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Compositional trends of fisheries in the River Ganges, India

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Abstract Monthly surveys of local fisheries from five principal landing sites on the River Ganges at Bhagalpur, India, were conducted from 2001 to 2007. Fishes of a range of sizes with mostly periodic-type life-history strategies, including many catfishes and carps, dominated the catch. Average annual yield (total mean monthly catch in units of biomass) was highly variable but trended downward during the study. Statistical ordination revealed associations between assemblage composition and hydrological seasons. Overall yields in this reach of the River Ganges tended to be greatest when the annual flood pulse was sustained longer. Patterns of average stock yields and inter-annual variability of yields were associated with species life-history strategies, with the most abundant and least variable species having periodic-type strategies of seasonal spawning, high fecundity, small eggs and no parental care. Although not appearing to have declined precipitously during the study, many stocks in this stretch of the River Ganges, including those of the largest and most valuable species, nonetheless seemed to remain below historical yield levels because of multiple impacts, including chronic intense fishing and other anthropogenic impacts.

KEYWORDS: assemblage structure, fish community, flood pulse, floodplain, life-history strategy.

Introduction

Fisheries of tropical lowland rivers are essential for the livelihoods and food security of millions of people around the world (Welcomme 2008). Fish populations of the middle River Ganges in eastern India make major contributions to the nutrition needs of millions of people (Sinha & Khan 2001) and are also critical for the conservation of the endangered Gangetic dolphin, *Platanista gangetica* (Roxburgh) (Chouldhary *et al.* 2006), yet few studies have addressed fisheries ecology in the region. The River Ganges supports a diverse fish fauna, with about 260 fish species reported for Indian waters (Sinha & Khan 2001). About 35 species have been identified as having highest commercial value, including carps (Cyprinidae), snakeheads (Channidae), and catfishes (Siluriformes) (Islam *et al.* 2006). There are indications that catches of these high-value species (primarily major carps and shad) have declined for a variety of factors associated with human population growth and environmental impacts, including fishing pressure, dams and pollution (Jhingran & Ghosh 1978; Payne & Temple 1996; Payne *et al.* 2003).

Studying the dynamics of floodplain fisheries of the lower River Ganges in Bangladesh, de Graaf (2003) found that fish catches were greater during the wet

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season (monsoon) than the dry season (summer). By contrast, Chouldhary *et al.* (2006) reported highest fishing intensity during the peak of the dry season in a stretch of the middle River Ganges in Bihar, India. High fish abundance in the middle Ganges near Patna and Allahabad, India, just prior to the monsoon season was associated with fish migrations (Payne & Temple 1996). In the middle and lower River Ganges, fish spawning tends to be associated with the annual increase in flow during the pre-monsoon season (May to July), with a second, smaller spawning peak during the post-monsoon (falling-water) season (October to December). Migrations of most cyprinids and catfishes are correlated with these two peaks (Payne *et al.* 2003). By contrast, the shad *Tenualosa ilisha* (Hamilton), one of the most exploited fishes of the lower Ganges in Bangladesh (Rahman 2001; Craig *et al.* 2004), spawns during the falling-water period. In tropical floodplain rivers, such as the Ganges, seasonally expanded aquatic floodplain habitats serve as nurseries for larvae and juveniles of many fish species (Lowe-McConnell 1987; Junk *et al.* 1989; Winemiller 2003), and the extent and duration of inundation often correlate positively with fishery yield (Welcomme 1985, 2008; Christensen 1993; Agostinho & Zalewski 1995). River fish species with divergent life-history characteristics respond to the annual flood pulse in different ways, with some species being more resilient to short-term environmental disturbances and others showing larger gains in recruitment under favourable flood pulse conditions (Winemiller 1989, 1996a, 2003).

This study analysed fishery data from surveys conducted between 2001 and 2007 in the middle River Ganges at five principal landing sites near Bhagalpur, India. This region lies within the Vikramshila Gangetic Dolphin Sanctuary in Bihar, and its fish stocks are vitally important for both people and dolphins. The primary aim of was to analyse trends in yield and species composition, and to assess their relationships with species life-history strategies and temporal patterns of rainfall. Rainfall determines the magnitude of duration of seasonal flood pulses, and the extent of floodplain inundation has been hypothesised to influence fisheries yields in tropical rivers throughout the world.

Materials and methods

Study area

Fish surveys were conducted at five landing sites near Bhagalpur, a city situated in the floodplain of the middle River Ganges in India (25° 15′ N; 86° 59′ E) (Fig. 1). Several streams that drain the hills of Santhal Parganas join the River Ganges in this stretch. The most extensive flooding generally occurs during the annual monsoon season (July to September). The slopes in the Bihar plains are gentle; thus, the flood waters spread over extensive areas (0.5–2 km wide on each side) (Singh 2007). Active braided channels, meanders and oxbow lakes, all of which result from hydrological dynamics within a low-gradient alluvial

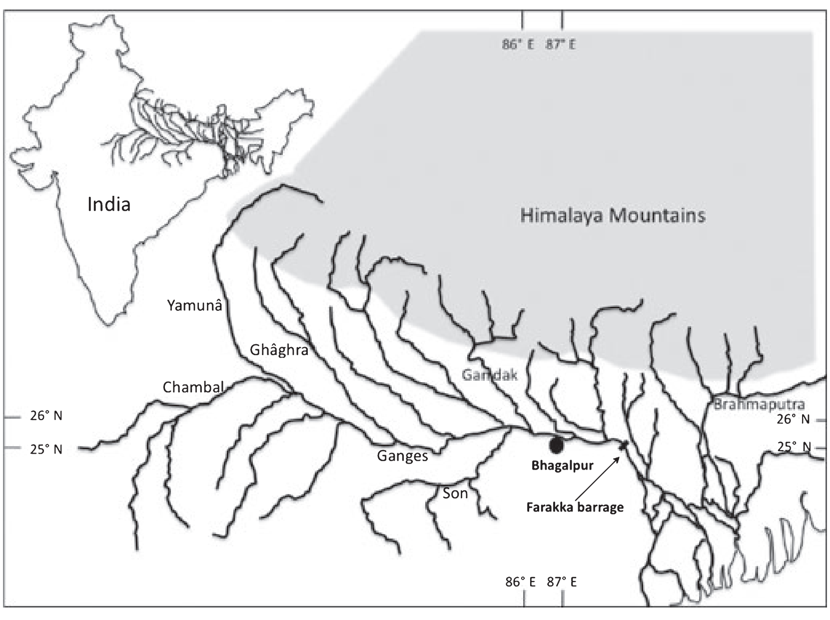

Figure 1. Map of the middle River Ganges in India showing location of Bhagalpur.

plain, characterise the geomorphology of the middle Ganges. During the monsoon season, water levels rise as much as 10 m and the main channel widens to 2–4 km (Chouldhary *et al*. 2006). The mean discharge from January 1965 to December 1973 at Farakka Barrage, located 115 km downstream from Bhagalpur, was 11 558 ± SD 14 553 $m^3 s^{-1}$ (range 1181–65 072 $m^3 s^{-1}$; hydrological data after construction of the barrage are held confidential by the Indian Government), with the lowest discharge during February to May and the highest during July to October (Vörösmarty *et al*. 1998). The river channel is not deeply incised in this area, and exposed bank sediments are those of the modern aggrading flood-plain system. Sewage from Bhagalpur and other urban centres discharges directly into the river. Other human impacts on water quality include bathing, clothes washing, boat traffic, brick making and immersion of human corpses for religious observance.

Fishery survey

The five most important fishery landing sites near Bhagalpur were surveyed regularly from 2001–2007: Maniksarkar Ghat (25° 15′ 47.7″ N; 86° 58′ 90″ E), Mont Ghat (25° 15′ 82″ N; 86° 59′ 85″ E), Mushari Ghat (25° 15′ 90″ N; 87° 00′ 52″ E), Panitanki Ghat or Waterworks Ghat (25° 16′ 13″ N; 87° 00′ 78″ E), Barari Ghat (25° 16′ 148″ N; 87° 01′ 528″ E). These five landing sites are the principal locations where full-time and part-time commercial fishermen bring their catches. A few part-time fishermen occasionally brought their catches to other landing sites, but survey data from those sites were not included here. Fishermen were intercepted in the morning (05:00–07:00 h) before they landed and could sell their fish, and once on shore the catches were recorded by species with corresponding weights. Fishermen were interviewed to determine what type of gear was used to catch each species, and how many fishermen participated. Each fisherman typically exploits a river segment that stretches no more than 5 km upstream or downstream from his landing site. Fishing effort is intense throughout the year, and fishermen adjust their gears and efforts to track changing spatio-temporal patterns of fish species abundance. According to the interviews, fishing effort and practices are strongly influenced by the relative availability of fish stocks in this stretch of the river; fishermen do not target fishes that are rare and thus difficult to catch, and virtually all species and size classes, even the smallest (approximately 6 cm standard length), are valued in the local market. Therefore, it is assumed that the local catch data reflected species relative yields of the Bhagalpur region. Based on interviews, the number of fishermen on a given day at a given landing site and during a given period varied (4–20 individuals per site per day). The number seemed to be influenced by fluctuations in fish availability (supply) more than by market demand, the latter being consistently high in this region. The catch from every fisherman who arrived at a given landing site on a given morning was examined. For the most part, the same group of fishermen returned to the same landing sites throughout the 7-year study interval, and this was because landing sites were near their villages. In no instance were any of the local fishermen perceived to be hesitant to interact with the survey team. These catch data should provide good estimates of species relative yield patterns within and between sampling periods. However, these data were not considered suitable for making inferences about stock densities (i.e. in terms of absolute numbers per unit area) between seasons within and among years. Fish species were identified using published taxonomic keys (Talwar & Jhingran 1991; Srivastava 1994) with nomenclature revised according to FishBase (2005). Specimens were weighed with a spring balance or, in a few instances, weight was estimated visually. Voucher specimens were archived at the Vikramshila Biodiversity Research and Education Center (VBREC) of Bhagalpur University.

Seven physico-chemical water parameters were measured in the River Ganges at Bhagalpur during surveys in 2003, 2004, 2006 and 2007 (Table 1). For each year, three hydrological seasons were considered: summer (March to mid June), monsoon (mid June to October), and winter (November to February). Water samples were collected at each site during the first day of the monthly fishery survey between 08:00 and 11:00 h (usually 09:00 h) and brought to the laboratory in 2.5-L containers. Physico-chemical environmental parameters, including temperature, pH, transparency and dissolved oxygen (DO) concentration, were estimated immediately after collection of a sample, whereas analysis of water samples for other chemical factors was carried out in the laboratory at Bhagalpur University. These analyses were performed following standard methods: transparency was measured with a Secchi disk (cm); surface water temperature was measured with a thermometer (°C); pH was measured with pH paper over a range of 1–10. DO was analysed by the modified Winkler method, and total hardness (TH) was determined by the EDTA titrimetric method (APHA 1998). Available phosphorus (PO_4) was measured by the stannous chloride method suggested by Wilde *et al*. (1972). Nitrate (NO_3) was determined by

Table 1. Mean values of physico-chemical variables recorded in the Middle River Ganges near Bhagalpur during 2003–2007. Except for pH, variables are expressed in mg L^{-1} unless otherwise mentioned

Variable	2003			2004			2006			2007		
	Summer	Monsoon	Winter	Summer	Monsoon	Winter	Summer	Monsoon	Winter	Summer	Monsoon	Winter
Temperature (°C)	27	29	16	30	28	19	32	26	20	32	24	17
Transparency (cm)	40.0	47.0	58.0	38.3	42.0	39.5	38.2	21.0	24.5	30.2	22.0	27.5
pH	6.0	6.0	6.5	6.5	7.0	6.3	7.5	7.3	7.5	7.5	7.5	7.5
DO mg L^{-1}	6.8	6.0	7.6	7.2	6.2	4.8	2.4	5.6	4.4	3.4	4.6	3.6
TH	160	174	150	97	90	188	132	144	166	162	164	148
Cl^- mg L^{-1}	37	24	15	13	22	18	17	10	17	21	30	12
PO_4 mg L^{-1}	0.02	0.02	0.03	0.03	0.02	0.02	0.03	0.03	0.05	0.05	0.06	0.11
NO_3 mg L^{-1}	0.02	0.04	0.03	0.04	0.03	0.03	0.04	0.02	0.01	0.03	0.03	0.03
COD	56.0	48.6	22.6	69.0	52.4	18.8	13.8	61.3	28.0	38.6	62.3	16.0

DO, dissolved oxygen; TH, total hardness; Cl^-, chloride; PO_4, phosphate; NO_3, Nitrate; COD, chemical oxygen demand.

the phenol-disulphonic acid method (Trivedy & Goel 1986).

Statistical analysis

The catches obtained by fisherman of the five zones over five consecutive days were combined as a single monthly survey. Here, the catches in these monthly surveys are referred to as monthly yields. Monthly yields of each species were averaged for each year, and the overall yield ranks of species were determined. Only data for the most common 30 species were used for subsequent statistical analyses. This eliminated species that were not present in samples during all 6 years of the survey. Data were log transformed to normalise distributions and increase linearity of correlations. Spearman's rank correlation (r_s) was used to evaluate inter-annual trends of species relative yields based on each species' contribution to the collective catch sample obtained for a given year. Rank correlation has been used extensively in studies of temporal change in vertebrate assemblages (Grossman *et al.* 1990; Winemiller 1996b), because it reduces the effects of subtle changes in yields that may result largely from sampling bias.

The coefficient of variation (CV) of average monthly yields by year was calculated and served as an indicator of the relative magnitude of inter-annual fluctuations. To examine the relationship between yield and variability, the CV was regressed against the annual average monthly yield. Pearson's correlation coefficient (r_p) was used to describe relationships between annual average monthly yield and annual rainfall (rainfall data were gathered from Meteorological Section, Bihar Agriculture College, Sabour, Bhagalpur).

Non-metric multidimensional scaling (NMDS) was used to examine similarity of species assemblage structure among three hydrological seasons during the 6-year study. Samples that are close to each other in ordination plots have similar species composition and species relative yields, whereas samples that are spaced farther apart have dissimilar species composition and/or yields. NMDS is considered well suited for analysing patterns in community structure without some of the problems associated with other methods, such as correspondence analysis, because it avoids assumptions of linearity (McCune & Grace 2002). The NMDS constructs a 2-dimensional ordination in a manner that best represents relationships among samples in a dissimilarity matrix (Field *et al.* 1982). Bray–Curtis dissimilarities were used as the distance measure, a metric demonstrated to be robust for ecological community applications (Faith & Norris 1989). A two-dimensional solution was used for computation of stress values. Guidelines for acceptance of stress values followed Clarke (1993): <0.05 = excellent, <0.10 = good, <0.20 = usable, >0.20 not acceptable. A Monte Carlo test randomization of stress values was performed using 100 iterations (McCune & Mefford 1999). Analysis of similarity (ANOSIM), a nonparametric procedure, was used to test the significance of the clustering of samples in the NMDS plot in relation to hydrological seasons and years (Clarke & Warwick 1994). Both NMDS and ANOSIM were performed with PRIMER 5 software (PRIMER-E, Plymouth, UK). To examine relationships between abiotic environmental conditions and species assemblage structure of fishery samples, log-transformed physico-chemical variables were correlated to NMDS axes 1 and 2 from the analysis of species yield data.

Species were categorised according to basic life-history strategies (Winemiller 1992; Winemiller & Rose 1992) to identify which strategies dominated the monthly sample yields during each year of the study period. In fisheries management, species life-history strategies have been used to explain the types of populations with high or low demographic resilience and production potential (Jennings *et al.* 1998; Rose *et al.* 2001; Winemiller 2005). Life-history information (e.g. adult body size, batch fecundity, spawning frequency, parental care and migratory behaviour) was obtained from Fishbase, Talwar and Jhingran (1991), Jayaram (1999) and other studies cited in this paper. Three life-history strategies were considered. Periodic strategists have relatively large body size, long generation time, large batches of small eggs, seasonal spawning, no parental care and sometimes are migratory. Periodic-type species respond better to large-scale variation and/or seasonal environmental variation. Opportunistic strategists are small species that have short generation times, fairly low batch fecundity, little migration and parental care and that should have good ability to rapidly colonise disturbed habitats. Finally, equilibrium strategists have low batch fecundity, well-developed parental care, and moderate to long generation times, and presumably have better competitive ability in relatively stable habitats with comparatively high densities of competitors and predators. When specific values were available for a species, the criteria of Rose *et al.* (2001) were adopted to categorise life-history strategies, and when values were lacking for a species, the strategy assigned was based on the most closely related species for which information was available.

Results

Seasonal and inter-annual catch composition

Seventy-six fish species (27 families) were recorded in the Bhagalpur area during the survey. Cypriniformes, Siluriformes and Perciformes were the dominant orders both in terms of species richness and yields (Table 2). The dominant fish species in the catch at Bhagalpur were *Wallago attu*, *Gudusia chapra*, *Salmostoma bacalia*, *Pseudeutropius atherinoides*, *Ailia coila*, *Sperata aor*, *Johnius coitor*, *Cirrhinus mrigala*, *Setipinna brevifilis* and *Mystus cavasius*. In 2001, *W. attu,* one of the most important catfish in floodplain fisheries in India and present in most tributaries of the River Ganges (Islam *et al.* 2006), had the highest annual average yield observed over the entire survey interval (353.9 kg). The average annual yield of *Wallago* decreased in 2002 followed by an increase in 2003 and then a decline in the following years (Table 2). Similarly, the major carps, including *Catla catla*, *C. mrigala*, *Labeo bata* and *Labeo rohita*, persisted in the catches, but annual average yields and rank positions fluctuated (Table 3). The major carp *Labeo calbasu* was present in all catches but with relatively low yields when compared with the other major carps. Thirty-five species, including the migratory *T. ilisha* and other small fishes, had annual average yields of < 10 kg.

Annual average yield tended to decrease over the course of the study. The highest average yield (3000 kg) was recorded in 2001, and the lowest average annual yields were recorded in 2006 (800 kg) and 2007 (900 kg), but the interval between fluctuated between 1100 and 2000 kg (Table 2). Average monthly yield was highly variable between seasons as well (Fig. 2). Yields were higher during summer, monsoon, and winter 2001–2002, and monsoon and winter 2003–2004, with the lowest yields during winter 2004–2005 and summer 2006 (< 25 kg). Significant ($P < 0.05$) correlations were found between annual rainfall and total yield in the same year ($r_p = 0.51$) and between annual rainfall and the total yield in the following year ($r_p = 0.39$). A significant correlation was found between the number of consecutive months with rainfall > 100 mm and total yield in the same year ($r_p = 0.63$).

Yield ranks were consistently high throughout the study period for the predatory catfish *W. attu* and the planktivorous shad *G. chapra* (Table 3). Spearman's correlation revealed significant correlations ($P < 0.01$) among years in terms of species annual average yields (Table 4). Samples from all the years were similar to one another, although several species showed a general pattern of declining average annual yields from 2001 to 2007: *P. atherinoides*, *A. colia, J. coitor, Chitala chitala, Corina soborna, Mystus tengra* and *Channa marulius* (Table 2).

The relationship between average monthly yield and the *CV* was inverse and weak (coefficient of determination, $r^2 = 0.18$) (Fig. 3). Three extreme patterns can be contrasted in Fig. 3: (1) species with high yield and low variability, a group that contains mostly periodic-type species (e.g. *L. calbasu*, *Puntius conchonius, W. attu, G. chapra*) and two opportunistic-type species (*Chanda nama* and *Pseudambassis ranga*); (2) species with high abundance and high variability, a group containing three periodic types (*Sicamugil cascadia*, *M. tendra* and *Macrognathus aral)* and two opportunistic types (*P. atherinoides* and *C. soborna*); and (3) species with low yield and high variability, a group including six opportunistic strategists (*Acanthocobitis botia*, *Lepidocephalichthys guntea, Botia dario*,

Table 2. Annual averages of yield (kg) and standard deviations (average ± SD) based on monthly samples of fishery landings from the Middle River Ganges near Bhagalpur, India, during the period 2001–2007

Family	Species	2001	2002	2003	2004	2006	2007
Siluridae	*Wallago attu* (Bloch & Schneider)	353.8 ± 439.7	152.8 ± 136.7	289.3 ± 468.0	139.0 ± 109.7	63.2 ± 70.6	135.7 ± 167.9
Clupeidae	*Gudusia chapra* (Hamilton)	258.2 ± 330.1	75.5 ± 86.7	161.1 ± 260.2	114.1 ± 168.6	66.4 ± 83.9	89.2 ± 206.2
Schilbeidae	*Pseudeutropius atherinoides* (Bloch)	154.9 ± 269.7	29.2 ± 28.4	23.2 ± 31.2	26.5 ± 41.4	8.5 ± 15.5	7.3 ± 15.8
Schilbeidae	*Ailia coila* (Hamilton)	151.8 ± 430.5	18.1 ± 18.0	43.2 ± 86.9	35.7 ± 64.8	66.8 ± 91.8	19.3 ± 23.6
Sciaenidae	*Johnius coitor* (Hamilton)	135.0 ± 225	10.5 ± 14.1	81.6 ± 104.5	34.9 ± 27.9	20.8 ± 32.5	12.2 ± 17.5
Engraulidae	*Setipinna brevifilis* (Valenciennes)	128.2 ± 119.5	35.9 ± 33.8	40.1 ± 44.8	55.1 ± 67.3	23.5 ± 23.5	20.5 ± 15.0
Bagridae	*Sperata aor* (Hamilton)	127.8 ± 136	55.3 ± 50.5	92.7 ± 137.4	33.8 ± 25.4	33.8 ± 40.1	40.1 ± 33.2
Cyprinidae	*Aspidoparia morar* (Hamilton)	119.7 ± 195.1	81.7 ± 74.4	62.2 ± 58.1	44.3 ± 61.8	72.0 ± 117.1	41.9 ± 34.3
Cyprinidae	*Salmostoma bacaila* (Hamilton)	116.8 ± 124.5	57.0 ± 62.4	53.7 ± 77.9	51.2 ± 59.7	35.8 ± 47.2	18.3 ± 30.7
Cyprinidae	*Cirrhinus mrigala* (Hamilton)	115.7 ± 190.4	41.9 ± 29.2	64.3 ± 85.4	36.7 ± 41.9	16.7 ± 20.9	36.3 ± 67.5
Bagridae	*Mystus cavasius* (Hamilton)	113.8 ± 73.1	56.8 ± 41.4	76.2 ± 73.4	43.2 ± 29.5	51.4 ± 50.8	32.1 ± 19.6
Cyprinidae	*Catla catla* (Hamilton)	98.5 ± 165.1	45.7 ± 61.5	138.1 ± 212.8	27.2 ± 32.0	31.6 ± 52.9	28.9 ± 37.5
Mugilidae	*Sicamugil cascasia* (Hamilton)	97.5 ± 140.3	17.5 ± 25.6	5.6 ± 8.9	9.0 ± 15.5	9.6 ± 20.7	5.0 ± 8.7
Bagridae	*Sperata seenghla* (Sykes)	93.2 ± 63.1	33.2 ± 27.2	86.1 ± 151.1	28.1 ± 41.1	24.5 ± 33.4	44.1 ± 70.3
Schilbeidae	*Clupisoma garua* (Hamilton)	90.1 ± 118.1	31.2 ± 48.4	45.0 ± 62.1	33.6 ± 47.4	27.9 ± 32.8	24.2 ± 34.1
Notopteridae	*Chitala chitala* (Hamilton)	86.1 ± 108.8	12.4 ± 17.1	88.6 ± 165.7	13.5 ± 19.6	11.2 ± 14.5	26.5 ± 33.9
Mastacembelidae	*Macrognathus aral* (Bloch & Schneider)	70.9 ± 115.7	5.3 ± 7.8	18.1 ± 54.2	3.1 ± 6.4	0.9 ± 2.5	7.1 ± 13.5
Clupeidae	*Corina soborna* (Hamilton)	66.3 ± 156	16.2 ± 47.7	6.8 ± 15.4	40.1 ± 86.7	14.4 ± 21.7	0.1 ± 0.3
Cyprinidae	*Labeo bata* (Hamilton)	53.6 ± 70.6	66.1 ± 79.6	149.8 ± 222.7	54.0 ± 32.6	16.5 ± 15.1	45.2 ± 66.0
Cyprinidae	*Puntius sophore* (Hamilton)	46.2 ± 38.4	18.0 ± 13.7	30.2 ± 34.0	20.2 ± 19.6	6.2 ± 6.8	12.8 ± 9.2
Channidae	*Channa punctata* (Bloch)	43.1 ± 46	16.4 ± 14.8	28.8 ± 56.9	10.3 ± 19.6	6.1 ± 10.1	41.3 ± 41.3
Mastacembelidae	*Mastacembelus armatus* (Lacepède)	38.0 ± 26.42	8.0 ± 4.7	27.4 ± 54.6	20.6 ± 22.6	6.4 ± 12.4	12.5 ± 13.5
Cyprinidae	*Labeo rohita* (Hamilton)	37.9 ± 71.9	21.1 ± 20.2	37.9 ± 47.8	11.9 ± 15.0	8.2 ± 7.8	11.9 ± 17.3
Schilbeidae	*Eutrophiicthys vacha* (Hamilton)	33.4 ± 38.7	6.3 ± 8.4	15.7 ± 25.0	20.0 ± 48.3	19.0 ± 36.9	11.9 ± 13.8
Cyprinidae	*Osteobrama cotio cotio* (Hamilton)	31.8 ± 31.9	11.6 ± 11.3	14.7 ± 22.6	7.5 ± 4.5	9.3 ± 14.3	19.9 ± 55.5
Clupeidae	*Gonialosa manmina* (Hamilton)	31.4 ± 75.5	95.6 ± 147.7	116.4 ± 216.5	25.3 ± 41.1	39.8 ± 75.5	27.8 ± 54.1
Bagridae	*Mystus tengra* (Hamilton)	30.4 ± 23.4	15.5 ± 14.8	19.6 ± 23.8	1.3 ± 2.2	0.0 ± 0.2	0.2 ± 0.4
Cyprinidae	*Puntius conchonius* (Hamilton)	28.7 ± 32.4	16.5 ± 13.3	33.4 ± 33.7	20.5 ± 24.6	11.3 ± 16.8	22.0 ± 26.9
Cyprinidae	*Puntius sarana sarana* (Hamilton)	27.9 ± 37.6	12.5 ± 9.6	32.2 ± 59.2	10.5 ± 11.8	4.4 ± 4.8	11.2 ± 19.8
Siluridae	*Ompok pabda* (Hamilton)	25.0 ± 26.3	7.4 ± 8.5	14.4 ± 26.6	4.1 ± 3.5	2.4 ± 4.1	8.9 ± 10.7
Channidae	*Channa marulias* (Hamilton)	22.8 ± 35.4	14.6 ± 14.8	23.3 ± 28.9	9.5 ± 7.5	4.5 ± 5.0	5.4 ± 7.0
Mastacembelidae	*Mastacembelus pancalus* (Hamilton)	19.1 ± 27.3	3.2 ± 2.4	11.7 ± 13.4	13.0 ± 25.1	4.9 ± 7.4	9.4 ± 17.1
Sisoridae	*Bagarius bagarius* (Hamilton)	17.7 ± 26.8	9.6 ± 21.5	10.0 ± 17.9	11.5 ± 31.2	2.8 ± 8.0	1.9 ± 1.9
Cyprinidae	*Labeo calbasu* (Hamilton)	17.4 ± 8.9	13.6 ± 15.0	25.2 ± 42.1	18.7 ± 19.2	12.1 ± 22.9	14.3 ± 14.9
Gobiidae	*Glossogobius giurus* (Hamilton)	16.3 ± 9.8	9.3 ± 7.4	16.1 ± 17.5	4.7 ± 3.8	12.5 ± 11.4	10.4 ± 10.0
Sisoridae	*Gogangra viridescens* (Hamilton)	14.8 ± 18.7	15.6 ± 26.6	3.7 ± 3.9	1.5 ± 2.3	2.6 ± 3.0	1.9 ± 2.3
Ambassidae	*Chanda nama* Hamilton	11.3 ± 13.5	6.9 ± 6.3	8.5 ± 11.1	5.7 ± 4.1	11.5 ± 16.2	4.9 ± 4.4
Mugilidae	*Rhinomugil corsula* (Hamilton)	11.0 ± 14.2	11.0 ± 17.0	1.6 ± 2.4	7.4 ± 11.9	1.5 ± 2.3	5.4 ± 10.5
Ambassidae	*Pseudambassis ranga* (Hamilton)	10.4 ± 13.3	6.6 ± 6.5	9.2 ± 12.5	6.7 ± 5.0	5.7 ± 6.3	4.9 ± 3.6
Notopteridae	*Notopterus notopterus* (Pallas)	9.7 ± 16.9	5.0 ± 6.9	5.1 ± 8.6	2.1 ± 1.5	5.3 ± 12.5	3.6 ± 5.0
Clariidae	*Heteropneustes fossilis* (Bloch)	9.1 ± 10.8	2.1 ± 3.6	4.2 ± 5.8	6.1 ± 15.1	0.3 ± 0.9	0.4 ± 0.6

Table 2. (*Continued*)

Family	Species	2001	2002	2003	2004	2006	2007
Pangasiidae	*Pangasius pangasius* (Hamilton)	8.6 ± 15.1	2.5 ± 4.5	3.8 ± 10.0	7.6 ± 20.5	10.1 ± 15.3	10.5 ± 34.7
Channidae	*Channa striata* (Bloch)	7.8 ± 22.2	7.8 ± 14.4	4.7 ± 6.6	4.6 ± 12.3	0.0 ± 0.2	1.3 ± 2.1
Schilbeidae	*Silonia silondia* (Hamilton)	6.2 ± 12.8	1.1 ± 1.2	1.2 ± 3.9	3.1 ± 7.3	4.2 ± 11.9	8.0 ± 11.0
Bagridae	*Rita rita* (Hamilton)	4.2 ± 6.1	1.9 ± 4.0	19.6 ± 30.7	5.1 ± 7.2	3.0 ± 4.6	3.4 ± 6.8
Bagridae	*Hemibagrus menoda* (Hamilton)	3.6 ± 4.8	1.5 ± 2.5	2.4 ± 2.9	0.3 ± 0.5	0.8 ± 0.8	18.2 ± 37.7
Belonidae	*Xenentodon cancila* (Hamilton)	3.6 ± 3.1	3.2 ± 4.5	4.2 ± 4.8	0.9 ± 0.9	0.6 ± 0.8	1.5 ± 2.0
Cyprinidae	*Crossochelius latius latius* (Hamilton)	2.9 ± 9.1	2.1 ± 4.0	2.4 ± 4.7	0.1 ± 0.1	0.4 ± 1.4	0.9 ± 1.5
Bagridae	*Mystus vittatus* (Bloch)	1.7 ± 18	0.7 ± 1.5	2.5 ± 3.5	19.6 ± 36.1	5.7 ± 7.6	13.7 ± 21.6
Cyprinidae	*Securicula gora* (Hamilton)	1.4 ± 2.4	0.2 ± 0.2	1.2 ± 3.0	0.4 ± 0.8	2.4 ± 6.7	0.4 ± 0.7
Cyprinidae	*Labeo gonius* (Hamilton)	1.2 ± 1.9	3.1 ± 5.2	1.0 ± 1.4	0.8 ± 2.4	0.3 ± 0.7	0.5 ± 1.6
Cobitidae	*Lepidocephalichthys guntea* (Hamilton)	0.9 ± 1.9	< 0.0 ± 0.1	1.1 ± 1.8	0.1 ± 0.2	0.1 ± 0.2	0.2 ± 0.3
Clupeidae	*Tenualosa hilsa* (Hamilton)	0.8 ± 1.7	1.1 ± 1.6	0.6 ± 1.5	< 0.01 ± 0.1	0.2 ± 0.8	0.1 ± < 0.01
Cyprinidae	*Chela atpar* (Hamilton)	0.7 ± 1.5	0.1 ± 0.1	0.5 ± 1.2	0.1 ± 0.3	0	< 0.01 ± < 0.01
Cyprinidae	*Amblypharyngodon mola* (Hamilton)	0.8 ± 2.4	0.2 ± 0.4	0.1 ± 0.2	0.1 ± 0.2	< 0.01 ± 0.1	0.1 ± 0.5
Balitoridae	*Acanthocobitis botia* (Hamilton)	0.7 ± 1.1	< 0.01 ± < 0.01	0.3 ± 0.5	< 0.01 ± 0.1	< 0.01 ± 0.1	< 0.01 ± 0.1
Clariidae	*Clarias batrachus* (Linnaeus)	0.5 ± 1.5	0	0	0	0	0
Sciaenidae	*Johnius gangeticus* Talwar	0.4 ± 1.2	0.3 ± 0.4	< 0.01 ± 0.1	3.5 ± 3.5	0.9 ± 2.5	0.4 ± 0.9
Cobitidae	*Botia Dario* (Hamilton)	0.3 ± 0.8	0.1 ± 0.2	0.4 ± 0.7	0.9 ± 1.9	0.1 ± 0.3	0.4 ± 0.5
Osphronemidae	*Colisa fasciata* (Bloch & Schneider)	0.2 ± 0.3	0.1 ± 0.2	0.6 ± 1.7	< 0.01 ± < 0.01	0	< 0.01 ± 0.1
Tetraodontidae	*Tetraodon cutcutia* Hamilton	0.2 ± 0.2	< 0.01 ± < 0.01	< 0.01 ± < 0.01	< 0.01 ± < 0.01	< 0.01 ± < 0.01	< 0.01 ± 0.1
Anabantidae	*Anabas testudineus* (Bloch)	0.1 ± 0.2	< 0.01 ± < 0.01	< 0.01 ± 0.1	0	0	0
Channidae	*Channa gachua* (Hamilton)	0.1 ± 0.2	< 0.01 ± 0.1	0	< 0.01 ± < 0.01	0.2 ± 0.1	0
Nandidae	*Nandus nandus* (Hamilton)	0.1 ± 0.1	< 0.01 ± 0.1	0.1 ± 0.2	0.3 ± 1.1	0	< 0.01 ± < 0.01
Cobitidae	*Botia lohachata* Chaudhuri	0.1 ± 0.1	< 0.01 ± < 0.01	< 0.01 ± < 0.01	< 0.01 ± 0.1	0	0.1 ± 0.2
Cyprinidae	*Chagunius chagunio* (Hamilton)	< 0.01 ± 0.2	< 0.01 ± < 0.01	0.2 ± 0.3	0.1 ± 0.3	< 0.01 ± 0.1	< 0.01 ± 0.1
Erithistidae	*Erethistes pusillus* Müller & Troschel	< 0.01 ± 0.1	0	0.1 ± 0.2	0.2 ± 0.6	< 0.01 ± < 0.01	< 0.01 ± < 0.01
Sisoridae	*Sisor rabdophorus* Hamilton	< 0.01 ± 0.1	0	0	0	0	0
Anguillidae	*Anguilla bengalensis* (Gray)	< 0.01 ± 0.1	< 0.01 ± 0.1	0.1 ± 0.3	< 0.01 ± < 0.01	0	0.9 ± 2.6
Cyprinidae	*Esomus danricus* (Hamilton)	< 0.01 ± 0.1	0	0.1 ± 0.2	0.1 ± 0.4	0	< 0.01 ± < 0.01
Sisoridae	*Glyptothorax telchitta* (Hamilton)	< 0.01 ± < 0.01	0	0	< 0.01 ± < 0.01	0	0
Cobitidae	*Somileptes gongota* (Hamilton)	< 0.01 ± < 0.01	0	0	0	0	0
Synbranchidae	*Amphipnous cuchia* (Hamilton)	< 0.01 ± < 0.01	0	0.1 ± < 0.01	0	0	0
Cyprinidae	*Tor tor* (Hamilton)	0	0	0	0.2 ± < 0.01	0	0
Chacidae	*Chaca chaca* (Hamilton)	0	0	< 0.01 ± 0.1	0	0	
	Unidentified species (5 spp.)	< 0.01 ± 1.5	0.5 ± 1.7	0.7 ± 2.0	0.4 ± 1.5	0	0
Total annual average of yield (kg)		3013.1	1195.0	2063.0	1110.9	801.3	936.3

Table 3. Abundance ranks of the 30 most common species in the Middle River Ganges fishery near Bhagalpur, India, during the period 2001–2007

Family	Species	2001	2002	2003	2004	2006	2007	LHS
Siluridae	*Wallago attu*	1	1	1	1	4	1	P
Clupeidae	*Gudusia chapra*	2	4	2	2	3	2	P
Schilbeidae	*Pseudeutropius atherinoides*	3	14	25	16	26	33	O
Schilbeidae	*Ailia coila*	4	16	15	4	2	17	P
Sciaenidae	*Johnius coitor*	5	30	9	11	13	24	P
Engraulidae	*Setipinna brevifilis*	6	11	16	3	12	15	O
Bagridae	*Sperata aor*	7	8	6	12	8	7	P
Cyprinidae	*Aspidoparia morar*	8	3	12	6	1	5	P
Cyprinidae	*Salmostoma bacaila*	9	6	13	5	7	18	P
Cyprinidae	*Cirrhinus cirrhosus*	10	10	11	10	15	8	P
Bagridae	*Mystus cavasius*	11	7	10	7	5	9	P
Cyprinidae	*Catla catla*	12	9	4	15	9	10	P
Mugilidae	*Sicamugil cascasia*	13	18	38	31	24	37	P
Bagridae	*Sperata seenghala*	14	12	8	14	11	4	P
Schilbeidae	*Clupisoma garua*	15	13	14	13	10	13	P
Notopteridae	*Chitala chitala*	16	27	28	24	22	12	E
Mastacembelidae	*Macrognathus aral*	17	39	37	43	45	34	P
Clupeidae	*Corina soborna*	18	21	3	8	17	56	O
Cyprinidae	*Labeo bata*	19	5	20	19	16	3	P
Cyprinidae	*Puntius sophore*	20	17	21	20	29	22	P
Channidae	*Channa punctata*	21	20	17	29	30	6	E
Cyprinidae	*Labeo rohita*	22	15	22	26	27	25	P
Mastacembelidae	*Mastacembelus armatus*	23	33	30	18	28	23	P
Schilbeidae	*Eutrophiichthys vacha*	24	38	31	21	14	26	P
Cyprinidae	*Osteobrama cotio cotio*	25	28	5	33	25	16	P
Cyprinidae	*Gonialosa manmina*	26	2	26	17	6	11	O
Bagridae	*Mystus tengra*	27	23	18	47	56	53	P
Cyprinidae	*Puntius conchonius*	28	19	16	19	21	14	P
Channidae	*Puntius sarana*	29	26	19	28	36	27	P
Siluridae	*Ompok pabda*	30	35	2	41	41	31	P

LHS, life-history strategy; E, equilibrium; O, opportunistic; P, periodic.

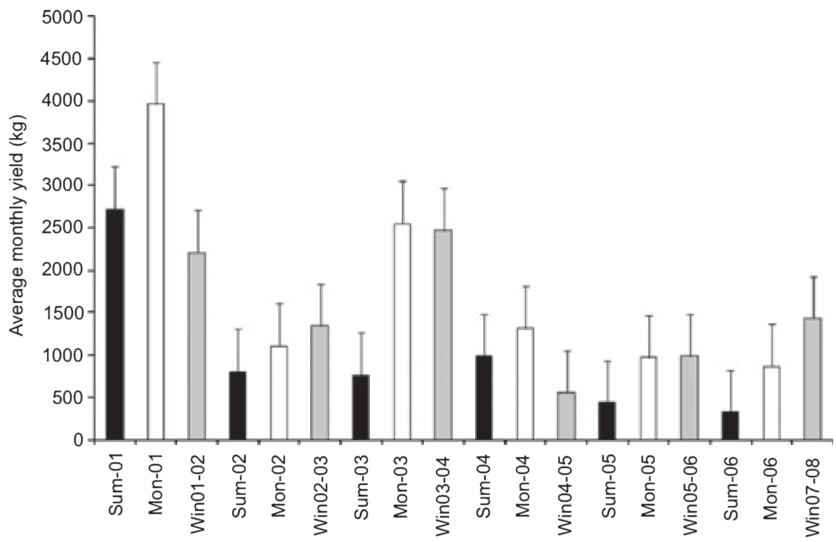

Figure 2. Seasonal trends in average monthly yield from fisheries landings at Bhagalphur over a 6-year period. Black bars, summer; white bars, monsoon; and grey bars, winter. Error bars are 1 SD.

Table 4. Spearman's correlations among years based on species annual average yields (for the 30 most common species) in fishery landings at Bhagalpur, India. Correlations are significant at 0.01 (**) and 0.05 (*)

Year	2001	2002	2003	2004	2006
2002	0.52**				
2003	0.49**	0.72**			
2004	0.70**	0.73**	0.66**		
2006	0.66**	0.74**	0.68**	0.78**	
2007	0.37*	0.70**	0.82**	0.59**	0.63**

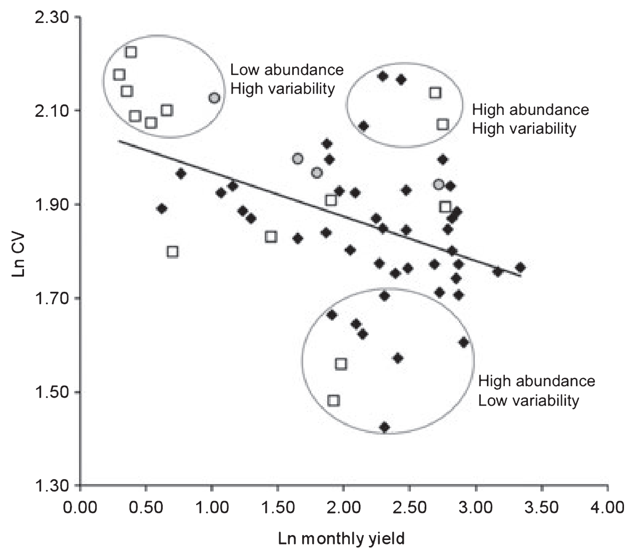

Figure 3. Relationship between the average monthly yield and the coefficient of variation (*CV*) of monthly yield for the 30 most common species in samples from the fisheries landings at Bhagalpur, India. Three extreme patterns of association between average and *CV* of biomass are contrasted with envelopes ($y = -1.94x + 5.63$, $r^2 = 0.18$). Symbols represent species life-history strategies: equilibrium, gray circle; opportunistic, empty square; periodic, black diamond.

Amblypharyngodon mola, Eresthistes pussilus and *Chela atpar*) and one equilibrium-type species (*Clarias batrachus*). When species were grouped according to life-history strategies, no significant between-group differences were found in terms of average monthly yield ($P > 0.30$).

Non-metric multidimensional ordination grouped samples according to hydrological seasons more than according to years (Fig. 4). Composition of the fish yields during the monsoon and winter periods were more similar than fish yields from the summer. The monsoon samples from 2002, 2003 and 2004 were more similar than those from 2001 and 2007 (Fig. 4). ANOSIM, which is based on random permutations of

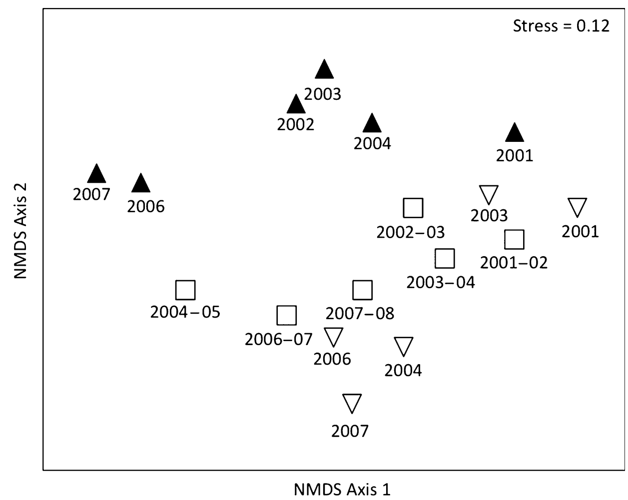

Figure 4. Non-metric multidimensional scaling (NMDS) ordination depicting the relative similarity of species biomass in seasonal fishery samples taken over a 6-year period at Bhagalpur, India. Symbols represent three hydrological seasons: summer, closed triangle; monsoon, inverted empty triangle; winter, empty square.

the survey data, gave a global value near to zero ($R = 0.013$, significance level = 49.7%), indicating significant differences in assemblage structure of the catch between these hydrological seasons.

Environmental variables and seasonal fish catches

pH was close to neutral (6–7.5) with highest values recorded during 2006 and 2007. Transparency was variable between years with the lowest values during the monsoon and winter 2006 and 2007. DO, nitrate (NO_3) and phosphate (PO_4) had high values during the entire period of study (DO ranging from 6 to 7.5 mg L^{-1}, NO_3 ranging from 0.02 to 0.04 mg L^{-1}, and PO_4 ranging from 0.02 to 0.11 mg L^{-1}), with the highest values (0.06 and 0.11 mg L^{-1}) during monsoon and winter 2007 (Table 1).

NMDS ordination of seasonal catch samples during the 3 years for which environmental data were collected resulted in two major axes that explained 55.3% of the original distances in n-dimensional space (stress = 0.02, instability < 0.0001, Fig. 5). Temperature was negatively correlated with Axis 1 during the summer in 2003–2004. pH and TH were positively correlated with Axis 1 during the winter and monsoon in 2006–2007 (Axis 1). Transparency and DO were negatively correlated with Axis 2, which indicates that most species collected during the winter and monsoon in 2003–2004 were associated with the decreasing transparency and DO. PO_4 was positively correlated

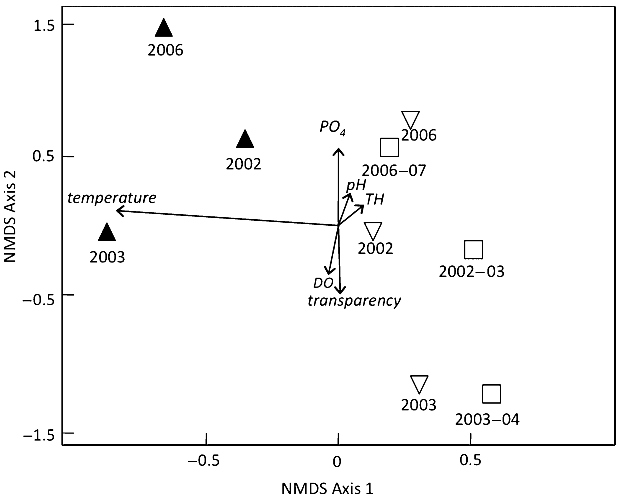

Figure 5. Non-metric multidimensional scaling (NMDS) ordination depicting the relative similarity of species biomass in seasonal samples for which environmental data were available. Correlations of key environmental variables with the two NMDS axes are shown as vectors (direction and magnitude). Summer, closed triangle; monsoon, inverted empty triangle; winter, empty square.

with Axis 2 during the winter and monsoon in 2006–2007, indicating that species collected during this period were associated with an increase in PO_4 concentration.

Life-history strategies of fishes in the Middle River Ganges

Forty-four of 76 species obtained during the survey were identified as having traits associated with the periodic life-history strategy, 20 were opportunistic strategists, and 12 were equilibrium strategists. Species with a periodic strategy usually spawn once or twice during the early wet season and have little or no parental care. Species with the equilibrium strategy have relatively small broods, parental care and aseasonal reproduction. The opportunistic strategy is characterised by maturation at small sizes, small broods and breeding at frequent intervals throughout the year. Among the 30 common species that were persistent in the catch during the entire study, 24 species are periodic-type, two are equilibrium-type, and five are opportunist-type (Table 3). The relationships between life-history strategies and the average annual yield and its *CV* were examined for 30 species (Table 3). Neither average fish yield (F = 0.05, d.f. = 2,37, P = 0.95) nor *CV* of yield (F = 0.99, d.f. = 2,37, P = 0.381) was significantly associated with life-history strategies.

Discussion

Composition and seasonal dynamics of the fish catch

The species composition of the fishery landings of the middle River Ganges appear to have shifted from dominance of major carps and large catfishes during the 1950s and 1960s (Payne *et al.* 2003) to a more diverse composition that includes smaller species of catfishes, cyprinids, shads, anchovies, croakers and spiny eels. *Tenualosa ilisha* used to be abundant in landings in sections of the river located upstream (12.1% of total catch) and downstream (up to 42% of total catch) from the Bhagalpur region (Payne *et al.* 2003), but the present study found very few *T. ilisha* in the landings (average annual yields 0.002–0.07% of total catch). This estuarine fish migrates upstream in the Ganges and other major rivers for spawning. Construction of the Farakka Barrage downstream from Bhagalpur has impacted fish migration, with some accounts attributed to the dam a 10% reduction in yields of *T. ilisha* in the upstream reaches (Payne *et al.* 2003).

The catfish, *W. attu* was the top-ranked species during every year of the study except 2006 when the cyprinid *Aspidoparia morar* was highest ranked. *Wallago attu* is distributed in floodplain rivers of southern Asia, IndoChina, and western Indonesia (Giri *et al.* 2002), and fishing pressure has caused a decline in the yield of this species throughout its range (Kurup 1992). Average yield of *W. attu* in middle Ganges landings was variable among years, with the lowest value observed in 2006. Recent catches of *W. attu* in the middle Ganges seem to show modest gains compared with the catch composition reported by Payne *et al.* (2003) and Jhingran (1991) at Patna from 1993 to 1994. In landings near Patna, this species constituted 8.5% of the catch composition during 1958, it declined to 1.3% of the catch in 1994, but from 2001 to 2007 at Bhagalpur this species constituted 8–14% of the total catch by biomass.

Summaries of fisheries catch data from the Ganges Basin from 1952 to 1995 were reported by Jhingran (1991), Temple and Payne (1995) and Payne and Temple (1996). Declining regional trends were observed for the Indian river shad, *G. chapra*, and the cyprinid *Salmostoma bacaila*, but these species were the second and ninth most important species in recent Bhagalpur landings. In the middle Ganges, the major carps formerly were the most important fish group in inland fisheries representing 53% of the catch at Agra, 45% at Kanpur and 38% at Allahaba, but were less abundant in the lower reaches (19–26%) at Patna (Jhingran 1991; Payne *et al.* 2003). In landings near Patna, the major carps represented 26.5% of the total catch in 1958–1966, and by 1993–1994 they had been reduced to 4.0% of the total catch. In the present survey, the percentage of major carps (*C. catla, C. mrigala, L. bata, L. calbasu, L. gonius, L. rohita and T. tor*) in the total annual catch varied between 9 and 15%, reflecting a small percentage compared with historical catches in the region. Reduced catches of these valuable species are attributed to large-scale exploitation of all life stages for direct consumption and stocks for aquaculture, and early life stages could be more vulnerable to impacts of pollution (Jhingran & Ghosh 1978; Sinha & Khan 2001). A study conducted in the Bhagalpur area by Chouldhary *et al.* (2006) identified the threat to sustainable fisheries posed by illegal fishing activities within the Gangetic Dolphin Sanctuary.

Seasonal flood pulses greatly influence ecosystem and fishery production in tropical rivers (Arthington *et al.* 2003). Floodplain aquatic habitats provide shelter in the form of submerged macrophytes and abundant food resources that facilitate rapid growth (Welcomme 1985; Neiff *et al.* 2009). Years with more extensive flooding may be associated with more dissolved nutrients and higher primary and secondary productivity (Junk 1997), higher fish growth rates (Bayley 1988; Halls *et al.* 1998), and greater fish recruitment (Agostinho *et al.* 2003; Bailly *et al.* 2008). More sustained flood pulses seem to be associated with greater catches of young-of-the-year fish in the Ganges (Payne & Temple 1996) and Ganges/Brahmaputra Delta (de Graaf 2003). Data on fish sizes and ages were not obtained in the present study, but the low correlation ($r^2 = 0.37$) between annual rainfall and the total annual yield may reflect strong contributions of young fish, which indeed was generally observed. Previous studies found that catches of high-value species in the middle and lower River Ganges consisted primarily of age-0+ fish (Jhingran & Ghosh 1978; Halls *et al.* 1999).

Catch variability and life-history strategies

Improved understanding of how fishing and environmental variability affect species with different life-history traits (Winemiller & Rose 1992; Jennings *et al.* 1998; Rose *et al.* 2001; Winemiller 2005) could help to conserve fish stocks in the middle River Ganges. Here, coefficients of variation of species annual yields were used to indicate temporal variability of exploited stocks. Although the influence of environmental variables on population dynamics was not examined directly in the present study, life-history traits can be used to infer responses of populations to harvest and other impacts (Winemiller 2005). The relationship between average monthly yield and the *CV* was weak and negative based on the 6-year data set, perhaps because fishing pressures varied among species, or simply because the survey data contain too much error. Consistently top-ranked species (high average yield and low *CV*) were mostly periodic strategists (Winemiller 1992; Winemiller & Rose 1992). The periodic strategy is associated with high compensatory reserve, but these species tend to show high inter-annual recruitment variation with poor conformity to stock–recruitment models (Winemiller 2005).

Migratory fishes are conspicuous ichthyofaunal components of large tropical rivers worldwide, and these species exploit seasonal variation in channel and floodplain habitats for spawning and feeding (Lowe-McConnell 1987; Winemiller 1989; Winemiller & Jepsen 1998). In fluvial ecosystems, migratory fishes have periodic-type life-history attributes and often display high inter-annual variation in recruitment in response to the timing, magnitude and duration of annual flood pulses (Winemiller & Rose 1992; Winemiller 2005; Tedesco *et al.* 2008). Fisheries that are dependent upon periodic strategists have the potential to be productive, because stocks could recover from overfishing rapidly during years with environmental conditions favourable for development of strong year classes (Adams 1980). However, maintenance of critical densities of adult stocks and the protection of juveniles and spawning habitats are essential for the management of long-lived, periodic species (Rose *et al.* 2001; Winemiller 2005).

The decline of major carps and other large, valuable species in catches from the middle Ganges has resulted in higher percentages of smaller species being landed (Payne & Temple 1996). The same pattern has been observed in other reaches of the River Ganges (Payne & Temple 1996; Sinha & Khan 2001; Payne *et al.* 2003) as well as in other tropical river fisheries (Welcomme 1975; Petrere *et al.* 2005). Fish species with an opportunistic life-history strategy (small size, early maturation, continuous and high reproductive effort, and short life span) appeared in all three of the groupings identified as extreme patterns of relationship between average monthly yield and variability of yield (Fig. 3). Because small fishes with opportunistic life histories tend to have relatively low economic value in most large-scale fisheries, they generally receive little attention from scientists and managers. Research on other Asian rivers with longstanding fisheries has revealed a tendency for large fishes with periodic-type life-history strategies to be replaced by smaller species with opportunistic-type strategies (Arthington *et al.* 2003). These shifts in fishery catches may reflect the composition of fish communities in floodplain habitats where fishing efforts increase after main channel stocks are depleted. As a result of their small size and ability to colonise newly formed aquatic floodplain habitats, opportunistic strategists have high demographic resilience. Some of these small species maintain viable populations in ephemeral, marginal habitats, whereas others persist in larger, permanent habitats where predation may at times be intense (Winemiller & Rose 1992; Winemiller 2005).

Only two species with an equilibrium-type life history (*Channa punctata, Chitala chitala*) ranked among the top 30 species in the Bhagalpur commercial fishery. Other equilibrium species, all of them exhibiting nesting and brood-guarding behaviour, ranked lower in terms of average annual yields (*Channa* species, *Clarias batrachus*, *Hepteroneustes fossilis*, *Anabas testudineus* and *Colisa fasciata*). Populations of equilibrium strategists are expected to be responsive to density-dependent environmental factors but with relatively low compensatory reserve (Winemiller 2005). Collectively, these eight equilibrium-type species comprised 1–5% of annual average yield in terms of biomass.

Environmental conditions and seasonal catches

Water quality of the River Ganges varies spatially and seasonally in response to watershed geology, topography, vegetation and hydrology (Singh 2007). pH values in the current study tended to be lower than those (7.3–8.8) reported by Sinha and Khan (2001). Water transparency was low, especially during the monsoon season, as expected because of the high concentration of sediments carried by the River Ganges. Low transparency reduces light penetration, which in turn limits algal production even when inorganic phosphorus and nitrogen are available as nutrients (Dokulil 1994). Most of the dissolved-oxygen values reported here for the middle River Ganges at Bhalgapur were below the India's water quality standards (Ref. IS 10500-1991). A general improvement in DO (4.7–8.0 mg L^{-1}) in the middle River Ganges (between Patna and Rajmnhal) from 1985 to 1990 was reported by Sinha and Khan (2001), but as shown here, lower levels still occur on a seasonal basis. Concentrations of dissolved PO_4 and NO_3 were relatively low compared with values recorded during the 1960s at Bhagalphur and Patna (Jhingran & Ghosh 1978) and at Patna and Allahabad (Khanna 1993). Domestic, industrial and agricultural wastes from local watersheds continue to flow into the River Ganges (Mukherjee *et al.* 1993). Local effects of this pollution vary seasonally because the river's enormous discharge during the monsoon (70–80% of annual rainfall is between July and September) dilutes and transports nutrients and other pollutants (Raj & Azeez 2009).

The multivariate statistical analysis revealed an association between low transparency and high DO and the yield and species assemblage structure of the catch during the monsoon (rising water) and winter (falling-water) seasons of 2003–2004. Species with relatively high yields during the monsoon and winter seasons of 2002–2004 included *W. attu*, *C. mrigala*, *S. aor*, *C. catla* and *L. bata*. In the River Ganges, the beginning of the monsoon and winter are accompanied by an increase in turbidity because of sediment delivery in runoff (Singh 2007). Rapidly changing environmental conditions during the monsoon induce behavioural changes in certain fish species, including large carps and catfishes that migrate upstream to spawn, thus making them more vulnerable to certain capture methods (Payne & Temple 1996). During the monsoon and winter of 2006–2007, fish yields tended to be lower, particularly those of *Wallago* and the major carps, and the underlying causes for this are unknown.

Management challenges

Fishing activity is intense in the middle Ganges, and a great variety of gear types are used with little effective regulation (Chouldhary *et al.* 2006). Both for the sustainability of fisheries and conservation of the Gangetic river dolphin that depends on fish as its food resource (Kelkar *et al.* 2010), better enforcement of fishery regulations are needed in the middle River Ganges. Otherwise, catches will continue to decline and the composition will shift further from large fish species towards smaller opportunistic species with greater demographic resilience. Activities other than fishing are likely also impacting fish stocks and aquatic habitats of the middle River Ganges. Irrigation, channel modification and sedimentation, among other factors, have damaged spawning grounds and reduced fishery yields in the middle River Ganges (Sinha & Khan 2001). Pollution from domestic, industrial and agricultural sources continues to be a serious problem (Agnihotri *et al.* 1993), and several water quality parameters were seasonally correlated with species composition of the catch. The Farakka Barrage disrupts longitudinal connectivity of the fluvial ecosystem and changes the flow regime downstream.

Before new dams are planned for other rivers in the basin, requirements of migratory species and influences on flow as a driver of ecological dynamics need to be assessed carefully (Arthington *et al*. 2003; Welcomme 2008).

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