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Transplantation of Icefish (Salangidae) in China: Glory or Disaster?

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Abstract

China has a long history of aquaculture, and it contributes the largest aquaculture production worldwide. Aside from expanding aquaculture area and maximizing unit yield, introducing new potential species is greatly encouraged. Icefish (Salangidae) from Taihu Lake have been introduced into other lakes and reservoirs throughout the country since 1979. *Neosalanx tangkahkeii* was introduced into the southern part of China, and *Protosalanx chinensis* was introduced into the northern part of China, and both species have been introduced into a small part of central China and Yunnan Province in southwest China. Only one-third of the transplantation was successful, and most of their yields experienced a burst-down course. Intrinsic traits of icefish including annual life cycle, higher fecundity, lower trophic level, together with sufficient environment capacity supported the population forming and burst, while overfishing, pollution and short of food could result in the failure of the transplantation. The introduction of icefish brought in economic benefits, but severely threatened biodiversity, especially in plateau lakes in Yunnan Province, caused possible hybridization and carried diseases. According to different environmental conditions and economic needs at regional scale, further transplantation of icefish would face respective fate as resource conservation, rapid development, limitation and insignificance. Increasing attentions on environmental protection and sustainable resource utilization require a fresh evaluation and adjustment of icefish transplantation to achieve an ecologically healthy aquaculture.

Key words: biodiversity, conservation, genetic bottleneck, invasion, taxonomy, transplantation.

Introduction

Fish, a rich source of proteins, essential fatty acids, vitamins and minerals, constitute a major staple food item for people. The constantly increasing aquaculture production would lead to greater dependence because it provides an important substitute for the declining production of capture fisheries to meet the growing demand for nutrition and economic performance (Naylor *et al.* 2000; De Silva 2003; Cressey 2009). Aquaculture began in China more than 2500 years ago with the culture of wild carp fingerlings in ponds in the Yangtze basin (Jeney & Jian 2009). Since then, farming of freshwater species has steadily expanded throughout China. China currently has the highest aquaculture output worldwide, accounting for about 67% of the world's total production (Subasinghe *et al.* 2009). Moreover, China is the only country wherein the aquaculture output exceeds the wild capture output (Zhong & Power 1997).

Generally, aquaculture expansion has mainly relied on increasing breeding areas, developing new techniques and introducing new species (Culliton 1979; Bostock *et al.* 2010). Many species and strains cultured worldwide are nonindigenous, that is, introduced from other regions (Naylor *et al.* 2001). Species with better characteristics such as good flesh quality, rapid growth rate, strong adaptability and higher disease resistance are the primary choices (Webber & Riordan 1976). Over the last three decades, more than 100 species have been introduced into China for aquaculture from other countries, and parts of them are very successful and now used commercially to meet the market demand (Li 2007): Tilapia (*Oreochromis niloticus*) was introduced from Africa in the 1970s (Eknath & Hulata 2009); bay scallop (*Argopecten irradians*) and Japanese scallop (*Mizuhopecten yessoensis*) were introduced from Mexico and Japan, respectively, in the 1980s (Guo 2009); turbot (*Scophthalmus maximus*) was introduced from Europe in the 1990s (Lei et al. 2005). Inside the country, four popular fish farming species as black carp (*Mylopharyngodon piceus*), silver carp (*Hypophthalmichthys molitrix*), bighead carp (*Hypophthalmichthys nobilis*) and grass carp (*Ctenopharyngodon idella*), widely distributed in most rivers and lakes in China, have also been introduced from their native ranges to other regions of China (Xie et al. 2001). *Brachymystas lenok tsinlingensis*, a remaining fish from glacial stage, was transplanted from Heihe (a branch of Yellow River) into Xishui (a branch of Yangtze River) and formed population (Li 1980).

China has a total area of more than 90 000 km^2 of lakes and reservoirs (Li et al. 2002), most of which are abundant in food organisms and available for fish culture. How to effectively use this idle water has been an urgent problem for administrative fisheries authorities, who aim to promote the food supply and economic development. Highly adaptive species thriving in lacustrine habitats were in a piror consideration.

Icefish (Salangidae) are primarily found in eastern Asia (Berra 2001). Freshwater icefish occur in the lentic bays, gulfs and estuaries of open lakes and reservoirs, and marine species are distributed in estuarine and coastal areas (Zhang et al. 2007a). China has the largest population of icefish worldwide, with the natural distribution ranging from Bohai Sea to Beibu Gulf and river systems such as Heilongjiang River, Yalu River, Liaohe River, Haihe River, Qiantang River, Pearl River and Yangtze River (Zhang et al. 2012). Affiliated lakes of the Yangtze River, including Poyang Lake, Dongting Lake, Taihu Lake, Hongze Lake and Chaohu Lake (the five biggest freshwater lakes in China in sequence), are the main icefish-producing areas (Wang et al. 2005). Icefish is zoophagous with a trophic level of 3–4 (e.g. phytoplankton–zooplankton – *Neosalanx tangkahkeii*; phytoplankton–zooplankton – small fish and shrimp – *Protosalanx chinensis*). Compared with large carnivorous fish, icefish use energy more efficiently. Although it is a good food resource for other predators, icefish have annual life cycles with time differences in spawning and preying, which increase their chances for survival, growth and reproduction.

Icefish has a long history to be commercially exploited as an essential component of historical fisheries worldwide. However, wild icefish resources have markedly decreased in almost all icefish-inhabited river basins in recent years because of overfishing, hydroprojects and water pollution (Wang et al. 2005; Zhang et al. 2007b). Traditional icefish fisheries have already diminished since late 1980s in Yellow River and Pearl River basins and lost commercial viability in Yangtze River and Yalu River estuaries recently (Dou & Chen 1994; Zhang et al. 2007b). To compensate for the decline in wild resources, icefish *Neosalanx tangkahkeii* was initially introduced from Taihu Lake in Jiangsu Province into Dianchi Lake in Yunnan Province in 1979 (Wang et al. 2002). Since then, icefish have been introduced into surface water bodies all over the country.

Taxonomy of Salangidae

Although Salangidae species have been studied for more than 100 years (Regan 1908; Wakiya & Takahasi 1937; Zhang 1993; Zhang et al. 2007a; Fu et al. 2012), the systematics of this family remains controversial, which may be partly attributed to their extensive distribution range from 53° 08′N to 20° 01′N (Wang et al. 2002), as well as their neoteny showing a morphologic plasticity during various life stages, for example the adults retain some larval features including an incomplete ossified skeleton with mass cartilage (Zhang 2008).

Salangids are widely believed to share a common ancestor with osmerids (Ishiguro et al. 2003). Fossils of ancient osmerids that evolved during the Late Palaeocene have been found at high latitudes in the northern hemisphere (Wilson & Williams 1991). Unfortunately, salangids have no fossil records because of their cartilaginous endoskeletons. Considering the interfamily and intrafamily evolution, salangids probably originated in the late Oligocene or early Miocene (Zhao et al. 2008). Given the extension of the icecap and decreasing water temperature during the glacial epochs in the Tertiary Period, the ancestors of salangids may have further migrated towards the continental coasts, probably forming the speciation and adaptive radiation of the anadromous salangids (Zhao et al. 2011).

After analysing and comparing available morphologic and molecular studies, we indicated that 15 of the 17 salangid species worldwide have been recorded in China (Table 1), among which *P. chinensis* and *N. tangkahkeii* have the widest distribution and the highest ecological plasticity.

Protosalanx chinensis Basilewsky, 1855 (Fig. 1a)
Eperlanus chinensis Basilewsky, 1855
Salanx hyalocranius Abbott, 1901
Protosalanx hyalocranius Regan, 1908
Paraprotosalanx andersoni Rendahl, 1923
Paraprotosalanx andersoni Fang, 1934
Protosalanx hyalocranius Zhang, 1955
Protosalanx hyalocranius Chen, 1956
Protosalanx hyalocranius Sun, 1982

Table 1 Taxonomy of icefish (Salangidae)

Species	Type locality	Distribution	Habitat
Salanx brachyrostralis	Nanjing, China	China	F
Salanx prognathus	Shanghai, China	China, Korea	M,B
Salanx ariakensis	Ariake Sea, Japan	China, Japan, Korea	M,B
Salanx cuvieri	—	China, Vietnam	M,B
Leucosoma chinensis	Guangzhou, China	China, Vietnam	M,B,F
Neosalanx anderssoni	Shanhaiguan, Hebei, China	China, Korea	M,B
Neosalanx argentea	Guangzhou, China	China	B,F
Neosalanx brevirostris	Tonkin, Vietnam	China, Vietnam, Korea	M,B,F
Neosalanx tangkahkeii	Xiamen, Fujian, China	China	B,F
Neosalanx tangkahkeii	Tianjin, China	China, Korea	B,F
Neosalanx pseudotaihuensis	Tianjin, China	China, Korea	F
Neosalanx jordani	Yalu River, Seisenko River, Rakutoko River, Korea	China, Korea	M,B,F
Neosalanx oligodontis	Taihu Lake, Jiangsu, China	China	F
Protosalanx chinensis	—	China, Vietnam, Korea	M,B,F
Neosalanx reganius	Ariake Sea, Japan	Japan	F
Salangichthys ishikawae	Miyagiken, Japan	Japan	M
Salangichthys microdon	Tokyo, Japan	Japan, Russia, Korea	M,B,F

M, marine; B, blackish; F, freshwater.

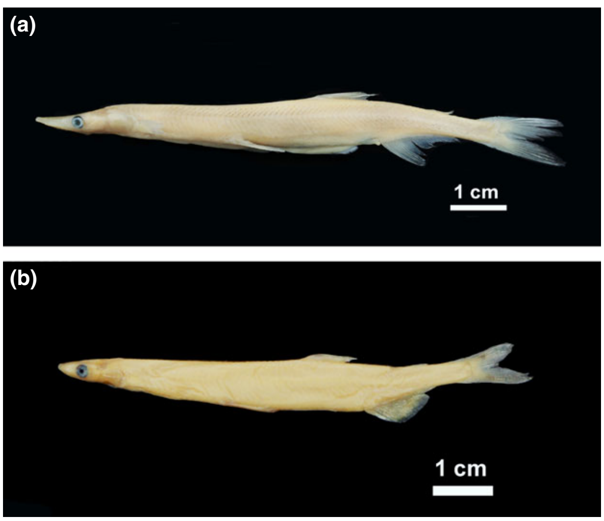

Figure 1 (a) *Protosalanx chinensis* Basilewsky, 1855. (b) *Neosalanx tangkahkeii* Wu, 1931.

Protosalanx chinensis Roberts, 1984

Protosalanx chinensis has 14–19 dorsal rays; 29–36 anal rays; 20–30 pectoral rays; 64–70 vertebrae, mostly 66–69; 12–17 gill rakers; and 20–33 anal scales. Its maximum standard length is 210 mm. This species has a pointed snout when viewed from above and its lower jaw projects beyond the upper jaw. It has teeth on its tongue in two series, and its caudal fin is sometimes more or less darkly coloured.

This species is widely distributed in the Western North Pacific from Korea and China to Tonkin and Vietnam. It inhabits in freshwater, brackish and marine water with salinities less than 30‰. Its spawning grounds are restricted to water with salinities less than 12‰. *Protosalanx chinensis* is a multiple spawner because its ovaries contain various sizes of yolk oocytes. The batch fecundity of this species ranges from 3090 eggs to 34 520 eggs per individual. The fertilized eggs hatch within 40 days to 50 days under natural conditions. *Protosalanx chinensis* is carnivorous, with the juveniles mainly feeding on zooplankton and the adults more than 70 mm long feeding on larval fish and mysid shrimp. *Protosalanx chinensis* can even become cannibalistic when food is not sufficient.

Neosalanx tangkahkeii Wu, 1931 (Fig. 1b)

Protosalanx tangkahkeii Wu, 1931
Neosalanx tangkahkeii taihuensis var. Chen, 1956
Neosalanx tangkahkeii taihuensis Sun, 1984
Neosalanx taihuensis Zhang, 1987
Neosalanx pseudotaihuensis Zhang, 1987
Neosalanx tangkahkeii Zhang *et al.*, 2007

Neosalanx tangkahkeii has 14–16 dorsal rays; 24–27 anal rays; 21–27 pectoral rays; 56–60 vertebrae; and 14–18 gill rakers. Its average standard length ranges from 50 to 80 mm. This species has a blunted snout when viewed from above and has an anteriorly protruding lower jaw. Its palate and tongue are toothless. Its pectoral fins are longer and more pointed in males, and the mature males have 14–25 anal scales.

Neosalanx tangkahkeii is endemic to China and is mainly distributed in the rivers and lakes of the Yangtze River Basin. It is rarely found in estuaries of the South China Sea and East China Sea. Its breeding seasons are from March to

May (spring spawning stock) and from September to October (autumn spawning stock). The optimum temperature of this species ranges from 8.5 to 21.6 °C in spring and from 23 to 15 °C in autumn. Its average fecundity is approximately 1400 per individual. Fertilized eggs hatch within 4 days to 6 days under natural conditions. *Neosalanx tangkahkeii* is a zooplankton feeder and occasionally feeds on shrimp and fish fry.

Practice

Historical dynamics of natural icefish populations

Factors that influence icefish population dynamics are complicated. The intrinsic traits of icefish, such as its yearly simple lifespan and different sensitivities, allow differently rapid responses of population size to environmental changes and habitat degradation (Magnuson *et al.* 1998; Wang *et al.* 2005). Water pollution from factory emissions and agrochemical pesticides is a key factor that leads to the heavy decline in *Salanx ariakensis* (Kim & Park 2002). The degradation of spawning and feeding habitats because of irrigation works, dams and farmland reclamation from lakes and sediment accumulation depletes *Neosalanx reganius* (Islam *et al.* 2006). Dou and Chen (1994) reported a considerable effect of historical overfishing on icefish assemblages in the Yellow River estuary.

Given the increasing fishing effort, the yield of target fish generally increases initially because of the increased harvest rate, but ultimately declines when the annual harvest exceeds the sustainable potential. Although overfishing generally diminished fish stocks, it will not necessarily lead to direct species extinction (Myers *et al.* 1995; Allan *et al.* 2005). Despite the very low population levels of target species, their innate biotic potential generally promotes recovery. Many studies show that lower population levels decrease the mortality or increase the survival of the larval and juvenile fish (Booth 1995; Myers *et al.* 1995; Conover & Munch 2002). The over-exploited stocks are often recovered by abating fishing pressure or providing better habitat condition (Welch *et al.* 2010). The recent habitat fragmentation caused by irrigation works and land use in the Yangtze River basin affects the icefish distribution and population dynamics, for example the icefish caught in Dongting Lake and Poyang Lake in the 1980s dramatically decreased to 3% and 1% of those caught in the 1960s, respectively, and some species are now facing extinction (Wang *et al.* 2009). Unlike overfishing, fishing bans could not fix the shortages caused by habitat degradation. In Taihu Lake, the icefish yield varied irregularly as indicated in the three phases. (i) from 1953 to 1984, the annual catch was stable at approximately 500–1000 tons, (ii) from 1985 to 1993, the annual catch sharply increased to 2000 tons, which could be attributed to intensive fishing and interspecific relationship. For example, lake anchovy *Coilia ectenes taihuensis*, sharing the same food choice for zooplankton with Salangidae, is considered to have inhibitional effects on icefish population (Yan *et al.* 1996). Meanwhile, *Erythroculter ilishaeformis*, feeding on anchovy with a portion more than 95% in volume, could benefit icefish population through feeding on anchovy and leaving sufficient niche for icefish (Liu *et al.* 2006), (iii) from 1994 to 2002, the annual catch dropped similar to the first phase, except for the second wave in 1998–2000 (Fig. 2a). The lowest icefish yield in percentage of the total Taihu Lake fisheries was observed after the aquaculture boom from 1985 to 1993 (Fig. 2b) (Zhu 1982).

Process of icefish transplantation

China's lake and reservoir fisheries are nearly dominated by the artificial stockings of four major Chinese carp species. In 1979, nine mature *N. tangkahkeii* individuals from Taihu Lake were captured for artificial propagation. A total of 6825 fries were hatched and then released into Dianchi Lake, Yunnan (Gao *et al.* 1982). Dianchi Lake is a eutrophic lake with an area of 310 km^2, an average depth of 4 m and an annual average temperature of 16 °C (Wang 1995). It is rich in zooplankton and poor in carnivorous species. This action resulted in a nationwide trend of icefish transplantation. According to an

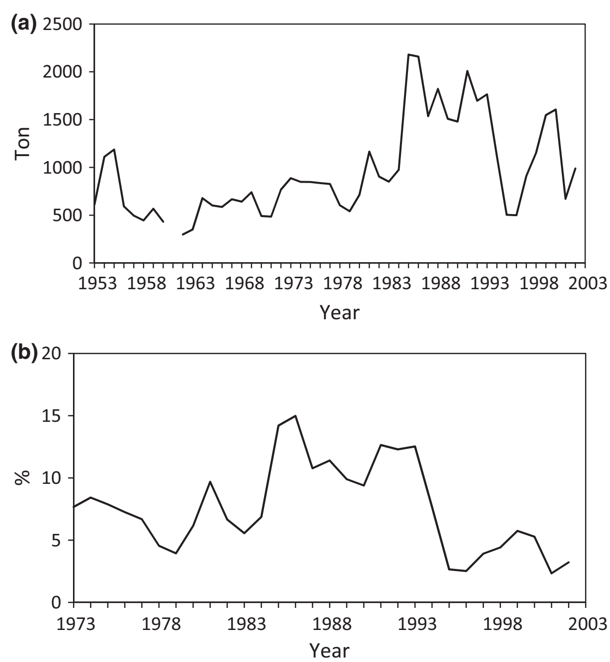

Figure 2 (a) Historical productions of icefish in Taihu Lake for 60 years (no data in 1961). (b) Variation of icefish proportions of total fisheries in Taihu Lake for 30 years.

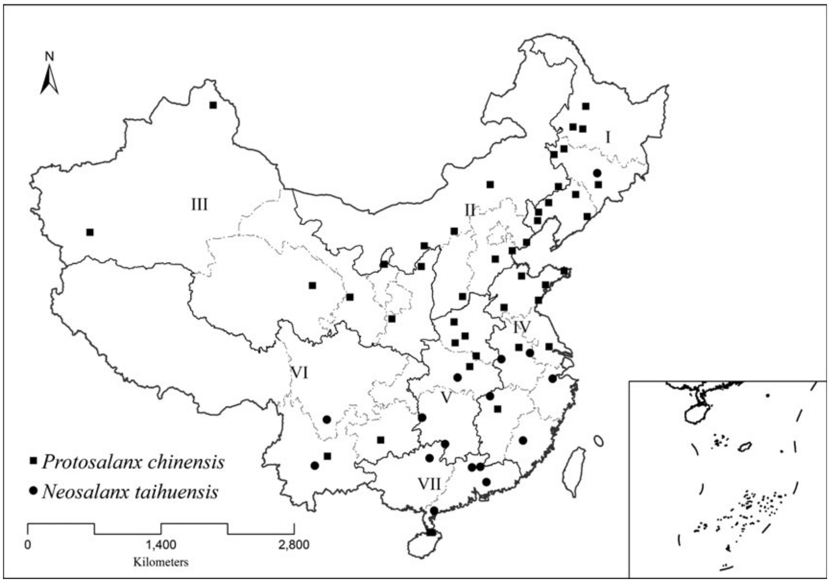

Figure 3 Distribution of introduced icefish in China. China is divided into seven parts according to geological characteristics, traditional customs and geopolitics: (i) Northeast China (including Heilongjiang, Jilin and Liaoning); (ii) North China (including Beijing, Tianjin, Inner Mongolia, Hebei and Shanxi); (iii) Northwest China (including Xinjiang, Ningxia, Gansu, Shannxi and Qinghai); (iv) East China (including Shanghai, Shandong, Jiangsu, Anhui, Zhejiang, Fujian and Jiangxi, Taiwan); (v) Central China (including Henan, Hunan and Hubei); (vi) Southwest China (including Chongqing, Sichuan, Yunnan, Guizhou and Tibet); and (vii) South China (including Guangdong, Guangxi, Hainan, Hongkong and Macau). Generally, *Neosalanx taihuensi* was introduced into the south part of China that has warm temperature and *Protosalanx chinensis* into the north part of China that has cold water. In a small part of central China, both species were introduced into the same water body.

incomplete statistics, icefish have been introduced into reservoirs and lakes in 27 provincial units (Fig. 3), with a total area of more than 10 000 km^2. The species production reached 25 000 tons in 1999, 70–80% of which came from the artificial yield (Li *et al.* 2002). The China's Fishery Statistical Yearbook (published by the Fisheries Bureau, Ministry of Agriculture) listed detailed information on seafood at the beginning, although freshwater played a more important function in fisheries support. Since 2001, the annual report individually has listed the production of economically important freshwater species including icefish yield.

China is divided into seven parts according to geological characteristics, traditional customs, and geopolitics: (i) Northeast China (including Heilongjiang, Jilin and Liaoning); (ii) North China (including Beijing, Tianjin, Inner Mongolia, Hebei and Shanxi); (iii) Northwest China (including Xinjiang, Ningxia, Gansu, Shannxi and Qinghai); (iv) East China (including Shanghai, Shandong, Jiangsu, Anhui, Zhejiang, Fujian and Jiangxi, Taiwan); (v) Central China (including Henan, Hunan and Hubei); (vi) Southwest China (including Chongqing, Sichuan, Yunnan, Guizhou and Tibet); and (vii) South China (including Guangdong, Guangxi, Hainan, Hongkong and Macau) (Fig. 3). Based on the water, temperature requirements for propagation, *P. chinensis*, suitable to lower temperatures, can be transplanted to North China, and parts of East China and Central China. By contrast, *N. tangkahkeii*, enjoying higher temperature, is suitable for transplantation into parts of South China, Southwest China, Central China, East China and even North China.

Northeast China

Heilongjiang Province has abundant lakes and reservoirs, and 2000 km^2 of that is suitable for fisheries. *P. chinensis* was first introduced in 1995 (Kong *et al.* 2007), and its output sharply increased to 450 tons in 2008, and then to 838 tons in 2010 (Fisheries Bureau, Ministry of Agriculture 2001–2011). The available water surface for fisheries in Liaoning Province is approximately 793 km^2. Icefish was also introduced in 1995 by the local government (Liu 2001), and the output showed a yearly increase to 1373 tons in 2010 (Fisheries Bureau, Ministry of Agriculture 2001–2011). Many vacant water bodies remain in this region, and the output can be further increased by intensive introduction activities (Fig. 4a).

North China

Up to 5 750 000 fertilized *P. chinensis* eggs were transplanted four times (1985, 1988, 1990 and 1991) into Daihai, Inner Mongolia. The presence of mature individuals in 1989 indicated successful icefish introduction in northern China, although no economically viable population formed. From 1991 to l994, icefish sharply increased

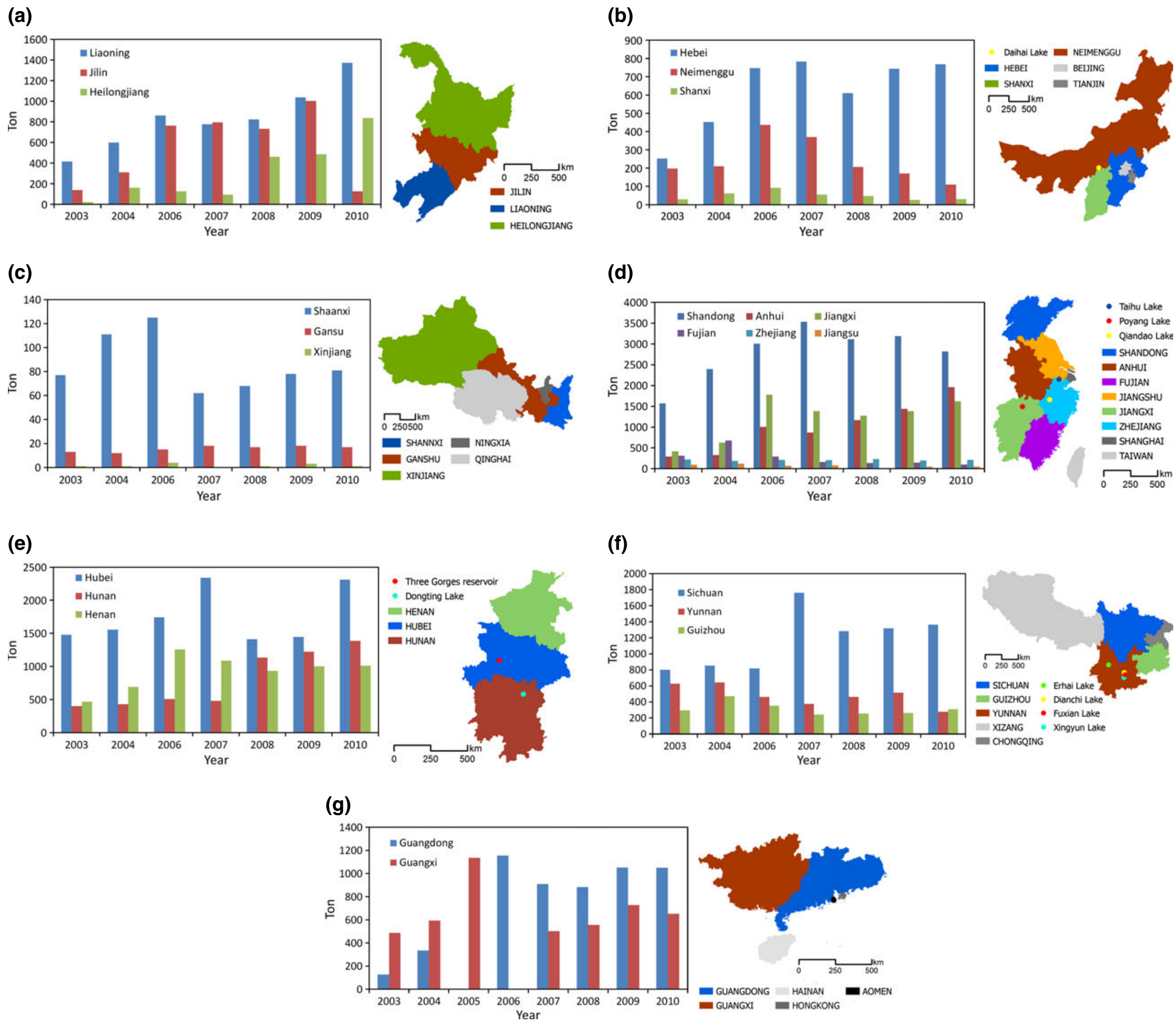

Figure 4 (a) Annual production of icefish in Northeast China. (b) Annual production of icefish in North China. (c) Annual production of icefish in Northwest China. (d) Annual production of icefish in East China. (e) Annual production of icefish in Central China. (f) Annual production of icefish in Southwest China. (g) Annual production of icefish in South China.

because of the removal of wild *Culter erythropterus* and reached a new national record production of 2550 kg km^{-2} in 1995 (Lan *et al.* 1998). The population of this species showed a typical 'J'-shaped growth curve within the 10-year period from 1985 to 1996. A 'J' growth curve means that the population density of an organism increases rapidly in an exponential or logarithmic form in a new environment, but then stops abruptly as environmental resistance (e.g. seasonality) or some other factors (e.g. the end of the breeding phase) suddenly become effective (Allaby 1998). In 1996, *P. chinensis* population in Daihai disappeared, which was attributed to feeding by the recovered predator population (Lan *et al.* 1998). By releasing a large amount of fertilized eggs, as well as protecting the eggs and larvae, icefish began to produce yield in 1997 and reached a new peak yield of 4500 kg km^{-2} in 2000. The output decreased again in 2001, forming the second 'J' population growth curve. In 2002, approximately 900 million fertilized eggs were released again, forming the third 'J' population growth curve (Ge *et al.* 2003). This indicates that icefish easily form 'bursts' depending on its reproductive ability and enough environmental capacity, causing wide fluctuations in quantity (Fig. 4b).

Northwest China

In Xinjiang, *P. chinensis* has been introduced since 1996, for example, in Hongshan Reservoir from 1996 to 1997, Nanhu Lake from 1996 to 1998, Bosten Lake from 1996 to

2000 and Bayi Reservoir and Xinier Reservoir in 2006 (Zhang *et al.* 2000). However, the introduction of this species was unsuccessful. The highest total yield was only 4 tons in 2006 (Fisheries Bureau, Ministry of Agriculture 2001–2011) (Fig. 4c).

East China

East China region is the origin of icefish, for example Taihu Lake in Jiangsu Province, Dongting Lake in Hunan Province and Poyang Lake in Jiangxi Province.

Shandong Province has approximately 5200 reservoirs, with a total area of 770 km^2 suitable for aquaculture (Cao & Liu 1999). In 1992, *P. chinensis* was initially introduced into this province, covering an area of 730 km^2, and the production reached 3534 tons in 2007 (Fisheries Bureau, Ministry of Agriculture 2001–2011) (Fig. 4d).

Qiandao Lake in Zhejiang Province was artificially formed in 1959 after the construction of Xinanjiang hydroelectric station. The lake has an area of 573 km^2, and the average temperature of the surface water (0 to 10 m depth) is 24 to 28 °C (Wang 1995). The lake has more than 80 fish species, for example *Aristichthys nobilis*, *Ctenopharyngodon idella*, *Erythroculter ilishaeformis*, *Anguilla marmorata* and *Siniperca chuatsi*. Aquaculture in this area has developed with an annual production capacity of over 3000 tons (Luo 2001). *N. tangkahkeii* was introduced into Qiandao Lake in 1991, and 600 000 individual fries were released into the Lake within the next 3 years. The first generation of introduced species was captured in late September 1992. In 1994, the yearly output was 50 tons and increased to 321 tons in 1996, 820 tons in 1997 and peaked at 1018 tons in 1998. However, in 1999, the production decreased to 620 tons and only 110 tons in 2000. No fishing was reported thereafter (Luo 2001). In Qiandao Lake, predatory fish mostly feed on icefish eggs, fry, juveniles and adults at different developmental stages. Moreover, regional and seasonal algal blooms cause aquatic hypoxia and water quality degradation, which ultimately result in low rates of egg hatching and larval survival (Xiang *et al.* 2002).

Central China

The transplantation of *P. chinensis* in Henan Province began in 1987 and succeeded in 1990. The transplantation were intermittent in 62 reservoirs, with an area of 700 km^2, and only 38% finally formed economically viable populations (Wang 1998). In 2006, the output peaked at 1254 tons (Fisheries Bureau, Ministry of Agriculture 2001–2011).

Hubei Province has 5778 reservoirs, with 1500 km^2 of available water for fishery. From 1995 to 1997, *N. tangkahkeii* has been gradually transplanted into 150 reservoirs with an area of approximately 700 km^2 (Feng *et al.* 2002). The output peaked at 2338 tons in 2007 (Fisheries Bureau, Ministry of Agriculture 2001–2011) (Fig. 4e).

The Three Gorges Dam is a remarkable engineering that has attracted worldwide attentions. Historically, *N. tangkahkeii* has been reported in the reservoir area and no yield. The hydrologic dynamics and habitat changes under dam operation threatened 44 endemic and indigenous fish, and six species even face extinction (Gong *et al.* 2009). Meanwhile, the increasing nutrient loads, primary productivity and consequent food resources have supported blooms of *N. tangkahkeii* to be commercially important fisheries since 2006. *N. taihuensis* mostly feeds on plankton, thus its outbreak could cause food shortages for other fish larvae, which results in a decline of other species resource (Wang *et al.* 2013). Exceptionally, four major Chinese carp species, particularly *H. molitrix* and *A. nobilis*, significantly increased with the icefish population outbreak in the reservoir (Gong *et al.* 2009).

Southwest China

Yunnan Province has nearly 400 species of freshwater fish, accounting for about 40% of the total freshwater species in China (Kang *et al.* 2013). With the rapidly changing environment over the past decades, most indigenous fish are becoming endangered. The original lake area was 1800 km^2, which shrank to 1200 km^2 in 1950, and then to 1100 km^2 in 1970 (Zhou & Huang 2005). The decrease in lake area seriously damaged fish habitats and spawning grounds.

In 1979, icefish was first introduced into Dianchi Lake in Yunnan. The *N. tangkahkeii* population rapidly increased with annual production reaching to 1200 tons in 1982, 2000 tons in 1983, and 3500 tons in 1984. The successful transplantation and resulting economic development earned the Scientific and Technological Second Prize issued by Ministry of Agriculture and People's Government of Yunnan Province (1984) and the National Scientific and Technological Progress Award (1985). The awards greatly encouraged the second wave of transplantation into 12 lakes all over the province in 1984. However, only the transplantation into Xingyun Lake was successful, with an annual yield varying between 78 tons and 400 tons, and an economic population burst also occurred in Fuxian Lake because of a 2 km connected channel between Xingyun Lake and Fuxian Lake, although icefish was not introduced into Fuxian Lake. At the beginning of 1989, the third wave of transplantation further covered Erhai Lake and other lakes, with an area of 430 km^2. This time transplantation in all lakes achieved success (Zhou & Huang 2005).

The specific conditions in plateau lakes caused *N. tangkahkeii* to modify its reproductive strategy, shortening its maturation period from 1 year to 1–8 months and increasing the spawning frequency to three times per year (spring, autumn and winter) (Yang *et al.* 1999). This change indicated that *N. tangkahkeii* is sufficiently plastic and has potential for introduction and expansion (Fig. 4f).

South China

Guangdong Province has more than 7000 reservoirs covering an area of 1150 km^2. In the mid-1980s, *N. tangkahkeii* eggs from Yunnan were unsuccessfully introduced to Guangdong. In 1996, icefish was released again into 28 reservoirs and formed population in 12 reservoirs (Liao 2002). In 2006, the output peaked at 1155 tons (Fisheries Bureau, Ministry of Agriculture 2001–2011).

Guangxi has a total reservoir area of 1330 km^2. In 1993, the government introduced *N. tangkahkeii* into more than 90 reservoirs with a total area of 530 km^2. The output peaked at 1135 tons in 2005 (Zhang 2006) (Fig. 4g).

Fate of icefish transplantation

The fate of icefish transplantation can be classified into three types: (i) complete success, with high and stable yields in several consecutive years; (ii) partial success, with temporary economic yield; and (iii) failure, with no commercial advantage, which has been observed in two-thirds of the lakes and reservoirs with introduced icefish (Hu *et al.* 2001). However, even in complete and partial successful transplantation, the icefish yield still decreased after a burst, which was mostly attributed to the biological traits as annual small species with higher fecundity. In water bodies with unsaturated fish populations, the introduced species can easily bloom after 2–3 years of propagation, and the reproductive individuals are supplementary population. After this burst, the population decreased gradually or sharply and fluctuated at lower yield.

For example, *P. chinensis* in a new environment in North China developed fecundity and widened reproductive conditions, for example, spawning ground water depth is up to 20–25 m, incubation temperature range was broadened covering 1–15 °C, and hatching rate increased even under a prolonged incubation period of 15–65 days (Sun 1982). Whether *P. chinensis* survives its early development in winter and early spring is the key factor in population fluctuation (Li 2003). In water body with abundant fish population, *P. chinensis* eggs and fry may become food for predatory fish in winter when zooplankton density is low. If *P. chinensis* fortunately reaches its larval stage in spring, it has a chance to burst because most predators are in breeding period, and zooplankton and the eggs of other fish serve as abundant food sources for *P. chinensis*. Icefish *N. tangkahkeii* feeds on plankton throughout its life cycle, and it shares the same feeding habitat only with adult bighead carp (Sun 1982). Thus, *N. tangkahkeii* has to avoid spatial and temporal competition with bighead carp to survive and further form a thriving population after introduction. Once *N. tangkahkeii* escapes danger from bighead carp, its population will rapidly burst. Moreover, *N. tangkahkeii* in plateau lakes in Yunnan Province increases its spawning frequency from 2 to 3 times (spring, autumn and winter) per year (Liu & Zhu 1994). This frequent spawning effectively compensates for population loss, especially during seasons when bighead carp is inactive or when zooplankton is abundant.

Both *P. chinensis* and *N. tangkahkeii* have been introduced into lakes and reservoirs with environment suitable for both species to achieve a good complementary relationship (Li *et al.* 2002). *N. tangkahkeii* could be used as food for *P. chinensis* and it forms productive population when *P. chinensis* decreases, thereby maintaining a stable icefish yield (Li *et al.* 2009). In the Luhun Reservoir in Henan Province in 1998, when nearly no *P. chinensis* was sampled, *N. tangkahkeii* still maintained a production of more than 50 tons (Wang 1998).

Besides the intrinsic traits mentioned above, fishing technique is also considered as an important factor to influence population (Shen & Yu 2002; Zhou & Huang 2005). In Daihai Lake in 1995, the intensive fishing covering a 45-day period and using 110 fishing boats heavily churned the sediment, and the floating detritus consumed excessive oxygen. Before the convection between the upper and the lower water layers, the lake froze. In the next 5 months of freezeup period, the closed Daihai Lake was always in anaerobic condition to stimulate the production of harmful H_2S, NH_3, No_2-N, thus ceased the hatching of icefish eggs. This directly resulted in the loss of icefish fisheries in 1996 (Lan *et al.* 1998). In Dianchi Lake, water pollution, scarce of food and overfishing were considered as the most threats to the unsustainable fisheries (Gao *et al.* 1989; Huang & Chang 2001), but this was then questioned by Li (2003). More researches are needed to elucidate the primary factors for achieving sustainably successful icefish transplantation.

Consequence

Economic benefits

Human activity is the main cause of freshwater fish movements across river basins and countries (Leprieur *et al.* 2008). The introduction of non-native species provides economic benefits and a means of feeding people as well as contributes to biodiversity (Cucherousset *et al.* 2012). A good example is the establishment of endangered or vulnerable freshwater fish species in their introduced range. Sunbleak (*Leucaspius delineatus*), a small cyprinid species, used to be abundant in central Europe but has dramatically declined throughout its native range. However, because this species was introduced in England in the mid-1980s, it has formed large populations and now is considered well established (Gozlan *et al.* 2003).

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Such a large-scale transplantation of two close relative species is rare worldwide. The transplantation of icefish provides significant economic benefits to the agriculture. For example, national icefish production in China increased from 5000 to 25000 tons in 1999, which is worth more than 300 million RMB (Ge *et al.* 2003). Although the yield significantly decreased in 2000, the national annual yield linear has kept growing since 2003 [$y = 1233.2x + 9404.7$ ($R^2 = 0.8302$)] (Fig. 5). The increase in fisheries in the next few years will be still expected in most unsaturated reservoirs and lakes.

Impacts of icefish transplantation

Aside from its economic benefits, introducing non-native species would inevitably cause ecological and environmental effects (Shaflanda 1996; De Silva 2012; Rico *et al.* 2012). Whether the introduction of non-native species is either good or bad and how to achieve a balance between them is continually debated (Mann 2005; De Silva *et al.* 2009; Cucherousset *et al.* 2012). Gozlan (2008) considered that only a small proportion of non-native freshwater fish species (about 6%) was associated with severe effects on native biota, whereas the rest of the species could integrate into existing communities with harmonious moderate effects (Ruesink 2005). However, Vitule *et al.* (2009) questioned this view after discussing data regarding Nile perch, common carp, tilapias, catfish and zebra mussels at a global scale. The ecological risk associated with freshwater fish introduction is variable across fish families according to their traits. For example, Percidae species cause high risk after introduction, whereas Acipenseridae species pose a fairly low risk (Gozlan 2008). The introduction of Nile perch (*Lates niloticus*) in Lake Victoria causes the extinction of hundreds of endemic cichlid species (Hauser *et al.* 1998). By contrast, transplantation of the planktivorous fish *Limnothrissa miodon* into Lake Kivu in the Democratic Republic of Congo, Lake Tanganyika in Tanzania, and the Zambezi River in Mozambique establishes highly successful fisheries with minor effects on the pre-existing fish communities or trophic ecology (Spliethoff *et al.* 1983). However, the deliberate release of non-native organisms for aquaculture generally affects the local ecosystem because of threats to native species, hybridization and the importation of parasites and diseases (Kolar & Lodge 2002; Magurran 2009).

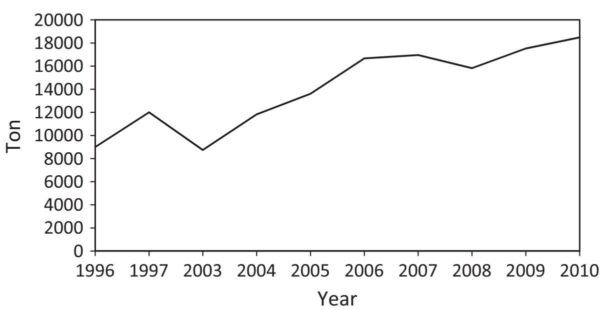

Figure 5 Annual production of icefish in China. The national icefish yield from 2003 to 2010 yearly increased and could be formulated as $y = 1233.2x + 9404.7$ ($R^2 = 0.8302$).

Threats to native species

Globally, tilapias are prized for aquaculture because they are physiologically tolerant, for example multiple spawning, parental care and extreme feeding plasticity (Welcomme 1986; De Silva *et al.* 2006; Arthur *et al.* 2010). Nile tilapia changes the native community structure, reduces the abundance of planktonic microcrustaceans and increases microalgal abundance (Okun *et al.* 2008). Catfish, favoured by many consumers, have spread rapidly worldwide for aquaculture. The mobility, amphibious habits and remarkably plastic diets of catfish have allowed escapees from aquaculture areas to establish populations in the wild (Cambray 2003; Lodge *et al.* 2012). They also affect native species through fierce carnivorous predation and destruction of natural habitats by burrowing into the earth.

Yunnan Province has many plateau lakes abundant in endemic species. Some species can even be found in only one lake in a long period of geological formation. As annual fish species, icefish can easily set up and adjust its population than other perennial species, which are incapable of adjusting between bursts and rapid declines. Bursting of introduced icefish populations can outcompete native lacustrine species for both food and living space. This phenomenon ultimately disrupts the simple food chain by directing the energy flow towards icefish, leaving no available niche for other planktivores. Furthermore, icefish even show feeding habitat on the eggs of other species, thus threatening the recovery of endemic fish population (Du 1999), which also occurs in other animals (Vredenburg 2004; Biro & Stamps 2008). This behaviour deprives the last chance of population recovery of native species, possibly leading to extinction. Of the 28 endemic species in Dianchi Lake, 13 can only be found in this lake in the world. The introduction of *N. taihuensis* was considered as one of the biggest threats, nearly resulting in the extinction of endemic species (Chen *et al.* 1998; Liu & Peng 2000). Protected species, such as *Sinocyclocheilus grahami*, *Spinibarbus sinensis*, *Anabarilius polylepis* and *Xenocypris yunnanensis*, have not been sampled for at least 20 years. In Erhai Lake, the populations of native species have increased because of persistent conservation since the 1990s, while the introduction of *N. tangkahkeii* effortlessly caused the extinction of endemic *Cyprinus* species such as *C. longipectoralis*, *C. megalophthalmus* and *C. daliensis* (Wu & Wang 1999; Du & Li 2001). In Fuxian Lake, pressure from icefish caused a sharp decline in the annual yield of rare *Zacco taliensis* from 400 to 500 tons in the 1960s to less than 1 ton in 2002 (Xiong *et al.* 2008). Coincidentally, the endemic *Schizothorax* that dominates Lugu Lake is now only observed occasionally (Chen *et al.* 1998). Icefish are incompatible with other members of family Salangidae and species from other taxa. The Yalu River estuary historically contains five coexisting Salangidae species, but the estuarine *Neosalanx jordani* and *Salanx prognathus* were outcompeted by introduced *P. chinensis*. Icefish *P. chinensis* was introduced into the reservoir connected to the upper Yalu River and eventually escaped and burst in the river and estuary because of its high salt tolerance. Unfortunately, estuarine icefish spawn during spring, thereby providing food for *P. chinensis* (Wang 1984; Xia & Shi 1985).

For maximum economic benefits, fishing this annual species is greatly enhanced. However, special fishing gear that catches icefish 4–5 cm long could also threaten endemic species. In Fuxian Lake in 1999, as every 10 kg of icefish caught, at least 1 kg of *Anabarilius graham*, which is endemic to Yunnan Province, was lost as bycatch (Zhou & Huang 2005).

Hybridization, founder effect and genetic bottleneck

Introducing nonendemic species may cause hybridization and genetic introgression of the invader into the indigenous species (Smith *et al.* 2010), which augments the variability and viability of the former, but is extremely deleterious to the latter. The distribution of each species is generally relatively concentrated within an advantageous range, because of long-term natural selection (Giske *et al.* 1998; Strauss *et al.* 2006). Human disturbances on the original distribution would definitely affect the ecological environment of the transplanted area, good or bad, more is bad. Introduced rainbow trout (*Oncorhynchus mykiss*) hybridized with many western North American native trout species, which is partly responsible for the threatened status of six *Oncorhynchus* species (Vitule *et al.* 2009). Sympatry is common in salangids, such as *P. chinensis*, *S. ariakensis*, *S. prognathus*, *N. jordani* and *N. anderssoni* in the Yalu River Estuary. In most cases, sympatric salangids are not monophyletic or usually have different microhabitat preferences (e.g. *N. jordani* and *N. anderssoni* have different preferences in salinity), or differentiate their spawning periods (e.g. *S. ariakensis* spawns in September, whereas *S. prognathus* spawns in spring) (Zhang *et al.* 2005), thus showing high genetic divergence and successful isolation of interspecific reproduction.

Introduced populations are also subject to founder effect and genetic drift, entailing the loss of genetic variation and inbreeding depression and reducing fitness of the introduced species (Salmenkova 2008), even with rapid increases in the populations of invasive species. However, a recent study on grass carp *C. idella*, a freshwater species native to China that has been introduced to many countries, indicated that some populations developed genetic bottlenecks and low genetic diversity, while others experienced rapid population expansion with potential genetic diversification within 50 years after its introduction (Chen *et al.* 2012). As previously mentioned, Taihu Lake is the main source of transplanted icefish. To obtain sufficient fertilized eggs for the national demand at a low price and maintain stable high production, many types of multiple transplantation frequently occurred, and the operations were disorderly. Some practices even used eggs from introduced population, for example Yunnan population (Xiao *et al.* 2000). More seriously, introduced population eggs were even released into original places, for example, 117.75 million of eggs were released into Hongzhe Lake from Heilongjiang Province in 2010–2011 (http://www.jsof.gov.cn/art/2011/5/23/art_58_75616.html). Adaptive changes in ecological traits and the formation of the genetic structure of the population in the new areas may occur very rapidly among salangids. Genetic diversity is urgently needed to be detected whether the founder effect or the rapid population expansion occurs within and among native and introduced salangid populations.

Parasites and diseases

Introducing non-native species can also introduce novel pathogens (Gozlan *et al.* 2005; Altizer *et al.* 2011), which can have serious consequences. The zebra mussel is the intermediate host for a trematode, and its introduction allows the parasite to infest native fish, causing high fish mortality (Pronin *et al.* 1997). Frozen rainbow trout shipped from Europe introduced *Myxobolus cerebralis* (Myxobolidae), and this myxozoan causes whirling disease first observed in North America in 1956 (Bergersen & Anderson 1997). The crustacean copepod parasite *Lernaea cyprinacea* (Lernaeidae) was introduced to Brazil with carp and then it subsequently affects a wide range of hosts (Ghiraldelli *et al.* 2006).

The natural production of *N. tangkahkeii* in Chaohu Lake irregularly varied in recent years because of parasitic infection (*Diagramma cholodkowski*, Diphyllobothriidae), and the gonads remain undeveloped in all infected individuals (Liu *et al.* 2009). As one of the important germplasm repositories, *N. tangkahkeii* from Chaohu has been widely transplanted. The introduced *N. tangkahkeii* population would probably cause the spread of parasitic infection. Moreover, the potential range of introduced fish species is much larger than the current range. This finding suggests that the detrimental changes in the ecosystem are likely to affect larger areas.

Perspective

According to the Government's plan for aquaculture, the main aim in the field of fisheries is to accelerate the transfer of scientific and technological breakthrough into commercial production (Luo *et al.* 2009). This aim includes the following: (i) setting up a complete system for developing good strain seed and the corresponding breeding technology; (ii) enhancing aquatic organism conservation and aquatic ecology, such as selective capture, pollution prevention and environmental restoration; and (iii) improving disease prevention and food safety control system. Therefore, more accurately evaluating biological, ecological and genetic factors and predicting transplant effects are urgently needed for future actions.

Successful transplantation should fulfil economic, geographic, biological and ecological criteria (Hu *et al.* 2001). First, the economic benefits of introduction, including fishery value, population dynamics and fishing potential, should be evaluated. Second, the selection of species for transplantation should consider the corresponding physical properties (water temperature, depth, discharge, flow velocity, etc.) and chemical properties (water quality) of recipient water body. Third, the biological criterion requires intensive knowledge of the traits of both the introduced species (food habitat, reproductive characters) and the recipient water body (food organisms, community composition). Lastly, the interspecific and intraspecific relationships within the ecosystem should be considered, particularly the appearance and distribution of predators and other species that share the same niche as the introduced species.

Icefish have attractive economic and nutritional values (Sun 1982) and serious ecological effects. Generally, successful icefish transplantation can be divided into five stages:

1. Survival of introduced species in the new environment
2. Reproduction and population formation
3. Population burst (normally after 2–4 years)
4. Competition between introduced species and other organisms
5. Formation of a new ecosystem.

The final ecosystem could be one of three types: (i) similar to the former if icefish failed to form a viable population, (ii) dominated by icefish with the loss of endemic species and (iii) a balanced ecosystem with a dynamic equilibrium among stable icefish populations and other species.

The environmental effects of icefish transplantation have also received considerable attentions, especially in cases where societal benefits are negatively affected by the consequences of unregulated development. The interaction between aquaculture and the surrounding natural and social environments must also be considered. To date, aquaculture aims to achieve a balance among economic development, environmental security and rational resource utilization (Welcomme 1986; Leprieur *et al.* 2008). In China, relevant standards for fisheries, such as standards for pollution-free aquatic products and standards for wastewater discharge in freshwater aquaculture, have also been set up (CSP 2000; Song 2009). Although eradicating icefish is greatly encouraged, catching icefish is hard, no matter what equipment is used. As a result, periodic icefish outbreaks occur repeatedly. If the burst-down period is shorter than the time needed for ecosystem recovery (which means icefish bursts occur before the ecosystem recovers from icefish decline), the ecosystem will be unable to recover.

Corresponding to the differences of environment, economy and aquaculture technique at regional scale, transplantations of icefish show different processes and probable future scenarios. Regions IV and V, the main origin and production areas of Salangidae, are definitely the preferred objects for icefish resource reparation and protection. A serial of measures including banning fishing in spawning period, releasing fry and water pollution treatment are in action in recent years. Region I is possibly the potential area to develop icefish transplantation, supported by a large vacancy of water body and governmental plan for both economic need and resource protection, especially the former. Regions II and III are also in the encouragement of icefish transplantation. The seasonal environment resistance and unresolved technical problems would cause unignored difficulties for successful development. Researches concerning to the success of transplantation in such a place should be greatly encouraged. Region VI, the pioneer of icefish transplantation, has ever made remarkable achievement, but now limits further transplantation for the damage, for example threats to native species, fauna homogenization, attributing to large-scale actions without reasonable planning. Region VII, a region with well-developed mariculture, has been paid less attention and seems to have no further plan on icefish transplantation. Provincial units without icefish transplantation before also have no actions in the near term.

Historical and current reports on icefish transplantation mostly focus on temporary achievements and benefits instead of further information on its consequences. However, the effects of species introduction may take a few years, or even decades to develop fully (Strayer *et al.* 2006). Thus, more research on biology, ecology and conservation biology are encouraged. The results obtained from research, together with the development of aquaculture techniques, will help us find new approaches for transplanting icefish to benefit both economy and environment, or at least achieving a balance. Thus, caution is needed because introducing non-native species is irreversible once they become established. Our findings can be viewed as an incentive to discover possible uses for native species with high economic and societal values. Furthermore, despite of laws and regulations for minimizing the spread of single species, the effective implementation of such laws can often be hampered by other factors. To date, the transplantation of icefish is still debated. We believe this issue deserves further consideration before the final decision, which may end in catastrophic failure or roaring success.

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