

1 Dynamic of *Tridacna* spp. population variability in northern SCS over
2 past 4500 years derived from AMS ¹⁴C dating

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21 **Abstract**

22 The marine bivalve, *Tridacna* spp. is an iconic invertebrate of the Indo-Pacific coral

23 reef communities from Eocene to present. However, field observations found that the

24 population of *Tridacna* spp. has declined in recent decades and some species are now
25 endangered in the northern South China Sea (SCS) of western Pacific, which are
26 speculated to be connected with the human overfishing and/or climate changes. Thus
27 distinguishing the impacts of human activities and climate changes on *Tridacna* spp.
28 populations is essential for understanding the dynamic of *Tridacna* spp. population
29 variability. Such effort will be important in launching conservation policies and
30 restoring population. Here, extensive sampling was applied on sub-fossil *Tridacna* spp.
31 shells at the North Reef of the northern SCS, and the long-lived (with a lifespan more
32 than 30 years) *Tridacna* spp. population index (LTPI) over the past 4500 years was
33 obtained based on the AMS¹⁴C dating method. The results show that LTPI has
34 experienced several short-term collapses (shorter than 200 years) over the past 4500
35 years, which may be associated with excessive cold winter temperatures. Remarkably,
36 LTPI usually recovered rapidly after the rewarming of temperatures, indicating a robust
37 self-recruitment mechanisms in response to natural climate changes. However, the last
38 catastrophic collapse of LTPI that occurred at around AD ~1820 – AD ~1900 didn't
39 rebound despite the significant rise in temperature over the recent 100 years. The
40 decoupling between LTPI and climate changes in recent hundred years was probably
41 induced by the increased commercial fishing in the SCS, which has overwhelmed and
42 exacerbated the self-recruitment mechanisms between *Tridacna* spp. population and
43 climate changes.

44 **Key words:** *Tridacna* spp.; EAWM; overfishing; endangerment

45 **1. Introduction**

46 In the Phanerozoic, five major extinctions occurred (Raup and Sepkoski, 1982), and
47 these events were attributed to natural force majeure ranging from maladaptation to
48 changing environments, such as colder or warmer climates, extreme volcanic activity,
49 external impact events by asteroids and meteors and more (Erwin, 1994; Trotter et al.,
50 2008; Barnosky et al., 2011; Jiang, 2016). There is emerging evidence that we now face
51 the sixth mass extinction: Hundreds of species have gone extinct since the Industrial
52 Revolution, largely due to significant human interventions and climatic changes
53 (Tilman et al., 1994; Thomas et al., 2004; Marzluff et al., 2008; Ceballos et al., 2015;
54 Jiang, 2016). It is reported that the extinction rate in modern times is much higher than
55 historical background levels (Pimm et al., 1995; Rosser and Mainka, 2010), and that
56 the extinction rate of mammals and birds on islands is much higher than those on
57 continents (Loehle and Eschenbach, 2011). Currently, about one million plants and
58 animals are at risk of extinction, and many of them may go extinct in the coming
59 decades according to the Intergovernmental Science-Policy Platform on Biodiversity
60 and Ecosystem Services (IPBES) (Tollefson, 2019).

61 *Tridacna* spp. is the largest bivalve in the world, and is also known as the “jade of
62 the sea”. Some species of Tridacnidae family have been listed as the “Vulnerable”
63 species in IUCN Red List of Threatened Species in 1996 (Wells, 1996). *Tridacna* spp.
64 are iconic invertebrates of Indo-Pacific tropical shallow coral reefs from the Eocene to
65 present (Rosewater, 1965; Neo et al., 2015). Most species can grow dozens of

66 centimeters and live for several decades (Rosewater, 1965), and the largest species,
67 *Tridacna gigas*, has been reported to reach a length of 137 cm (Rosewater, 1965).
68 *Tridacna* spp. are associated with unicellular algal symbionts (Zooxanthellae).
69 Zooxanthellae serve the symbiotic function of synthesizing the host's waste molecules
70 (CO₂) to photosynthesize organic molecules, which are shared with the host (Yonge,
71 1936; Fisher et al., 1985; Norton et al., 1992). *Tridacna* spp. serve numerous ecological
72 roles on coral reefs, for example, they represent a food source for predators and
73 scavengers, provide shelter for small invertebrates and coral reef fish, and serve as
74 controllers of eutrophication (Neo et al., 2015). In addition, their hard and dense
75 aragonite shells with annual and even daily growth lines in their inner shell layer have
76 been developed to provide important high resolution paleoenvironment archives from
77 tropical oceans (Sano et al., 2012; Yan et al., 2013; Yan et al., 2020).

78 *Tridacna* spp. are often attached to coral reef using their byssal strings during early
79 life, and meld into the coral reef during adulthood, then deposited *in-situ* after death
80 (Fankboner, 1971). Their sedentary lifestyle leads to a poor adaptability to
81 environmental changes. The optimum water temperature for the growth of *Tridacna*
82 spp. ranges from ~26 °C to ~30 °C (Mingoa, 1990; Junchompoo et al., 2013; Apte et
83 al., 2019), and sustained high or low temperatures outside their tolerance limits can
84 cause mortality through the loss or death of symbionts which provokes the whitening
85 of the mantle tissue (Lucas et al., 1989; Mingoa, 1990; Blidberg et al., 2000; Buck et
86 al., 2002; Andréfouet et al., 2013; Maboloc and Villanueva, 2017). In addition, the

87 immobility of *Tridacna* spp. assists their easy exploitation. The adductor, gonad, muscle
88 and mantle tissues of *Tridacna* spp. are harvested as a delicacy (Lucas, 1994), and the
89 shells of *Tridacna* spp. are made into various works of art and crafts (Larson, 2016).
90 Therefore, *Tridacna* spp. are considered as a valuable fishery in many countries. For
91 example, the Fijian fishery harvest 49.5 tons of shell in 1984 for commercial purposes
92 (Lewis et al., 1988).

93 Field observation suggested that the long-lived *Tridacna* spp. in the northern South
94 China Sea (SCS) has suffered a catastrophic population crash in recent decades (Dong
95 et al., 2015), which is in pace of the global warming. However, the current *Tridacna*
96 spp. population collapse has also coincided with the increased commercial fishing in
97 recent decades (Larson, 2016), making it is difficult to distinguish the impacts of human
98 disturbances and climate changes on the *Tridacna* spp. populations. Thus investigating
99 the variability of *Tridacna* spp. populations before the introduction of mass harvesting
100 by humans is essential.

101 Theoretically, by collecting the sub-fossil shells from top to bottom in coral reef
102 systems, we can obtain continuous “sedimentary sequences”. Then the time series of
103 long-lived *Tridacna* spp. population can be obtained in accordance to the age
104 distribution of these sub-fossil shells. Finally, together with the anthropogenic and
105 paleoclimatic archives, the impacts of climate changes and human activities on the
106 population of *Tridacna* spp. in northern SCS can be assessed.

107 2. Materials and methods

108 2.1 Site description, sample collection and long-lived sample selection.

109 The South China Sea (SCS) is one of the largest semi-enclosed marginal seas off
110 the Asian continent, with an area of 3.6 million km², located in the Western Pacific (Fig.
111 1). It is studded with numerous islands, coral reef, atolls and shoals. All samples used
112 in this study were collected from North Reef (17°04'39" N, 111°28' 36" E), Xisha
113 Islands, northern South China Sea, which is about 300 km distant from the largest island
114 in the SCS, Hainan Island (Fig. 1). Instrumental data show that the mean annual air
115 temperature, sea surface temperature (SST) and rainfall are 26.7 °C, 27.6 °C and
116 1450.55 mm, respectively.

117 *Tridacna* spp. do not move during their lifetimes (Fankboner, 1971) and their shells
118 are deposited in situ after death. Extensive sampling was applied from a circular area
119 with a radius of ~100 m in North Reef (17°04'39" N, 111°28' 36" E) from top to bottom
120 to obtain a continuous "sedimentary sequence". For each sub-fossil shell, a radial
121 section about ~0.5 cm-thick was cut from its umbo to the ventral margin along the
122 maximum growth axis (Fig. 2) (Yan et al., 2013). The annual growth bands can be easily
123 observed from the sections of the *Tridacna* spp. shells (Fig. 2c) and the lifespan of each
124 *Tridacna* spp. shell can be determined by counting the number of annual growth bands,
125 one annual growth line for one year. Although a total of 1406 samples were collected
126 from top to bottom from North Reef systems, our analysis focuses primarily on long-

127 lived shells. Here, the sub-fossil samples with more than 30 annual growth layers were
128 defined to be the long-lived clam samples. A total of 245 sub-fossil samples with a
129 lifespan greater than 30 years were obtained in this study. The 245 shells were divided
130 into 4 groups randomly and sent to the accelerator mass spectrometry (AMS) ^{14}C dating
131 laboratory respectively from 2015-2019, 69 samples in 2015, 60 samples in 2016, 61
132 samples in 2017 and 55 samples in 2019. Each selected radial section was photographed,
133 cleaned with deionized water and dried, and then ~50 mg carbonate powder was milled
134 from the middle part of the inner layer (Fig. 1b) by a dental drill for AMS ^{14}C dating.

135 **2.2 Radiocarbon dating**

136 AMS ^{14}C dating was applied to determine the periods in which the samples were
137 alive. Three groups of the *Tridacna* spp. shells (i.e., with 190 carbonate powder samples)
138 were dated at the Institute of Earth Environment, Chinese Academy of Sciences at
139 Xi'an in 2015, 2016 and 2017, respectively by the AMS ^{14}C dating method, and one
140 group of 55 samples were dated at Beta Analytic in 2019 by the AMS ^{14}C dating method.
141 The results were calibrated by the marine ^{14}C yield model using Marine13 of Calib Rev
142 7.0.4 (<http://www.calib.org>) with a regional $\Delta R=18$ and $\sigma=37$ (John et al., 2002). The
143 calibrated results show that the youngest *Tridacna* spp. lived around 1765 AD, while
144 the oldest lived around BC 2426, thus spanning almost the last 4500 years (Fig. 3a).

145 **2.3 The numbers of long-lived *Tridacna* spp. samples in each 100 years.**

146 A moving 100-year window with a 10-year sliding time step (e.g. the time windows
147 were set as AD 2000-AD 1900, AD 1990-AD 1890, AD 1980-AD 1880, ..., until BC
148 2450-BC 2550) was used in this study, and the long-lived sub-fossil samples in each
149 time window were counted according to the distribution of calibrated ^{14}C ages (Fig 3b).
150 Then the time series of the amount of the long-lived *Tridacna* spp. sub-fossil shell
151 samples in each 100 years was used as “long-lived *Tridacna* spp. population index
152 (LTPI)” in this study (Fig 3b). In addition, in order to verify the representativeness and
153 reproductivity of *Tridacna* spp. population index, the LTPI were also calculated for the
154 4 dating groups, respectively, as shown in figure 3c (2019), d (2017), e (2016) and f
155 (2015).

156 **2.4 Details of the anthropogenic activity and climate proxy data.**

157 Human impacts on wild animal populations began perhaps 50,000 years ago and
158 increased significantly 500 years ago with the arrival of more humans and efficient
159 hunting tools (Jiang, 2016; Dirzo et al., 2014). The History Database of the Global
160 Environment (HYDE 3.2, Goldewijk et al., 2017) provided an integrated record of the
161 co-evolving human-environment system from 10000 BC to AD 2017
162 (<https://easy.dans.knaw.nl/ui/datasets/id/easy-dataset:74467>). In this study, the total
163 human population of main countries around the SCS, including China, Philippines,
164 Malaysia, Vietnam and Thailand, over the past 4500 years was used to represent the
165 combined anthropogenic effects on *Tridacna* spp. populations in the northern SCS (see
166 Fig. 4a). In addition, elemental Hg flux during the past 600 years in northern SCS was

167 adopted as a proxy to reflect human activities around the region (Fig. 4a).

168 Species survival in a given area may be influenced by climate change (Thomas et
169 al., 2004; He, 2012). However, reliable paleoclimate records for the northern SCS area
170 with high-resolution over the past 4500 years currently do not exist. The winter
171 temperature variability in the northern SCS is largely influenced by atmospheric
172 circulation patterns from the Northern Hemisphere middle-high latitudes (Yan et al.,
173 2015), therefore the paleoclimate records from mainland China and the Northern
174 Hemisphere (e.g., Ge et al., 2006; Vinther et al., 2006; Kang et al., 2018) were used to
175 investigate the connection between LTPI and natural climate variability over the past
176 4500 years. The time resolution of paleoclimate records ranges from hundreds to
177 decades, so a 100 years low-pass filter was applied on the LTPI for the convenience of
178 the comparison between LTPI and paleoclimate records (Fig. 4b, 4c and 4d).

179 **3. Results and discussion**

180 **3.1 Dynamic of long-lived *Tridacna* spp. population variability over the past 4500 years.**

181 The calibrated ^{14}C ages of the 245 long-lived sub-fossil shells are mainly
182 concentrated in the BC ~200- BC ~2000 period and had no obvious clustering during
183 the most recent 2000 years (Fig. 3a). As shown in figure 3b, LTPI increased from BC
184 ~2000 to BC ~800 and then shows a decreasing trend. Four short-term crashes existed
185 at AD ~2000 – AD ~1820, AD ~1390 –AD ~1230, AD ~640 – AD ~500 and BC ~80

186 – BC ~170, which are usually followed by rapid recoveries except for the most recent
187 one (Fig. 3b).

188 Although just 245 samples were dated in total, the population indices calculated by
189 four groups respectively show similar trends and patterns over the past 4500 years (Fig.
190 3c, d, e and f), indicating that the LTPI in the North Reef obtained by AMS¹⁴C dating
191 method was in general replicated. Even if more samples are dated, they are likely to be
192 on the existing distribution curve, indicating that “long-lived *Tridacna* spp. population
193 index” based on 245 sample ages have the potential to provide a representative
194 reflection on the dynamic of *Tridacna* spp. population in the North Reef.

195 **3.2 Climatic impacts on dynamic of *Tridacna* spp. population during AD ~1900 –** 196 **BC ~2550**

197 Paleoclimate records, including the temperature record from the China mainland
198 (Ge et al., 2006), the $\delta^{18}\text{O}$ record of Greenland ice-core (Vinther et al., 2006), and the
199 East Asian Winter Monsoon (EAWM) archive (Kang et al., 2018), were employed to
200 discuss the possible link between the *Tridacna* spp. population and climate changes
201 (Fig. 4b, 4c and 4d, respectively). As shown in figure 4b, 4c and 4d, these paleoclimate
202 records show similar variation to the LTPI, indicating that the *Tridacna* spp.
203 populations in the North Reef, northern SCS, is likely influenced by the climate change.
204 The highest correlation coefficient ($R=0.40$, $p<0.01$) between LTPI and $\delta^{18}\text{O}$ record of
205 Greenland ice-core occurred when LTPI lags ~150 years behind the $\delta^{18}\text{O}$ record, and

206 the highest correlation coefficient ($R=0.72$, $p<0.01$) between LTPI and temperature
207 anomaly of China mainland occurred when LTPI lags ~180 years behind the
208 temperature anomaly. Meanwhile, the LTPI was negatively associated with EAWM
209 intensity, with a correlation coefficient $R=-0.59$ ($p<0.01$) when the LTPI lags ~480
210 years behind the EAWM record. The physical-biological time lags between LTPI and
211 proxy-climate records can be explained with the following reasoning:

212 First, the marine “reservoir effect” in the northern SCS has not been completely
213 solved and the calibration curve in Calib Rev 7.0.4 remains imperfect. [Yu et al. \(2010\)](#)
214 examined the regional marine ^{14}C reservoir in the SCS using paired measurements of
215 AMS ^{14}C and TIMS ^{230}Th on corals. The results showed that the regional marine
216 reservoir corrections (ΔR) of the SCS (i.e., including three sites: Leizhou Peninsula,
217 Sanya Island, Nansha Islands) during the Holocene varies from -18 ± 73 to 362 ± 58 .
218 Thus the single, constant ΔR value ([John et al., 2002](#)) as used in the calibration program
219 cannot completely account for the marine “reservoir effect” for the sample location.
220 Such an unstable “reservoir effect” leads to the temporal mismatch of the climate-
221 population relationship. Second, chronological uncertainties exist for the paleoclimate
222 records themselves. For example, the ages of the EAWM record in Fig. 4d was
223 determined by optically stimulated luminescence (OSL) from quartz with errors from
224 10 to 340 years, and the continuous chronology over past 4500 years was calculated by
225 interpolation based on 11 measured OSL ages ([Kang et al., 2018](#)). Both the dating
226 method and the interpolation process can lead to additional uncertainties. Third,

227 *Tridacna* spp. has a long life span, and the population recruitment often requires a
228 relatively long period after being hard hit by negative factors. So the LTPI expectedly
229 lags climate changes in a biologically determined manner. Overall, it is reasonable that
230 there is a chronological deviation and time shift between paleoclimate records and LTPI.
231 To simplify the discussion, phase adjustments were applied for Fig. 4b, 4c and 4d
232 (~150-year, ~180-year and ~480-year, respectively) to remove the time-lag between
233 paleoclimate records and the LTPI. In the following discussion, all mentioned ages are
234 based on the age profile of LTPI.

235 Figure 4b shows that the long-lived *Tridacna* spp. were abundant in the northern
236 SCS around BC ~800 – BC ~1100. Meanwhile, the temperature reconstructions for the
237 China mainland reveal warm conditions during BC ~800 – BC ~1100 (Ge et al., 2006).
238 The $\delta^{18}\text{O}$ data from the Greenland ice-core (Vinther et al., 2006), which is usually used
239 to represent the temperature record for the Northern Hemisphere high latitude region,
240 also shows a warm period during BC ~800 – BC ~1100. In addition, the mean grain
241 size of loess during the last 4500 years at Weinan, Shaanxi Province, has been
242 demonstrated to show a weakened EAWM intensity during BC ~800 – BC ~1100
243 (Kang et al., 2018). Thus, the high LTPI during the BC ~800 – BC ~1100 period
244 probably benefited from the warm climate and a weak EAWM.

245 LTPI decline from BC ~800, in concert with the temperature records (Ge et al.,
246 2006; Vinther et al., 2006). Meanwhile, the decline of LTPI was also accompanied by
247 an increased EAWM (Kang et al., 2018). Notably, the decline of LTPI during AD ~1900

248 - BC ~800 is marked by four “pre-Industrial *Tridacna* spp. endangerment” stages (Fig.
249 4b, 4c and 4d, with ~150-year, ~180-year and ~480-year phase adjustments,
250 respectively): AD ~1820 – AD ~1900, AD ~1390 – AD ~1230, AD ~640 – AD ~500
251 and BC ~80 – BC ~170. As shown in figure. 4b, 4c and 4d, these four periods are
252 characterized by a relatively low temperatures and/or a strong EAWM circulation (Fig.
253 4b, 4c and 4d, with ~150, ~180 and ~480 years of phase adjustment, respectively),
254 suggesting that cooler temperature and/or stronger EAWM circulation may trigger a
255 collapse of *Tridacna* spp. populations. In addition, the low and stable human population
256 around the SCS before AD ~1900 (Fig. 4a) seems to rule out the influence of human
257 disturbance during AD ~1900 – BC ~2550, which reinforces the hypothesis of climate-
258 induced collapse of *Tridacna* spp. populations.

259 Despite some evidence that ocean warming is negatively impacting *Tridacna* spp.
260 populations (Neo et al., 2017; Apte et al., 2019), there are no reports on bleaching-
261 induced mortality from ocean warming in the northern SCS. Northern SCS is the
262 marginal area for the occurrence of *Tridacna* spp. (Fig. 1a). Seasonal climate variation
263 in the northern SCS is dominated by the East Asian Monsoon and tropical climate
264 systems. The modern instrumental data show that the SCS usually merges into the
265 Western Pacific Warm Pool during the summer, and its climate variability is mainly
266 controlled by the state of the warm pool (Yan et al., 2015), with a stable summer Sea
267 Surface Temperature (SST). Monthly mean maximum SST often occurs in June, at
268 about 29.5 °C (Fig. 4e), which is still within the optimum temperature range (~26 °C to

269 ~30 °C) for *Tridacna* spp., but the potential risk under future sustained warming cannot
270 be completely ruled out. During winter, with the southward migration of the Western
271 Pacific Warm Pool, the temperature in the northern SCS is greatly affected by large-
272 scale atmospheric circulation patterns from the Northern Hemisphere middle-high
273 latitudes (Fig. 4g). This effect is usually achieved by the East Asian Winter Monsoon
274 through cold surges (Yan et al., 2015). When a strong cold surge develops from the
275 Siberian High and moves southward, the winter air temperatures around the China
276 mainland and the northern SCS decrease rapidly, as well as SST (Fig. 4f and 4g). The
277 monthly mean SST in January is about 24.5 °C (Fig. 4e), and the lowest daily SST
278 during AD 2010–2015 is 21.02 °C, which could threaten the *Tridacna* spp. populations,
279 especially juveniles. Although the recent global warming is considered to be
280 unprecedented for recent centuries (Marcott et al., 2013; Kaufman et al., 2020), the
281 modern minimum SST in winter in the northern SCS is lower than the optimum growth
282 temperature of *Tridacna* spp. Therefore, in certain cold periods, winter SST in northern
283 SCS was probably lower than present (Yan et al., 2015), which may cause the occurring
284 of short-term crash of *Tridacna* spp. population. These paleoclimate interpretations, as
285 well as the analyses in figure 4b, 4c and 4d suggest that the four short-term collapses in
286 LTPI during AD ~1900 – BC ~800 is attributable to the low winter temperatures in
287 these certain cold periods.

288 As shown in figure 4b, 4c and 4d, LTPI usually recovered quickly from the short-
289 term crashes with the weakening of EAWM and the consequent temperature rebound

290 except for the last one. For example, LTPI experienced a short-term collapses around
291 AD ~1230, which lasted more than 100 years (Fig. 4d). However, with the weakening
292 of the EAWM after AD ~1400, the LTPI rebounded quickly, indicating that *Tridacna*
293 spp. populations have robust self-recruitment mechanisms in response to natural
294 climate changes. The results are consistent with the recent study about the coral reef
295 growth of the Hainan Island over the past 7000 years, which also identified temperature
296 limitations in northern SCS (Yan et al., 2019).

297 **3.3 Overfishing disruption on recruitment mechanisms of *Tridacna* spp.** 298 **population.**

299 Self-recruitment mechanisms of *Tridacna* spp. populations was prominent for the
300 first three short-term crashes, but not for the most recent one. *Tridacna* spp. populations
301 did not recover from the latest ~AD 1820 - AD ~1900 collapse, although the
302 temperature has risen significantly in the past ~100 years (Yang et al., 2002; Mann et
303 al., 2009; Marcott et al., 2013; Kaufman et al., 2020) (Fig. 4b and 4c). The increased
304 human population and anthropogenic Hg flux around the SCS after AD ~1700,
305 especially after AD ~1900 (Liu et al., 2012, Goldewijk et al., 2017) (Fig.4a), suggest
306 increased human activities and impacts around the SCS in recent centuries. For
307 centuries, fishermen around the SCS harvested *Tridacna* spp. for subsistence purposes,
308 the adductor, gonad, muscle and mantle tissues of *Tridacna* spp. are all used for food
309 (Lucas, 1994). The shells are also used for prayer beads, jewelry, salad bowl and other
310 ornaments, which are popular in East and South-East Asia, especially after the

311 improvement of carving techniques (Larson, 2016). In addition, *Tridacna* spp. are
312 popular aquarium animals, and they are listed in the top ten of the most traded
313 ornamental invertebrates worldwide (Wabnitz et al., 2003). Overfishing by humans for
314 commercial and recreational purposes is most likely to account for the modern
315 depletion of *Tridacna* spp. in the northern SCS. It is reported that modern long-lived
316 *Tridacna* spp. (> 30 years) are now rarely found in the northern SCS (Neo et al., 2018;
317 Yu 2020).

318 **4. Conclusions**

319 In order to fully understand the survival threats to modern *Tridacna* spp. population
320 vulnerability in the northern SCS, the dynamic of *Tridacna* spp. population over the
321 past 4500 years was investigated. The results show that the LTPI in the northern SCS
322 increased from BC ~2000 to BC ~800 and then followed a declining trend. Four “pre-
323 Industrial *Tridacna* spp. endangerment” stages were identified during the BC ~800 -
324 AD ~1900 interval, attributing to low temperatures and strong EAWM circulation.
325 *Tridacna* spp. populations usually recovered quickly from the short-term crashes when
326 the EAWM weakened and the temperature rebounded, suggesting robust recruitment
327 mechanisms in response to favourable climatic changes. However, the potential for
328 population recovery was probably overwhelmed by human activity (especially over-
329 harvesting), as demonstrated by the catastrophic population crash during the recent
330 global warming period.

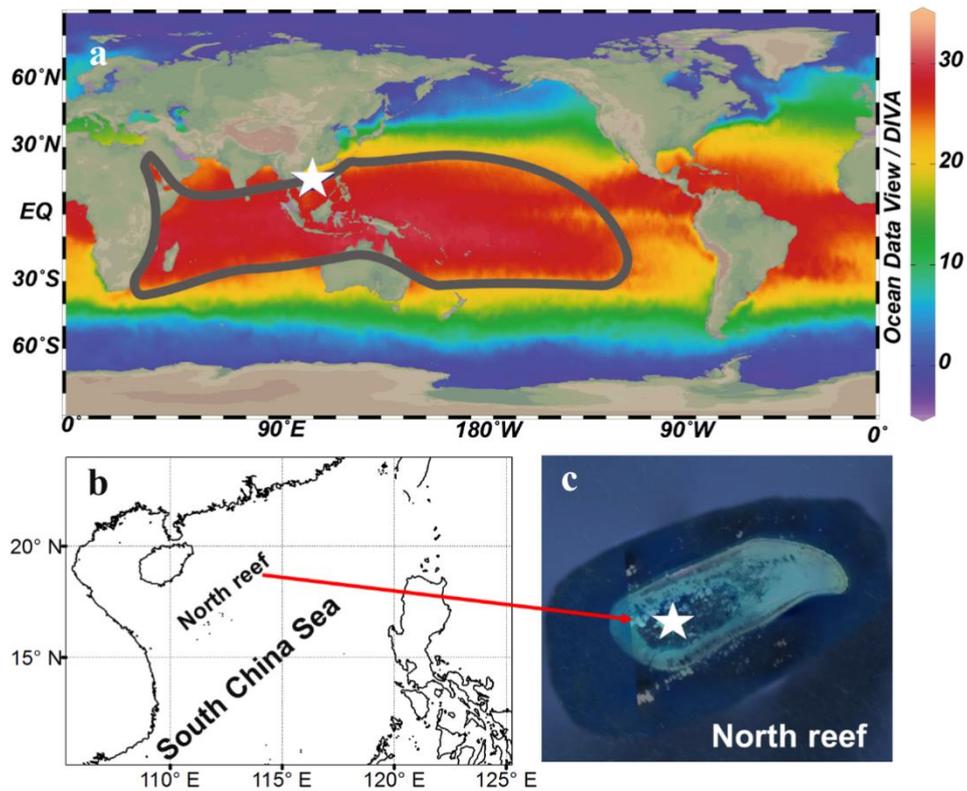
331 Human activity has been demonstrated to be the dominant cause of most
332 contemporary environmental and ecological changes in recent hundred years, and thus
333 unique from other geological periods (Crutzen, 2002; Hughes et al., 2017; Lewis et al.,
334 2015). Human induced climate change, habitat loss and over-harvesting have resulted
335 in species extinctions some 100 to 1000 times higher than background rates, and the
336 sixth great extinction is probably under way (Barnosky et al., 2011; Ceballos et al.,
337 2015; Pimm et al., 1995; Dirzo et al., 2014). *Tridacna* spp. populations of the northern
338 SCS could be hit hard under a global wave of anthropologically driven biodiversity
339 losses. Fortunately, the situation regarding *Tridacna* spp. in the northern SCS has
340 attracted wide attention in recent decades. In order to protect these populations,
341 conservation polices have been launched. For example, the Chinese government has
342 listed *Tridacna* spp. as a key protected species. The Convention on International Trade
343 in Endangered Species of wild Fauna and Flora has listed *Tridacna* spp. in order to limit
344 illegal trade. Hainan Province has banned the harvest, transport, and sale of *Tridacna*
345 spp. and *Tridacna* spp. shell products since 2017. Meanwhile, artificial breeding of
346 *T.squamosa*, *T.derasa*, *T.maxima*, *T.nova*, *T.crocea* and *T.hippopus* species have been
347 somewhat successful (Zhang et al., 2020; Zhou et al., 2020; Yu, 2020), and a release
348 program is in progress (Yu, 2020). The enhanced protection and the release of the
349 cultivated *Tridacna* spp. should be a net benefit for *Tridacna* spp. in the wild, perhaps
350 resulting in a full recovery of populations.

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357 DQGG0105).

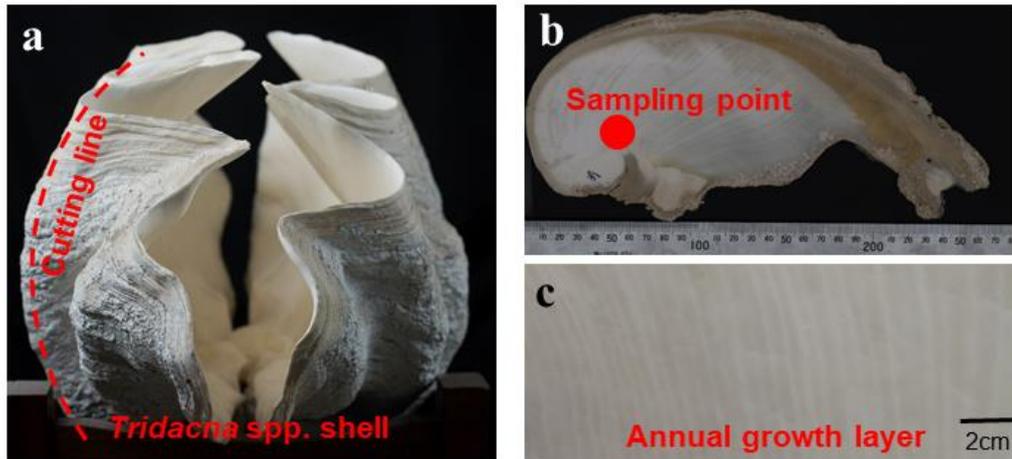
358 **Figures.**



359

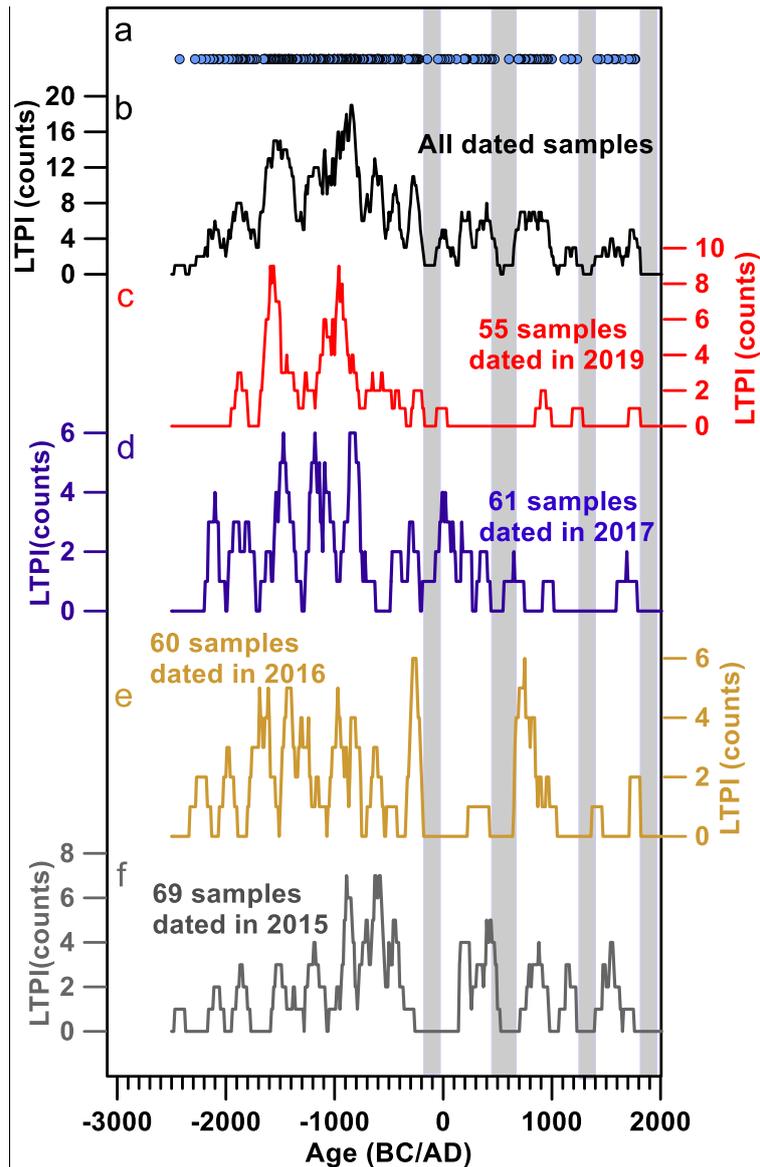
360 Fig. 1 Location of sampling site, Xisha Islands, South China Sea. (a) Distribution map
361 of *Tridacna* spp. and sampling site at North Reef. The grey contour marks the
362 boundary where *Tridacna* spp. thrive and the white star marks the sampling site at the

363 North Reef of Xisha Islands, northern South China Sea. (b) Map of the northern South
364 China Sea showing the location of Xisha Islands. (c) Map of the North Reef, white
365 star is the sampling site.



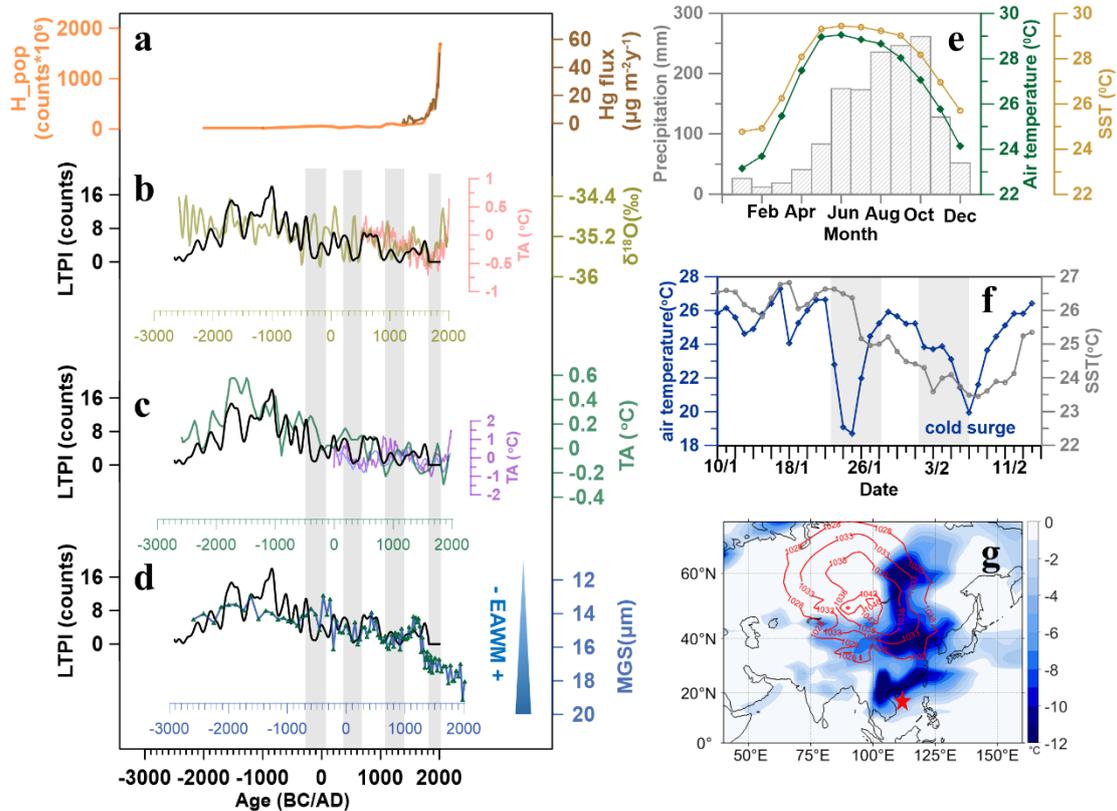
366

367 Fig. 2 (a) Sub-fossil *Tridacna* spp. shell. For each sub-fossil shell, a ~0.5 cm-thick
368 section was cut from the umbo along the maximum growth direction. (b) Cross-
369 section photo of the *Tridacna* spp. shell. The red contour marks the sampling point for
370 carbonate powder. (c) Annual bands can be observed clearly from the inner layer in
371 section and the lifetime of each shell can be determined by counting the number of
372 annual growth layers.



373

374 Fig. 3 (a) Calibrated age distribution of 245 long-lived sub-fossil samples. AMS ^{14}C
 375 dating results were calibrated by the marine ^{14}C yield model using Marine13 of Calib
 376 Rev 7.0.4 (<http://www.calib.org>) with a regional $\Delta R=18$, $\sigma=37$ (John et al., 2002). (b)
 377 Long-lived *Tridacna* spp. population index (LTPI) calculated by 245 ages of shell. (c),
 378 (d), (e) and (f) Four LTPI calculated by four sample groups divided randomly during
 379 the AMS ^{14}C dating experiments.



381

382 Fig. 4 Long-lived *Tridacna* spp. population index (LTPI), human population (H_pop)
 383 of counties around SCS, paleoclimate records and modern climatic characteristics
 384 around the sampling site. A 100-year low-pass filter was applied on LTPI to remove the
 385 inter-decade variance (black line). (a) Human population of countries around SCS
 386 (orange line), and elemental Hg flux during past 600 years in northern SCS (brown line,
 387 Liu et al., 2012). (b) 100 years low-pass filtered $\delta^{18}\text{O}$ of Greenland ice-core (olive line,
 388 Vinther et al., 2006) and temperature anomaly of Northern Hemisphere (soft pink,
 389 Mann et al., 2009). (c). Temperature anomaly of China (green line, Ge et al., 2006;
 390 majestic purple line, Yang et al., 2002) and winter temperature anomaly of eastern

391 China (pastel blue line, [Ge et al., 2002](#)). (d). Mean grain size (MGS) of loess in Weinan,
392 Shaanxi province (navy blue line, [Kang et al., 2018](#)). The grey bars in (b), (c) and (d)
393 are the short-term collapses of LTPI. The ~150-year, ~180-year and ~480-year phase
394 difference or time delay that exists between LTPI and climatic records were discussed
395 in the main text. (e). Long time-averaged, monthly mean surface air temperature and
396 precipitation (forest green line and grey bar, respectively, 1958–2005 average) and
397 monthly mean SST (gold line, 1982-2014 average) of the Xisha islands. (f). Time
398 evolution of the abrupt cooling process during the cold surge from January to February
399 of 2016 (grey line: SST, deep blue line: air temperature). (g). Spatial distributions of air
400 temperature anomaly during the cold surge from 21th January (75°N–60°N latitude
401 band) to 25th January (15°N–0°N latitude band), 2016 (air temperature anomaly = daily
402 air temperature – January mean temperature). The red contour lines denote the Siberian
403 High in January, 2016 (monthly mean sea level pressure higher than 1028 hPa), and the
404 red star marks our sampling site.

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