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Assessing impacts of introduced aquaculture species on native fish communities: Nile tilapia and major carps in SE Asian freshwaters

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ABSTRACT

Herbivorous or omnivorous tilapia and carp species form the backbone of tropical inland aquaculture and fisheries enhancement and have been introduced widely outside their natural ranges. Perceptions of their impact on native fish faunas vary widely, but there have been few rigorous assessments. To quantify the impact of tilapia and carp stocking on native fish communities in freshwater wetlands of the Mekong region, we conducted observational and experimental impact–control studies replicated at the wetland level, at a total of 46 sites in Lao PDR. The studies were designed as paired comparisons of wetlands where the non-native species (Nile tilapia *Oreochromis niloticus*, mrigal *Cirrhinus cirrhosus*, rohu *Labeo rohita* and bighead carp *Hypophthalmichthys nobilis*) were stocked in substantial numbers with similar wetlands where the species were absent. Stocking of these non-native species was associated with significant increases in total fish biomass, by 180% in the observational study and by 49% in the experiment. Native fish biomass was not affected by stocking of the non-native species. No significant impacts on native fish species richness, diversity indices, species composition or feeding guild composition were detected, except for moderately negative effects on Simpson diversity and equitability in the observational study. In the experiment, no effect had a point estimate exceeding −14%, or a 95% confidence limit exceeding −35% of the non-impacted value. Use of these non-native tilapia and carp species in fisheries enhancement in mainland SE Asia supported substantial increases in harvestable biomass while having only mild impacts on native fish communities. Escapes of the same species from pond and cage aquaculture facilities are likely to result in lower biomass in the wild and have lower impacts than enhancement stocking. We encourage building on our results through a systematic and stakeholder-participatory evaluation of the significance and acceptability of benefits and risks associated with the use of these non-native species. This evaluation should be extended to the relative benefits and risks of replacing non-native species with native ones in aquaculture and enhancement, considering that risks associated with using the current set of non-native species are increasingly well known and appear mild-to-moderate, whilst ecological and genetic risks of releasing domesticated types of native species are poorly known.

1. Introduction

Although a large number of fish species are being cultured, the bulk of aquaculture and fisheries enhancement production is accounted for by a small number of species which have been introduced widely beyond their native ranges (Welcomme, 1988; DIAS, 2004). Herbivorous or omnivorous tilapia and carp species are a case in point, having been introduced throughout the tropics and accounting for about 80% of tropical inland aquaculture production. Like the common agricultural animal domesticates, these species have attributes that make them particularly attractive for raising in captivity (Bilio, 2008). In addition, many of these species have been selectively bred to enhance traits such as growth (Hulata, 2002). There are thus good reasons for raising these species.

Introductions always carry risks for the native biota. Interactions with non-native species rank second only to habitat modification as a threat to freshwater fish biodiversity (Miller et al., 1989; Harrison and Stiassny, 1999). Although aquaculture confines fish in ponds, cages, or tanks, accidental releases into natural waters tend to occur from pond and cage systems (typically at a small percentage of the cultured stock per year, Naylor et al., 2004). Fisheries enhancement involves deliberate stocking of cultured juveniles into natural water bodies (Welcomme and Bartley, 1998; Lorenzen, 2008). Concern about impacts of releases into the natural environment has led to calls for

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restricting the use of introduced species in aquaculture and fisheries enhancement and fueled interest in the development of native species for such purposes (Ross and Beveridge, 1995; Naylor et al., 2001; Ross et al., 2008). However, only a small proportion (about 6–22%) of non-native fish species are associated with severe impacts on native biota, while the majority of such species integrate into existing communities with at best moderate effects (Williamson, 1996; Ruesink, 2005; Gozlan, 2008). Moreover the alternative, culture and accidental or deliberate releases of native species may also have significant ecological and genetic impacts (McGinnity et al., 2003; Naylor et al., 2004; Lorenzen, 2005). While concerns regarding the impacts of non-native species focus on interspecific interactions, those regarding native species focus on intraspecific interactions between partially or fully domesticated types and wild types. Where a choice can be made as to whether a particular native or non-native species should be cultured, it is not clear *a priori* which option poses the lesser risk to native biota.

Given that different non-native species pose very different levels of risk to native biota when used in aquaculture and fisheries enhancement, effective risk management strategies should differentiate between the "damaging minority" of species that require strict control and species of lesser concern for which benefits of judicious use may justify or outweigh risks (Van Driesche and Van Driesche, 2000; Dudgeon and Smith, 2006; Hill and Zajicek, 2007). Differentiation between risk categories needs to take account of the likelihood of establishment of a species and the consequences of its establishment for native biota. Both aspects tend to be very uncertain for species not yet present in the wild, so that a highly precautionary approach is indicated and widely implemented with respect to new introductions (Leprieur et al., 2009). By contrast, once non-native species have been released, risks of establishment and its consequences can be quantified through observational or experimental field studies. The resulting information will reduce uncertainty, thereby paving the way for differentiated management measures such as active eradication of problem species on the one hand and minimal regulation of species for which risks are demonstrably low and balanced by benefits on the other. Decision making in this respect should be informed by rigorous impact assessments but will also require value judgments by stakeholders as to the significance of impacts and acceptability of levels of uncertainty (Hill and Zajicek, 2007).

Impacts of non-native on native fish populations may arise from competition for resources, predation, habitat and water quality alterations, hybridization, and the importation of parasites and diseases (Moyle et al., 1986; Arthington, 1991; Canonico et al., 2005). The strongest impacts on the receiving communities are typically associated with introductions of predators (Eby et al., 2006). Where interactions are weak, non-native species may integrate into native communities without causing severe impacts such as species extinctions. Communities that can integrate additional species in this way may be viewed as offering 'unused niche opportunities' that the introduced species can utilize (Williamson, 1996; Shea and Chesson, 2002). Whether or not this occurs depends on characteristics of the non-native species as well as on those of the native community. In either case, the non-native species may be present at noticeable abundance. Non-native fish presence therefore is not a sufficient indicator of impact, which must be established from changes in the abundance or composition of the native community. This requires temporal and/or spatial controls (non-impacted reference sites) and ideally, replication (Parker et al., 1999). Moreover, impacts may become fully apparent only years or decades after first introduction (Strayer et al., 2006; Spens et al., 2007). This is particularly so where populations of introduced species increase slowly before reaching levels of abundance that cause major impacts, or where impacted species are long-lived and impacted in their early life stages. Such factors must be considered in the timing and duration of impact studies. Unfortunately, rigorous impact studies are rare. Much information on impacts of non-native species is based on casual observations or on studies that lack controls or replication and have been conducted over very short time periods (Strayer et al., 2006; Vitule et al., 2008). Hence despite good conceptual understanding, knowledge of impacts of particular introductions and our ability to predict impacts of new introductions remain very limited (Williamson, 1996; Moyle and Light, 1996). This makes it difficult to derive useful generalisations that could help to discriminate between high and low-impact species because, in the absence of systematic studies, lack of documented impacts does not imply a positive demonstration of low impact.

In mainland SE Asia, non-native tilapia and carp species are widely used, often in polyculture, in pond and cage aquaculture systems (Edwards et al., 1997; Michielsens et al., 2002; Amilhat et al., 2009) and in fisheries enhancements in natural and modified freshwater wetlands (Lorenzen et al., 1998a,b; De Silva et al., 2006). Our study was carried out in the Lao PDR, where non-native carp and tilapia species had been introduced by the 1970s. However, large-scale aquaculture development and fisheries enhancement are relatively recent phenomena in Lao PDR, having expanded rapidly since the mid-1990s. While the bulk of aquaculture and fisheries enhancement production is currently based on non-native species, there is a drive for the development of native species for these purposes by governments, regional management bodies such as the Mekong River Commission and NGOs (e.g. MAF, 2006). This is partially due to a perception that stocking of native species would cause less harm to native biota than the use of non-native species (e.g. MAF, 2006), and perhaps a perception that this would be more 'natural' (c.f. Simberloff, 2003). In the Lao PDR, intentional and quantitatively significant releases into the wild occur only in selected wetlands, typically those that are actively managed for fisheries production by local villages (generally known as 'community fisheries'; Garaway et al., 2006). While non-native species have thus been released in high densities in selected wetlands, they have not dispersed widely and remain absent from most. Freshwater wetlands in the Lao PDR therefore offer excellent opportunities for assessing impacts of tilapia and carp releases through replicated impact-control studies.

In the present study, we assess the impacts of fisheries enhancement with non-native carp and tilapia species on the abundance and diversity of native fish communities in mainland SE Asia. We conducted observational and experimental studies, designed as a paired comparison of relative biomass, species richness and structural indicators of native fish communities between wetlands with substantial populations of the non-native species and associated control sites where non-native species were absent. Our studies are thus replicated at the whole-wetland level and use spatial controls to provide statistically robust information on impacts. We discuss implications of our results for the use of non-native species in aquaculture and fisheries enhancements in SE Asia and encourage wider debate on the methods and criteria by which risks of continued use of non-native species can be assessed and management strategies devised.

2. Material and methods

2.1. Study area

The study was carried out between 1999 and 2002 in southern Lao PDR. The climate in Lao PDR is tropical with an average daily temperature of 31 °C and an average annual precipitation of 1500 mm, about 75% of which occurs in the monsoon season (May to October). The study area forms part of the lower Mekong basin, where the regional pool comprises some 760 fish species (Kottelat, 2001). Wetlands in the region are intensively fished and are increasingly being modified in the course of agricultural intensification

(Claridge, 1996; Nguyen Khoa et al., 2005). All study wetlands were located in lowland areas of the provinces of Khammouane and Savannakhet.

2.2. Study design

The study comprised three main elements: (1) exploratory surveys of wetlands and associated fisheries to support the design of quantitative impact studies, (2) an initial observational study involving wetlands where non-native species were well established from earlier releases and (3) an experimental study involving deliberate stocking of wetlands in order to generate consistent treatments. Both quantitative studies were based on paired comparisons between wetlands where non-native species had been established with similar control wetlands where the species were absent. The study was thus replicated at the whole-wetland level. For simplicity we refer to the initial observational study as 'observational' and to the subsequent experiment as 'experimental'. However, both studies were primarily observational in the sense that treatments could not be allocated at random to experimental units (Eberhardt and Thomas, 1991). The total number of wetlands that could be sampled was limited to about 50 by logistical constraints. Many wetlands included in the exploratory surveys turned out to have been stocked previously and were thus unsuitable as control sites. Hence even in the experimental study, treatment allocation was constrained by historical stocking patterns and the majority of wetlands that were deliberately stocked already had non-native species present. A paired design was chosen to minimize environmental variation and maximize the statistical power of the comparisons. Controls were located in the same watershed, normally in close vicinity to the wetlands were non-native species were present. The exploratory survey was carried out in September 1999, the observational study from October to December 1999, and the experimental study from June 2000 to June 2002.

2.3. Exploratory survey

Exploratory surveys were carried out to determine physical characteristics, presence or absence of non-native species, and fisheries management regimes for a set of potential study lakes. The surface area of wetlands was calculated from their dimensions, which were measured directly for smaller wetlands or on maps for larger ones. Multiple depth measurements were undertaken in all wetlands and averaged to obtain mean depth. Total phosphorus (TP) concentration was measured as a trophic status indicator. Three samples were taken in different locations in each wetland and processed according to APHA (1989).

Information of non-native species presence and fisheries management was obtained through semi-structured interviews with local fishers (Chambers, 1992). This information was used to provide *a priori* information on the presence or absence of non-native species in wetlands and their fisheries management regimes.

2.4. Observational study

A total of 23 wetlands where non-native carps or tilapia species were present were identified during the exploratory survey. Each of these wetlands was paired with a local control wetland where the non-native carps and tilapia were absent. In all 46 wetlands (23 'treatment' and 23 control sites), relative biomass, diversity and composition of the fish communities were assessed using standardized test fishing with monofilament gill nets, a common sampling gear (e.g. Kurkilahti and Rask, 1996). All test fishing in the observational study, and subsequently, was conducted using a standard multipanel monofilament gillnet consisting of six panels, each 5 m long and 1.5 m deep with mesh sizes of 10, 20, 40, 60, 80 and 100 mm (stretched mesh). These nets were constructed by a local fisherman using locally available netting. For each sample, nets were set by local fishermen at about 1800 h and retrieved the following morning at about 0600 h. Fish were recorded individually by species. Total catch by weight was determined for each fishing event to provide an estimate of catch per unit of effort (CPUE), a measure of relative biomass. For the initial observational study, only one test fishing event was carried out in each water body. Subsequently, repeated test fishing was carried out in six wetlands to establish relationships between the number of fishing events and the cumulative number of species recorded. Three events consistently yielded over 90% of the asymptotic number of species recorded, hence three fishing events were carried out quarterly in all wetlands during the experiment. Field data collection was carried out by trained staff of the Livestock and Fisheries Section of Savannakhet Province. Species identification was carried out by two staff members trained as para-taxonomists at The Natural History Museum, London, UK.

2.5. Experimental study

Out of the 46 wetlands included in the observational study, 14 were selected for experimental stocking and paired with 14 controls were non-native species were known to be absent. Selection of wetlands for stocking was based on patterns of non-native species presence and on the preferences of local villages which have *de facto* management authority over wetlands within their immediate area. Most pairings of treatment and control sites remained the same as in the observational, but some controls had to be re-allocated for logistical reasons or because small numbers of non-native species had been found in the observational study.

Experimental stocking of wetlands was conducted annually in 2000 and 2001 and test fishing was carried out for a total of four times in 2001 and 2002. Wetlands were stocked with carps only, Nile tilapia (*Oreochromis niloticus*) only, or 50:50 carps and tilapia, all at the same total stocking density (3500 ha^{-1} of 3–5 cm juveniles, equivalent to a total biomass of about 2 kg ha^{-1}). The 'carps' treatment comprised equal numbers of three species, the Indian major carps mrigal (*Cirrhinus cirrhosus*) and rohu (*Labeo rohita*), and the Chinese bighead carp (*Aristichthys nobilis*). Experimental stocking was carried out primarily to evaluate yields from different stocking regimes, but the study also provided further data on impacts of native wild fish. While our study involved experimental releases of non-native fish species into selected wetlands, all species used were already present in the wild in the study area and no releases were made into wetlands where non-native species were absent.

Test fishing was carried out in the same way as in the observational study (see above).

Fishing effort was monitored in all stocked wetlands, where fishing was under strictly controlled by communal organisations and could thus be monitored easily. It was not possible to monitor fishing in the non-stocked wetlands where access was open to all and extensive household surveys would have been required to quantify fishing effort. However, in order to gain an indication of the level of fishing effort in such wetlands, we used data from a household fishing survey conducted previously (1995–1997) in the same area (Garaway, 1999; Lorenzen et al., 2006). Fishing involved a variety of different gears (principally gill nets, cast nets, lift nets and seines) and measures of fishing effort expended by different gears therefore had to be standardized (Gulland, 1983). The fishing power P_g of gear g relative to standard gear s was calculated as the average of the CPUE ratio for the two gear types over all wetlands i where both gears were used:

$$P_g = \frac{1}{n}\sum_{i=1}^{n} \frac{CPUE_{g,i}}{CPUE_{s,i}} \tag{1}$$

Table 1
Comparison of environmental variables and fishing intensity in non-impacted (control) and impacted wetlands. Means with 95% confidence intervals.

Variable	Non-impacted (control)	Impacted
Surface area (ha)		
Observational study	8.66 [2.23, 15.10]	6.44 [2.33, 10.64]
Experiment	2.81 [1.63, 3.99]	2.90 [1.73, 4.06]
Mean depth (m)		
Observational study	1.85 [1.37, 2.33]	1.77 [1.44, 2.00]
Experiment	1.79 [1.30, 2.27]	1.84 [1.26, 2.41]
Total phosphorus concentration (mg l^{-1})		
Observational study	0.08 [0.02, 0.14]	0.13 [0.04, 0.22]
Experiment	0.11 [0.05, 0.18]	0.18 [0.03, 0.34]
Fishing intensity (h ha^{-1} $year^{-1}$)		
Experiment		163 [88, 303]
Household survey	283 [113, 708]	

The combined fishing effort E_i of all gears in wetland i is then given by:

$$E_i = \sum_g E_{g,i} P_g \tag{2}$$

Fishing effort was standardized in units of experimental gill net effort and divided by wetland area in order to obtain a measure of fishing intensity.

2.6. Data analysis

Species richness was determined as the cumulative number of genera recorded from all samples from a given lake. Different numbers of fish were caught across the sites and therefore sample sizes across sites differed, a factor that could potentially affect the results of any analysis into species diversity given that more species are likely to be recorded with increasing numbers of individuals sampled (Bunge and Fitzpatrick, 1993). In order to mitigate against this sampling effect, rarefaction was used to compensate for differences in sample size and calculate the expected number of species for a standard sample size (Gotelli and Colwell, 2001). Rarefaction is based on the distribution of individuals among species and uses an algorithm to calculate the mean richness of computer generated re-samples of 30 fish (the minimum number of fish caught in the samples included in the analysis). Both raw and rarefied species richness results are reported. In addition to species richness, Simpson's diversity index (D) and equitability index (E) and the Shannon diversity index (H) and equitability index (J) were used to quantify native fish diversity (see Magurran, 2004). The indices were calculated for the number of individuals (not biomass) of each species.

To assess effects of stocking on ecological characteristics of fish communities, the composition of samples was described in terms of the proportional abundance of major feeding groups Classification of species by these characteristics was based on information from FishBase (Froese and Pauly, 2009; Rainboth, 1996; Kottelat, 2001).

The main impact assessment was based on differences in the above indicators between paired lakes with and without substantial populations of the non-native species. For each indicator, the mean value in non-impacted (NI) sites is given as a baseline, and the effect of the non-native species is reported as the mean and 95% confidence interval of differences between the paired, impacted and non-impacted wetlands (see Table 4). In the paired design, the mean effect is not the same as the difference between the means in impacted and non-impacted sites, and the non-impacted (baseline) means are given only as an aid to interpretation. All confidence limits were generated using a nonparametric bootstrap (Efron and Tibshirani, 1993).

Regression analysis was used to explore possible relationships between impact indicators, the trophic status indicator TP and fishing intensity. Results allowed to assess the magnitude of possible confounding effects of these variables.

3. Results

3.1. Wetland and fish community characteristics

The study wetlands included oxbow lakes, natural depressions and swamps, ranging from 0.5 to 7.5 ha in area, and from 0.5 to 3.5 m in depth. Statistical analysis indicated that there were no significant differences between stocked and non-stocked water bodies in terms of the area, depth, total phosphorus, or fishing intensity (Table 1). The observational study included some wetlands of larger area than the experiment, but impacted and control wetlands were of similar mean area in both cases. As mentioned above, fishing intensity estimates for non-impacted wetlands were derived from an earlier study and are indicative only. Most wetlands where non-native species were absent (control wetlands) were open to individual fishing by local villagers, while most wetlands where non-native species had been released and built up substantial populations were managed as community fisheries (see Garaway et al., 2006 for more detail on the management arrangements). These differences in access underlie the noticeably, if not significantly higher average levels if fishing intensity in non-impacted wetlands. All wetlands classified as 'impacted' in the observational study had been previously stocked, the majority (15) repeatedly and for at least four years.

Five non-native fish species were caught in test fishing or known to have been released (Table 2). In total, 3422 fish of 83 species representing 17 different families were caught during test fishing in the paired sites (see Table 3 for the most common species and their characteristics). The most dominant family of fish caught in the test fishing were the Cyprinids which accounted for 46 of the 76 species caught in the sampling programme (60.5%), including two introduced species (*C. carpio* and *C. cirrhosus*). One family, the Cichlidae, was composed entirely of non-native fish in the form of *O. niloticus*.

3.2. Impacts of non-native carps and tilapia

Results of the observational and experimental studies were broadly similar and are therefore presented together (Fig. 1; Table 4). Examination of the species richness data for individual waterbodies shows noticeable co-variation between the paired impacted and control sites, indicating that the paired design successfully controlled for spatial variation in richness and thus, improved the statistical power of the impact assessment (Fig. 1). In general, effects measured in the experimental study have narrower confidence limits than those measured in the observational study, reflecting higher sampling effort during the experiment (Table 4).

Table 2
Non-native fish species captured in test fishing or known to have been released in the study area.

Species	Family	Origin	Trophic guild	Max. length (cm)	Experimental stocking
Oreochromis niloticus (Linnaeus 1758)	Cichlidae	Africa	Planktivore	60	Yes
Cirrhinus cirrhosus (Bloch 1795)	Cyprinidae	Indian subcontinent	Planktivore	100	Yes
Labeo rohita (Hamilton 1822)	Cyprinidae	Indian subcontinent	Herbivore	200	Yes
Hypophthalmichthys nobilis (Richardson 1845)	Cyprinidae	China	Planktivore	112	Yes
Cyprinus carpio (Linnaeus 1758)	Cyprinidae	Europe and Asia	Omnivore	120	No

Table 3
Native fish species most frequently encountered in test fishing events.

Species	Family	Trophic guild	Max. length (cm)	Frequency (%)
Parambassis siamensis (Fowler 1937)	Ambassidae	Planktivore	6	47
Esomus metallicus (Ahl 1923)	Cyprinidae	Planktivore	8	40
Anabas testudineus (Bloch 1792)	Anabantidae	Omnivore	25	33
Puntius brevis (Bleeker 1850)	Cyprinidae	Omnivore	12	30
Trichogaster trichopterus (Pallas 1770)	Osphronemidae	Insectivore	15	28
Systomus aurotaeniatus (Tirant 1885)	Cyprinidae	Planktivore	6	24
Channa striata (Bloch 1793)	Channidae	Carnivore	100	17
Cyclocheilichthys repasson (Bleeker 1853)	Cyprinidae	Insectivore	28	16
Hampala dispar (Smith 1934)	Cyprinidae	Carnivore	35	16
Systomus sp	Cyprinidae	Omnivore		16
Mystus mysticetus (Roberts 1992)	Bagridae	Carnivore	13	15
Rasbora paviei (Tirant 1885)	Cyprinidae	Insectivore	12	14
Barbonymus gonionotus (Bleeker 1850)	Cyorinidae	Omnivore	40	12
Macrognatus siamensis (Guenther 1861)	Mastacembelidae	Omnivore	30	12
Hemibagrus cf. nemurus (Valenciennes 1840)	Bagridae	Carnivore	65	7
Labiobarbus leptocheilus (Valenciennes 1842)	Cyprinidae	Planktivore	30	7
Osteochilus hasseltii (Valenciennes 1842)	Cyprinidae	Planktivore	32	7
Ompok bimaculatus (Bloch 1794)	Siluridae	Carnivore	45	6
Parachela oxygastroides (Bleeker 1852)	Cyprinidae	Insectivore	20	6

Judging from measured impacts on CPUE, non-native species added significantly, by 180% in the observational study and by 49% in the experiment, to total fish community biomass without affecting native fish biomass (Table 4). No significant impacts on native fish species richness, diversity indicators, species composition or feeding guild composition were detected, except for reductions in Simpson diversity (−24%) and equitability (−18%) in the observational study. In the experiment, no adverse effect was significant, had a point estimate exceeding −14%, or a 95% confidence limit exceeding −35% of the non-impacted value.

3.3. Possible confounding effects of trophic status and fishing intensity

Regression analysis showed no effect of wetland trophic status as measured by total phosphorus concentration on native fish CPUE or diversity indices. Fishing intensity (Fig. 2) had a significant ($P<0.05$), negative effect on native fish CPUE that was well described by ln (CPUE) = −0.06–0.26ln(FI). This implies that the difference in mean fishing intensity between impacted and control wetlands (163 vs. 283 h ha^{-1} year^{-1}) could account for a 14% higher CPUE in the impacted wetlands. Fishing intensity had no effect on diversity indices. It therefore is unlikely that the results of the paired comparisons have been significantly influenced by confounding effects of trophic status or fishing intensity.

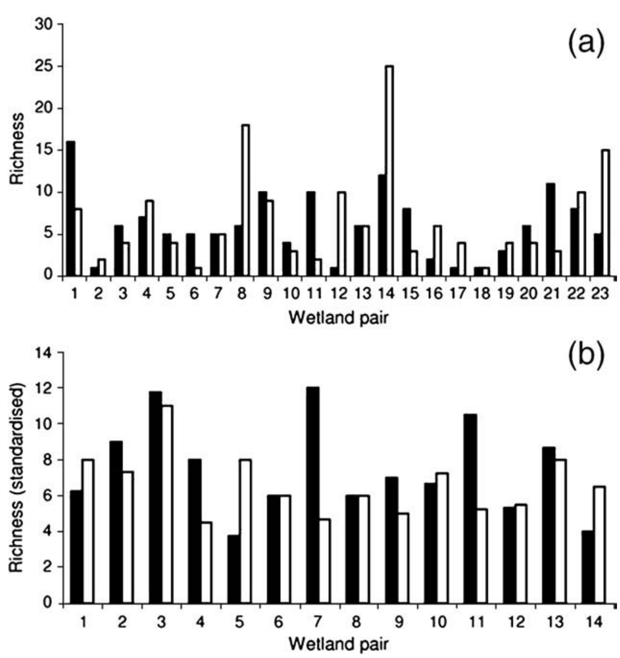

Fig. 1. Wild fish species richness recorded in each wetland site during the initial observational study (a) and the experiment (b). Solid bars denote water bodies where the non-native species were absent, closed bars those where they were present. Richness is shown as raw values for the exploratory study and as standardised (rarefied) values for the experiment.

4. Discussion

4.1. Study design

To the best of our knowledge, this is the first control–impact study replicated at wetland level to assess impact of non-native carp and tilapia species on native fish communities. By quantifying abundance (biomass) of the native and non-native species in addition to structural aspects of the native communities (richness, diversity indices, and trophic guild composition), the study demonstrated that non-native species raised total biomass substantially without measurably displacing native species.

Both quantitative studies, including the experiment, were essentially observational in the sense that prior presence of non-native species had to be taken into account in design and therefore, treatments could not be allocated at random to experimental units. Observational studies are more susceptible to biases than experiments because treatment allocation may have been influenced by response variables (Eberhardt and Thomas, 1991). In our case, impacts on native fish communities could have been underestimated if non-native species had been released preferentially in wetlands with above-average abundance or diversity of native species. There is no indication that this would have been the case. The paired design successfully reduced environmental variation and increased the statistical power of the impact study, as is evident for example from the noticeable correlation species richness values between impacted and control sites (Fig. 1). Comparison of wetland characteristics between impacted and control sites indicated that mean total phosphorus concentration and fishing intensity were slightly, but not significantly higher in impacted sites. Regression analysis of relationships between impact indicators, TP and fishing intensity showed that observed differences in the latter are unlikely to confound the impacts estimated from the paired comparisons.

Impacts of species introductions may take time (years, possibly decades) to become fully apparent (Strayer et al., 2006). The majority of 'impacted' wetlands had first been stocked at least four years prior to the observational study and thus, at least seven years prior to the end of the experiment. Over that period, the non-native species had

Table 4
Paired comparisons of non-native and native species catch per unit of effort (CPUE), raw and standardized native species richness, native species diversity indices, and native species trophic guild composition. Mean values for non-impacted (NI) sites are given as a baseline, and effects are shown as the mean difference between paired, impacted and non-impacted sites. Mean effects are also shown as a proportion of the NI value. Effects in bold are significant at $P<0.05$.

	Observational study (23 pairs)		Experiment (14 pairs)	
	NI	Effect [95% CI]	NI	Effect [95% CI]
Total CPUE ($g\ m^{-2}\ h^{-1}$)	**0.73**	**1.32 [0.29, 2.33] (+180 [40, 319] %)**	0.51	**+0.25 [0.04, 0.45] (+49 [8, 88] %)**
Native CPUE ($g\ m^{-2}\ h^{-1}$)	0.73	0.22 [−0.51, 0.86] (+30 [−70, 118] %)	0.51	−0.01 [−0.15, 0.10] (−2 [−29, 20] %)
Native richness (raw)	6.04	0.74 [−1.65, 3.41] (+12 [−27, 56] %)	13.64	−1.21 [−4.64, 2.46] (−9 [−34, 18] %)
Native richness (standardized)			7.49	−0.85 [−2.38, 0.73] (−12 [−32, 10] %)
Native Simpson diversity (D)	**3.24**	**−0.85 [−1.73, −0.05] (−26 [−53, 5] %)**	2.77	−0.37 [−0.98, 0.25] (−14 [−35, 9] %)
Native Simpson equitability (E)	**0.61**	**−0.11 [−0.23, −0.01] (−18 [−63, 2] %)**	0.41	+0.02 [−0.08, 0.11] (+5 [−20, 27] %)
Native Shannon diversity (H)	1.14	−0.18 [−0.55, 0.16] (−14 [−48, 14] %)	1.29	−0.10 [−0.31, 0.13] (−8 [−24, 10] %)
Native Shannon equitability (J)	0.59	−0.04 [−0.21, 0.12] (−7 [−36, 20] %)	0.66	0.00 [−0.12, 0.11] (0 [−18, 17] %)
Native carnivores (%)	5.4	0.4 [−10.0, 8.1]	4.1	−0.4 [−2.2, 1.4]
Native herbivores (%)	0.1	0.3 [−0.3, 1.4]	0.3	0.1 [−0.5, 0.9]
Native insectivores (%)	9.6	−1.1 [−11.4, 8.3]	15.7	−5.4 [−14.9, 5.3]
Native omnivores (%)	15.6	−0.7 [−13.3, 12.8]	23.7	−8.3 [−21.8, 5.1]
Native planktivores (%)	69.3	1.1 [−17.2, 17.7]	56.1	14.1 [−4.6, 32.6]

build up very substantial biomass (almost two thirds of the total in the observational study and one third in the experiment) without measurably affecting the biomass or diversity of the native fish community. It should also be noted that the majority of native species in the wetlands are small and short-lived, so that even impacts on early life stages are likely to become apparent fairly rapidly. Both the timeframe of the study and the high biomass build-up of non-native species indicate that the design offered good ecological and statistical power to detect strong impacts. This does not exclude the possibility that more subtle or long-term impacts could emerge.

4.2. Impacts

Stocking of the non-native species was associated with significant increases in total fish biomass, by 180% in the observational study and by 49% in the experiment. Despite this large effect on total biomass, native fish biomass was not affected by stocking of the non-native species. Of the richness measures and diversity indices studied, only Simpsson diversity and equitability were significantly impacted in one of the studies (26% and 19% reduction respectively in the observational study). Overall this suggests that even where the non-native species account for a large or dominant share of total biomass, their impacts on native fish communities are mild-to-moderate. We encourage broader debate as to the ecological significance and acceptability of the impacts measured and the associated uncertainty.

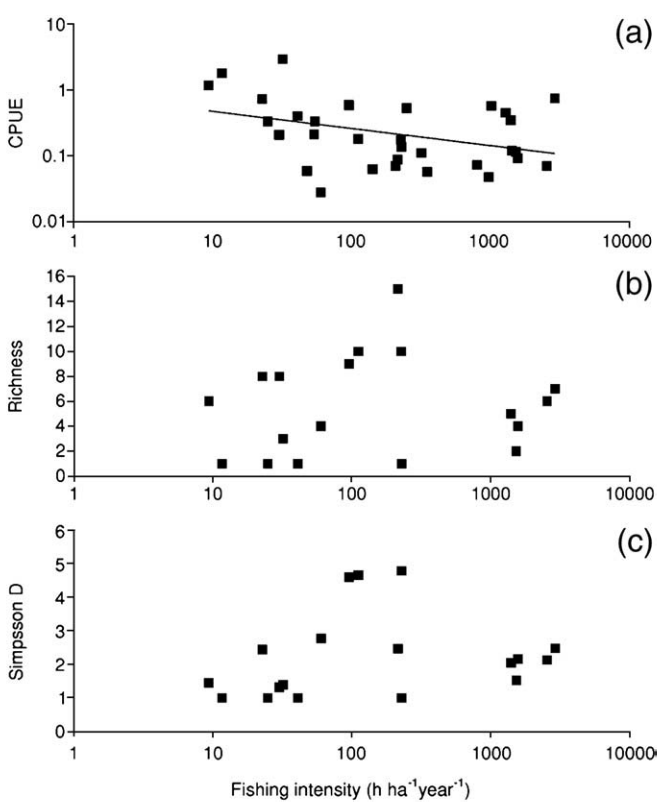

Fig. 2. Effect of fishing intensity on CPUE (a), species richness (b) and Simpsons D (c). Only the impact on CPUE is significant ($P<0.05$).

The primary reason for the limited impact on native fish communities may be low niche overlap between non-native and native species present in the wetlands. Nile tilapia *O. niloticus* for example are known to utilize phytoplankton and blue green algae that are under-utilized by the native species in the region (Moreau, 1999). It is also possible that fishing, which reduces community biomass substantially relative to the unexploited level, may have contributed to excess resource availability. However, a comparative study of wetlands under different levels of fisheries exploitation found no evidence for replacement of native with non-native fish biomass regardless of exploitation level (Lorenzen et al., 1998a).

The results of our study are consistent with reviews by Welcomme and Vidthayanon (2000) and De Silva et al. (2005, 2006) which concluded that there was little evidence of impacts on biodiversity caused by commonly used exotic fish in SE Asia. Where tilapias have been implicated in biodiversity impact in the region, this has involved the Mozambique tilapia (*O. mossambicus*) which has a greater tendency that *O. niloticus* to prey upon small fish and fish larvae (Hardjamulia and Wardoyo, 1992; Balayut, 1999; Welcomme and Vidthayanon, 2000). Other studies on the impact of stocking these carp species have also found no evidence of negative impacts on fish biodiversity in either small water body or floodplain fisheries at stocking densities similar to those used in this study (Islam, 1999; Haque et al., 1999; Barthelmes and Braemick, 2003).

It is important to bear in mind that the results from our study are specific to the non-native species released and the receiving ecosystem and native fish community. The same species could interact significantly with native species if released in a different biogeographic region. Indeed, significant impacts e.g. of non-native tilapias have been documented for other regions (Canonico et al., 2005). Likewise, other non-native species could have significant impacts on native communities in the Mekong region, notwithstanding the fact that our study suggests that these communities offer unused niche opportunities. As mentioned before, the strongest impacts can be expected from releases of piscivores (Eby et al., 2006).

4.3. Policy and management implications

Release of non-native tilapia and carp species added substantially to total fish community biomass, but had at best mild impacts on native fish communities. We encourage wider debate to judge the significance and acceptability of the impacts and associated uncertainty measured here. The process should consider whether continued use of these non-native species in SE Asia poses significant conservation concerns and if so, how these should be managed. Given the importance of aquaculture in regional fisheries programmes (e.g. MAF, 2006; Bush, 2008) it is crucial that, in addition to assessing risks from non-native species, the risks and benefits of alternatives, in particular the development of native species, should also be carefully considered. The release of partially domesticated native fish brings with it new, different, and, as yet, poorly quantified ecological and genetic risks (Naylor et al., 2004; Lorenzen, 2005). In promoting such an approach we recognise that the issue of acceptable risk involves value-based judgements and that these decisions are a matter of societal choice. In the case that we describe, systems where aquaculture and culture-based fisheries have been promoted for poverty alleviation, it is vital that these debates are inclusive. 'Expertising' these debates (c.f. Friend, 2009), risks excluding concerned stakeholders and marginalising elements of society in these debates, the outcomes of which may have considerable impact on their livelihoods. Design of such a process could draw on, for example, the Generic Nonindigenous Aquatic Organisms Risk Analysis Review Process (Generic Analysis) implemented in the USA (Orr, 2003; Hill and Zajicek, 2007).

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