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Long-term density dependent effects of the Chinese mitten crab (*Eriocheir sinensis* (H. Milne Edwards, 1854)) on submersed macrophytes

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ABSTRACT

The Chinese mitten crab (*Eriocheir sinensis* (H. Milne Edwards, 1854)), is a highly invasive species and poses a great threat to endemic species and infrastructure in Europe and North America. Although it is partly herbivorous and prefers to live in lakes with abundant submersed macrophytes, little is known about its effect on macrophytes. We used its native range, the mid-lower Yangtze Basin where the species has been cultured intensively for decades, as our study site to test the hypotheses that (1) high crab densities weaken the positive feedback between macrophytes and water transparency, and that (2) the effects of crabs become apparent only on decadal timescales and (3) are density dependent. We used correlative analyses based on 12 years of monitoring and multi-lake comparisons among 20 sub-areas in 4 lakes. High crab densities were found to cause negative effects on submersed macrophytes and transparency, and to weaken the positive relation between macrophytes and transparency. High densities of macrophytes showed resilience to disturbance from crabs. This resilience, however, reduced with continuous presence of high crab densities. Crab densities were strongly positively related with total phosphorus and negatively with transparency and total nitrogen. Phosphorus concentrations and transparency were not related with phytoplankton chlorophyll *a*, suggesting that crab's bioturbation strongly influences water quality. The apparent resilience of the dense macrophyte stands should however, not delay attempts to eradicate the crab where it is invasive as this becomes more difficult once they have become established. When macrophyte abundance is already low at the time of invasion, immediate loss of macrophytes may occur.

1. Introduction

Loss of submersed macrophytes has been widely reported in shallow lakes (Blindow, 1992; Körner, 2002; Schallenberg and Sorrell, 2009; Baastrup-Spohr et al., 2013). Excessive nutrient (nitrogen and phosphorus) loading is a well-known cause (Scheffer, 1998; Carpenter, 2003) but herbivory has received ample attention as a causal factor as well (Lodge, 1991; Wood et al., 2012a,b). Waterfowl, for instance, can exert a strong top-down effect on submerged macrophytes. Its effect increases with waterfowl density and can even lead to an elimination of the above-ground biomass at high waterfowl densities (Wood et al., 2012b). Other herbivores such as grass carp, crayfish, and mammals have been reported to cause negative effects on macrophytes as well (e.g., Lodge and Lorman, 1987; Olsen et al., 1991; Prigioni et al., 2005; Van der Wal et al., 2013; Law et al., 2014), sometimes triggering a complete shift from macrophyte dominance to phytoplankton dominance (Rodríguez-Villafañe et al., 2003).

Although not primarily herbivorous, the Chinese mitten crab (*Eriocheir sinensis* H. Milne Edwards, 1854), may also contribute to the loss of submersed macrophytes in lakes. The crabs are opportunistic but preferentially feed on macroinvertebrates and detritus (Wen et al., 2000). They also forage on submerged macrophytes, although their importance to the total diet of the crab is limited (3.5–7.5% dry weight) (Jin et al., 2001, 2003). Hence, indirect impacts likely play a more important role than direct consumption. These indirect impacts include damaging the macrophytes while foraging on macroinvertebrates and causing sediment resuspension with their burrowing activity thereby deteriorating

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underwater light conditions. In the absence of crabs, macrophytes typically enhance the water clarity (Kosten et al., 2009) which improves light conditions, thereby enhancing photosynthesis and macrophyte growth. This positive feedback is the primary mechanism maintaining a macrophyte-dominated clear-water state in shallow lakes (Scheffer et al., 1993). We hypothesize that Chinese mitten crabs' bioturbating activities weaken this positive feedback (hypothesis 1).

The crab is a catadromous crustacean native to East Asia. This species has long been a fashionable table delicacy in China. True aquaculture of this species began in the 1980s (Zhao, 2000), characterized by stocking of either hatchery reared or wild propagules to shallow lakes. In its native range, it lives in coastal waters and shallow lakes with abundant vegetation (Zhang et al., 2001; Rudnick et al., 2003). Because of its high reproductive rate and wide range of physiological tolerances (Rudnick et al., 2003), this species successfully invaded Europe over one century ago, mainly through ballast water, and more recently in the 1990s, North America and Western Asia. The crab is still expanding its invasive range (Herborg et al., 2003, 2005, 2007). From reports on the invasive character of the crab, it is known that it negatively impacts biodiversity and fisheries, contributing to the extinction of native invertebrates by preying on them and possibly by competing with native invertebrates and fish (Leppäkoski et al., 2002). Additionally they are capable of destroying dikes and other infrastructure through burrowing (Rudnick et al., 2003; Dittel and Epifanio, 2009). However, little is known about its potential impact on macrophytes in both native and invaded areas.

A short term mesocosm (Jin et al., 2001) and a presence-absence study in the field (Xu et al., 2003) indicated negative effects of high densities of crabs on macrophytes. Instant negative effects of crayfish were also found on macrophytes in short-term enclosure experiments (Lodge and Lorman, 1987; Lodge et al., 1994). In a reservoir where Chinese mitten crab was introduced, however, no effects on submersed macrophyte biomass (*Potamogeton maackianus* and *Ceratophyllum oryzetorum*) were observed until the second year (Yu and Jiang, 2005). The effect of the crabs is likely also density dependent as has been shown in a study in systems where rice and crab culturing is combined: the biomass of plants declined significantly with increasing stocking density (Li et al., 2007). We still lack insight in how crabs affect macrophytes in natural lakes over a decadal scale and at which densities they cause a problem. We hypothesize that the effect of crabs becomes apparent only on a timescale of years and that their effect is likely to be crab and macrophyte density dependent (hypotheses 2 and 3).

In this study, the mid-lower Yangtze Basin was used as an experimental site to study the effects of crabs. In this area, crab culture has been practiced for decades in numerous shallow lakes and many of these lakes have experienced loss of submersed macrophytes, providing an excellent opportunity to look into the effect of crabs on submersed macrophytes. In this study, we relate crab density to macrophytes density and water quality using a dual approach based on (1) monitoring data of a lake with a decadal crab culture (further referred to as the time series analyses) and; (2) a 1-year detailed field-study in 20 sub-areas of 4 large middle-Yangtze shallow lakes supporting crab cultures of different intensity (further referred to as the multi-lake analyses).

2. Methods

2.1. Study sites

Decadal data were available for Lake Biandantang (Hubei Province), a lake in the middle Yangtze Basin. It forms a part of Lake Bao'anhu and has an area of 333 ha, a maximum depth of 2.5 m, and an average depth of 2.1 m. This is the only lake on which decadal (12 years) data of crab and environmental are available. Multi-lake comparisons were conducted on data from isolated sub-areas of the lakes Bao'anhu, Niushanhu, Luhu and Western Liangzihu for which data were gathered in 2001–2002. All four lakes are located in the middle Yangtze Basin (114°08′–48′ E, 30°07′–23′ N) (see Wang et al. (2006) for a detailed description of the locations). Nets and dykes divide the lakes into 20 sub-areas. These divisions are already in place for years or decades. The areas of the sub-areas range from 145 to 6667 ha and they have average depths ranging from 1.8 to 3.3 m (Table 1). Exchange of water among the sub-areas is limited, if occurring at all, which is demonstrated by the considerable variation in environmental conditions such as nutrient levels and transparency among the sub-areas (Table 1). A one-way ANOVA analyses (Wang et al., 2005) underlined the significant difference in environmental conditions. We therefore treated each of the 20 sub-areas as separate water bodies. A warm, humid subtropical climate dominates in this region, with an annual mean air temperature ca. 19 °C and precipitation ca. 1030 mm.

2.2. Stocking and harvest of crabs

Stocking of Chinese mitten crabs started in the late 1980s in Lake Biandantang and in around the year 2000 in the other lakes. Artificially propagated crab juveniles weighing 10 (5–15) (mean (min–max)) g ind^{-1} were transported from Nantong, Shanghai and released into the lakes during winter and early spring (December–May). Their escape is prevented by placing fences made of plastic sheets along the shoreline. Adult crabs are caught with cage traps in autumn of the same year (September–November). Harvest data in Lake Biandantang from 1991 through 1999 were collected from Jin et al. (2001). Data for subsequent years of this and the other sub-areas were obtained from the local farmers directly (Table 1). Stocking rates (SR) were only available for the 20 sub-areas included in the multiple-lake comparison and were calculated as individuals of stocked crabs divided by area. Crab yield (CY) was available for all lakes and calculated as weight of caught adult crabs divided by area. For Lake Biandantang no stocking rate data was available, however, stocking rate tends to be strongly positively correlated to crab yield (between CY and SR in 2001, $r = 0.88$, $n = 16$, $p < 0.001$) when macrophyte biomass is high (with biomass in December 2001 higher than 100 g m^{-2}), we therefore use crab yield here as an indicator for crab density. Harvest effort remained equally high throughout the entire study period (farmers may take up to one month to remove as many crabs as possible).

2.3. Sampling and analyses

Historical data (before 2000) from Lake Biandantang regarding biomass (B_{Mac}, wet weight) of submersed macrophytes were collected from the literature (1991–1993, 1994–1995 and 1996–1999 were collected from Su et al. (1995), Yu and Zeng (1996) and Jin et al. (2001), respectively). Data of Secchi depth (Z_{SD}) and coverage of submersed macrophytes (C_{Mac}) (visual estimation from a boat of the percentage area occupied by submersed macrophytes) were collected from Jin et al. (2001). The data from these references were all reported as averages. The number of sampling sites (n) of Z_{SD} was not specified in Jin et al. (2001); that of B_{Mac} and C_{Mac} was 15 (on 3 transects and 5 for each) in Su et al. (1995), and not specified in Yu and Zeng (1996) and Jin et al. (2001). The methods applied in these references are similar to those we have applied and explained in the following.

Fieldwork was carried out from December, 2001 to December, 2002 (Table 1). Total nitrogen (TN), total phosphorus (TP) and phytoplankton chlorophyll *a* (Chl *a*) were measured seasonally. Winter sampling took place in December 2001 in lakes Bao'anhu,