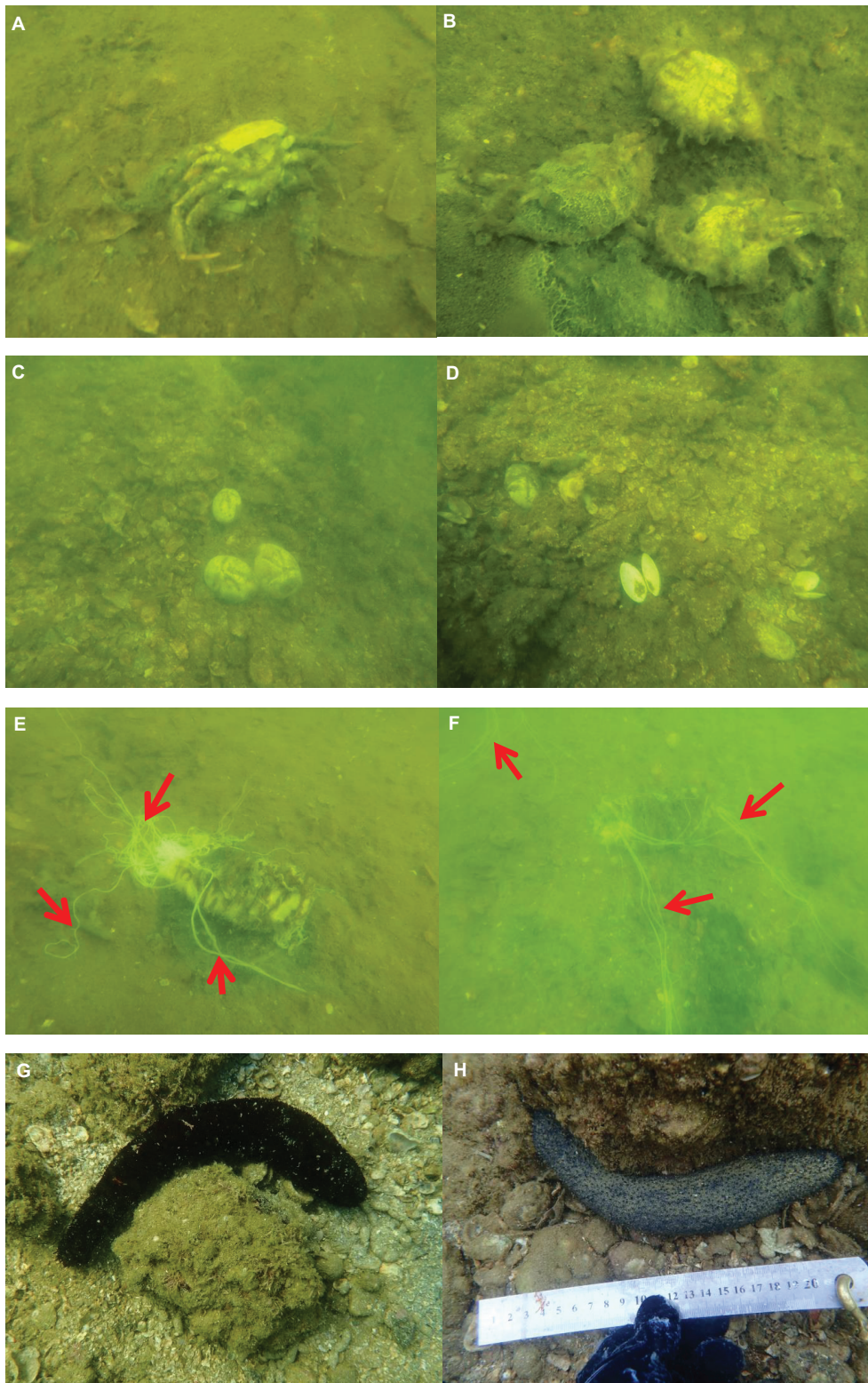


FIGURE 4 | Representative benthic invertebrates at S1 in summer 2017. Decaying corpses of crabs *Charybdis japonica* (A) and *Portunus pelagicus* (B) at DS 30–50 m; tests of the heart urchin *Echinocardium* spp. (C) and shells of the bivalve *Asaphis violascens* (D) at DS 30–50 m; dead *Holothuria leucospilota* at DS 20–40 m (E,F), with arrows indicating Cuvierian tubules; live *H. leucospilota* at DS 0–10 m (G,H).

sediments, and most at > 30 m DS had their anus (at the posterior end of body) oriented upward (Figures 5A–D). In contrast, individuals observed < 20 m DS usually had normal posture (Figures 5E,F). All sea cucumbers had normal posture in 2020 summer sampling, and no benthic invertebrate corpses were found along any 10 m transect increment at either site.

Abundance

Average sea cucumber abundance at S1 varied with time (one-way ANOVA, $P = 0.000$) (Figure 6). Abundance increased from winter to spring in 2017, but then decreased over time, with abundances in autumn 2019 ($0.06 \pm 0.00 \text{ ind m}^{-2}$) and summer 2020 ($0.02 \pm 0.01 \text{ ind m}^{-2}$) significantly lower than those during four sampling events in 2017 (0.18 ± 0.02 , 0.20 ± 0.04 , 0.15 ± 0.01 , and $0.14 \pm 0.03 \text{ ind m}^{-2}$). The rate at which abundance decreased accelerated over time, by 61% from autumn 2017 to autumn 2019, and 58% from autumn 2019 to summer 2020. Average sea cucumber abundance in 2020 was about 10% of 2017 values.

Average sea cucumber abundance at S2 varied with time (one-way ANOVA, $P = 0.019$) (Figure 6), and increased by 84% from summer 2017 ($0.33 \pm 0.12 \text{ ind m}^{-2}$) to summer 2020 ($0.60 \pm 0.07 \text{ ind m}^{-2}$). Average sea cucumber abundance at S1 was significantly lower than it was at S2 in spring and autumn 2017, and summer 2020 (t -test, $P = 0.004$, $P = 0.002$, and $P = 0.005$, respectively). Average abundances at S2 were 1.8–2.8× those at S1 in 2017, and 25.8× those of S1 in summer 2020.

Population Structure

Summertime sea cucumber body lengths at S1 ranged 11–34 cm in 2017 and 16–30 cm in 2020; at S2 these values were 10–40 cm in 2017 and 7–36 cm in 2020. Relationships between sea cucumber wet weight (W , g) and body length (L , cm) for summer 2017 are described by a positive linear correlation: $W = 10.715L - 65.421$ ($n = 35$, $R^2 = 0.618$, $P = 0.000$). We derive wet weights of sea cucumbers along each transect during summers of 2017 and 2020 using this equation.

Wet-weight population structure at each site in summer of 2017 and 2020 is shown in Figure 7. Sea cucumbers of medium size were prevalent at both sites, excepting S2 in summer 2017, where large individuals were proportionally more abundant (67.86%). The percentage of small-sized sea cucumbers at S1 decreased from 10.29% in 2017 to 0% in 2020, while values at S2 increased from 4.59 to 24.72%. Proportions of large-sized individuals at S1 decreased from 39.71% in 2017 to 28.57% in 2020, while values at S2 decreased from 67.86 to 33.58%.

DISCUSSION

Most tropical sea cucumber species in China are intensely fished to meet growing market demand for their products (Purcell et al., 2012; Harith et al., 2018; Huang et al., 2018). Of these, *H. leucospilota* occurs widely throughout tropical and subtropical oceans, but limited information existed regarding natural stocks of this species in the South China Sea. We report the tendency of one population in an area open to the public (S1) to aggregate in

shallow water from winter to summer, but to disperse to deeper water in autumn. From a fishery perspective, the rate of decline in abundance of this species increased from 2017, no small-sized animals were found in 2020, and we consider that the local extinction of this species is an eventual possibility. In contrast, *H. leucospilota* abundance in a protected area (S2) increased by 84% from summer 2017 to summer 2020, and the percentages of small-sized, recently recruited sea cucumber increased by 20% over this same period.

Distribution

The distribution of sea cucumbers is influenced by various environmental (e.g., water temperature, salinity, substratum, depth, hydrodynamics) and biological (e.g., reproduction, predators, and even the presence of other holothurian species) factors (Massin and Doumen, 1986; Zhou and Shirley, 1996; Drumm et al., 1999; Mercier et al., 2000; Woodby et al., 2000; Harith et al., 2018; Tanita and Yamada, 2019). Relationships between sea cucumbers and their environment also vary geographically, such as the presence of juvenile *H. leucospilota* being positively correlated with seagrass cover at Pai Island, Indonesia (Setyastuti et al., 2018), but being absent from seagrass beds at Laing Island, Papua New Guinea (Massin and Doumen, 1986). The distribution of coral reef-dwelling *H. leucospilota* in tropical oceans can be also regulated by physicochemical parameters, substratum type, and hydrodynamics (Massin and Doumen, 1986; Harith et al., 2018; Setyastuti et al., 2018). No comparable information is available for *H. leucospilota* in coastal waters of China. We report sediment types to comprise relatively homogeneous sands and shell/rubbles from 10 to 50 m DS at each sampling site, and for sea cucumber density to not be very high, especially at S1. Therefore, substratum type and/or food availability might not be key factors regulating the distribution of this species at DS > 10 m at either site. Similarly, no relationship was observed between sea cucumber density and sediment type in the coastal waters of Ishigaki Island (Tanita and Yamada, 2019).

Coastal hypoxia and anoxia represent major stresses for benthic marine species. Mobile fauna can actively avoid hypoxia by migrating from these conditions to more oxygenated waters, with migrations and avoidance behaviour generally starting at $\text{DO} < 3.0 \text{ mg L}^{-1}$ (Wu, 2002; Riedel et al., 2012, 2014; Cosme and Hauschild, 2016). Echinoderms are aerobic animals with only moderate tolerance to environmental anoxia (Gray et al., 2002; Levin et al., 2009; Riedel et al., 2014; Cosme and Hauschild, 2016), and their threshold for escape responses to hypoxic conditions varies: e.g., the ophiuroid *Amphiura filiformis* abandons its burrow at $\text{DO} < 1.2 \text{ mg L}^{-1}$, but *A. chiajei* emerges from sediments at 0.8 mg L^{-1} (Rosenberg et al., 1991); and the sea urchin *Psammechinus microtuberculatus* begins to discard its camouflage and move from beneath bioherms at $\text{DO} < 2.8 \text{ mg L}^{-1}$, while the infaunal *Schizaster canaliferus* begins to emerge onto the sediment surface at $\text{DO} < 1.4 \text{ mg L}^{-1}$ (Riedel et al., 2014).

We report DO levels at S1 to decrease with DS during spring and summer (Table 2). Although we did not directly observe sea cucumber escape behaviours during sampling, hypoxia stress

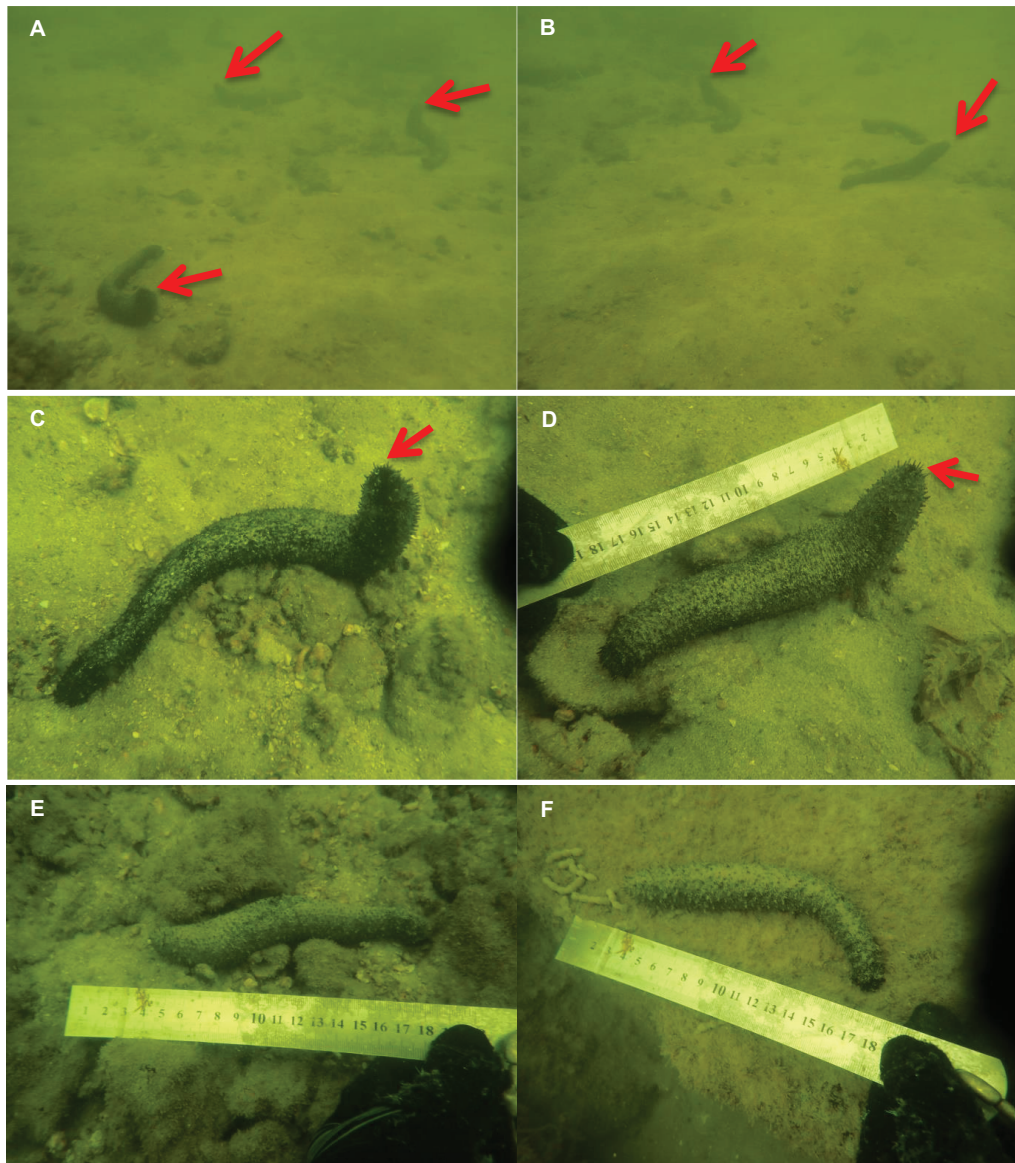
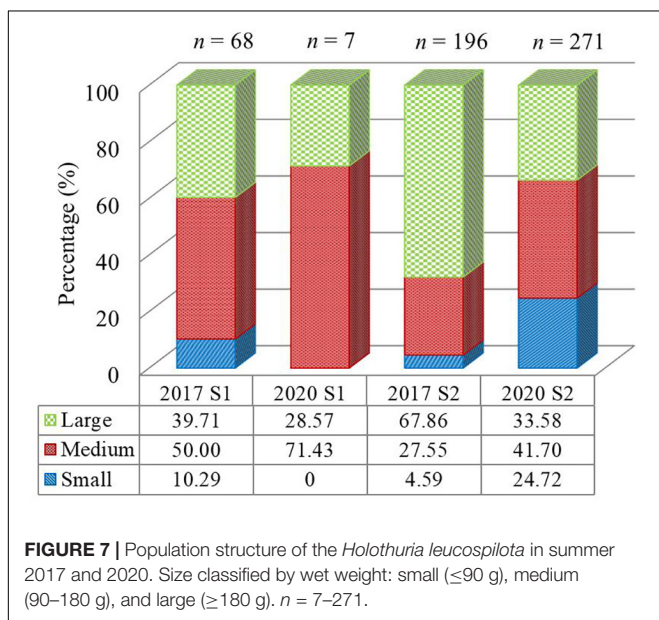
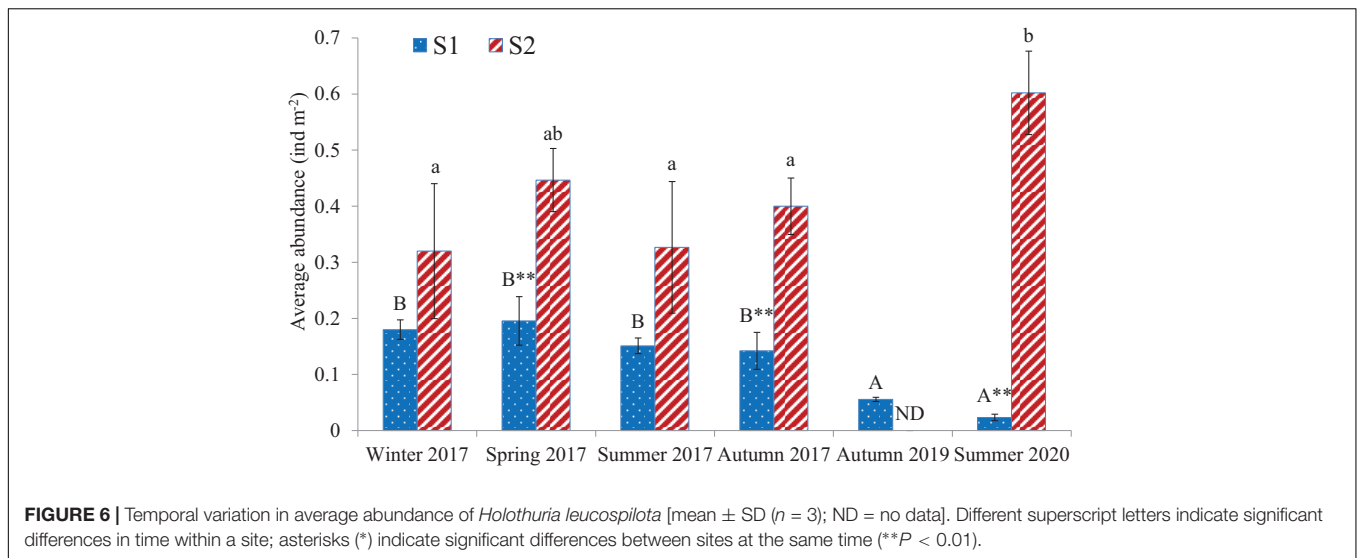


FIGURE 5 | Sea cucumber *Holothuria leucospilota* at S2 in summer 2017: **(A–D)** DS 30–50 m, with arrows indicating anus; **(E,F)** DS 0–20 m.

should have already forced *H. leucospilota* to migrate from deeper into shallower waters (with higher DO), particularly in summer, when specimens aggregated at DS < 20 m (**Figure 3A**). Decreased pH can also significantly influence benthic macrofaunal fitness and survival (Riedel et al., 2012). We report low pH in summer 2017, especially at S1, which possibly also influenced the distribution of *H. leucospilota*.

At S2 the seabed was largely flat, lacking refuge atop elevated substrata at >15 m DS (**Figure 2**). Additionally, S2 bottom waters had higher DO levels, possibly exceeding concentrations that would initiate escape behaviour for *H. leucospilota*, with no mass migration or avoidance reaction triggered during spring or summer. Sea cucumbers obtain most of their oxygen via their respiratory trees – blind-ended evaginations of the posterior

digestive system – which rhythmically inflate with seawater that is drawn in through the anus located atop the posterior end of the body (Conand et al., 1997; Jaekle and Strathmann, 2013; Weinrauch and Blewett, 2019). Most sea cucumbers at DS > 30 m may have elevated their anus to source oxygenated water from higher in the water column during periods of summer hypoxia (**Figure 5**). Sea cucumbers were absent from 0 to 10 m DS at S2, where rock prevailed during winter and autumn. This distribution is consistent with (Massin and Doumen, 1986), who reported *H. leucospilota* preferred non-rocky substrata. However, a few individuals could be observed on rocks in shallow water during spring and summers. The occurrence of *H. leucospilota* on nearshore rocks might also be explained by their seeking shallow water refuges when DO was low during spring and



summer. While the onset and extent of hypoxia disturbance is difficult to forecast and study in the field, animal behaviour can be used to assess hypoxia stress in marine ecosystems (Riedel et al., 2014). The typical “escape” and/or “anus-lifted” behaviours of *H. leucospilota* may serve as early warning signals of hypoxic conditions.

Abundance

The sea cucumber is a common and conspicuous animal in tropical and subtropical coastal areas. Comparatively high abundances of *H. leucospilota* can be observed on tropical reefs: e.g., 0.5–1.2 ind m⁻² at Reunion Island, Indian Ocean (Conand et al., 1997; Gaudron et al., 2008), 0.8 ind m⁻² at One Tree Reef, Great Barrier Reef, Australia (Schneider et al., 2011), and 2.6 ind m⁻² at Satang Besar Island, Sarawak,

Malaysia (Harith et al., 2018). The abundance of this species appears much lower in subtropical areas, where, for example, on a reef fringing Ishigaki Island, southern Japan, it reaches only 0.31 ind m⁻² (Tanita and Yamada, 2019). We report average abundances at S1 from 0.14 to 0.20 ind m⁻² in 2017 in an area closed to the public (deemed “virgin abundance”), but for densities at this site to decrease to 0.02 ind m⁻² (about 10% of 2017 levels) by summer 2020 after the area was opened to public for fisheries and tourism in 2018. This decrease suggests that this population has been severely over-exploited (a stock between 10 and 30% of virgin abundance) (Friedman et al., 2011; Purcell et al., 2013). In contrast, abundance at S2 (protected from both fisheries and tourism) increased by 84% from 2017 to 2020, and reached 0.60 ind m⁻² by summer 2020.

Hypoxia can seriously affect marine life and the ecological balance of coastal waters, mortality of benthic fauna occurs at DO concentrations <2.0–0.5 mg L⁻¹ (Gray et al., 2002; Vaquer-Sunyer and Duarte, 2008). In Gullmarfjord, Sweden, all macrofauna died at DO < 1.4 mg L⁻¹ (Josefson and Widbom, 1988). Benthic macrofauna most resistant to hypoxia include molluscs, followed by polychaetes, echinoderms, and crustaceans (Gray et al., 2002; Levin et al., 2009). Sublethal hypoxia thresholds for echinoderms range 0.7–1.7 mg L⁻¹ (Chu and Tunnicliffe, 2015). For *H. leucospilota*, survival rate decreases by 18% after 4 d hypoxia exposure (2 mg L⁻¹), and 80% after 22 d exposure (Zamani et al., 2018). We previously reported bottom-cultured *H. leucospilota* and *Apostichopus japonicus* to be able to endure high levels of organic and sulphide pollution beneath a fish farm in Dapeng Cove, but not sustained summer hypoxia, and for all individuals to have died after late July when DO concentrations in bottom water dropped below 2.5 mg L⁻¹ (Yu et al., 2013, 2014).

Field studies have shown that DO < 1.0 mg L⁻¹ prevailing for days to weeks can significantly affect benthic community structure (Levin et al., 2009). We report DO < 1.04 mg L⁻¹ at DS > 20 m in summer 2017 (Table 2), and

concomitant mass mortality of benthic invertebrates (e.g., crabs, sea cucumbers, sea urchins, bivalves) (Figure 4). While short-term hypoxia does not induce evisceration in sea cucumbers, long-term hypoxia can, and the *H. leucospilota* can reject the Cuvierian tubules when confront prolonged hypoxia stress (Zamani et al., 2018; Weinrauch and Blewett, 2019). We report dead *H. leucospilota* at S1 with expelled Cuvierian tubules, indicating long-term exposure to hypoxia. While Cuvierian tubule expulsion could indicate severe hypoxia and the collapse of benthic ecosystems, summer hypoxia-induced mortality may not be the main cause of sea cucumber population decline at S1. Because bottom water oxygen depletion is typically a slow and gradual process, and sea cucumbers at S1 tended to aggregate in shallow water from winter to summer (Figure 3A), most of them could have found shelter from hypoxia at DS < 20 m before severe hypoxia or anoxia occurred in summer 2017. No apparent decline in *H. leucospilota* abundance occurred in 2017, prior to S1 being opened to the public, but it did decline afterward, with few individuals being found in summer of 2020 when DO levels were relatively high, and there had been no apparent mass mortality of benthic fauna.

Although macrobenthic species biomass and richness in the lower portion of Daya Bay, particularly Dapeng Cove, was negatively influenced by coolant water (heated) discharged from nuclear power plants (Wang et al., 2008), it is unlikely that the abundance of *H. leucospilota* was directly affected by discharge plumes in recent years. It is more likely that the decrease in abundance of *H. leucospilota* at S1 was due to other anthropogenic disturbances, particularly fishing pressure from fishermen and tourists, with summer being the tourist season, and with swimming and snorkelling being popular aquatic sports in Daya Bay. Many fishermen and tourists visited S1 in summer from 2018, when *H. leucospilota* would have migrated to shallow waters within the range of snorkellers. These individuals would be easily captured, possibly explaining why no individual was observed at DS < 10 m (with high DO), and few individuals were found at DS 10–20 m (greater depth along a transect would afford increased protection from fishing) in summer 2020. During summer of 2017, the highest sea cucumber densities occurred at DS < 10 m in waters with increased DO. Concurrently, *H. leucospilota* abundance increased at S2, which was closed to the public and protected from fisheries and tourism, over this same period.

Wild sea cucumber stocks are easily affected by fisheries, and marine reserves can assist in conserving their declining populations (Uthicke and Benzie, 2000; Anderson et al., 2011; Purcell et al., 2012, 2013; Wolfe and Byrne, 2017; Ramírez-González et al., 2020). In Ngardmau State, Palau, a decline in sea cucumber abundance occurred in one area open to fishing, while recovery occurred within a marine reserve (Rehm et al., 2014). On the Great Barrier Reef, densities of the sea cucumber *Holothuria nobilis* on reefs protected from fishing were about four times those on reefs open to fishing (Uthicke and Benzie, 2000). We consider S2 functions to an extent as a reserve for sea cucumbers in Daya Bay.

Population Recruitment

Hypoxia can negatively affect reproduction, larval supply, settlement and recruitment of benthic invertebrates: e.g., the brittle star *A. filiformis* spawning is affected by low DO (2.7 and 1.8 mg L⁻¹) (Nilsson and Skold, 1996), and larvae of the spionid polychaete *Paraprionospio pinnata* do not settle until DO exceeds 2.0 mg L⁻¹ (Powers et al., 2001). *H. leucospilota* breed in Daya Bay in summer (Huang et al., 2018), at which time the water column is stratified and pollution (organic enrichment from fish and oyster aquaculture inside the bay, and coolant water from nuclear power plants) could exacerbate hypoxia in Dapeng Cove (Tang et al., 2003; Wang et al., 2008; Yu et al., 2013, 2014). Severe summer hypoxia at S1 might negatively affect spawning and subsequent settlement of larval *H. leucospilota*, which, combined with broodstock depletion because of fishing pressure and/or hypoxia-induced mortality, might limit recruitment. Abundance declined by 90%, and the proportion of small *H. leucospilota* decreased from 10.29% in 2017 to 0% (no recruitment) in 2020 at S1.

Sea cucumbers might experience an Allee effect – a correlation between population size or density and mean individual fitness – induced by large reductions in abundance, resulting in slow and negligible recovery, and even population collapse (Uthicke and Benzie, 2000; Uthicke et al., 2009; Anderson et al., 2011; Wolfe and Byrne, 2017). As a traditional fishery target species, *H. leucospilota* in the open area of Daya Bay will continue to be exploited heavily by local fishermen and tourists. Overfishing and a lack of fisheries and tourism regulations at S1 are typical of the situation throughout China with regard to tropical sea cucumber resources. Recovery of *H. leucospilota* in this area is unlikely, unless fisheries and tourism desist. In contrast, higher DO concentrations and abundant sea cucumber broodstock in the breeding season at S2 favour recruitment of *H. leucospilota*, with abundance at this site tending to increase between 2017 and 2020. Site S2 might function as a nursery ground for sea cucumbers, and provide planktonic larvae for recruitment into nearby areas, although it is unknown if these larvae will disperse to areas that are fished. An improved understanding of the biology, ecology, and conservation of tropical sea cucumbers in China is required.

CONCLUSION

Our results demonstrated that the summer hypoxia at the mouth of a subtropical bay (S1) could force sea cucumber *H. leucospilota* to aggregate in shallower waters, where they were easily captured by fishermen and tourists after this area was opened to the public. The hypoxia at S1 could negatively influence *H. leucospilota* spawning and larval settlement, which combined with depletion of broodstock because of fishing pressure and/or hypoxia-induced mortality, could inhibit recruitment. In contrast, higher DO concentrations and abundant broodstock during summer favoured recruitment of *H. leucospilota* at the protected open-water area (S2). Overall, hypoxia and anthropogenic disturbance impede recovery of *H. leucospilota* at S1, while the protected

S2 might function as a nursery ground for sea cucumbers of the nearby area.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

ZY: conceptualisation, funding acquisition, investigation, data curation, writing – original draft, review, and editing. YZ: data curation, writing – original draft, review, and editing. LZ and HS:

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