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Increase of a hypoxia-tolerant fish, *Harpadon nehereus* (Synodontidae), as a result of ocean deoxygenation off southwestern China

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Abstract We report a sudden explosive rise in abundance off southeastern China of a fish species that is hypoxia-tolerant, Bombay duck (*Harpadon nehereus*, Family Synodontidae), belonging to an Order (the Aulopiformes) encompassing overwhelmingly deep-sea fishes, but which predominantly occurs in coastal water. We suggest that this is made possible by the very high water content of its muscle and other tissues (about 90%, vs 75–80% for other coastal fish), which reduces its oxygen requirements and allows it to outcompete other fish in low-oxygen neritic and estuarine waters. We suggest that the extent to which this drastic shift in abundance and in the resulting community structure in a very extensive and extremely important coastal marine ecosystem offer evidence of growth of ocean deoxygenation along the western edge of the North Pacific Ocean. Also, we suggest that this episode may represent an instructive example of similar disruptions of established marine biological community structures and interlinked life support and natural resource systems that may be expected to emerge under current global trends of climate/environmental change.

Keywords Hypoxia · Water content · Population explosion · Dissolved oxygen · Jellification

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The international marine scientific community has become increasingly concerned over a perceived trend toward serious loss of dissolved oxygen from the world's oceans (Diaz and Rosenberg 2008; Keeling et al. 2010; Bakun 2017). A case in point is the East China Sea Large Marine Ecosystem, a major upwelling zone (Hu et al. 2018), which has become one of the largest near-coastal low-oxygen areas in the world's oceans (Chen et al. 2007). For example, 18-year time series of dissolved oxygen measurements assembled for two locations along the Minjiang River Estuary shows a strong decline (Fig. 1).

Bombay duck (*Harpadon nehereus*) is a somewhat confusingly named fish species that has long been an important resource for Indian marine fisheries (Bapat 1970) as well as a major component of the marine ecosystem off western India, where hypoxic, and even totally anoxic, zones are particularly pervasive

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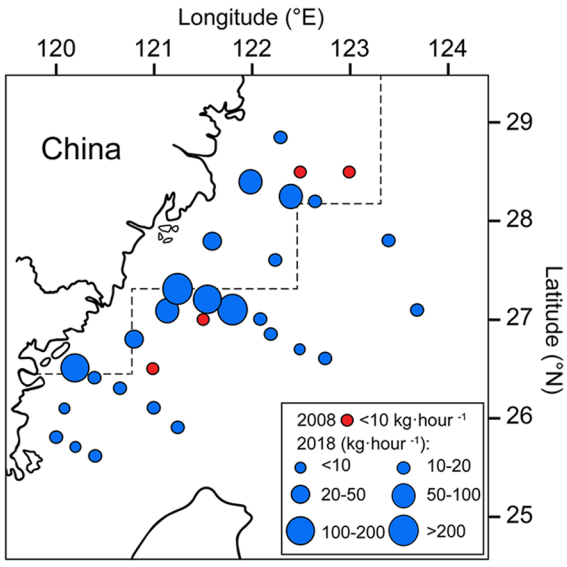

Fig. 1 Catch rates of Bombay duck (*Harpadon nehereus*) in scientific bottom trawl surveys conducted in the autumn of 2008 (red dots; from Luo 2012) and 2018 (blue dots; data field sampled by Longshan Lin) in the southeast of the East China Sea. The Minjiang River Estuary (see text) is where the southernmost dotted line (representing the southern part of "Subregion R1" in Fig. 3 of Kong et al. 2019) meets the coastline

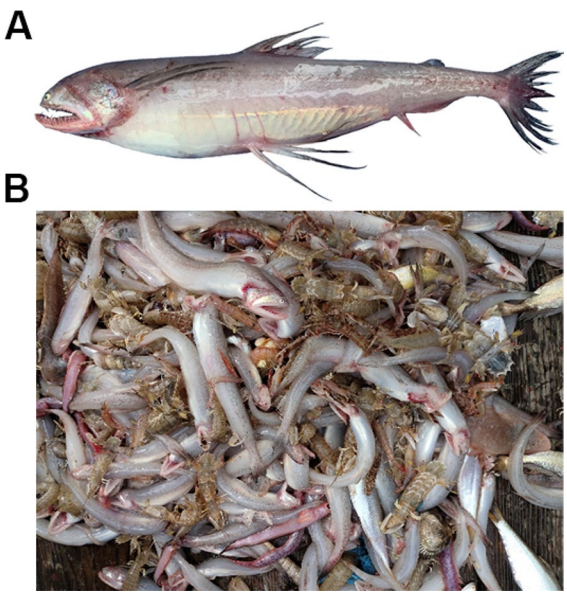

Fig. 2 Bombay duck (*Harpadon nehereus*); **A** individual specimen of 24 cm (note the wide gape of the mouth, and the small eyes at the tip of the snout); **B** a trawler's catch, completely dominated by *H. nehereus* as is currently the case in many, if not most commercial trawl operations off the southeastern coast of China (Photos by Bin Kang)

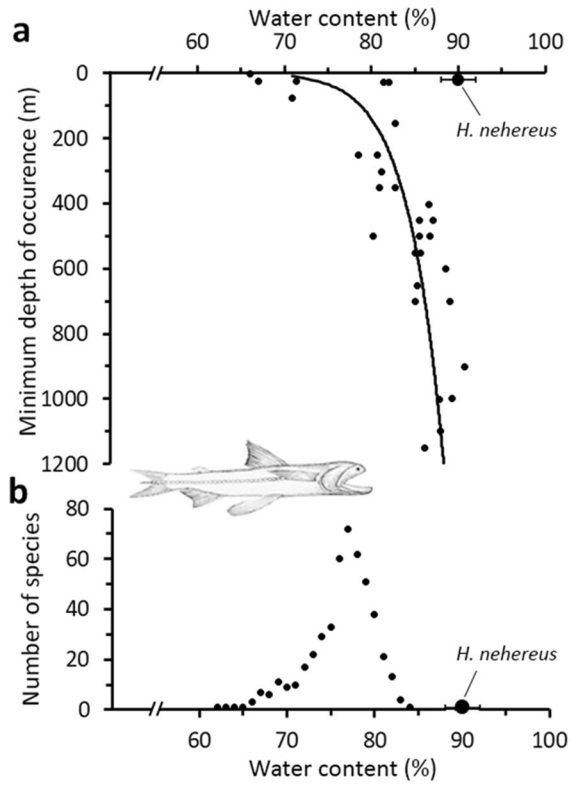

Fig. 3 Illustrating the exceptional nature of Bombay duck (*Harpadon nehereus*); **A** water content of 29 species of mesopelagic teleosts (without gas bladder) as a function of their minimum depth of occurrence (adapted from Fig. 1 in Childress and Nygaard, 1973) contrasted with the depth occurrence and water content of Bombay duck (from Bykov 1983; Gopakumar 1997; see also * www.fishbase.org); **B** water content of the meat/fillet of 474 species of predominantly neritic teleosts (from www.fishbase.org , based mainly on Bykov 1983), contrasted with the muscle water content of Bombay duck

(Bakun et al. 1998). Bombay duck (Fig. 2A) is quite a remarkable fish in its extremely flaccid, jelly-like body, caused by a very high water content of muscle and other tissue, of around 90% (Bykov 1983; Gopakumar 1997), compared to 70–80% in other neritic fishes (Bykov 1983, and Fig. 3). Indeed, in spite of living in relatively shallow waters, Bombay duck has a water content similar to midwater and deep-water fishes, notably of the Order Aulopiformes (Childress and Nygaard 1973; Drazen 2006; also see FishBase, www.fishbase.org).

The high water contents of midwater and deep-sea fishes allow them to "cheaply" grow relatively large bodies allowing them to have large mouth armed with long fangs (Olson 2017) for ambushing

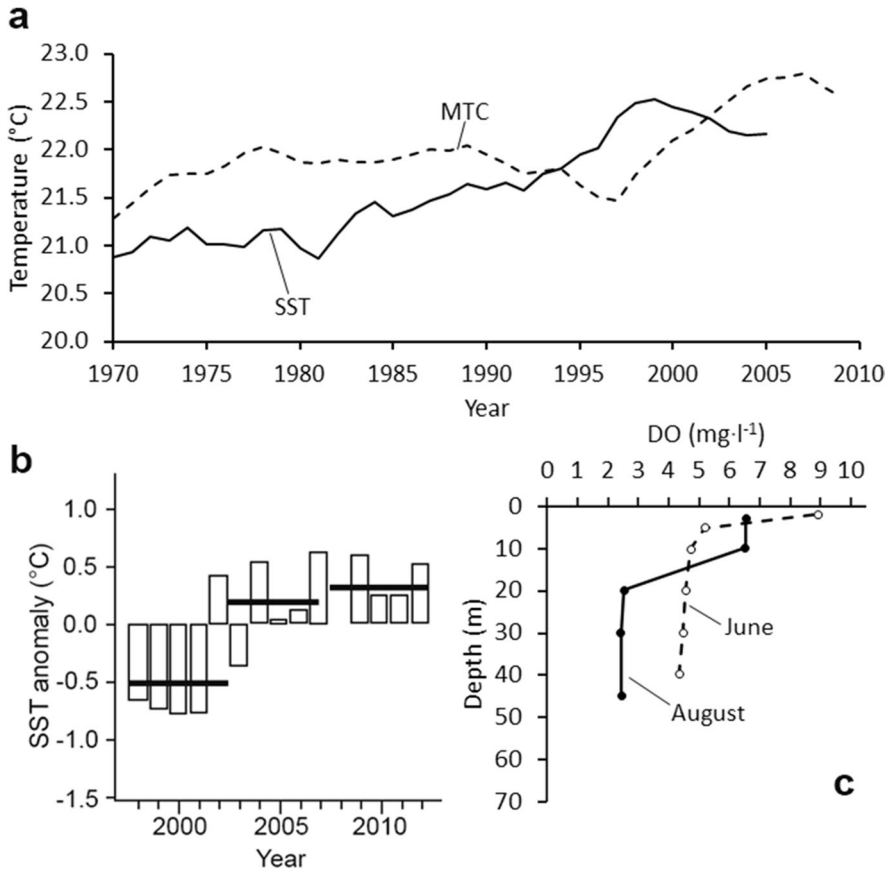

Fig. 4 Illustrating the decline of habitat suitability of the coastal areas of the East China Sea for most teleosts and other water-breathing ectotherms; **A** trends in sea surface temperature (SST; Belkin 2009) and in the mean temperature of the catch (MTC), inferred from the contribution of various species to the catch from the East China Sea LME and their preferred temperature (Liang et al. 2018); **B** SST increase in Subarea R1 of Fig. 1 (modified from Fig. 6 in Kong et al. 2019); **C** seasonal decreases in dissolved oxygen at depth at Station 20 (in 2003 (adapted from Fig. 3 in Chen et al. 2007) in 2003 at about 31°20′N and 124°E (from Chen et al. 2007)

large prey in an ecosystem where potential prey are exceedingly rare. This adaptation to food scarcity may also be seen as an "exaptation" sensu Gould and Vrba (1982), i.e., a trait evolved by natural selection which is co-opted for another use, given that it also reduces oxygen demand (Pauly 2019). From a metabolic standpoint, Bombay duck could perhaps be characterized as a quasi-analog to a jellyfish, which are known to be particularly well adapted to tolerating low-oxygen conditions due to their body mass being composed of about 98% water (Palomares and Pauly 2009; Richardson et al. 2009).

In the waters off western India, Bombay duck inhabits sandy mud bottom for most of the year; however, during the monsoon, it moves into coastal estuaries. Because of this habitual exposure to a variable range of environmental conditions and circumstances, this species has had to evolve a high level of physiological resilience. Bombay duck, which has a wide Indo-Pacific range, used to play only a minor role in Chinese domestic marine fisheries, such that it was not recorded in national statistics as an independent species. Recently, however, Chinese marine fishery landings have showed a transition from such traditional food fishes as large-headed hairtail and large yellow croaker (*Larimichthys crocea*) which are severely overfished (Liang and Pauly 2017) to a profusion of small pelagic fishes and to a growing dominance of the hypoxia-tolerant Bombay duck (Lin 2009; Yang et al. 2013; Deng et al. 2018; Kang et al. 2018; Li and Kang 2020).

Thus, Bombay duck abundance in fish survey catches (Fig. 1) and in commercial catches has increased (Kang et al. 2018; Fig. 2B), resulting from a spatial expansion northward and a temporal extension, from former confinement within the summer season, to a wider temporal spread lasting from spring into autumn. The massive population growth that this implies has imposed a greatly increased competition for available prey resources within the formerly dominant complex of more traditional food

fish species. Indeed, field observations from the early 2010s indicate that about 90% of Bombay duck stomach contents consist of fishes (Zhang and Jin 2014).

Current global ocean trends of climatic warming and of declining available oxygen would seem to favor the evolved adaptations of the Bombay duck (Fig. 4). Moreover, the expanded Bombay duck population off southeastern China seems to be following an emergent global pattern (Koel et al. 2019), wherein a natural multi-species biological community is changed step by step toward a community largely based on a single dominant species, thereby losing resilience to external interferences that might be much more easily maintained in conjunction with a more diverse species complex.

This regional-scale ecosystem regime shift (Bakun 2005) does offer a warning that ocean deoxygenation may be continuing to progress along the subtropical and temperate western boundary of the Pacific Ocean. This experience might harbinger a future in which the biological resource communities of many marine ecosystems of the world might become less diverse and much more dominated by hypoxia-tolerant forms such as jellyfish (Richardson et al. 2009) and squids (Gilly et al. 2006).

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