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Long distance migration and marine habitation in the tropical Asian catfish, *Pangasius krempfi*

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A synthesis of catch data from southern Laos and life-history information indicate that adult *Pangasius krempfi*, an important Asian catfish, migrates up the Mekong River from the South China Sea in Vietnam past Cambodia, arriving in southern Laos each year in May. Strontium concentrations in the otoliths of river-caught *P. krempfi* are, on average, three to four times higher than the levels of strontium in the otoliths of related freshwater species, indicating marine and estuary habitation for fish caught in southern Laos. *Pangasius krempfi* muscle tissue samples from the same fish also exhibit stable isotope ($\delta^{15}N$ and $\delta^{13}C$) values characteristic of marine environments. The results of this investigation support the conclusion that *P. krempfi* is anadromous, spending a part of its life at sea and in the brackish water of the Mekong Delta before returning to spawn in fresh water. The fish travels at least 720 km to the Khone Falls in southern Laos, and possibly further. Spawning probably occurs in fresh water from June to August at which time young fish move down the Mekong River to the Mekong Delta. The data answer a previously unresolved question (the long-distance migratory behaviour of *P. krempfi*) and have important implications for the management and conservation of Mekong River fishes.

Key words: anadromy; Asia; conservation; fragmentation; Mekong River; migration.

INTRODUCTION

Dispersal and migration are critical to the persistence of natural populations (Ruckelshaus *et al.*, 1997). Specifically, information about migratory patterns of fishes is important when managing for viable populations (Hill & Hill, 1994). Without information about migratory patterns, threats such as habitat degradation, the

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proliferation of dams and overfishing can unwittingly lead to rapid declines in fisheries and to species extinction or extirpation (Xie, 2003). In fact, worldwide, >100 migratory fish stocks have gone extinct as a result of poor management, overfishing, dam building and habitat degradation (Leidy & Moyle, 1998).

Pangasius krempfi Fang & Chaux, 1949, a large-bodied catfish in the family Pangasiidae, is one of many potentially migratory fish species in the Mekong River Basin (Roberts & Vidthayanon, 1991; Roberts, 1993*a*; Roberts & Baird, 1995). Little information exists, however, on the migratory patterns of *P. krempfi* (or any other Mekong River species), though it has been suggested that *P. krempfi* is an anadromous species that migrates long distances to spawn (Roberts & Baird, 1995). Past evidence for anadromy was inferred from sightings of this species at different locations at different times within the Mekong Basin. The need for information about the migratory behaviour of this catfish and other migratory fishes in the Mekong River is especially acute, because proposed dam developments, overfishing and habitat degradation now threaten fish populations that are a key source of protein to millions of people (Hogan *et al.*, 2004; Allan *et al.*, 2005).

Pangasius krempfi is a member of a commercially important family of catfishes Pangasiidae (Roberts & Vidthayanon, 1991) and is distributed along coastal Vietnam in the South China Sea and in the Mekong River as far upstream as Luang Prabang Province in northern Laos (Poulsen & Valbo-Jorgensen, 2000). Roberts & Baird (1995) reported *P. krempfi* spends part of its life in coastal marine waters, unlike other species in this genus. They hypothesized that *P. krempfi* exhibits a single migratory pattern and spawn exclusively in fresh water (Roberts & Baird, 1995). These ideas have been corroborated by field observations. In Vietnam, *P. krempfi* is reported in the ocean from January to April (Roberts & Baird, 1995). Two 4 kg specimens caught 10 km off the coast of Vung Tau, Vietnam were observed on 4 January 1994. Similarly, Lenormand (1996) stated that adult *P. krempfi* move upstream of the estuarine zone in February or March. Lenormand (1996) also found that from January to March is the only noteworthy period of *P. krempfi* fishing near the Cambodia–Vietnam border. In Laos, Baird (1996) reported that, 'only adults. . . .weighing over 1·5 kg' are found in southern Laos, and only from May to October while Lenormand (1996) emphasizes the absence of fish over 2 kg from the Vietnam estuary from March until August. Based on this information, Roberts & Baird (1995) suggested that *P. krempfi* begins to move upstream to spawn in February and March, reaching the Khone Falls, 720 km from the sea, in mid-May. The fish spawn upstream of the Khone Falls, perhaps along the Thai-Lao border, between June and August. After spawning, the adult fish probably migrate downstream, swimming through Laos, Cambodia and Vietnam to the estuary and the South China Sea (Fig. 1). None of these fish, however, have been reported or observed being caught when moving downriver. This may be because water levels are so high then that there is very little fishing in the middle of the river. The young fish (probably larval fish) presumably drift or swim downstream to the Mekong Delta with the high water flows that persist during the rainy season (Roberts & Baird, 1995).

The purpose of this study was to investigate the migratory patterns of *P. krempfi*. Catch data, otolith microchemistry and the analysis of carbon and

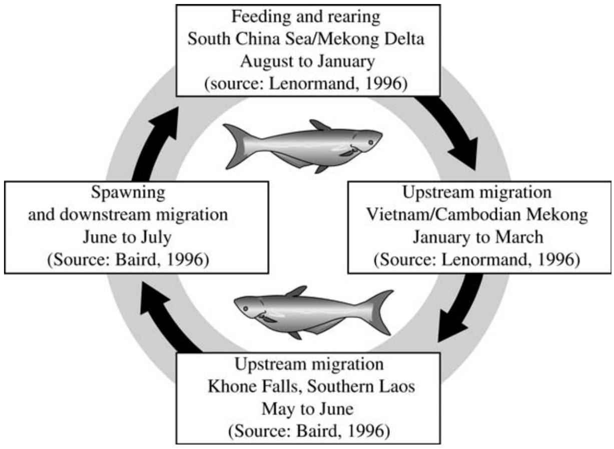

FIG. 1. The life history of *Pangasius krempfi* based on Baird (1996) and Lenormand (1996).

nitrogen stable isotopes were used to test the hypotheses that *P. krempfi* inhabits both marine and freshwater environments, is anadromous and undergoes long-distance spawning migrations up the Mekong River. Finally, the findings were analysed in relation to the management of migratory fish species within the Mekong River Basin.

MATERIALS AND METHODS

STUDY SITE

The Mekong River runs *c*. 4200 km from its origin in upland China to the Mekong Delta in Vietnam. The Mekong River is the twelfth longest river in the world and it is the sixth largest in terms of total discharge. It passes through southern China, a small part of Burma, Laos, Thailand, Cambodia, and finally southern Vietnam before emptying into the South China Sea (Pantulu, 1986). The Mekong River supports one of the most diverse fish faunas in the world. About 1200 species of fishes occur in the Mekong River Basin, including brackish-water areas, although many remain undescribed (Rainboth, 1996; Van Zalinge *et al.*, 2000). Several species undertake seasonal migrations between the Tonle Sap Lake and the Mekong River in Cambodia (Baird *et al.*, 2003, 2004; Hogan *et al.*, 2004).

For this study, catch data and fishes from the Khone Falls area and nearby locations in southern Laos were collected (Fig. 2). The Khone Falls includes a complex system of channels, wetland forests, rapids and waterfalls of various sizes in the mainstream Mekong River. Situated just north of the border between Laos and Cambodia, the Khone Falls represents an important biogeographical barrier for some species of fishes (Roberts, 1993*a*). Many others, including all the highly migratory species found along the Lao and Cambodian border, however, are able to migrate up certain channels of the Khone Falls region (Roberts & Baird, 1995). The Khone Falls also supports some of the most important family-scale fisheries in Laos and the Mekong River Basin (Roberts, 1993*a*; Roberts & Warren, 1994; Roberts & Baird, 1995; Baird *et al.*, 2001, 2003, 2004).

Three independent techniques were used to better understand the behaviour and life history of *P. krempfi*. First, catch rates for the fish at the Khone Falls, southern Laos, were recorded between 1993 and 1998. Catch rates indicate the magnitude and frequency of upstream migration of *P. krempfi* each year. Second, the stable nitrogen and carbon

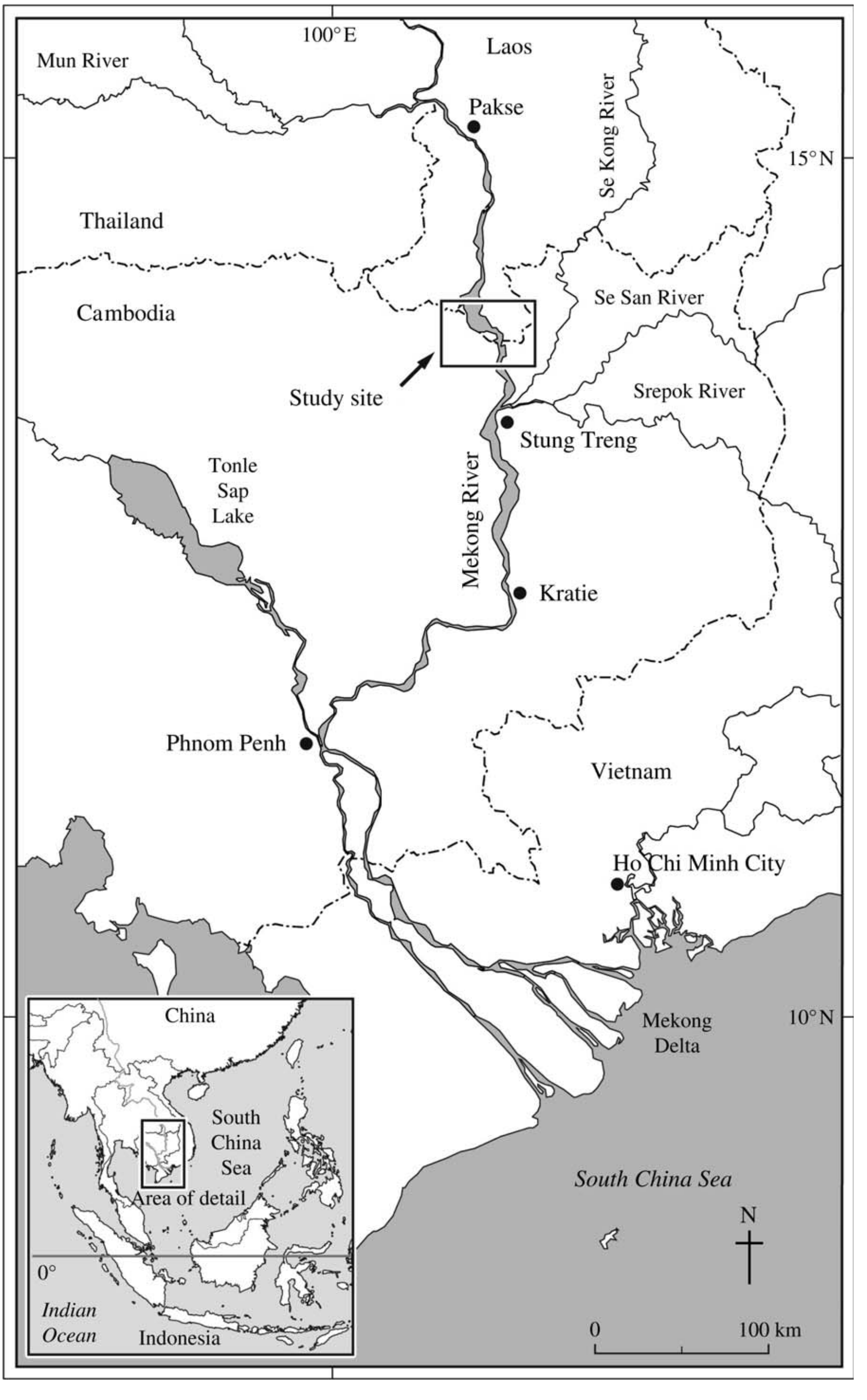

FIG. 2. The Mekong River Basin. The study and sampling site, Khone Falls, is located on the Lao and Cambodian border. Fishes were collected from the Mekong River (fresh water) at Khone Falls, *c*. 720 km upstream from the South China Sea.

isotope signatures of *P. krempfi* and five other species of catfishes were analysed. Stable isotope ratios of carbon and nitrogen characterize the food source and environment of *P. krempfi* in relation to that of other Mekong River fishes. Third, the strontium to calcium ratio in otoliths of *P. krempfi*, *Pangasius conchophilus* Roberts & Vidthayanon, 1991, *Pangasius larnaudii* Bocourt, 1866, *Pangasius macronema* Bleeker, 1851 and *Helicophagus waandersii* Bleeker, 1858, were measured. Strontium to calcium ratios provide a chronological record of marine and freshwater habitat use throughout the life of the fish. Other Pangasiidae species, apart from *P. krempfi*, found in the Khone Falls were included in the assessment in order to indicate that *P. krempfi* is the only one that spends time in marine environments.

CATCH DATA

From 1993 to 1998, work was conducted in conjunction with the Lao Community Fisheries and Dolphin Protection Project and the Environmental Protection and Community Development in Siphandone Wetland Project to identify, count and weigh *P. krempfi* captured in the 120–160 mm mesh set mono- and multi-filament nylon gillnet fishery by 10 fishers from Hang Khone Village, which is in the Khone Falls area. Minor changes in fishers supplying the data over the years arose due to unforeseen family related problems, but overall, the catch data represent a relatively uniform catch effort from year to year. Each year this fishery operates over essentially the same season, and although these nets are sometimes used in other seasons, *P. krempfi* have never been caught outside the specific fishing season for the species. Fish mass was recorded daily using a spring scale. The total mass of the fish for each day was then calculated and plotted through time in order to visualize the magnitude and seasonality of *P. krempfi* catches.

CARBON AND NITROGEN STABLE ISOTOPE ANALYSIS

Measurement of carbon (^{13}C:^{12}C;$\delta^{13}C$) and nitrogen (^{15}N:^{14}N;$\delta^{15}N$) stable isotope ratios provide a time-integrated measure of food web-relationships based on assimilated rather then ingested prey (Peterson & Fry, 1987). Nitrogen isotope ratios become enriched at successive trophic levels, thereby providing an estimate of consumer trophic position (Minagawa & Wada, 1984; Vander Zanden & Rasmussen, 2001). Stable carbon isotopes can be used to indicate dietary differences and carbon flow pathways because there is little fractionation from prey to predator, while different food items often have distinct $\delta^{13}C$ values (Hecky & Hesslein, 1995; Vander Zanden & Rasmussen, 1999).

Animals incorporate isotopic signatures into their tissues that reflect the food source or their environment. Provided environmental or food-web isotope signatures vary spatially or across habitat gradients, animal migrations can be inferred using isotope techniques (Hansson *et al.*, 1997; Hobson, 1999). In particular, marine food webs are enriched in $\delta^{13}C$ and $\delta^{15}N$ relative to freshwater systems (Hesslein *et al.*, 1991; Doucett *et al.*, 1999*a,b*). Thus, a fish captured in fresh water that exhibits elevated $\delta^{13}C$ and $\delta^{15}N$ signatures, particularly, if incongruent with the range of observed freshwater isotopic values, can be presumed to have recently migrated from a marine habitat.

Six species were considered in this analysis: *P. krempfi* and five species of closely related freshwater catfishes (*P. conchophilus*, *P. macronema*, *Pangasius pleurotaenia* Sauvage, 1878, *P. larnaudii* and *H. waandersii*) as well as one prey species, the small cyprinid *pa soi Henicorynchus* spp. Approximately 10 samples from adults of each species were collected in May 1999 from the Khone Falls, Laos. Fishes were captured using gillnets and fence-filter wing traps. They were measured (total length, L_T) and weighed. A 20 mm strip of dorsal muscle tissue was taken from each fish. This muscle tissue was immediately dried and stored at room temperature until analysis. The samples were re-dried at 75° C for 48 h, then ground into a fine powder using a mortar and pestle. Ground tissue samples were sent to the Stable Isotope Laboratory, University of California, Davis, U.S.A. (http://stableisotopefacility.ucdavis.edu) for automated carbon and nitrogen analysis (ANCA) combined with continuous flow isotope ratio mass spectrometry (CF-IRMS).

Stable isotope ratios are expressed in delta (δ) notation, defined as parts per thousand (‰) deviation from a standard material; $\delta^{13}C$ or $\delta^{15}N = 1000[(R_{sample}R^{-1}_{standard}) - 1]$, where $R = {}^{13}C{:}{}^{12}C$ or ${}^{15}N{:}{}^{14}N$. A more positive (less negative for carbon) isotopic value is said to be isotopically enriched, meaning that the sample contains proportionally heavier stable isotope (${}^{13}C$ or ${}^{15}N$). The standard material used was Pee Dee belemite (PDB) limestone for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$ (both standards have a constant value arbitrarily set at zero). Twenty per cent of the samples were analysed in duplicate; the S.E. of the mean for replicates was 0·13 ‰ for $\delta^{13}C$ and 0·15 per mil for $\delta^{15}N$.

OTOLITH ANALYSIS

Otoliths are often used to age fishes, because successive layers of calcium carbonate are deposited throughout a fish's ontogeny. Radtke & Kinzie (1996) have shown that fish otoliths can serve as records of physio-chemical events that occur while a fish matures, based on the observation that other elements (*e.g.* strontium and barium) can be deposited in place of a small number of the calcium ions in the carbonate structure. Habitat transitions, particularly the change from fresh to salt water, can be documented by observing variations in the chemical composition of an otolith along the time axis (Radtke *et al.*, 1988; Rieman *et al.*, 1994). Strontium concentrations in fresh water are typically *c.* 0·02–0·11 mg l^{-1}, whereas seawater strontium concentrations are one to two orders of magnitude greater, *c.* 8 mg l^{-1}. Consequently, the strontium:calcium ratio of the otolith records fish habitat, either salt water or fresh water, throughout the life of the fish. Radtke & Kinzie (1996) and Radtke *et al.* (1996) have used this method successfully to document freshwater-marine transitions.

To verify the hypothesis that individual *P. krempfi* are anadromous, strontium to calcium ratios in the otoliths of migrating fish captured in the Mekong River between 700 and 800 km upstream of the South China Sea were analysed. Otoliths were collected from individuals caught in southern Laos between 1 June and 15 August 1998. During this period, *P. krempfi* migrate upstream to spawn (Roberts & Baird, 1995; Lenormand, 1996). Otoliths from 33 *P. krempfi* were removed and stored dry in envelopes for analysis. For comparison, seven samples were taken from five potamodromous (migratory solely within fresh water) species: *P. conchophilus*, *P. macronema*, *P. larnaudii*, *P. pleurotaenia* and *H. waandersii*.

For microprobe analysis, sagittae (single otoliths) were mounted on 25·4 mm diameter glass discs using a heat-polymerized resin, 'Petropoxy 154' (Palouse Petroproducts, Palouse, WA, U.S.A.). Sagittae were then ground to the midplane using wet and dry carborundum paper (600 and 1200 grit) and highly polished on a Buehler Ecomet III grinding wheel with 0·05 µm deagglomerated alumina paste. Prepared specimen discs and standards (strontianite and calcite with known elemental concentrations) were coated with carbon in a Denton DV-502 carbon evaporator to a thickness of 25 nm. Carbon coating is necessary to further dampen diffraction of the resultant X-rays and increase electron conductance.

Standards and samples were analysed with an X-ray wavelength dispersive electron microscope using an incident beam of 10 µm, an accelerating voltage of 15 kV and a beam current of 8 nA (Radtke & Kinzie, 1996). The probe (1992 CAMECA SXSO electron microprobe; Cameca, Courbevoie, France) was calibrated with strontium and calcium standards five times both before and after specimen analysis to correct for any possible instrument error. X-rays characteristic of strontium and calcium were counted for 30 s and the background measurements were recorded for 15 s (Radtke & Kinzie, 1996). Elemental concentrations were analysed at intervals of 5 µm across the chosen axis from the core to the margin of each otolith.

RESULTS

CATCH DATA

The 120–160 mm mesh set gillnet fishery targets *P. krempfi* in the Khone Falls area of southern Laos. Over the six consecutive years between 1993 and 1998 that the fishery was monitored at Hang Khone Village, *P. krempfi* made up between 64 and 87% of the catch for each year, with a mean of 73% of the landings by mass for all years (the largest individual *P. krempfi* weighed 10 kg, the smallest was 1·5 kg and the mean ± S.D. mass was 3·9 ± 1·2 kg).

Apart from the gillnet catch, *P. krempfi* was the fourth most abundant species in the catches for one fence-filter wing trap at the Khone Falls monitored in 1994, 1995, 1998 and 1999, making up an average of 4·7% of the catch by mass. In that fishery, the minimum mass recorded for an individual *P. krempfi* was 1·00 kg, the largest was 8·67 kg, and the mean ± S.D. mass was 3·36 ± 1·69 kg (Baird *et al.*, 2004).

Confirming reports received from fishers, no *P. krempfi* were recorded between December and April in any of the over 30 different fisheries monitored at Hang Khone Village between 1993 and 1999. A total of 6732 kg of *P. krempfi*, however, were caught between May and November, mainly in 120–160 mm mesh set nylon gillnets, with a lesser amount in the fence-filter wing-trap fishery (Fig. 3). Over 98% of the *P. krempfi* were caught between mid-May and June (34% in May and 64% in June). Just 1·5% were landed in July and only three fish (weighing a total of 8·7 kg or 0·13% of total catch) were landed in August. Only one fish weighing 3·6 kg and another weighing 2·4 kg were caught in October and November respectively. For the 120–160 mm mesh gillnet fishery, the first fish for each season were caught between 7 May (in 1996) and 29 May (in 1998). In each year, the majority of the catch were landed in June,

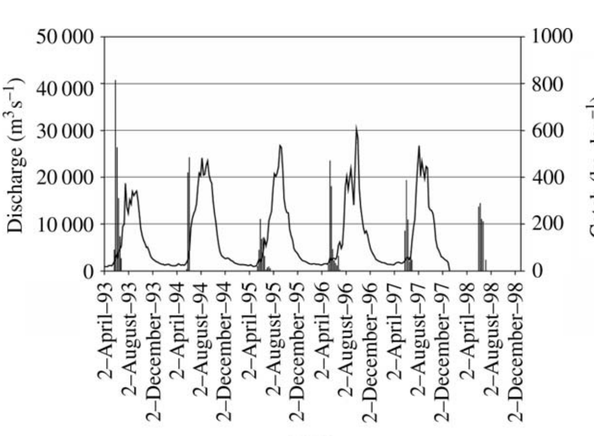

FIG. 3. Catch data–vertical bars (plotted with discharge–continuous line) for *Pangasius krempfi* in the 120–160 mm mono- and multi-filament gillnets in southern Laos, 1993–1998. The seasonality of the catch, coupled with the information about the seasonality of catches of *P. krempfi* in other stretches of the Mekong River indicates that *P. krempfi* migrate passed the Khone Falls once per year, probably on a spawning migration.

except for in 1996, when the majority were landed in May. The sudden arrival and disappearance of *P. krempfi* in fisheries at Hang Khone Village is consistent with the hypothesis that the species is highly migratory. In addition, peak *P. krempfi* catches at Hang Khone coincide with increases in river discharge (Fig. 3), indicating that these increases in discharges could act as a trigger for these migrations (Baran *et al.*, 2005).

CARBON AND NITROGEN STABLE ISOTOPE ANALYSIS

ANOVA comparing three size classes of *P. conchophilus* revealed no significant difference in $\delta^{15}N$ (ANOVA, d.f. = 252, $P > 0{\cdot}05$) and $\delta^{13}C$ (ANOVA, d.f. = 252, $P > 0{\cdot}05$) among size groups. In addition, $\delta^{13}C$ and $\delta^{15}N$ values did not vary as a function of L_T for *P. krempfi* ($\delta^{13}C$; linear regression, d.f. = 6, $P > 0{\cdot}05$ and $\delta^{15}N$; linear regression, d.f. = 6, $P > 0{\cdot}05$) or *P. larnaudii* ($\delta^{13}C$; linear regression, d.f. = 4, $P > 0{\cdot}05$ and $\delta^{15}N$; linear regression, d.f. = 4, $P > 0{\cdot}05$). As there were no significant isotopic differences as a function of body size, hereafter species-specific means are used for all further analyses.

Mean ± S.D. $\delta^{13}C$ *v.* $\delta^{15}N$ values for the seven species of pangasiid catfish and *Henicorynchus* spp., a common prey species, were plotted (Fig. 4). Values clustered within a relatively narrow range of $\delta^{13}C$ (−24 to −26‰) and $\delta^{15}N$ (8 to 10‰), with the exception of *P. krempfi*, which exhibited elevated $\delta^{13}C$ and $\delta^{15}N$ values relative to the other fishes ($\delta^{15}N$ = 12‰, $\delta^{13}C$ = −17·5‰). Fishes (other than *P. krempfi*) $\delta^{13}C$ values overlapped with the three 'sources' sampled from the Mekong River: terrestrial plant material, periphyton and particulate organic matter (Fig. 4). The similarity between source and fish $\delta^{13}C$ values of the presumed non-anadromous fishes contrasts dramatically with *P. krempfi*, which does not overlap with any source $\delta^{13}C$ values. The elevated $\delta^{13}C$ and

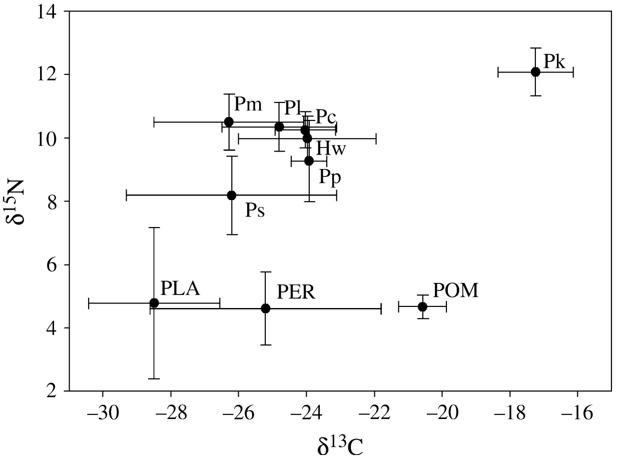

FIG. 4. Food web of Mekong River based on stable carbon and nitrogen isotopes. Fishes: Pk, *Pangasius krempfi*; Pl, *Pangasius larnaudii*; Pc, *Pangasius conchophilus*; Pm, *Pangasisus macronema*; Pp, *Pangasius pleurotaenia*; Hw, *Helicophagus waandersii* and Ps, *Henicorynchus* spp. Sources: PLA, terrestrial plants; PER, periphyton; POM, particulate organic matter. The values of stable carbon and nitrogen isotopes from the tissue of *P. krempfi* are typical of marine fishes.

$\delta^{15}N$ values for *P. krempfi*, dissilimilar to any sources sampled in the Mekong, is highly suggestive of marine habitation, as marine habitats are known to exhibit elevated $\delta^{13}C$ *v.* $\delta^{15}N$ values relative to freshwater habitats (Hesslein *et al.*, 1991; France, 1995*a,b*; Secor *et al.*, 1995; Doucett *et al.*, 1999*a,b*).

OTOLITH ANALYSIS

Strontium:calcium ratio measurements in all otoliths of *P. krempfi* ranged from 0·00 to 26·14 (mean ± S.D. 5·54 ± 0·92). Strontium:calcium ratio measurements in all otoliths of freshwater species (*H. waandersii*, *P. conchophilis*, *P. larnaudii and P. macronema*) ranged from 0·00 to 6·76 (mean ± S.D. 2·23 ± 0·62). All *P. krempfi* otoliths were further characterized by a peak strontium:calcium measurement of at least 7·68 and a decreasing strontium:calcium ratio at the otolith edge, indicating a transition from the sea to a freshwater environment. Furthermore, strontium:calcium measurement showed high variability, including multiple increases and decreases of the Sr:Ca ratio (Fig. 5).

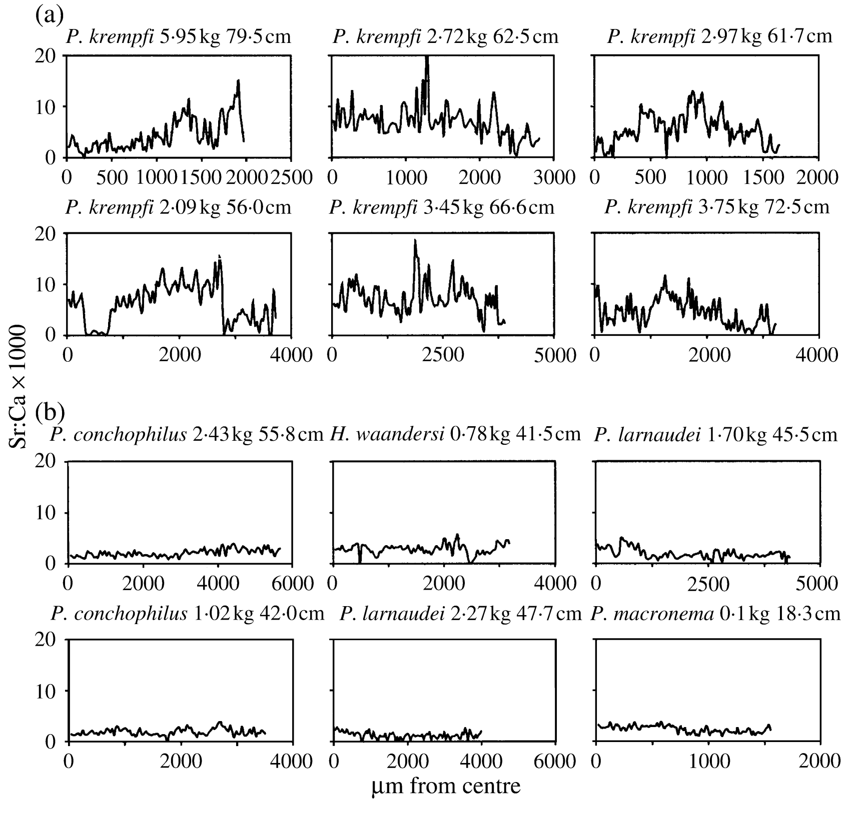

FIG. 5. Strontium:calcium ratio measurements in otoliths of (a) *Pangasius krempfi* and (b) related freshwater species (*Helicophagus waandersii*, *Pangasius conchophilus*, *Pangasius larnaudii* and *Pangasius macronema*). The values Sr:Ca ratios in the otoliths of *P. krempfi* are siginificantly higher than the Sr:Ca values in the otoliths of related freshwater species, strong evidence of marine habitation by *P. krempfi*. Values of total length and mass of each fish are provided.

Mean strontium concentrations in the otoliths of *P. krempfi* were significantly different than freshwater species (pair-wise *t*-test, d.f. = 27, $P < 0{\cdot}001$) and, on average, two to three times higher than the concentrations found in freshwater species. These results are consistent with the hypothesis that *P. krempfi* spend part of their life in a marine environment. Nonetheless, the high levels of strontium in the otoliths of *P. krempfi* together with high variability in the Sr:Ca ratio indicate that *P. krempfi* may move regularly between marine and brackish waters. This contradicts the hypothesis of Roberts & Baird (1995) who suspected that non-migrating *P. krempfi* reside exclusively in marine waters.

DISCUSSION

THE LIFE HISTORY OF *P. KREMPFI*

This study provides strong evidence that *P. krempfi* inhabits both marine and freshwater environments, is anadromous and undergoes long distance spawning migrations up the Mekong River. The migration of *P. krempfi*, characterized by adult fish moving into fresh water to spawn, is the first documented case of anadromy, and one of the few recorded examples of long distance migration in a Mekong River species. McDowall (1988) reports that anadromous behaviour is common in 28 families of fishes, yet only one species of Pangasiidae (*P. krempfi*) is thought to potentially be anadromous (McDowall, 1988). Worldwide, McDowall (1988) notes few species of anadromous catfishes, making *P. krempfi* unusual among catfishes.

While this study does not provide conclusive evidence that young and adult *P. krempfi* move downriver to the Mekong Delta after spawning, there is a considerable amount of information that points to such a conclusion. The otolith data from adult fish collected in southern Laos indicate that *P. krempfi* inhabit salt water repeatedly and from a very early life stage, even though spawning occurs far from the sea. Young fish probably move downstream quickly and arrive in the Mekong Delta before significant growth occurs. Local fishers in southern Laos also report that they do not see juvenile *P. krempfi* (Roberts, 1993*a*; Roberts & Baird, 1995), while fishers in the Mekong delta in Vietnam do report small fish (Lenormand, 1996).

Researchers, especially in the Mekong region, currently rely on catch statistics and repeated surveys to gather information about the ecology and migrations of fish species (Lieng *et al.*, 1995; Baird *et al.*, 2003, 2004). The concurrent use of multiple ecological tracers, combined with life-history information and catch data, provide a comprehensive means of inferring fish migrations and habitat use. This study demonstrates the value of using chemical techniques to provide answers about fish life history and also highlights the value of combining different approaches to build conclusive evidence, especially in a large, tropical system like the Mekong River (Baird *et al.*, 2004).

While marine and freshwater habitats differ in average $\delta^{13}C$ and $\delta^{15}N$ values, isotopic information alone cannot provide unequivocal evidence for migration between freshwater and marine systems. Isotopic values at the base of the food web within both freshwater and marine ecosystems can vary considerably. Thus, an alternative explanation for the difference in average $\delta^{13}C$ and $\delta^{15}N$

values between *P. krempfi* and other species of pangasius catfishes is that *P. krempfi* feeds on an unsampled benthic food source, while all other species rely on some mix of the three potential 'sources' sampled in this study. Examination of diet data does not support this explanation (Lenormand, 1996; unpubl. data). *Pangasius krempfi* feeding behaviour was found to be similar to that of other large-bodied pangasiid catfishes (omnivore and carnivore that does not feed while migrating). Thus, the high δ^{13}C and δ^{15}N concentrations found in the muscle tissue of *P. krempfi* are probably indicative of feeding that occurred before migration (*i.e.* a marine environment).

Similarly, δ^{15}N values at the base of the food web can also vary among sites within freshwater or marine habitats (Vander Zanden & Rasmussen, 1999). In particular, anthropogenic and sewage-derived nitrogen have distinct (typically enriched) 15N values relative to natural or background nitrogen sources (Cabana & Rasmussen, 1996; McClelland *et al.*, 1997; McClelland & Valiela, 1998), and microbial processes such as denitrification can produce elevated δ^{15}N values (Owens, 1987; Peterson & Fry, 1987). Thus, an alternative explanation for the enriched δ^{15}N of *P. krempfi* could be migration from a freshwater area with elevated δ^{15}N, rather than a marine habitat. Anthropogenic sources of nitrogen, however, are assumed to be diffuse in Cambodia and Laos, because most of the population of the country lives in widely distributed rural areas with few point source pollutants. Finally, if *P. krempfi* undergo long-distance migrations and do not eat during this period, the energy fuelling the migration would be derived from catobolizing their own tissues, which would result in elevated tissue δ^{15}N (Doucett *et al.*, 1999*c*). Though this is an alternative explanation for the elevated nitrogen isotopes values, it is also consistent with the hypothesis of long-distance migration in this species. The most likely explanation, therefore, is that enriched δ^{15}N concentrations found in the muscle tissue of *P. krempfi* indicate feeding in a marine environment. These isotope results, when examined in the context of the catch data and information already available about *P. krempfi*, provide a compelling argument that the species is anadromous.

MANAGEMENT AND CONSERVATION

Many important large-bodied migratory fish species occur in the Mekong River Basin, noteably *P. krempfi* and other species of Pangasiidae (Lieng *et al.*, 1995; Baird & Flaherty, 2004; Hogan *et al.*, 2004). While migratory fish species are extremely important in the Mekong River Basin (they make up the majority of harvest of many fisheries), they are vulnerable to both overfishing and habitat degradation (Roberts, 1993*a*; Roberts & Baird, 1995; Ahmed *et al.*, 1996; Baird & Flaherty, 2004).

Although there is currently little quantitative evidence to support the hypothesis that *P. krempfi* is overfished in the Khone Falls area, there is a considerable amount of evidence (including reports from fishers) that supports the conclusion that a number of fish stocks in the Mekong Basin have declined due to overfishing (Hogan *et al.*, 2004; Baird & Flaherty, 2005).

Habitat alteration and degradation also constitute a significant threat to *P. krempfi* and other species. Threats to fish habitat include channel alteration and dredging, inorganic and organic pollution, and wetland vegetation removal and alteration (Roberts, 1993*b*; Hill & Hill, 1994). The construction of large hydroelectric dams, however, potentially represents the most significant threat to highly migratory species in the mainstream Mekong River (Roberts, 1993*b*; Hill & Hill, 1994; Roberts & Baird, 1995; Baird & Flaherty, 2004). Large dams threaten to alter hydrological regimes and block the movements of fishes up and down the Mekong River (Hill & Hill, 1994; Baird & Flaherty, 2004). They could also seriously disrupt the drift of larvae downriver (Bartham & de Brito Ribeiro, 1991; Bartham & Goulding, 1997). Fortunately, no dams have yet to be built in the lower or middle Mekong River, but if any are, it seems highly likely that *P. krempfi* would be greatly impacted or the species might even disappear from the Mekong River. Similarly, many species of poorly studied migratory fishes in other rivers is Asia, and worldwide, are probably at risk due to habitat fragmentation (Nilsson *et al.*, 2005). The lack of information about the ecology of migratory tropical fishes, combined with the level of fragmentation of these systems (>50% fragmented by dams), underscores the need to address the risks to understudied migratory fish species (Nilsson *et al.*, 2005).

Given the importance of migratory fishes, the management of transboundary fish stocks is one of the primary biodiversity and food security issues in the Mekong River Basin (Rabinowitz, 1995; Baird *et al.*, 2003; Baird & Flaherty, 2004). All countries in the region are interconnected, united by common borders and major rivers, especially the Mekong. As an anadromous species that migrates through Vietnam, Cambodia, Laos and Thailand, *P. krempfi* highlights the immediate need for transboundary co-operation between countries within the Mekong River Basin. Several regional agreements exist for the management and conservation of straddling stocks of species. The International Convention on Migratory Species and the Convention on Biological Diversity both provide guidelines for the management and conservation of transboundary species. These agreements, as well as fisheries laws and local fisheries management agreements, can serve as a framework for the regional management of aquatic biodiversity in the Mekong River Basin.

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