Journal of Fish Biology (2005) **67** (Supplement B), 23–34
doi:10.1111/j.1095-8649.2005.00927.x, available online at http://www.blackwell-synergy.com

Habitat use, migration pattern and population dynamics of chevron snakehead *Channa striata* in a rainfed rice farming landscape

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Habitat use, migration, mortality and growth of the chevron snakehead *Channa striata* in a rainfed rice farming landscape of north-east Thailand were studied through a tagging experiment. A total of 751 fish were captured, tagged and released during three distinct events in the late dry season, and in the beginning and at the end of the wet season. Rice fields provided the major wet season habitat for *C. striata*. Small trap ponds built to provide dry season habitat on farms provided 20% of catches and, if not harvested, could increase recruitment to the spawning stock by >30% despite accounting for <1% of dry season habitat by area. Migrations were localized (mostly <500 m). Up-migration from perennial to seasonal water bodies at the beginning of the wet season involved longer distances and took place over a longer time than down-migration at the end of the wet season. Natural mortality rates were extremely high, particularly during the period of down-migration. Fishing mortality rates were high in absolute terms, but contributed only 6–36% to the total mortality. Growth was seasonal with a maximum towards the end of the wet season. Snakeheads have successfully colonized the rainfed rice farming landscape, where populations can withstand intensive exploitation and respond well to aquatic habitat management on farmland.

Key words: floodplain; habitat; mark-recapture; mortality; rice fields.

INTRODUCTION

Rainfed rice farming landscapes are major, man-made wetlands and their aquatic biological resources are often intensively exploited. Rice farming systems and their aquatic ecosystems are among the oldest cultural landscapes, having evolved over 6000 years (Ruddle, 1982; Koohafkan & Furtado, 2004). Rice is the staple food for 40% of the world's population, and rice-based farming systems dominate land use in the lowland areas of tropical Asia. Asian rice fields cover an area of 115 million ha (Koohafkan & Furtado, 2004), which represents >50% of the continent's total wetland area of 204 million ha (Finlayson & Spiers, 1999). About 57% of rice cultivation occurs in natural wetlands, while the remainder occurs on land that has been converted to retain rainfall and runoff (Hook, 1993).

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Rainfed and flood-prone rice fields constitute temporary wetlands with many functional similarities to natural floodplains, and support diverse assemblages of wetland associated organisms (Heckman, 1979; Lawler, 2001). Rainfed and flood prone rice fields serve as important feeding and nursery areas for fishes (Coche, 1967; Heckman, 1974, 1979; Little *et al*., 1996). Many fish species migrate into rice fields at the beginning of the wet season to feed and spawn, and return to permanent waterbodies as water levels decline (Coche, 1967; Fernando, 1993; Meusch, 1996). Rice farming landscapes often support very productive fisheries, with intensive harvesting of wild fishes in the rice fields, along drainage lines (the principal migratory pathways), and in natural streams and wetlands. Such fisheries contribute significantly to livelihoods of rice farming areas (Tan *et al*., 1973; Garaway, 1999; Gregory & Guttman, 2002; Nguyen Khoa *et al*., 2005). Not surprisingly therefore, rice farmers often create and manage aquatic habitats on their land specifically for fisheries purposes. This includes the construction of trap ponds in which fishes aggregate during the down-migration, to be harvested later in the dry season or provide spawning stock for the next season (Little *et al*., 1996; Edwards *et al*., 1997).

The chevron snakehead *Channa striata* (Bloch) is the most common snakehead species found in the rice farming areas of north-east Thailand. The species is carnivorous, air breathing and able to migrate over wet ground. It is thus well adapted to life in rice farming landscapes with their pattern of seasonal and temporary wetlands (Wee, 1982). Snakeheads are also the most highly valued fish in rice farming areas and are therefore, a prime focus of fisheries exploitation and habitat management by local people.

Despite their ecological interest and importance as fisheries resources, little is known about the ecology and population biology of snakeheads *Channa* sp. in rice farming areas. Such knowledge is becoming increasingly important to underpin habitat and harvest management, as the physical environment of rice farming areas is modified by agricultural intensification and fishing becomes increasingly intensive and commercialized. The present study aimed to analyse habitat use, migrations and population dynamics of snakehead in a rainfed rice farming landscape.

MATERIALS AND METHODS

STUDY AREA

The study was carried out during 1 year from May 2003 to April 2004 in two adjacent villages (14° 55′ N; 104° 35′ E) near the River Kayoong in Sisaket Province, north-east Thailand. Aquatic habitats in the study area included open water bodies (river, reservoirs and swamps) with an area of 68–120 ha in the dry and wet seasons respectively, 622 ha of rainfed rice fields and 0·8 ha of trap ponds. Trap ponds are built within farm land to provide dry season habitat for wild fishes, thus ‘trapping’ fishes in private ponds during down-migration. Trap ponds were distributed throughout the rice field area and averaged 62 m^2 in surface area and 1–3 m in depth during the dry and wet seasons respectively. Of the total of 130 trap ponds in the study area, 77 were perennial while the remainder dried up sometime during the dry season. Most trap ponds were harvested completely by dewatering, but some were harvested only partially to maintain spawning stock for the following season. North-east Thailand is characterized by the strongest seasonality in rainfall and thus, the most variable aquatic habitat availability in south-east Asia (Heckman, 1979). The rainfall data at the study site during 2002–2004 are shown in Fig. 1. Irrigation is very limited and agricultural activities are highly dependent on the monsoon cycle. Farming is limited to one rainfed rice crop per year during the monsoon months (Little *et al.*, 1996).

HOUSEHOLD SURVEY

A household survey was conducted throughout the study period to collect detailed information on fishing effort and catch. Of a total of 274 households on the study area, 60 were selected at random. The time spent fishing by household members, number and length distribution of *C. striata* collected, and the precise location of harvesting were recorded. These data were used to provide an overview of fishing activities and some biological data.

TAGGING

A tagging experiment was carried out to provide detailed information on chevron snakehead migrations and population dynamics. Tagging was carried out between 7 May and 14 November 2003, in three distinct events: (1) during the dry season when fish were captured in trap ponds, (2) at the start of the rainy season when fish were captured during their up-migration and (3) at the end of the rainy season when fish were captured during their down-migration. A total of 751 fish were tagged, of which 19% were recovered (Table I). All fish for tagging were captured by local fishermen using common methods such as dewatering trap ponds in the dry season, and employing traps and cast-nets in the wet season. Fish captured in good condition were measured for total length (L_T) and, if >18 cm, tagged with T-bar anchor tags of 3 cm length inserted in the dorsal musculature. Fish were then released at the capture location. The duration of tagging activities at each event varied with the availability of fish, but did not exceed 16 days. Recaptures were monitored continuously from May 2003 to June 2004. All recaptures occurred as part of normal fishing activities by villagers in a total area of *c.* 10 km^2, there was no experimental fishing (other than to obtain animals for tagging as described above). Only a very small reward was offered for reporting recaptures and allowing measurements to be taken of the recaptured fish. Information campaigns and the small reward encouraged tag reporting, but there was no indication that they influenced the level of fishing activities as such. In each village, one farmer was hired to maintain interest in the village and record recaptures of tagged fish (exact location, L_T and tag number). Detailed maps

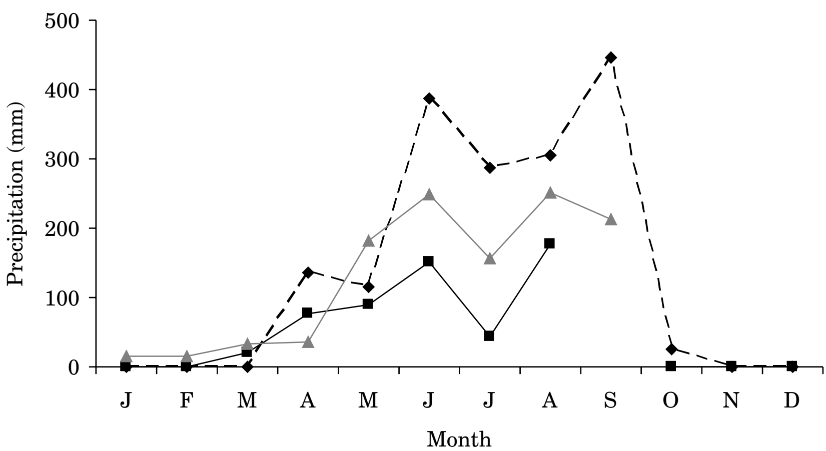

FIG. 1. Monthly rainfall in the study area (Namklieng District) in 2002 (◆) 2003 (■) and 2004 (▲).

TABLE I. Number of *Channa striata* marked and recaptured

Tagging events	Number released	Number recaptured	Percentage recaptured
1. Up-migration from the ponds (10 locations) (7 May to 14 May 2003)	297	83	28
2. Up-migration from the rice fields (13 locations) (28 August to 12 September 2003)	156	26	17
3. Down-migration from the rice fields (11 locations) (30 October to 14 November 2003)	298	31	10
Total	751	140	19

of the study area were drawn using information from aerial photographs, farmer mapping of rice fields and GPS positions. This map allowed recapture locations to be recorded fairly precisely.

HABITAT USE AND MIGRATION

Habitat use was assessed directly from the recapture locations of tagged fish. Migrations were represented by straight arrows on maps, and migration distance calculated as the straight line distance between the release and the recapture locations. The time taken for migrations was calculated from release and recapture dates. Fish released during the first tagging event in May were unable to migrate before onset of the wet season in June, which was thus considered as the start of migrations for fish released in this study.

MORTALITY AND EXPLOITATION RATES

Natural and fishing mortality rates were estimated through tag-recapture modelling (Lebreton *et al.*, 1992; Julliard *et al.*, 2001). All releases were analysed separately. The post-release monitoring period was divided into weekly intervals from time t to $t + \Delta t$ (where Δt equals 1 week). The probability $Q(t)$ of a tagged fish surviving and retaining its tag to time t is given by: $Q(t) = e^{-(M+F+L)t}$, where M and F are the natural and fishing mortality rates respectively and L is the rate of tag loss. The probability $P(t)$ of a tagged fish being recaptured and reported during the interval $[t,\ t + \Delta t]$ is given by: $P(t) = q\ Q(t)\ F\ (M + F + L)^{-1}\ (1 - e^{(-\ (M\ +\ F\ +\ L)^{\Delta t}})$, where q is the probability of a recaptured tag being reported. Using this model it was possible to predict the probability of a tag being recaptured and reported for all intervals in the monitoring period. The probability of a tag not being recaptured and reported at all equals one minus the sum of probabilities $P(t)$ for all intervals monitored. Omitting a multinomial term which does not depend on the parameters, the negative log likelihood L of the observed data given a set of model parameter values is thus given by: $L = -\sum_{t=1}^{t\max} C(t)\ln(P(t)) - \left(R - \sum_{t=1}^{t\max} C(t)\right)\ln\left(1 - \sum_{t=1}^{t\max} P(t)\right)$, where R is the number of tagged fish released, and $C(t)$ is the number of recaptures actually reported in interval $(t,\ t + \Delta t)$. The maximum likelihood estimate of the model parameters was obtained by minimizing L through numerical search. Confidence limits for the parameters were determined from likelihood profiles (Hilborn & Mangel, 1997).

This recapture model as formulated here assumes that all captured fish are retained rather than re-released, as was the case in the fishery monitored. It also assumes that monitoring covers the full area of distribution of the released fish. This condition is likely to have been met given wide spatial coverage of monitoring and evidence that migrations were very localized.

It was not possible to separate the effects of natural mortality and tag loss, hence the combined $M + L$ was estimated from the data and M calculated for different assumptions about L. Published studies on T-bar tag loss in a variety of species suggest loss rates of $<0{\cdot}5$ year^{-1} (Fabrizio *et al.*, 1999; Adam & Kirkwood, 2001). The level of reporting of recovered tags was judged to be very high in the field, and it was thus assumed that $q = 1$. The exploitation rate $E = F(M + F)^{-1}$ was calculated to assess the relative importance of fishing as a source of mortality.

GROWTH AND CONDITION

The L_T increments between release and recapture were plotted against recapture time to assess seasonality of growth. Condition (K) were calculated as $K = 100WL_T^{-3}$, where W is the mass (g) and L_T is in cm. ANOVA was used to test for significant differences in K among tagging events.

RESULTS

FISHING

The total number of chevron snakehead harvested in the study area over 1 year was estimated as 5900 individuals (1770 kg) based on the household survey. This corresponds to 7·8 individuals ha^{-1} (2·4 kg ha^{-1}) of aquatic habitat area. Of the total chevron snakehead catch, 54% was obtained from rice fields, 25% from open waters, and 20% from trap ponds and other farm ponds. Fishing effort directed at chevron snakehead varied seasonally, being highest at the beginning and the end of the wet season.

MIGRATION AND HABITAT USE

Observed migrations of the tagged fish are illustrated in Fig. 2 for the three tagging events. Chevron snakehead dispersed in all directions within the wetland area, without any clear seasonal pattern. The majority of recaptures (70%) occurred within 500 m of their released site (Fig. 3). The maximum migration distance observed was 3 km, for two specimens at the beginning of the rainy season. During the last tagging event (down-migration), a significantly higher proportion of recaptures (90%) occurred within 500 m of their released site. This is likely to indicate more restricted movement during this period when aquatic habitat connectivity is rapidly declining and fishing effort increased locally on the few water ways left. All recaptures from the last tagging event were recorded within 2 months of release, while recaptures of fish tagged prior to or during the up-migration were still recorded after 6 months (Kruskal-Wallis, d.f. $= 2$, $P < 0{\cdot}01$).

Information on habitat use is summarized in Fig. 4, which shows the habitat types in which fish were recaptured or found dead. Recaptures from open water bodies did not show a strong seasonal pattern. Overall recapture locations were dominated by rice fields in the wet season, and trap ponds in the dry season. A total of 21 tagged fish (15% of all tags recovered) were found dead. The highest number of dead fish was found at the end of the wet season, obviously as a result of stranding in isolated locations. No marked fish were recovered after February 2004, although monitoring continued until June.

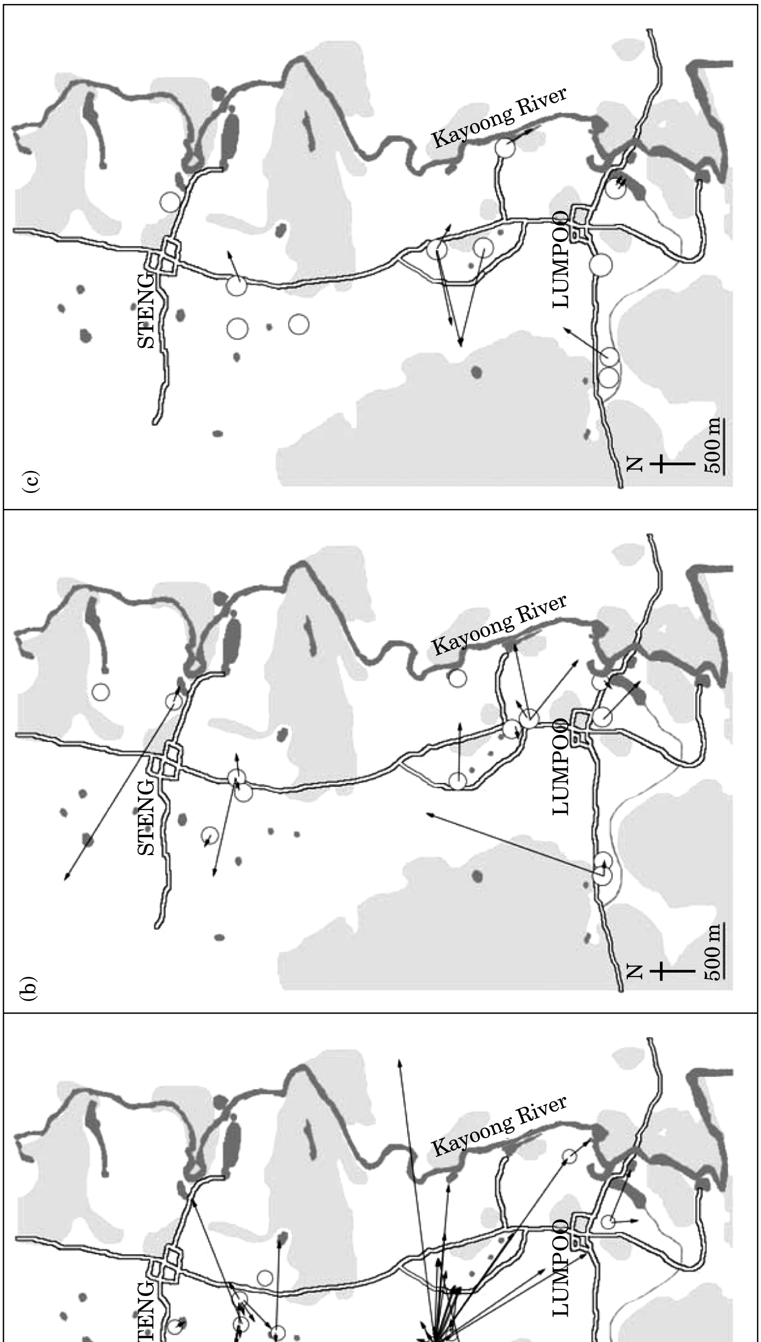

FIG. 2. Recaptures of tagged fish at the study site. (○, the release locations for each tagging event): (a) up-migration from trap ponds, (b) up-migration from rice fields and (c) down-migration from rice fields. Arrows connect the release and recapture locations. Lowland (mostly rice fields) (□), upland (mostly forested) (▢) and open water bodies (■) are indicated. Migrations <100 m are not represented.

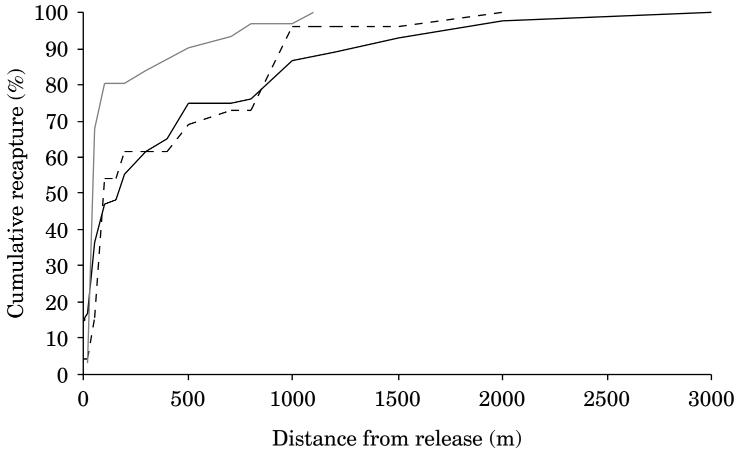

FIG. 3. Cumulative recapture of marked snakehead as a function of distance from the release site for the three tagging events: up-migration from trap ponds (—), from rice fields (--) and the down-migration (———).

MORTALITY AND EXPLOITATION RATES

The model provided a reasonably good fit to observed recaptures over time (Fig. 5). The parameter estimates show very high rates of natural mortality and tag loss ($M + L$) of *c.* 3·6–4·2 year^{-1} during the wet season and 25·8 year^{-1} during the period of down-migration (tagging event 3) (Table II). Fishing mortality rates were estimated at 0·5–1·7 year^{-1} and not significantly different

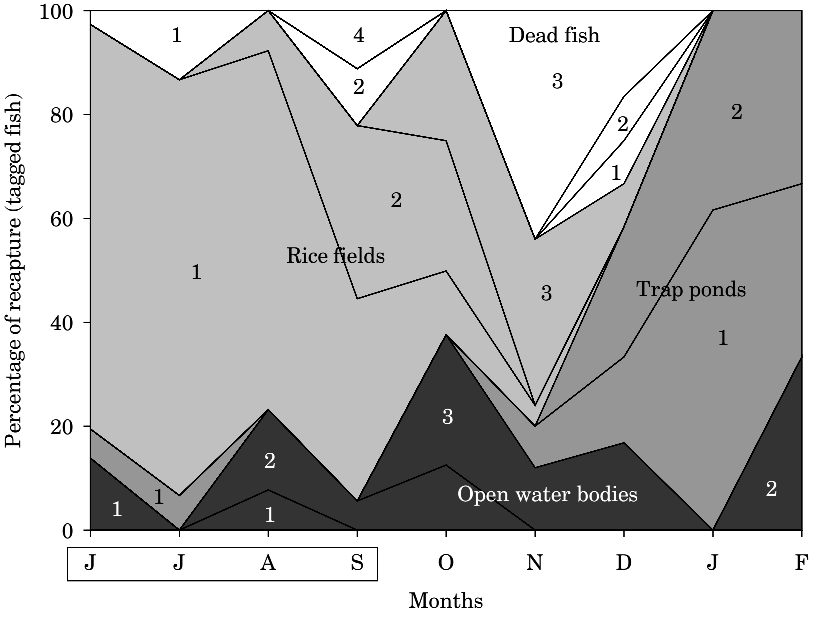

FIG. 4. Recapture habitat of tagged fish. Numbers indicate the event at which the recovered fish were tagged: 1, up-migration from the ponds; 2, up-migration from rice fields; 3, down-migration. Months with precipitation are enclosed in a rectangle.

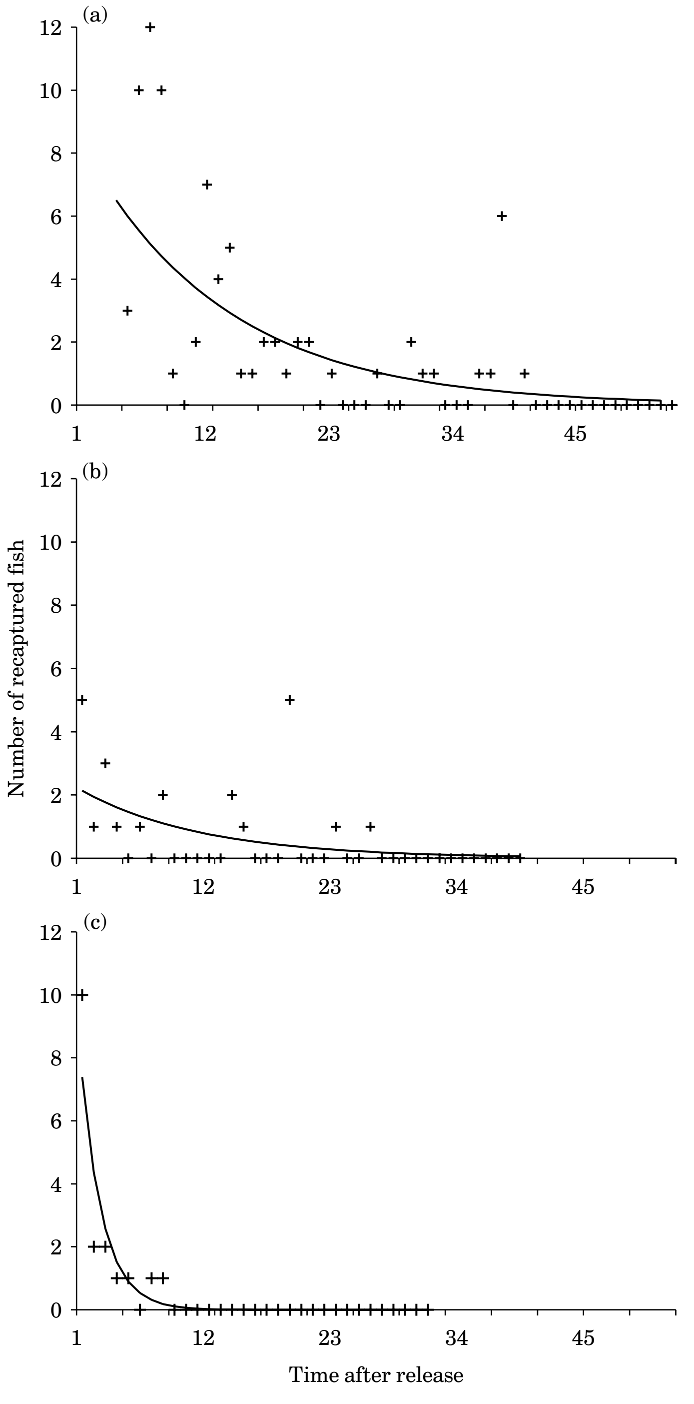

FIG. 5. Observed (+) and predicted tag returns (—) over time after release. Predicted returns are calculated as the predicted probability of recapture $P(t)$ multiplied by the number released R. Tag returns were monitored over 52, 40 and 31 wk respectively for tagging events (a) 1, (b) 2 and (c) 3.

TABLE II. Estimates of the instantaneous natural mortality plus tag loss ($M + L$), instantaneous fishing mortality (F) and exploitation rate (E). Numbers in parentheses are 95% CL

	$M + L$ (year^{-1})	F (year^{-1})	E
Up-migration (from ponds)	3·04 (2·66; 3·30)	1·7 (1·16; 2·45)	0·36
Up-migration (from rice fields)	4·16 (2·72; 5·51)	0·75 (0·40; 1·30)	0·15
Down-migration (from rice fields)	25·76 (18·49; 34·41)	1·66 (0·83; 3·06)	0·06

between periods (tagging events). Fishing mortality was thus high in absolute terms but accounted for only 6–36% of the total mortality. This result was insensitive to tag loss within reasonable limits (0·5–1·0 year^{-1}).

GROWTH

Increments in L_T (Fig. 6) suggested a seasonal pattern of growth, with the largest increase in L_T occurring towards the end of the wet season. Fish tagged during the up-migration also had a significantly lower K than those tagged during the down-migration (ANOVA, d.f. = 2, $P < 0·001$).

DISCUSSION

Snakeheads have successfully colonized the man-made habitats of the rainfed rice farming landscape. Rainfed rice fields themselves provided the major wet season habitat of snakehead in the study area, being colonized from perennial water bodies. Migrations were mostly localized, rarely exceeding a distance of 500 m, and not strongly directional. This migration pattern is broadly similar to that described by Halls *et al.* (1998) for *C. striata* in a Bangladesh floodplain system. Body growth occurred primarily towards the end of the wet season, suggesting that biomass production in the fishery occurs mainly during the wet season and thus, within rice fields.

Whilst it was not possible to separate the natural mortality and tag loss rates, the combined rate of >3 year^{-1} suggests that natural mortality is very high even if tag loss rates of 0·5 or 1·0 year^{-1} are assumed, far in excess of the values typically found in the literature (Fabrizio *et al.*, 1999; Adam & Kirkwood, 2001). Natural mortality rates were particularly high at the end of the dry season when 'stranding' in isolated locations appeared to be a major source of mortality. The very high mortality rates at down-migration were only a short period. Similar patterns and overall levels of natural mortality have been observed in natural floodplain systems (Arthington *et al.*, 2005). Fishing mortality rates, although high in absolute terms, accounted for only a moderate share of total mortality. This suggested that the population was only moderately exploited.

Colonization of rice fields and trap ponds is largely dependent on stock from open waters (river, reservoirs and swamps) which provide the principal dry season refuges (Magoulick & Kobza, 2003). Trap ponds, the main dry season aquatic habitat created within rice field systems, are small in area (<1% of dry season habitat area), but contribute very disproportionately to catches and

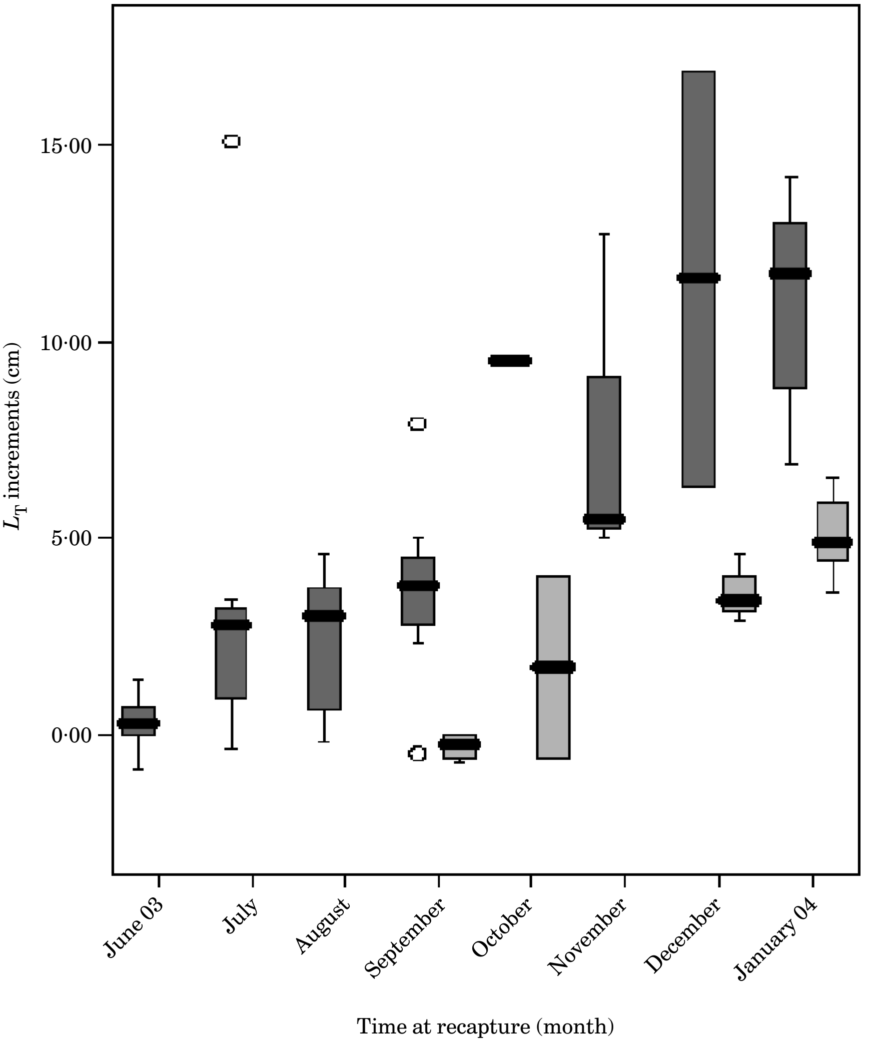

FIG. 6. Box-plot of total length increment between release and recapture as a function of recapture time, for tagging events 1 and 2. The box contains 50% of observations, error bars are the 25th and 75th percentiles and open symbols are outliers.

potentially, recruitment. Trap ponds account for 20% of all catches during the year, and *c*. 90% of those taken in the dry season. Given that most trap ponds are harvested completely, their contribution to recruitment in the next wet season is likely to be negligible at present. If all 77 perennial trap ponds were left unfished and contributed an average of 88 fish (unpubl. data) each to recruitment in the following season, however, this would provide a total of 6776 additional recruits. The current level of recruitment may be estimated at *c*. 21 000 fish (given that 5900 fish were harvested during the year, and only *c*. 28% of recruits present at the beginning of the wet season were captured, Table I). Protection of fish in trap ponds from harvesting could thus increase total recruitment to the spawning stock by *c*. 32%. That does not necessarily imply that protecting recruits in trap ponds will provide overall benefits to the fishery, but it illustrates the potential for small man-made habitats to contribute to the maintenance of spawning stock.

External threats to the chevron snakehead population and fishery arise primarily from changes in agricultural practices that may reduce water retention in rice fields (Nguyen Khoa *et al.*, 2005). Given that rice fields play a major role in fisheries production but appear to contribute little to the replenishment of populations in open waters, a reduction in rice field habitat is likely to affect fisheries yield more strongly than population persistence.

We thank S. Wongpen, P. Choorerd, S. NgaoSri, S. Khamseantea, B. Maneerat, T. Viriyaphap, S. Laosingla, D. Turongruang, A. Yakupitiyage, S. Komolmarl, J. Morales, D. Little and H. Demaine for support and fieldwork assistance. Constructive comments from two anonymous referees improved the manuscript. This research was supported by the Department for International Development of the U.K. (Grant R7917).

References

Adam, M. S. & Kirkwood, G. P. (2001). Estimating tag-shedding rates for skipjack tuna, *Katsuwonus pelamis*, off Maldives. *Fishery Bulletin* **99,** 193–196.

Arthington, A. H., Balcombe, S. R., Wilson, G. A., Thoms, M. C. & Marshall, J. (2005). Spatial and temporal variation in fish-assemblage structure in isolated waterholes during the 2001 dry season of an arid-zone floodplain river, Cooper Creek, Australia. *Marine and Freshwater Research* **56,** 25–35.

Coche, A. G. (1967). Fish culture in rice fields, a world-wide analysis. *Hydrobiologia* **30,** 1–44.

Edwards, P., Little, D. C. & Yakupitiyage, A. (1997). A comparison of traditional and modified inland artisanal aquaculture systems. *Aquaculture Research* **28,** 777–778.

Fabrizio, M. C., Nichols, J. D., Hines, J. E., Swanson, B. L. & Schram, S. T. (1999). Modeling data from double-tagging experiments to estimate heterogeneous rates of tag shedding in lake trout (*Salvelinus namaycush*). *Canadian Journal of Fisheries and Aquatic Sciences* **56,** 1409–1419.

Fernando, C. H. (1993). Rice field ecology and fish culture – an overview. *Hydrobiologia* **259,** 91–113.

Finlayson, C. M. & Spiers, A. G. (1999). *Global Review of Wetland Resources and Priorities for Wetland Inventory*. Wageningen: Wetlands International.

Garaway, C. J. (1999). Small waterbody fisheries and the potential for community-led enhancement: cases studies in Lao PDR. PhD Thesis, University of London.

Gregory, R. & Guttman, H. (2002). The ricefield catch and rural food security. In *Rural Aquaculture* (Edwards, P., ed.), pp. 1–13. Wallingford, UK: CABI Publishing.

Halls, A. S., Hoggarth, D. D. & Debnath, K. (1998). Impact of flood control schemes on river fish migrations and species assemblages in Bangladesh. *Journal of Fish Biology* **53** (Suppl. A), 358–380. doi: 10.1006/jfbi.1998.0827

Heckman, C. W. (1974). The seasonal succession of species in a rice paddy in Vientiane, Laos. *International Revue der Gesamten Hydrobiologie* **59,** 489–507.

Heckman, C. W. (1979). *Rice Field Ecology in Northeastern Thailand: The Effect of Wet and Dry Seasons on a Cultivated Aquatic Ecosystem*. The Hague: Dr W. Junk.

Hilborn, R. & Mangel, M. (1997). *The Ecological Detective: Confronting Models with Data*. Princeton, NJ: Princeton University Press.

Hook, D. D. (1993). Wetlands: history, current status and future. *Environmental Toxicology and Chemistry* **12,** 2157–2166.

Julliard, R., Stenseth, N. C., Gjosaeter, J., Levke, K., Fromentin, J. M. & Danielssen, D. K. (2001). Natural mortality and fishing mortality in a coastal cod population: a release-recapture experiment. *Ecological Applications* **11,** 540–558.

Koohafkan, P. & Furtado, J. (2004). *FAO Rice Conference 04/CRS.17*. Rome: FAO.

Lawler, S. P. (2001). Rice fields as temporary wetlands. *Israel Journal of Zoology* **47,** 513–528.

Lebreton, J.-D., Burnham, K. P., Clobert, J. & Anderson, R. D. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* **62,** 67–118.

Little, D. C., Surintaraseree, P. & Innes Taylor, N. (1996). Fish culture in rainfed rice fields of northeast Thailand. *Aquaculture* **140,** 295–321.

Magoulick, D. D. & Kobza, R. M. (2003). The role of refugia for fishes during drought: a review and synthesis. *Freshwater Biology* **48,** 1186–1198.

Meusch, E. (1996). Participatory assessment of rice field fisheries in Atsapanthong District, Savannakhet province, Lao PDR. MS Thesis, Auburn University, Alabama, USA.

Nguyen Khoa, S., Lorenzen, K., Garaway, C., Chamsingh, B., Siebert, D. J. & Randone, M. (2005). Impacts of irrigation on fisheries in rain-fed rice-farming landscapes. *Journal of Applied Ecology* **42,** 892–900.

Ruddle, K. (1982). Traditional integrated farming systems and rural development: the example of rice-field fisheries in Southeast Asia. *Agricultural Administration* **10,** 1–11.

Tan, C. E., Cheaon, B. J., Sier, H. K. & Moulton, T. (1973). A report on paddy fields fish production in Krian, Perak. *Ministry of Agriculture and Fisheries Malaysia Bulletin* **128**.

Wee, K. L. (1982). Snakeheads – their biology and culture. *In Recent Advances in Aquaculture* (Muir, J. F. & Roberts, R. J., eds), pp. 179–213. London: Croom Helm Ltd.