

5 Dynamics of Floodplain Fish

5.1 Introduction

This central chapter of the report outlines the research results on the dynamics of floodplain fish. The chapter begins by looking at the spatio-temporal variability in the productivity of the two study sites. Following this, each stage of the productive cycle is considered in detail, in an attempt to *explain* the observed differences in productivity, and demonstrate the impacts of FCD/I schemes, and the implications of different fishery management approaches.

The 'explanatory variables' covered in this chapter include the abundances of fish, and the resulting overall community structures, followed by the detailed components of the life history ecologies of six key species of fish at each study site. Each stage of the life history is covered in turn, from recruitment, feeding and growth rates, reproduction and mortality, and finally to migration cycles and dry season survival strategies. This investigation into the productive potential of impounded floodplains thus considers both their accessibility to floodplain fish, and their productive capacity for those fish present.

The chapter is self-contained, but includes material from the PhD and its Sub-Projects 2 and 4 (Appendices D and F), and also from Sub-Projects 1 and 3 (Appendices C and E). The analysis is far more thorough for the Bangladesh study site, where the Biological Surveys and Sub-Projects were carried out, but comparative material is also presented for Indonesia wherever possible.

5.2 Spatio-Temporal Variability in Productivity

This section examines the spatio-temporal variation in productivity at the two study sites. At the Bangladesh site, floodplain areas of the 'Inside' and 'Outside' study regions were available from the detailed mapping of location codes, obtained by ground truthing with GPS technology (Section 3.4). This approach was made possible in Bangladesh by the many roads and paths crossing the floodplains, but was prevented in Indonesia due to the inaccessibility of the unpopulated Lempuing floodplains.

Productivity is therefore measured for the Bangladesh site as catches per unit area (CPUA), and compared both spatially, inside and outside of the FCD/I scheme, and temporally, across the two study years. In Indonesia, productivity is simply measured as the total catches of the three study regions, and only compared across the years.

5.2.1 Spatio-temporal variability in productivity - Bangladesh

As shown below, total annual productivity in Bangladesh, measured as catch per unit area, was higher in the Outside region than the Inside region, and higher in 1996 than in 1995.

<u>Region</u>	<u>1995</u>	<u>1996</u>
Inside	51 kg/ha/yr	81 kg/ha/yr
Outside	104 kg/ha/yr	130 kg/ha/yr

Outside catches particularly exceeded those Inside over the 1995 flood season (July to November 1995), and during the following dry season up to June 1996 (Figure 5.1). Productivities over the 1996 flood season were more similar between the two regions, showing a relative increase in Inside catches, though October and November catches were again higher Outside.

Though the PIRDP study site was selected for the nominal similarity of its Inside and Outside floodplains, part of the observed differences in fish catches may be due to habitat differences between the regions. As discussed further in Chapter 6, the low catch in the Inside region reflects the relative absence of catches from *beel*, floodplain and canal habitats (Figures 6.7, 6.8, Chapter 6). This absence may be partly due to the lack of *beels* or canals inside, or - more likely - to sampling errors if the respondent fishermen simply did not fish these habitats. Field staff also noted that the inside floodplains were more used for rice production, which inhibited the use of certain gears such as seine nets on the floodplains.

5.2.2 Temporal variability in productivity - Indonesia

In Indonesia, catches varied significantly between the two study years, with the 1995 flood season producing a high total catch of 1183t, and '96 producing a reduced catch of only 718t. The 1996 season was thus only 61% as productive as 1995, with catches being particularly reduced to only 51% in both the Lake and Forest regions, and being maintained at 75% in the Savanna river region (Figure 5.2).

5.3 Fish Abundances - Bangladesh

With CPUA productivities at 60-104% greater in the Outside Bangladesh floodplains, compared to Inside², it was hypothesised that relative fish abundances could explain the additional productivity detected outside. As a measure of overall fish abundances (all species combined), overall catches per unit effort (CPUE) were thus calculated on a monthly basis for each different gear type. Average CPUE ratios³ were then estimated among the four regions for comparison of fish abundances (since CPUE does not involve any area term, all four regions can be compared):

1995 Abundance Comparisons

Comparison	Ratio	Confidence Interval	n	Implication
In / Out	0.83	0.63 - 1.10	25	Outside 20% > Inside
Adj / Out	0.95	0.55 - 1.64	20	Outside _ Adjacent
In / MR	0.55	0.34 - 0.89	12	Main River 82% > Inside
Adj / MR	0.89	0.24 - 3.26	6	Main River 12% > Adjacent
Out / MR	0.79	0.52 - 1.19	17	Main River 27% > Outside
Adj / In	1.43	0.74 - 2.77	17	Adjacent 43% > Inside

These average ratios are imprecise, with five of the six confidence intervals including unity (indicating no significant difference). The overall picture, however, is internally consistent. The Main River CPUEs, for instance, are higher than for all the other regions, while the Outside CPUEs are higher than the Inside ones. The overall impression is quite clearly that CPUEs were higher outside the FCDI scheme in 1995, particularly in the Main River. Assuming that the gears are equally effective wherever they are fished, these results suggest that the overall fish community was more abundant Outside in 1995.

In 1996, effort levels were more similar inside and out (18% higher outside - Chapter 6), and outside CPUAs exceeded inside ones by only 60%, compared to the 104% seen in 1995. This shift in direction may also be explained by the overall fish abundances which changed in 1996, as shown below:

1996 Abundance Comparisons

Comparison	Ratio	Confidence Interval	n	Implication
In / Out	1.28	0.85 - 1.95	22	Inside 28% > Outside
Adj / Out	1.19	0.71 - 2.01	21	Adjacent 19% > Outside
In / MR	1.55	0.73 - 3.31	16	Inside 55% > Main River
Adj / MR	0.69	0.22 - 2.14	11	Main River 45% > Adjacent
Out / MR	0.81	0.43 - 1.48	19	Main River 23% > Outside
Adj / In	0.98	0.60 - 1.59	22	Adjacent _ Inside

In 1996, CPUEs in the Main River were thus again higher than the Outside and Adjacent regions, but Inside CPUEs were higher than both the Outside and Main River ones. Though these figures are again very imprecise, they suggest a significant shift in relative fish abundances, compared to those in 1995.

² A greater difference than can be explained by fishing effort - see Chapter 6

³ Average calculated on log-transformed data within gear-month categories only to avoid seasonal variations in catchability; with approximate 95% confidence interval (CI) calculated as +/- 2*SE, before back transformation.

5.4 Fish communities

5.4.1 Introduction

Tropical fish communities are noted for their high diversity (Lowe-McConnell, 1987). The floodplain river systems in Bangladesh contain more than 260 species of teleost fish within 145 genera and 55 families (Rahman, 1989). Fish communities are influenced by biotic and abiotic factors which are continually changing through space and time. These changes may occur gradually, for example in response to geomorphological change (land form and levels), climatic change or more rapidly in response to anthropological effects such as pollution, exploitation and hydraulic engineering (Lowe-McConnell, 1987).

Bearing in mind this high natural variability, this section compares the fish community structures between different locations, in an attempt to determine the likely accessibility implications of FCD/I schemes. An initial section describes the different types of fish species found in floodplain river systems. Fish communities are then compared across the whole of Bangladesh, using the data recorded by FAP17 (FAP17, 1994a). Subsequent sections examine the local fish communities within the project study regions in both the Pabna and Lempuing sites.

5.4.2 Categories of Floodplain Fish Species

Species inhabiting floodplain-river systems have been categorised into two ecologically distinct groups based largely on their behaviour in response to seasonal changes in the floodplain environment (Welcomme, 1985):

- **Whitefish**

Species belonging to this category are generally reophilic, inhabiting rivers and other fluvial bodies. The majority undertake seasonal spawning and/or feeding migrations either longitudinally (upstream) or laterally onto the floodplain, or a combination of both. Longitudinal migrations may be upstream or downstream; some are local covering only small distances, others, usually upstream, may be substantial. Upstream spawning locations offer a number of advantages, including higher dissolved oxygen concentrations and fewer predators. Furthermore, the duration of the downstream drift of developing fry may take several weeks allowing time for individuals to grow beyond a size which is particularly vulnerable to predation. Fry may move onto the floodplain either passively or actively, or in the case of the anadromous *Hilsa ilisha*, be swept downstream to the sea. Adults of other species often return, usually before the eggs and young, to downstream floodplain habitats soon after spawning to take advantage of the rich feeding. Lateral migrations are active rather than passive and in an ordered sequence of species when returning to the main channel. Whitefish species are generally intolerant of the extreme conditions that exist in the floodplain habitat during the dry season (low oxygen and pH levels and high temperatures) and hence they must undertake lateral migrations to fluvial environments each year (Welcomme, 1979; 1985; Ward and Stanford, 1989).

- **Blackfish**

Species belonging to this category are generally limnophilic, 'still-water fishes' (MRAG, 1994a). Because their migrations between wet and dry-season habitats are limited, they are normally confined to the floodplain habitat, dispersing within it during the flood to spawn and feed and inhabit residual water bodies during the dry season. At most, their migrations are lateral to fringes of main channel. Many species are adapted to surviving low oxygen concentrations, high temperatures and even desiccation (see Welcomme, 1985; Lowe-McConnell, 1987 for reviews).

- **Greyfish**

This black/white categorisation has been extended by Regier *et al* (1989) to include 'greyfish' species. 'Greyfish' species inhabit backwaters or the fringes of the main channel during the dry season and undertake lateral migrations to the floodplain for feeding and spawning. However, unlike 'whitefish' species, they are capable of residing on the floodplain during the dry season if suitable conditions prevail. Species of fish are often also classified according to the main processes which control their populations; the intrinsic rate of population increase and the environmental carrying capacity (the parameters r and K of the logistic population model).

- **r -selected Species**

The ' r -selected' species are characterised by their small size, short-lifespan, rapid growth, early maturity, high fecundity and high natural mortality rates (Pitcher and Hart, 1982). Their populations rely on the ability

to colonise new habitats and increase rapidly to exploit unpredictable environments (for example, inundated floodplain habitat). A consequence of these 'life history characteristics' is that their populations contain few age-groups and are intrinsically variable, 'tracking' the environmental variation. They can sustain high levels of exploitation but are susceptible to sudden collapse. Their small size makes them less mobile.

- **K-selected Species**

Conversely, *K*-selected species are generally regarded as large, slow-growing, long-lived species, maturing later in life and usually being less fecund. These species also tend to exhibit lower natural mortality rates. Their populations contain several age-classes and are therefore less susceptible to sudden collapse, but they cannot sustain heavy exploitation. They are unable to take advantage of favourable environmental conditions but are better suited to surviving long periods of adverse conditions. (Garrod and Knights, 1979; Pitcher and Hart, 1982).

Size is seen as the most important trait of an individual's life history and hence a good indicator of its position within the 'r/K spectrum'. As size decreases, metabolic rate per unit weight increases, leading to a decrease in longevity. The size of an organism has also been shown to be strongly positively correlated with its generation time and equally strongly negatively correlated with its intrinsic growth rate (Begon and Mortimer, 1986).

5.4.3 Catch species composition - Bangladesh

This section summarises the differences between 'inside' and 'outside' fish communities across the whole of Bangladesh, as revealed by analysis of the FAP17 catch database (see Appendix J for full details).

Initial studies confirmed as expected that species communities in Bangladesh exhibit dissimilarities both between geographical region and habitat type.

In addition to the regional and habitat variability, fish caught in inside and outside floodplain/beel sites in the NW and NE of Bangladesh were also found to be significantly different ($p < 0.05$). There was no evidence that fishing intensity was responsible for these differences. Instead, the patterns were better explained in terms of the migratory behaviour of the fish assemblages. FCD/I schemes appear to act as obstacles to migrations and movement and thereby reduce the abundance of large, migratory, high value, whitefish species including the highly prized Indian major carp species, in favour of small, low value, resident, blackfish and greyfish species. The inside species are mostly of the *r*-selected, rapid response type.

Though significant differences were detected as described above, FCD/I schemes in Bangladesh did not exclude all migratory species, rather they simply reduced their abundance. This implies either that sluice gates and other 'regulators' do allow some access to impoundments across embankments or that the migratory species are able to survive inside.

Due to the low values of the small fish species most common inside FCD/I schemes, the unit value (Tk/kg) of the fish communities was 20% lower in fully functioning schemes and 6% lower in partially functioning schemes. Despite these losses in value, the nutritional value of the fish communities inside modified sites may actually be higher, because the small species are generally eaten whole (see Appendix J).

5.4.4 Catch species composition - PIRDP study site, Bangladesh

- **Numbers of fish species**

At the Bangladeshi PIRDP study site, a total of 92 different fish species were recorded during the two year investigation, not including crustacea (Table 5.1). Slightly more fish species (not including the abundant shrimp families, found in all regions) were caught outside the FCDI scheme than inside:

Region	Number of species sampled in:	
	1995	1996
Adjacent	46	47
Inside	62	74
Outside	69	76
Main River	37	66

The above data suggest that more fish species were caught in 1996 than in 1995, but this difference may also reflect the taxonomic expertise gained by the field staff during the project. The low species counts from the Adjacent regions also reflect the low sampling effort applied to that region, with only around one fifth of the samples taken in the Inside region.

Bearing in mind that the sampled parts of the Adjacent and Inside regions may be less habitat-rich than the Outside one (having mainly *beel* and riverine habitats respectively - see Chapter 6), a combined species total for both inside regions still only gives 64 fish species to compare with the 69 found in the Outside waters in 1995. In 1996, 74 fish species were caught in both the inside regions, compared with the 76 from Outside. As might be expected, with its single habitat type, the Main River was the least rich of the four regions in 1995. However, combining the Main River with the Outside region produces a total of 73 and 80 distinct fish species caught outside the FCDI scheme in 1995 and '96 respectively, compared with the 64 and 74 inside.

- **Species compositions**

Considering next the relative species compositions of the regional catches, the Inside and Outside regions produced a similar diverse mixture of fish species in both 1995 (Figure 5.3) and 1996 (Figure 5.4). Species commonly found in both these regions included *Channa punctatus*, *Puntius sophore*, *Wallago attu* and shrimps. *Channa striatus* formed the main catch Inside in 1995, while *Wallago attu* was particularly common Outside in 1996. The Adjacent region appears to differ from the other two floodplain regions, having reduced communities more dominated by the *beel*-resident blackfish *Channa punctatus* and *Puntius sophore*. In clear contrast, the Main River region is overwhelmingly dominated by the single species *Hilsa ilisha*, and also contains the riverine catfish *Pangasius pangasius*, absent from the three other regions.

The abundances of individual species were compared between the Inside and Outside regions (for which the most data exist) using the average CPUE ratios for gears sampled in the same months in both regions.

Among 18 species in 1995 and 19 species in '96 with six or more (maximum 18) gear-month pairs to estimate an average CPUE ratio from, the following species were more than twice as abundant in the regions indicated:

Year	> Twice as abundant Inside	> Twice as abundant Outside
1995	<i>Anabas testudineus</i>	<i>Catla catla</i> , <i>Glossogobius giuris</i> , <i>Labeo rohita</i> , <i>Mystus vittatus</i> , <i>Wallago attu</i> , shrimps
1996	<i>Colisa fasciatus</i> , <i>Chanda nama</i> , <i>Lepidocephalus guntea</i> , <i>Mastacembelus pancalus</i> , <i>Xenentodon cancila</i>	<i>Cirrhinus reba</i> , <i>Pseudeutropius atherinoides</i> , <i>Wallago attu</i>

In overall terms, these results confirm - as found above for Bangladesh as a whole - that the small, floodplain-resident species are more common inside the FCDI scheme, while the major carps and riverine catfish predators are more common outside. Comparing the years, the figures show that the increase in abundances in the Inside region in 1996 was attributable to the smaller floodplain species, which presumably recruited well in the large floods of both 1995 and 1996.

Fish abundances could not be reliably compared between the Inside and Main River regions due to the lack of gear-month-species combinations to examine. It is however very likely that the common *H. ilisha* is far more abundant in the main river than inside the FCDI scheme.

5.4.5 Catch species composition - River Lempuing study site, Indonesia

- **Numbers of fish species**

At the unmodified Indonesian study site, a total of 42 different fish species were recorded including some family groups (Table 5.2), the most downstream Savanna River habitat region was found to be the most species rich in both study years:

Region	Number of species sampled in:	
	1995	1996
Lake District	27	29
Forest River	28	30
Savanna River	37	34

While the downstream river habitat may be more species rich, the differences between regions may also be partly due to the sampling effort applied by field staff: 154, 243 and 477 catch composition (CE3) samples were taken from the Lake district, the Forest river and the Savanna river respectively. The small differences observed between the two study years were not considered to be significant.

The relatively lower numbers of fish species at the Indonesian study site, compared to Bangladesh, may be due to the smaller size of the Lempuing River, or more likely to the relative taxonomic rigour applied by the field staff in each country (in Bangladesh, only 0.5% of the total recorded catches were identified as 'other' species, compared to 5.9% in Indonesia).

- **Species compositions**

As expected, species compositions showed notable differences between the Indonesian habitat study regions (Figures 5.5, 5.6). Certain species, such as *Pristolepis fasciatus*, *Pangassius micronema*, *Rasbora* spp and *Thynnichthys polylepis*, were most common in the Lake habitat region. Other species, including *Cryptopterus* spp, *Mystus nemurus*, *Macrobrachium rosenbergii* and *Wallago leeri* were more found in the riverine habitats, and only occasionally found in the Lake region. Within the riverine species, some species also showed longitudinal preferences: *Dangila ocellatus*, *Osteochilus hasselti* and *Trichogaster trichopterus* were most common in the upstream Forest river region, while *Trichogaster pectoralis* and *Mystus nemurus* were most common in the Savanna river region. Certain species, including *Channa striatus* and *Helostoma temmincki* showed no consistent habitat preferences, being found in all three habitat types.

Between the two study years, the species compositions remained broadly similar in the two riverine regions. In the Lake region, however, the 1996 catches became dominated by *Channa striatus*, *Helostoma temmincki* and *Thynnichthys polylepis* (Figure 5.6), with several other species being relatively reduced from their 1995 levels (Figure 5.5).

Notably, two of the most valuable species of the River Lempuing, *Notopterus chitala* and *Osphronemus gurami* were not recorded in any of the 1995 or '96 catches. These two fish species were recorded in the 1993 samples of ODA Project 4791 (MRAG, 1994a), in very small numbers, and must now be considered extremely close to local extinction.

5.5 Recruitment dynamics

The recruitment of fish means the arrival of the new year class or cohort of fish into the fishery. The magnitude of each year's recruitment indicates the success of spawning and of the early survival of eggs, larvae and fry before they enter the fishery. High levels of recruitment are thus vital to maintain the productivity of any fishery. In Bangladesh, some changes in the annual levels of recruitment are qualitatively indicated by the higher overall abundances in 1995 and the increases in abundance of the smaller fish species in 1996.

Unfortunately, due to high levels of environmental noise, the relationship between recruitment and the exploitation of the stock is also usually the least well understood component of the population dynamics of any given species. For multispecies stocks, recruitment success varies between species, and to some extent, different species balance each other out so that overall recruitment may remain high, even though species compositions change between the years.

This section presents results on the stock-recruit relationship for one species *P. sophore*, obtained during field experiments at BAU, Mymensingh. Material is then presented on the seasonality of recruitment, to improve the understanding of the seasonality of reproduction. Finally, the relative importances of different sources of recruitment are considered for floodplain regions inside impounded FCD/I schemes.

5.5.1 Stock recruit relationship of *P. sophore*

The experiment undertaken to examine the effect of density (intraspecific competition) on the growth of *P. sophore* (Appendix F) also yielded important information on the recruitment dynamics of this species under different stock sizes. This information is reported in detail elsewhere (Halls, PhD thesis), but the main conclusions are given here.

The relationship between the spawning stock size (numbers of eggs) and subsequent recruitment in unfertilized ponds suggested that a Ricker (1954) stock-recruitment model best fitted the data (Figure 5.7). In this relationship, recruitment is increased when the densities of fish are reduced, implying that *P. sophore* are able to compensate for low fish abundances experienced during extreme dry seasons. In the small stock ponds, the estimated numbers of eggs at the start of the experiment ranged from 16,000 to 2.3 million, while the subsequent recruitment varied between 175 and 7,500 fish!

For those *P. sophore* held at the lowest densities in fertilized ponds, recruitment was much increased over the levels observed in the unfertilised ponds (Figure 5.8). A highly significant ($p < 0.001$) relationship was thus found between recruitment and pond productivity, measured as chlorophyll concentration. As noted in Section 5.7.5, some of the *P. sophore* spawned at the start of the experiment in these ponds were able to grow to sexual maturity and spawn themselves within only 12 weeks of hatching! These observations suggests that species such as *P. sophore* are well adapted to respond rapidly to seasonal conditions on floodplains, and that recruitment success may even be increased when long droughts increase floodplain fertility levels due to decomposition.

5.5.2 Seasonality of recruitment

The seasonality of recruitment was investigated by simple examination of the bi-monthly samples of length frequency data collected from the fisheries. New recruits were identified as the smallest fish seen in length frequencies, which were subsequently seen to grow steadily from the length frequency samples in the following months.

- **Bangladesh**

Fish recruitment in Bangladesh was observed to occur in July of 1995 and '96 for *Anabas testudineus* (Figure 5.9), *Catla catla* (Figure 5.10), *Channa striatus* (Figure 5.11) and *Wallago attu* (Figure 5.14); and to occur slightly earlier with the early flood in May 1996 (Figure 4.7) for *Glossogobius giurus* (Figure 5.12) and *Puntius sophore* (Figure 5.13). The latter two species are thus identified as *r*-selected, small species, having particularly quick responses to early flooding events.

Fish in Bangladesh recruit at very small sizes, as little as 1-2cm, due to the small mesh sizes in the fishery. They must therefore be recruited into the fishery almost immediately after spawning, suggesting that spawning takes place during the May-July flood season.

- **Indonesia**

The Indonesian length frequency data showed that all of the five key *fish* species recruited most strongly in January of each year (Figures 5.15 to 5.18, and 5.20). A handful of very small *Mystus nemurus* were also recorded in the riverine barrier catches in November of each year (Figure 5.18). *Channa striatus* also recruited over an extended period from September 1995 to January 1996 (Figure 5.16), possibly reflecting the mid-drawdown re-flood event experienced in July 1995 (Figure 4.4a).

The giant freshwater prawn, *Macrobrachium rosenbergii*, in contrast, recruited before the fish species in November in both study years and also in July 1995, presumably, like *Channa striatus*, also in response to the early reflooding in that month.

In Indonesia, fish recruit at a slightly larger size than in Bangladesh, due to the relatively larger mesh sizes in use. The smallest recruits measured from fish catches were 9cm long for *C. striatus*, and 3-4cm long for the other fish, though most recruits were at least twice this size. Recruitment for these fish species is then approximately 2-3 months behind the start of the flood season, and a more immediate 1 month or so after the floods for the prawn *M. rosenbergii*.

5.5.3 Sources of recruitment in unmodified floodplains

The length frequency data for the Indonesian key fish species was mostly insufficient to draw strong conclusions on spatial differences in recruitment sources, due to the small sample sizes in the Lake and Forest regions. It was tentatively observed, however, that *H. temmincki* and *O. hasselti* both recruited strongly in both the Lake and the riverine regions (Figures 5.17 and 5.20), while *C. striatus* and *M. nemurus* both recruited mainly in the downstream Savanna river region (Figures 5.16 and 5.18).

A clearer pattern was observed for the giant prawn *M. rosenbergii*. This species was never found in the Lake habitat region, and appeared as new recruits in November and after the July '95 reflooding in the downstream Savanna river. In the following months, January and March, larger prawns were then detected in the upstream Forest river region. This pattern is in agreement with the estuarine spawning behaviour generally reported for *Macrobrachium* species (see further discussion in section 5.11).

5.5.4 Sources of recruitment inside modified floodplains

In Bangladesh, fish of all species clearly recruited both inside and outside the FCD/I scheme at the same times (Figures 5.9 to 5.14). In May 1996, *Puntius sophore* even recruited inside the FCD/I scheme in response to the early 1996 flood, when it had not yet recruited outside (Figure 5.13).

Further information on recruitment sources in Bangladesh is available from the Sub-Project studies on dry season waterbodies (Appendix C) and sluice gates (Appendix E). The first Sub-Project indicated that approximately 0.6-2.2 tonnes of fish survived over the dry season in the deepest floodplain waterbodies inside the FCD/I scheme, compared to 2.9t outside (not including survival in the main river). Such Inside survivors were nearly all maturing adults, which would have gone on to produce many more tonnes of young fry with the new flood.

For comparison, the sluice gate Sub-Project indicated that approximately 0.9-4.0 tonnes of young fry migrated passively in to the FCD/I scheme mostly during July and August of the 1996 flood season. In comparison to the similar weight of pre-spawning fish remaining in the dry season waterbodies in May, this weight of immigrant fish later in the year was comprised of already spawned fry. Assuming that the Inside spawners do reproduce many times their own weight of fry, the relative contribution of the inside sources of recruitment is likely to be substantially greater than those from outside. This conclusion - that modified floodplains may be largely self-recruiting - is supported by the catches in the 1995 flood season. The 1995 Inside catches, though not as good as those Outside (Figure 5.1) were achieved even with the main Talimnagar sluice gate being closed for virtually all of the 1995 flood season (Figure 4.6).

Though fish survival in dry season waterbodies may thus provide the bulk of recruitment in modified floodplains, both inside and outside sources of recruitment are nevertheless thought to be important. Species compositions in the dry season waterbodies were shown to become depleted towards the end of the dry season, presumably as the less hardy species became unable to tolerate the increasingly anoxic conditions (see Appendix C). Recruitment from outside the FCD/I scheme is then likely to be of key importance for maintaining the biodiversity of stocks inside. The relatively higher catch in the Inside region in the 1996 flood season, compared to Outside (Figure 5.1) may also partly reflect the much more open sluice gates in that year (Figure 4.7).

5.6 Feeding dynamics - Bangladesh

5.6.1 Introduction

Both the quantity and the quality (nutritional and energy value) of food available to floodplain fish have the potential to affect their growth rates and productivity. In this section, the relative feeding rates - and their seasonality - and the diet composition of the key species is therefore compared between the Inside and Outside sampling regions in Bangladesh.

In the routine biological surveys, a semi-quantitative 'points' method was used to determine stomach fullness and diet composition (Appendix A), as recommended by Hyslop (1980) and Wootton (1990). The method used was based upon a subjective allocation of points firstly for stomach fullness (the stomach fullness index - SFI - ranging from 0 to 10 for full), and then by subdividing the contents by each food category in proportion to their visually estimated contribution to the total. Though food intake depends on digestion rates (not measured and probably seasonally variable following mean temperatures) as well as stomach fullness, the SFI was interpreted as a rough index of feeding differences between the different

months and areas.

5.6.2 Spatial variability in diet composition

As discussed in the following paragraphs, and shown clearly in Figures 5.21 and 5.22, the diet compositions varied significantly between the key species, but showed very little differences inside and outside the FCDI scheme.

- **Diet of *A. testudineus***

Insects form the bulk of the diet of *A. testudineus*, both inside (45%) and outside (46%) the FCDI scheme (Figure 5.21). Mud is also important, forming 31% and 25% of the diet for the inside and outside locations, respectively, though this may be ingested accidentally. Crustacea (shrimps), fish (including *Puntius* species), algae, higher plants, molluscs and phytoplankton are also present, each forming less than 4% of the diet in both sampling locations. Mud forms a marginally higher proportion of the diet inside the FCDI, replacing seeds and phytoplankton which are more prevalent in the diet outside the FCDI scheme. Other than this small difference, diet composition is very similar in both sampling locations.

- **Diet of *C. catla***

In descending order of mean percentage stomach volume, the diet of *C. catla* comprises zooplankton, algae, mud and phytoplankton (Figure 5.21). The relative contributions of each of these items is very similar in both sampling locations except for algae which forms approximately 18% of the diet inside compared to 11% outside. This difference is balanced by a 7% larger unidentified proportion of the diet.

- **Diet of *C. striatus***

The diet of *C. striatus* in both sampling locations is dominated by fish (73% inside and 72% outside) (Figure 5.21) including *Chanda ranga*, *Chanda nama*, *Chanda baculis*, *Channa punctatus*, *Colisa fasciatus*, *G. giuris*, *Puntius* species, *Mastacembelus pancalus*, *Mystus* species and *Xenentodon cancila*. Insects, crustacea (shrimps and crabs), amphibians (frogs) and algae form less than 6% of the diet in both locations.

Mud, water and higher plants are also present, perhaps ingested unintentionally with target food items. Insects form marginally more of the diet (6%) compared to inside (3%) as do crustacea which form 4% of the diet outside compared to 3% inside. Other than these very small differences, the diet composition is the same in the two locations.

- **Diet of *G. giuris***

Glossogobius giuris is also largely piscivorous in both sampling locations (Figure 5.22). Fish species form 82% of the diet inside compared with 80% outside the FCDI scheme. In addition to being cannibalistic, *G. giuris* consumes a highly diverse range of species including *Amblypharyngodon mola*, *Brachygobius nunus*, juvenile *C. catla*, *Chanda ranga*, *Chanda nama*, *Channa punctatus*, juvenile *Labeo bata* and *Labeo rohita*, *Mystus cavasius*, *Mystus tengra*, *Mystus vittatus*, *Puntius conchoniis*, *Puntius gelius*, *P. sophore* and *Puntius ticto*. The remaining components of the diet comprise mainly crustacea (shrimps) in very similar proportions inside (15%) and outside (14%) the FCDI scheme.

- **Diet of *P. sophore***

Algae, zooplankton, phytoplankton and mud are the most important components of the diet of *P. sophore* (Figure 5.22). The relative proportions of these components are very similar between the two sampling locations. The only significant divergence between the two locations is for phytoplankton, which forms marginally more of the diet inside (16%) compared to outside (10%).

- **Diet of *W. attu***

Wallago attu is mainly piscivorous, but outside the FCDI scheme, this species also consumes amphibians (frogs) in small quantities (Figure 5.22). Fish form a larger component of the diet inside (67%) compared to outside (61%) as do crustacea (shrimps) which form 4% inside and 2% outside. Species of fish consumed by *W. attu* include *Ailia coila*, *Chanda nama*, *Chanda ranga*, *Clupisoma garua*, *Corica sorborna*, *Cyprinus carpio*, *G. giuris*, *Labeo rohita*, *Labeo bata* and *Labeo guntea*, *Mastacembelus pancalus*, *Mystus cavasius*, *Mystus tengra*, *Mystus vittatus*, *Ompok pabda*, *Puntius conchoniis*, *Puntius gelius*, *P. sophore*, *Tetradon cutcutia*, and juvenile *W. attu*. Assuming that the other main components (water, mud and higher plants) are non target food items, consumed whilst taking prey items, then the combined prey items comprise a slightly larger proportion of the diet inside (71%) than outside (68%).

5.6.3 Spatio-temporal variability in feeding rates

Feeding intensity varied significantly between the key species, as described in the following sections.

The number of stomach fullness samples recorded in each month varied due to availability, both among species and between sampling regions. In some months, no samples were available, particularly for *C.catla* and *G.giuris*. In other months, the target sample size (24 fish) in each sampling region was exceeded by nearly three times. In the figures accompanying the following text (Figures 5.23 and 5.24), mean monthly SFIs comprising based on only one fish have been excluded; the vertical bars around each monthly SFI give the approximate 95% confidence interval around the estimates, calculated as 2 times the standard error (SE) of the mean.

- **Feeding rates of *A. testudineus***

Anabas testudineus showed a consistent seasonal pattern of feeding both inside and outside the FCDI scheme (Figure 5.23). Feeding increases rapidly with the rising flood to reach peak levels which coincide with the period of floodplain inundation. Feeding then declines with the falling water to reach low levels by the end of the dry season. However, feeding does increase mid-way through the dry season (months 2 and 14) for a short period. The mean SFI is significantly higher ($p < 0.05$) outside the FCDI compared to inside, during March 1995 and June 1996. For the remaining sampling period, SFI is not significantly different in the two sampling locations. Overall, the mean SFI is generally higher during the 95/96 flood year compared to the 96/97 year.

- **Feeding rates of *C. catla***

The seasonal pattern of feeding described above is also evident for *C.catla* but less pronounced (Figure 5.23). Outside the FCDI scheme during 1995, the SFI remained relatively constant during the dry season period (months 1-5), and higher than in the two following dry season periods. Mean SFIs are consistently higher outside between months 2 - 7, but this difference is difficult to quantify given the lack of samples inside the scheme. On average, stomach fullness is higher during 95/96 compared to 96/97, particularly outside the FCDI scheme.

- **Feeding rates of *C. striatus***

Although more complex, the pattern of feeding of *C.striatus* is also seasonal (Figure 5.23). Unlike the previous two species, feeding intensity reaches a peak at two different times of the year. The first corresponds with the rising water period (months 5-9 and 19-20), which is followed by a decline in the SFI during the beginning of the drawdown (months 9-12 and 21-23). The second occurs during the latter stages of the drawdown (months 12-13 and 24). This second peak is succeeded by a progressive decline in the SFI for the remainder of the dry season (months 14-17), presumably as prey become increasingly depleted. Although there is no indication of any significant differences in mean SFI between the two sampling locations in any of the sampling months, the mean SFIs are, on average, greater during 95/96 compared to 96/97, particularly outside the FCDI scheme.

- **Feeding rates of *G. giuris***

Glossogobius giuris shows a very similar pattern of feeding to *C.striatus*, characterised by two intense periods of feeding during each flood cycle (Figure 5.24). This is particularly evident for the inside population where the SFI first peaks around month 6 (month 20 in the following year) and then again around month 13 (month 24 in the following year). The mean SFI is generally higher in each month during the 95/96 compared to 96/97, although there is no evidence that mean SFI is significantly different between the two sampled populations.

- **Feeding rates of *P.sophore***

A seasonal pattern of feeding is less pronounced in *P.sophore* but feeding intensity does increase during the flood period and is lowest towards the end of the drawdown and at the end of the dry season (Figure 5.24). However, in common with *A.testudineus*, feeding does not cease during the dry season but often intensifies for a short period between December and March. Indeed, the highest SFIs were recorded during the latter half of the 94/95 flood year dry season. Overlapping confidence intervals in every month, except month 6, imply that there are no significant differences in feeding intensity of the two populations. Furthermore, there are no obvious differences in feeding intensity between 95/96 and 96/97.

- **Feeding rates of *W.attu***

The feeding pattern of *W.attu* is not strongly seasonal but the SFIs are slightly higher during the flood season, especially during the 96/97, and generally low at the end of the each dry season (Figure 5.24). Feeding intensity is consistently higher outside the scheme between month 6 and month 17, though this

difference is not significantly different. Feeding intensity is generally higher during the 96/97 flood compared to the previous year.

5.6.4 Summary of feeding dynamics of Bangladeshi key species

Summarising the preceding sections, it is clear that no strong differences exist in the feeding potential of the Inside and Outside regions. Diets were almost identical inside and outside for all of the species investigated, and only *W. attu* showed consistently different SFIs between the two regions (see later).

Compared to these minimal spatial differences, slightly greater variation was seen in the SFIs between the two years, with the large '95 flood generally producing higher feeding rates than the '96 one.

With regard to their diet compositions, *A. testudineus* was mainly insectivorous, *C. striatus* and *W. attu* were both mainly piscivorous, *G. giurus* ate both fish and crustacea, and *C. catla* and *P. sophore* both ate mainly plankton and algae.

5.7 Growth rates - Bangladesh

5.7.1 Introduction

Growth, the total elaboration of tissue, is an important component of biological production, and often varies strongly due to both endogenous and exogenous factors. Endogenous factors include the genetic component of fish growth that ultimately limits the maximum size of a given species. The other main intrinsic factor controlling fish growth is body size, with growth rates generally declining with increasing fish size (age). Exogenous factors affecting growth are better understood, and of more relevance to this project. Growth depends largely on food availability and feeding rates and the nutritional value of the food ingested. The feeding rate itself is influenced by temperature through its effect on metabolism, and on the rate of gastric evacuation.

Feeding rates may also be influenced by the physiological state of the fish. Feeding rate or consumption may decrease or cease completely as fish become reproductively active. Predator density is also likely to affect feeding rates. When predator densities are high, prey species must be more attentive, reducing the time available for foraging (Bayley, 1988; Belk, 1993). Inter- and intra-specific competition for food will also determine feeding rates, though inter-specific competition is believed to be less important because of the inherent flexibility in trophic organisation among floodplain communities (Welcomme, 1985). Intra-specific competition is likely to be more important and will be largely governed by the density of fish. Because biomass density is known to vary significantly both inter- and intra-annually, the existence of intra-specific density-dependent growth has important implications for determining the dynamics of floodplain fish populations. Sub-Project 4 (Appendix F) investigates this subject in depth for *Puntius sophore*.

Growth is also seasonal, being fastest during the flood or high water season and slowest, often ceasing completely, during the dry season. In the Amazon floodplain, Bayley (1988) found that mean weight increments of 12 species were 60% higher during the rising water period than during the remainder of the year. Seasonality in growth has been explained in terms of changes in food availability, temperature, competition for food, fasting prior to spawning activity and "deep physiological rhythms" (Welcomme, 1985). It is difficult to distinguish the relative importance of these factors since they often occur at the same time.

In addition to the inherent intra-annual variation described above, the growth of floodplain fish often exhibits significant inter-annual variation. These variations have been correlated with flooding intensity and duration, and temperature during the dry season (Dudley, 1972; Kapetsky, 1974). During exceptionally poor flood years in the Senegal river system, *Citharinus citharinus* failed to reach sexual maturity, achieving less than 50% of its normal size, resulting in recruitment failure (Welcomme, 1985). As shown in this section, fish populations at the project site are almost entirely comprised of 0+ aged fish, reaching maturity at the end of their first year. Failure to reach sexual maturity due to poor growth could thus have terminal implications for these populations.

In the following sections, the growth performance of the Bangladeshi key species is compared between both the years and the study regions, and an attempt is made to correlate the observed growth differences with explanatory factors. The factors investigated in this regard include the hydrological flood index, competition (fish density), diet composition and feeding intensity. In section 5.7.5 and Appendix F,

detailed consideration is given to the density dependence of growth for the key species *Puntius sophore*.

5.7.2 Spatio-temporal variability in growth rates - methodology

This section describes the methodology used to compare the growth performance of the six key species inside and outside the FCD/I scheme based on the analysis of length frequency and body weight data collected during routine sampling (Appendix A).

The length frequency data was collected from a number of different gear types, as seasonally available at different times of year. Since no single gear type provided sufficient data to construct a full time series of bi-monthly length frequencies for any of the species, it was necessary to combine data across different gears in each sampling period to obtain enough data for the analyses. This procedure assumes that any observed differences among length frequencies collected from different gears in each bimonthly period reflects spatial variation in the size of fish as opposed to any selectivity characteristics of the gear. Combining the data in this way should therefore provide length frequency data which approximately represents the true length structure of the population. To maximise the validity of this assumption, only the samples from the least selective gear types were aggregated, with samples from gill nets being excluded from analysis.

Initial attempts were made to model the growth of each species using the seasonal version of the von Bertalanffy growth function (VBGF) (Pitcher and Macdonald, 1973) allowing for sinusoidal variation in growth rates throughout the year. The parameters of the VBGF were estimated from the aggregated length frequency data using a version of the Electronic Length Frequency Analysis method (ELEFAN), Pauly and David (1981) in Version 4.1 of the Length Frequency Distribution Analysis (LFDA) software (Holden *et al*, 1995).

Unfortunately, this approach proved unsuccessful. Most of the distributions examined were dominated by a single mode. Growth patterns were easily detectable from this mode, but, because the parameters K (the growth rate) and L_{∞} (the asymptotic length) are negatively correlated, curves with quite different sets of parameter estimates fitted the data equally well. In the majority of cases, due to annual variability, curves could also be fitted to the growth pattern in one year but not the other. In other cases, the fitted curve failed to adequately describe growth in either year. Overall, the VBGF failed to adequately describe the growth of the key species because (i) inter-annual variations in growth were significant in most cases (ii) inter-annual variations in the time of recruitment (spawning time) were also common and (iii) the majority of distributions contained only a single mode (cohort), making it very difficult to obtain reliable estimates of K and L_{∞} . Further details on these problems, and the alternative fits for the VBGF curves for each species are given in Ashley Halls' PhD thesis.

Because of the inadequacy of the VBGF model, growth performance comparisons were instead made by comparing the mean length of fish in length frequency distributions sampled in November (\bar{L}_{Nov}).

November samples were selected for the comparison because (i) for all the species, most of the years growth is achieved by this month, after which growth virtually ceases during the dry season and (ii) two hydrologically split years (95/96 and 96/97) could be compared for which flood index and abundance data were available to assist interpretation.

This approach assumes that the length frequency distributions comprise fish of the same age. In most sampling months this assumption appeared to be well met. In cases where there was evidence of a second (1+) cohort, or of additional, unseasonal recruitment pulses, the corresponding length frequencies were omitted from the aggregated distributions.

The estimates of \bar{L}_{Nov} for the two sampling locations and for the two hydrological years were compared using two-way ANOVA. Unlike one-way ANOVA, this test allows valid comparisons of \bar{L}_{Nov} between the two factors: sampling location (inside or outside the FCDI scheme) and time (hydrological years) simultaneously, based upon the ideas of 'main effects' and 'interaction'. The main effects measure differences between levels of a factor, having been averaged over the levels of the other factor. The interaction terms measures how differences between the levels of a factor vary with the levels of the other factor (Brown and Rothery, 1993). Because of the degree of subjectivity required to estimate \bar{L}_{Nov} , the overall approach should be regarded as semi-qualitative and the results treated with some caution.

The growth performance of the key species was also compared based on their condition factors (Tesch, 1971; Wootton, 1990). Fish condition was quantified using the parameters of the fitted relationships between weight (W , in g) and length (L , in mm):

$$W = aL^b$$

The parameters of the model for each species and sampling location were estimated using simple linear regression from log-transformed pairs of length and weight data collected as part of the biological sampling programme. Data were pooled across the 24 month sampling period since there was no reason to believe that factors that might influence the condition of the species at the two sampling locations should change between years. For each species, the model parameter estimates for the two sampling locations were compared using analysis of covariance, ANCOVA (Zar, 1984; Brown and Rothery, 1993).

5.7.3 Spatio-temporal variability in growth rates - results

- **Growth in length**

Though sample sizes were variable, due to seasonal availability, the aggregated length frequency data from the non-selective gear types (Figures 5.9 to 5.14) proved more than adequate to reveal the patterns of growth for each species in the two sampling locations.

The length frequency distributions of all the key species except *Glossogobius giurus* are thought to be dominated by a single mode (cohort) which increases in mean length over the course of the year, as typical of intensely exploited, short lived species (Gulland and Rosenberg, 1992). As discussed in section 5.5.2, the new cohorts appear in July (or May in the case of *P.sophore*, 1996, inside, see Figure 5.13) corresponding to the time of floodplain inundation, before, or just after, the previous cohort disappears. This pattern is consistent with the growth of a single cohort.

The pattern shown in the distributions for *G.giuris* is less clear. A single mode dominates the distributions for most of the year with the new cohort appearing between July and September which is largely consistent with the other key species. However, much larger fish appear in the distributions between May and September (Figure 5.12). It is unlikely that these fish are the previous cohort because they are often at least twice as large as the new cohort. This runs counter to the knowledge of fish growth rates which decline with increasing fish size. For this reason, the growth of *G.giuris* may not be adequately described by the VBGF. Explanations for the patterns shown in these distributions are explored further in later sections.

In general, growth is highly seasonal, with the majority of the year's growth achieved between July and November, corresponding with the period of floodplain inundation. Very little growth occurs during the dry season, from November to April (Figures 5.9 to 5.14).

The results of the empirical ANOVA test on the differences in the mean length of the 0+ cohort in November (\bar{L}_{Nov}) are given in Table 5.3. For each species, the table gives the mean length for each level and factor combination, the overall means for each level, the difference in the means of the levels for each factor and the significance level of each effect, including interaction. Both main effects were significant for all the species except *A.testudineus* and *G.giuris* for which the location and year effects were not significant ($p > 0.05$) respectively. Interaction between the location and year factors was significant ($p < 0.05$) for all the species examined except *A. testudineus*.

With the exception of *G. giuris*, \bar{L}_{Nov} for all the key species was significantly ($p < 0.0001$) larger in the 95/96 hydrological year compared to 96/97. Differences in \bar{L}_{Nov} ranged from 0.2cm (4%) for *P.sophore* to 8.4cm (23%) for *W.attu*. The \bar{L}_{Nov} was also significantly ($p < 0.0001$) larger inside the FCD/I scheme compared to outside for *C.striatus*, *G.giuris*, *P.sophore* and *W.attu*, though the differences were marginally smaller than the between-year differences, ranging from 0.4cm (7%) for *P.sophore* to 7.7cm (18%) for *W.attu*. *Anabas testudineus* showed no significant ($p=0.687$) difference in \bar{L}_{Nov} between the two sampling

locations and for *C.catla*, \bar{L}_{Nov} was significantly ($p < 0.0001$) larger outside the scheme compared to inside.

- **Condition factors (growth in weight)**

The length/weight regression models for each species and sampling location (Figure 5.25) were found to be highly significant ($p < 0.0001$) with coefficient of determination (r^2) values ranging from 0.96 to 0.99, and sample sizes ranging from 195 to 618 fish.

The ANCOVA tests of the equality of slopes and elevations of the length/weight relationships between the sampling locations showed that the condition of *A. testudineus* and *C. striatus* is the same in both sampling locations ($p > 0.05$). For the remaining species, condition is better inside the FCD/I scheme compared to outside, though only marginally in the case of *P.sophore*. As shown below and in Figure 5.25, *Wallago attu* and *G. giuris* exhibit the largest differences in condition, followed by *C. catla*. For *G. giuris* and *C. catla*, the differences in condition arise from higher slope values and for *P. sophore* and *W.attu*, from higher intercept values.

The fitted parameters of the length/weight relationship for each of the species and sampling location(s) are as follows:

Species	Population	a	b
<i>A.testudineus</i>	Inside & Outside	1.78E-0.5	2.99
<i>C.catla</i>	Inside	5.34E-06	3.26
	Outside	9.70E-06	3.15
<i>C.striatus</i>	Inside & Outside	4.28E-06	3.11
<i>G.giuris</i>	Inside	6.31E-06	3.05
	Outside	1.05E-05	2.94
<i>P.sophore</i>	Inside	8.14E-06	3.21
	Outside	7.90E-06	3.21
<i>W.attu</i>	Inside	2.37E-06	3.17
	Outside	1.88E-06	3.17

5.7.4 Explanations for variability in growth performance

Summarising the preceding sections, growth performance, measured as the mean length of the 0+ cohort in November (\bar{L}_{Nov}) was, with the exception of *G.giuris*, found to be significantly higher during the 95/96 flood year compared to the 96/97 year. Differences in performance ranged from 4% larger for *P.sophore* to 23% larger for *W.attu*. During this flood year, growth performance of four of the six species was also significantly higher inside the FCD/I scheme than outside. These differences in performance were comparable with those between the two flood years, ranging from 7% for *P.sophore* to 18% for *W.attu*. In contrast, *Catla catla* grew 6% larger outside the scheme compared to inside and *A.testudineus* showed no significant difference in growth in the two locations.

The condition (weight at length) of *C.catla*, *G.giuris*, *P.sophore* and *W.attu* was also found to be significantly higher inside the scheme compared to outside, for the 24 month sampling period. No significant differences in condition were found for *A.testudineus* and *C.striatus*.

In an attempt to explain these observed differences, it may first be noted that none of the key species showed any significant differences in diet composition in the two sampling locations. Feeding intensity, measured as the mean monthly stomach fullness index (SFI), was also found to be not significantly different inside and outside the PIRDP FCDI scheme for any of the key species. There is some qualitative evidence that suggests that feeding intensity was, however, greater during the 95/96 flood year compared with 96/97, eg for *A. testudineus* and *G. giurus*, though *W. attu* fed better in 96/97.

Relative in/out abundances were also examined for the key species between the two flood seasons in the

manner of section 5.3, but only within the hydrologically split flood years (June to May). Abundances were thus found to be higher outside in the 95/96 flood year for *C. catla*, *G. giurus*, *P. sophore* and *W. attu* and higher inside in the 96/97 flood year for *A. testudineus*. Abundances were not significantly different for other species/year combinations.

The growth performance measures of the key species and the explanatory variables that were found to be significantly different in relation to the sampling location and hydrologically split year are summarised below. More extensive flooding (FI) explains the larger mean lengths (\bar{L}_{Nov}) found in 95/96 for five of the six key species, but fails to explain, with the exception of *C. catla*, the larger mean lengths found inside the FCDI scheme. The latter are much better explained by CPUE, the proxy of density, which also explains all the observed differences in condition. The SFIs correspond with the larger flood of 95/96, potentially explaining four of the larger mean lengths for this year.

Summary table indicating where the growth performance measures and explanatory variables were found to be significantly greater in relation to the sampling location and hydrological split year (NS - no significant difference).

	Growth performance variables			Explanatory variables*		
	\bar{L}_{Nov}		Condition	CPUE		SFI
Species	Year	Location	IN/OUT	95/96	96/97	Year
<i>A. testudineus</i>	95/96	NS	NS	NS	IN	95/96
<i>C. catla</i>	95/96	OUT	IN	OUT	NS	95/96
<i>C. striatus</i>	95/96	IN	NS	NS	NS	95/96
<i>G. giuris</i>	NS	IN	IN	OUT	NS	95/96
<i>P. sophore</i>	95/96	IN	IN	OUT	NS	NS
<i>W. attu</i>	95/96	IN	IN	OUT	NS	96/97

* Flood index : 95/96 > 96/97 IN < OUT in both years

These results imply that both the flood index and fish density are important factors determining the growth performance of the key species, while stomach fullness is more likely to reflect the effects of these two factors.

Contrary to what might be expected as the result of lessened flooding levels and period of floodplain inundation inside the PIRD P FCD/I scheme, the growth performance of the key species in this location has been shown to be significantly higher. This greater growth performance has been explained by lower levels of abundance at this location implying that intraspecific competition is an important component of floodplain fish growth.

5.7.5 Density dependence of growth

The previous section demonstrated clearly that the growth of several of the key species in the 1995/96 flood year varied between the inside and outside regions, as best explained by variations in fish densities. To quantify this result for the detailed modeling of the hydrological impacts of fish production potential, a collaborative pond experiment was undertaken at BAU, Mymensingh during Sub-Project 4 (Appendix F).

Briefly, this experiment confirmed that the growth of the key species *P. sophore* was highly dependent on its density, with the functional response apparently mediated by competition for food resources. Growth was highly responsive to pond conditions, presumably reflecting an adaptation to the unpredictable conditions of floodplain river systems. Under favourable conditions with low densities and high primary productivities (in the most fertilised ponds), recently spawned *P. sophore* were able to grow to sexual maturity and spawn within only 12 weeks of hatching! These results demonstrate the enormously high potential productivity of small species such as *P. sophore*, especially when reduced to very low numbers, either by fishing or natural hydrological conditions.

5.8 Reproduction Dynamics

The reproductive strategies of fish, particularly the age and time at which they spawn, coupled with their mortality rates, determine how many fish survive to mature and reproduce future cohorts. In the strongly seasonal floodplain environment, reproduction must be strongly adapted to environmental conditions to ensure that enough eggs are released at the right time to take advantage of seasonal opportunities for feeding and growth. This section compares the reproductive dynamics - the age and length at maturity, the fecundity and the time of spawning - for the key species in Bangladesh inside and outside the PIRDP.

5.8.1 Age and length at maturity

The average length at maturation for each key species (males and females) inside and outside the PIRDP FCD/I scheme was estimated from the length at which half the sampled individuals were sexually mature (L_{m50}), as fitted using the logistic function.

As shown in Figure 5.26, and tabulated below, lengths at maturity varied between the sexes for five of the six species, excluding only *W. attu*:

Species	Female		Male	
	In	Out	In	Out
<i>A.testudineus</i>	11.5 (341)	11.5 (166)	12.5 (200)	13.5 (99)
<i>C.striatus</i>	29.0 (162)	30.5 (148)	37.5 (198)	39.5 (157)
<i>G.giuris</i>	10.5 (155)	9.0 (206)	22.0 (182)	19.5 (278)
<i>P.sophore</i>	6.0 (430)	6.0 (386)	5.5 (138)	5.5 (108)
<i>W.attu</i>	60.0 (112)	54.0 (218)	56.0 (87)	54.0 (187)
<i>C.catla</i>	67.0 (27)	62.5 (34)	* (56)	46.5 (88)

Sample sizes in parentheses. * no model fit

Mature males of the most sexually dimorphic *C.striatus* and *G.giuris* were approximately 30% and 100% larger than females respectively. The average size of maturity for male *A.testudineus* also appears slightly larger than for females. For *P.sophore* and *C.catla*, length at maturity for females is marginally larger than for males.

In contrast, there is no strong evidence to suggest that L_{m50} is significantly different inside and outside the FCD/I scheme for any of the key species. Estimates of L_{m50} for *A.testudineus* (female) and *P.sophore* (male and female) are identical. Small differences, relative to average length, exist for the remaining species of each sex, though judging by the degree of variability in the data (Figure 5.26), these differences are unlikely to be significant. Insufficient data from mature fish were available to make comparisons across the FCD/I scheme for *C.catla*.

Combining these maturity data with the observed patterns of growth discussed in Section 5.7, all the key species except *C. catla* are seen to reach sexual maturity by the end of their first year. Insufficient data were available from large *C. catla* to determine reliable ages at maturity.

5.8.2 Fecundity at length

Fecundity - the number of eggs - in the female prior to spawning (Wooton, 1990), was estimated from 1.0g ovary sub-samples taken during the first two weeks of April 1995 just prior to the 95/96 spawning season. Sampling over this short period of time was designed to ensure that all the specimens were near the same stage of development and condition (Bagenal, 1978). Sample sizes for each key species and sampling location ranged from 14 to 41. Despite extensive searches at markets and landing centres, no ovary samples were obtained for *C.catla*, and *W.attu* and few were found for *C.striatus*.

Batch fecundity (gonad weight for *G. giurus*) was described as a function of fork length, L , as:

$$F = aL^b$$

and fitted to the data using log-transformed linear regression. The length-fecundity relationships for each species and sampling location were found to be significant ($p < 0.01$) except for *C.striatus* (inside) ($p = 0.08$). Because, the latter was only marginally non-significant, it was still included in the following comparison.

Fecundity at length relationships were not significantly different between fish inside and outside the FCD/I scheme for *C. striatus*, *G. Giurus* or *P. sophore* (ANCOVA, $p > 0.05$). For *A. testudineus*, the slopes (b) of the relationships were significantly different, implying that individuals were more fecund at length inside the FCDI scheme (Figure 5.27).

The parameters of the common (pooled, Zar, 1984) length-fecundity relationships for each species and sampling location were as follow:

Fecundity at length relationship parameters for PIRDP fish

Species	Location	a	b
<i>A.testudineus</i>	IN	4.53E-08	5.37
<i>A.testudineus</i>	OUT	1.26E-07	5.05
<i>G.giuris</i>	IN & OUT	1.51E-07	3.30
<i>C.striatus</i>	IN & OUT	9.89E-08	4.10
<i>P.sophore</i>	IN & OUT	4.50E-09	6.20

5.8.3 Seasonality of spawning

- **Biological survey data**

Spawning patterns in fish are commonly defined by changes in gonadosomatic index (GSI) (Welcomme, 1985; Wooton, 1990) which is a measure of the relative size of the gonad with respect to total body (somatic) weight:

$$GSI (\%) = \frac{\text{weight of gonad}}{\text{total body weight}} \cdot 100$$

Increases in the GSI during the reproductive cycle reflect the growth of developing oocytes during vitellogenesis. GSI is highest just prior to spawning, after which the GSI declines as increasingly more of the population contain spent females.

Changes in mean monthly GSI, calculated from gonad and body weight data collected as part of the biological sampling programme (Appendix A), were thus plotted to describe the pattern of breeding of the key species and to compare the timing of spawning in relation to sampling location (inside and outside the FCD/I scheme) and water height during the 24 month sampling period.

Changes in mean monthly GSI, with 95% confidence intervals, for each of the key species and the two sampling locations are illustrated in Figures 5.28 and 5.29. Where no confidence intervals are shown for the monthly GSI estimate, only one fish was sampled. The GSI data showed that *A. testudineus*, *C.striatus*, *P.sophore* and *W.attu* all have discrete, relatively short breeding seasons (May - June) coinciding with rising water levels. In a number of cases; *A.testudineus* (outside, 95/96); *C.striatus* (outside, 95/96); *P.sophore* (outside 95/96 and inside 96/97); and *W.attu* (outside 95/96); maximum spawning activity coincides with the time of floodplain inundation when flood levels reach bankfull height. Spawning seasonality is less pronounced in *G.giuris* (Figure 5.29) though the trend in the data suggests that spawning activity is concentrated during the higher water periods between July and August, rather than during the rising water period. Insufficient GSI data are available to draw any conclusions regarding the breeding patterns of *C.catla* (Figure 5.28, see following section).

The overlapping confidence intervals around the times of spawning and an absence of samples for some

months prevent reliable estimates and in/out comparisons of the actual month of spawning for any of the key species. However, there is no evidence in the GSI data to suggest that spawning time is significantly different inside and outside the FCD/I scheme for any of the key species (Figures 5.28, 5.29), nor is there any evidence of inter annual differences in these two hydrologically similar years.

For *P. sophore*, two spawning peaks are apparent in the GSI plots outside the FCD/I scheme in 95/96 and inside the scheme during 96/97. The effect of the latter spawning pattern is clearly reflected in the corresponding length frequency distribution (Figure 5.13) which shows two recruitment pulses; the first appearing May and the second in September. As discussed in Section 5.5.1, this small, most common species may grow to maturity and spawn more than once in each season.

- **Savar Net Catches of Carp Fry**

The spawning seasonality of the major carp, *Catla catla* could not be determined reliably above due to the lack of samples available of mature fish from the floodplain sampling regions. Additional data are, however available from the catch sampling programme on the reproduction of this species.

The fry of the major carps, particularly *C. catla* and *Labeo rohita* in the Pabna region, are caught in the main river waters using special mosquito fyke nets known as *savar* nets. Only one of the project's 40 CE respondents fished with *savar* nets, a man living in Protappur (PR19, see Figure 3.6) close to the main Jamuna River. The *savar* catches per unit effort of respondent PR19 show that carp fry were present in the Jamuna main river waters during May and June of 1995, and May, June and July of 1996 (Figure 5.30). Carp fry are thus generally available at the times of the rising floods (cf hydrological curves in Figures 4.6 and 4.7), and appear to have been spawned earlier in 1996 than in 1995, reflecting the slightly earlier flood in 1996. Since the Talimnagar sluice gates were closed for nearly all of May, June and July 1995, and flood waters did not flood on to the floodplain in 1996 until mid-July, due to the slow rise in water levels, it is evident that the carp fry spawned outside were largely prevented from moving in to the PIRDP in both years.

5.8.4 Spatial organisation of spawning

The general lack of differences between GSIs, Lm_{50} s and fecundities inside and outside the PIRDP FCD/I scheme indicate that reproduction occurs for most of the key Bangladesh species in both regions. Fish inside FCD/I schemes therefore do contribute to their own recruitment, and such schemes are not wholly reliant on immigration of recruits from outside through sluice gates.

For the largest species, *C. catla* and *W. attu*, the largest individuals were invariably found outside the FCD/I scheme (see Figures 5.25 and 5.26). Since *W. attu* do mature at the end of their first year, and since many mature fish were found inside the FCD/I scheme (Figure 5.29) it is concluded that this species does spawn both inside and outside the FCD/I scheme, but that more large fish survive outside (probably in the main river) due to the lower catchabilities in that habitat. For *C. catla*, in contrast, since hardly any mature fish were found either in the inside or the outside floodplain habitats, and since carp fry are only caught in *savar* nets in the main river, it is concluded that *C. catla* usually do not spawn in floodplain regions, but instead use such areas as nursery grounds.

5.9 Mortality and survival rates

5.9.1 Introduction

Mortality in exploited fish populations is due to both fishing and natural causes. The main causes of natural mortality in floodplain fish populations include stranding in isolated pools, or other extreme abiotic conditions such as high temperatures or low dissolved oxygen concentrations particularly for the whitefish species unadapted to cope with them (Welcomme, 1985; 1989). Such fish kills are rarely observed at the project sites, where predation is believed to be the major cause of natural mortality. Fishing mortality is of course extremely high at the project sites, due to the multitude of fishing activities (see Chapter 5), and the absence of mortality due to stranding is probably because the fish are usually removed from the waterbody before such conditions arrive!

The major factors influencing mortality rates; fishing, stranding, abiotic factors and predation vary strongly with the flood cycle, intensifying during the drawdown and with the progression of the dry season. (Welcomme, 1985; 1989). During this time, fish become concentrated in channels or pools as water recedes from the floodplain. These periods of high concentrations or densities of fish, with high catchability (q), are exploited by both fishermen and other predators (see Welcomme, 1985; MRAG 1994a). Abiotic conditions are also likely to reach extremes during this period leading directly, or indirectly, through greater vulnerability to disease (and thereby predation), to increased mortality rates. Conversely, during the high water period, the floodplain offers abundant food resources, space to escape from predators, tolerable abiotic conditions and low fish densities. Mortality rates during this period are therefore assumed to be low. Under these assumptions, it would appear that mortality is closely dependent upon fish density, both due to competition and to predation. This component of the dynamics of floodplain fish was studied in depth during Sub-Project 2 (Appendix D), as described briefly in Section 5.9.6.

The overall mortality rate arising from the various density-dependent and seasonal natural and fishing mortalities has strong implications for the sustainability and management of these fisheries. The following sections briefly examine the between-year variability in overall mortality rates at the study site, and then proceed to determine the relative contributions of both fishing and natural effects on the total mortality rates observed.

5.9.2 Annual variability in mortality

Qualitative indications on annual variabilities in total mortality rates are available from the Indonesian catch data and length frequency data. In 1995, for example, catches in the Lake District region were very high during the long dry season, and at the start of the October/November flood season: catches in the 1996 season in the Lake District were then substantially reduced compared to the previous year (Figure 5.2). In 1996 in contrast, the short dry season was followed by relatively good catches in the riverine regions, suggesting that mortality was relatively low that dry season (compare Figure 5.52 with Figure 5.47). Finally, the September and November 1994 length frequency data for three of the Indonesian key species (Figures 5.17, 5.18 and 5.20) shows that the largest, oldest fish were all heavily caught in this driest ever dry season on the River Lempuing, and then not caught in subsequent years. Though their capture at this time may reflect annual variations in recruitment strength, it seems more likely that the oldest fish are most adept at surviving over the dry season (see Hoggarth & Utomo, 1994), but that even they suffer high mortality rates in extreme hydrological conditions in some years.

5.9.3 Longevity

The approximate longevity of the key species at each study site is revealed by the time series of length frequency data, by following cohorts or age classes from their initial recruitment into the fisheries (Section 5.5.2). Though it is hard to be precise with this information, in the absence of formally fitted growth models (see Section 5.7.2), it is clear from the general unimodality of the length distributions in Bangladesh, that nearly all the Bangladesh key species only survive in significant numbers up to their first birthday (Figures 5.9 to 5.14).

In Indonesia, in contrast, far more of the length frequency distributions for the key *fish* species⁴ show

⁴ The distribution for the prawn *M. rosenbergii* (Figure 5.19) suggests an annual, catadromous life history strategy, as discussed elsewhere.

bimodality, indicating that significant numbers of fish do survive into their second year (Figures 5.15 to 5.18, and 5.20). The September 1994 length frequency distribution for *Mystus nemurus* even shows that one Indonesian catfish survived to almost three years of age (Figure 5.18).

5.9.4 Empirical estimates of total mortality rates

- **Materials and Methods**

Total annual instantaneous mortality rates, Z , were estimated for the Bangladesh study site, using the standard mortality relationship (Gulland, 1982):

$$N_1 = N_0 e^{-Z}$$

where N_0 is the initial number and N_1 is the number after one unit of time (one year, for annual mortality rates). Estimates of Z were made from the unaggregated (single gear type) length frequency data collected for each key species from low selectivity gear types, such as dewatering, *katha*, *kua*, small mesh seines and traps.

Gulland and Rosenberg (1992) reviewed length based approaches to estimating mortality rates, and concluded that, for the pattern shown in the length frequencies by all of the key species, ie a single mode for the majority of the year with a progressively increasing mean length (Type B distribution, based upon the classification of Shepard *et al*, 1987), Z is most reliably estimated using distributions which show two clear modes assumed to represent numbers of new recruits (N_t) and relative numbers of survivors from the previous years recruitment (N_{t+1}). By distinguishing two such modes, Z is estimated as:

$$Z = -\ln \frac{N_{t+1}}{N_t}$$

This method assumes 'steady state' population dynamics, that is, that recruitment and mortality are both constant in the two years. It also assumes that the length frequency samples are representative of the true population size structure. To maximise the latter assumption, only samples which exhibited a clearly bimodal pattern coinciding with the overall growth pattern were used included in the analysis. Where modes were overlapping, numbers in each mode (cohort) were estimated using the NORMSEP (Hasselblad, 1966), normal distribution separator routine of the FISAT programme (Gayanilo *et al*, 1996).

No attempt was made to estimate Z for *G.giuris* due to the absence of a reliable growth interpretation. Furthermore, because of the 'steady state' assumptions underlying the estimation method, no attempt was made to relate differences in Z estimates to fish density or environmental conditions (which clearly vary between the years).

- **Results**

A total of 64 estimates for Z were calculated from the 402 individual length frequency distributions examined (see Halls, PhD thesis for individual estimates), including 30 from inside the FCD/I scheme, and 34 from outside. Most of the estimates (45) were derived from length frequencies collected from dewatering, *katha*, *kua*, lift and seine net gears. The remainder were collected from dragnet, castnet, trap and longline catches. There were no obvious differences in the types of gear for which estimates were derived between the two sampling locations. The 64 estimates were divided approximately equally across each bimonthly sampling period and hydrological year. Those distributions for which no estimate could be made either contained two few fish to detect reliable modes, or simply comprised a single mode. Since the many samples comprising a single mode indicate infinitesimal mortality, on an annual basis, the average mortalities from the 64 bimodal distributions should be interpreted as a lower limit to the true mortality rates.

The estimates of Z for individual gear and month/year combinations ranged between approximately 2 and 6, with only 4 estimates below 2 and only one estimate above 6. This observed range is equivalent to between only 14 and 0.4% survival per year. Mean Z estimates, for each species and sampling location, were higher outside the FCD/I scheme compared to inside (Table 5.4). However, because of the high degree of variability in the individual estimates, this difference is only significant ($p < 0.05$) for *P.sophore*, and this estimate also depends on one estimate for Z which is very low in comparison to the other estimates for this species (Halls, PhD thesis). No significant ($p = 0.06$) differences exist between the

populations if this estimate is omitted from the comparison.

Because of the absence of significant differences in \bar{Z} between the two sampling locations, estimates for Z from both sampling locations were pooled, to give an overall mean value for each species. Total mortality rates are then highest for *C. catla* ($\bar{Z} = 4.7$) implying a survival rate of just below 1%. The remaining species show marginally lower mortality rates between 3.2 for *P.sophore* and 3.9 for *C.striatus*, equivalent to between 4 and 2% survival respectively (Table 5.4).

These very low (upper limits to) annual survival rates are consistent with the dry season survival rates estimated in Sub-Project 1 (Appendix C), at between 0.54-1.9% inside the FCD/I scheme, and 0.6% outside.

5.9.5 Fishing mortality rates

Relative indications of fishing mortality rates are available for the two project study sites from the tag return rates achieved in the mark-recapture programme (see sections 5.10.3 and 5.11.3). The overall tag return rates *reflect* the fishing mortality rates, but do not give actual estimates because some tags become missing due to both tag-induced mortality and tag losses from fish after release (see Appendix I). Recapture rates also vary seasonally, being particularly high when fish become fully enclosed in dry season waterbodies. Overall recapture rates then depend on the seasonality of tag releases, which varied due to availability, both between species, study sites and years (see Tables 5.5 and 5.12). The application of rigorous tagging models developed for such situations (see Seber, 1982) are difficult to apply to the floodplain study sites due to their open situation, with possible immigration and emigration of fish. Tag recapture rates are thus compared as simple indications of the lower limits of relative fishing mortality rates.

Comparing the two study sites is further complicated by the facts that different selections of species were used in each, and that different field staff did the tagging work (who's practices may have differed slightly, influencing tag losses and tag-induced mortality rates), and finally that different fishermen caught and returned the tags. As noted in Sections 5.10.3 and 5.11.3, two different tag designs were also used in both countries, with the less recaptured streamer tags (see Tables 5.8 and 5.15) being most used for the smaller individuals and the smaller species including *H. temmincki* and *O. hasselti* in Indonesia, and *G. giurus* and *P. sophore* in Bangladesh.

The most comparable overall tag recapture rates from the well-recaptured anchor tags only for the full two-year study periods, are then as follows⁵ (sample sizes and seasonality of recaptures are given in Tables 5.5, 5.12, 5.6 and 5.13):

Overall tag recapture rates for anchor-tagged key species

Taxonomic Group	Bangladesh Species	Recapture Rate	Indonesia Species	Recapture Rate
Carp	<i>C. catla</i>	51%	<i>O. hasselti</i>	24%
Snakehead	<i>C. striatus</i>	46%	<i>C. striatus</i>	11%
Catfish	<i>W. attu</i>	36%	<i>M. nemurus</i>	33%
Perch	<i>G. giurus</i>	44%	<i>H. temmincki</i>	16%
	<i>A. testudineus</i>	47%	<i>A. testudineus</i>	6%

With up to 51% of tags returned to the project, these recapture rates indicate that fishing mortality is likely to be extremely high in both the study sites. Studies of fish species in coastal systems, using similar tag designs (eg Buxton & Allen, 1989; Bryant *et al*, 1989, Funicelli *et al*, 1989) generally do not achieve recapture rates above 2-3%!

⁵ Recapture rates of species only tagged with streamer tags were 7% for *P. sophore* in Bangladesh, and 28% for *M. rosenbergii* in Indonesia.

Two key species were available and selected for study at both sites: *A. testudineus* and *C. striatus*. The recapture rates of these species indicate that fishing mortalities may be up to four to eight times greater in Bangladesh than in Indonesia for these species. This result may be unreliable for the smaller *A. testudineus*, though, as this species was only included at the Indonesian study in the second study year, and only 67 releases were made due to its low availability. The comparison for *C. striatus* still indicates a four-fold difference between the sites, though.

Of the other species, the strongly migratory major carp, *C. catla* (see Sections 5.10 and 5.11 for migration patterns) was most recaptured in Bangladesh, confirming its high total mortality rate, as observed in the preceding section. The smaller carp, *O. hasselti* in Indonesia shows only half the recapture rate of Bangladeshi *C. catla*. Similarly, the Indonesian *H. temmincki* was recaptured less than half as well as the Bangladeshi perciforme *G. giurus*. In contrast, the strongly migratory Indonesian catfish *M. nemurus* was recaptured by the Indonesian barrier traps (see Chapter 6) almost as much as the Bangladeshi catfish *W. attu*.

Within the Bangladesh site, recapture rates were similar for all species inside and outside the FCD/I scheme (Table 5.7).

5.9.6 Natural mortality rates

The natural mortality rate of *Puntius sophore* in Bangladesh was studied at the PIRDP field site by Sub-Project 2, supported by data from Sub-Project 4. This research is written up in Appendix D, from which the main summary points are copied here.

The influence of density on the natural mortality rate of *P. sophore* was examined in 20 naturally existing dry season water bodies, from both inside and outside the PIRDP flood control embankment, over the 1995/96 dry season. Fishing activities were restricted in these waterbodies over the period of the experiment by paying compensation payments to their owners.

There was no evidence to suggest that the natural mortality rate, at fixed density, was different in waterbodies sampled from inside and outside the FCD/I scheme.

A highly significant ($p = 0.003$) relationship was found between mortality and density, though based partially upon mortality rates with negative values. Evidence suggested that the bias extended to all estimates of natural mortality in the same direction, equally, and it was therefore argued that the underlying relationship was genuine, although the value of the intercept of the model remains uncertain.

Because of difficulties experienced in this experiment, the mortality-density response of *P. sophore* was further explored using data derived from the density-dependent growth experiment (see Appendix F). These data yielded a highly significant ($p = 0.002$) linear relationship between density and mortality, not significantly different from the relationship obtained from wild stocks above, reinforcing the existence of this observed density-dependent process and the authenticity of the models.

At the fish densities observed in the field - up to 10 *Puntius sophore* per m^3 - natural mortality levels were up to $M=0.05$ per week, during this dry season period. For the whole 20 week dry season, this stock would thus have experienced an overall mortality of $M=1.0$, equivalent to a survival rate of 37%.

5.9.7 Summary and comparison of mortality rate studies

The above studies have shown that mortality rates are enormously high for floodplain fish, and significantly different between Bangladesh and Indonesia, but not different within the PIRDP Inside/Outside regions.

At the Bangladeshi study site, total mortality rates were such that only up to 1-4% of the key species survived between years. In the dry season waterbodies, only 0.5-1.9% of fish survived to the end of the dry season to spawn next year. This suggests that most of the mortality does occur over the dry season period, as indicated by annual differences in mortality rates correlated with drought conditions in Indonesia. As a result of such high mortality rates, the Bangladesh stock was comprised almost entirely of fish less than one year old.

In contrast, at the Indonesian site, more fish were seen to survive into their second year, and the tag recapture data showed that fishing mortality rates for some key species could be up to four times lower

than in Bangladesh. Other species, including the most migratory *M. nemurus* and *M. rosenbergii* were, however, both highly exploited by the barrier traps in Indonesia, though still less than equivalent species in Bangladesh.

Overall tag recapture rates indicate the lower limits to fishing mortality rates, since tag losses and tag-induced mortalities reduce the number of tagged fish actually available for recapture. The tag recapture rates of 36-51% in Bangladesh, and their correlation with the estimated total mortality rates (both being highest for the migratory *C. catla*), imply that fishing is the major component of the very high mortality at this site.

In comparison to these very high rates of total and fishing mortality, natural mortality rates, studied in field and experimental conditions for the most abundant Bangladeshi species, *P. sophore*, were relatively low. Though still high compared to other resource systems at approximately $M=1.0$, natural mortalities were such that 37% of the *P. sophore* proved capable of surviving over the full dry season period, at the densities observed in the field. This suggests that restraints on dry season fishing could significantly increase the numbers of fish contributing to the recruitment in the following year. Though it is difficult to quantify this relationship due to multispecies effects, and density dependent processes, it is likely that a sacrifice of a few tonnes in the dry season catches could easily double the pre-spawning stock at the start of the next flood (Appendix C).

In Bangladesh, no significant differences were seen in any of the total, fishing, or natural mortality rates between the Inside and Outside PIRDP regions, suggesting that the hydrological differences between them were insufficient to influence mortality processes in the two study years.

5.10 Spatio-Temporal Migration Cycles - Bangladesh

The migration cycles of floodplain fish provide key evidence on their life history strategies for breeding, feeding, and survival over the critical dry season period. This information was required to determine the potential utility of reserves or other management measures for protecting these fish stocks. Due to the volume and complexity of the spatio-temporal data collected on this subject, and the ecological differences between the two study sites, the Bangladesh and Indonesian data are presented in separate sections.

5.10.1 Introduction

In Bangladesh, the spatio-temporal migration cycles of the key species were studied by the mark-recapture programme, supported by Sub-Project 3 'Fish Migrations through Flood Control Sluice Gates'. The Sub-Project results are attached as Appendix E, and summarised in the following section. The Bangladesh mark-recapture programme is then described in section 5.10.3, followed by the detailed results and conclusions.

5.10.2 Fish migrations through flood control sluice gates

The migrations of fish through two flood control sluice gates at the study site were studied in Sub-Project 3. Detailed information on this study is given in Appendix E, while the summary and main conclusions are included in this section.

Data were collected at the main Talimnagar sluice gate and the small Baulikhola sluice gate for the full 5-month flood season from July to November 1996. Daily records were taken of inside and outside water heights, sluice gate apertures and flow directions, along with the fishing efforts of three interceptory gears (lift nets, bag nets and jumping traps), and the weights, species compositions, length frequencies and directions of movements of their fish catches.

In 1996, the flood started early on 23 March, but did not reach the floodplain height until much later at the end of June. Outside water levels then rose until mid/late July and gradually fell until the end of November.

Due to the low water levels, the sluice gates were partly or fully open on all days up until mid August, thereby allowing water to pass into the PIRDP scheme. The gates were closed (though leaking) over the higher water period, and then opened again to allow water out from early/mid September.

Fishing gear use varied between the two sluice gates depending mainly on their size. Lift nets and bag nets were fully utilised at the small Baulikhola gate, but not at the larger Talimnagar gate due to the strong River Badai currents. Jumping traps caught fish attracted towards the sluice gates by the outflowing water

at the start of the ebb season, while the expensive bag net gear caught fish emigrating from the PIRDP at the end of the ebb. Lift nets were set in various positions on either side of the sluice gates to catch fish moving in both directions in different seasons.

Migrating fish displayed four different migration phases, including both passive and active responses in both inward and outward directions. During the early flood, small fish, such as *Puntius sophore*, *Glossogobius giurus* and shrimps drifted in passively with the current. Towards the end of the flood season, when the gates were closed but leaking, some of the same species were then attracted towards the gates and moved back out of the system. During the early ebb season, the major carps *Labeo rohita*, *Catla catla*, *Cirrhinus reba*, and *Labeo calbasu*, in addition to the predatory catfish *Wallago attu* were attracted in to the PIRDP, while other small species migrated out. The largest migration, including virtually all the species previously recorded, was a passive drift out with the ebb, particularly coinciding with the final fall in water levels below the floodplain height.

The vast majority of all migrating fish were the juvenile 0+ cohort, born at the beginning of the 1996 flood. Significant numbers of older *P. sophore* and *G. giurus* were also found moving in to the PIRDP early in the season, but only accompanied by the juvenile fish, suggesting they had already spawned outside. The larger *Catla catla*, *Labeo rohita* and *Wallago attu* in contrast, were not caught moving in with the young fish early in the season, but a few of the larger major carps were caught moving against the ebb current just after high water suggesting that they move upstream at this time.

The largest catches of migrating fish were taken during the late ebb passive emigrations at the small Baulikhola gate. Surprisingly, more fish were caught trying to migrate against the flows in to the PIRDP after high water, than passively at the beginning of the flood. Due to the difficulty of fishing the large Talimnagar gate, though, it was concluded that many fish both entered and escaped from the PIRDP waters through this route, without capture. The weight of young fish migrating in to the PIRDP during the early flood was roughly estimated between 0.9 and 4 tonnes, mostly through the Talimnagar gate, compared to the 0.6t catch from the existing fishing gears.

5.10.3 The Bangladesh mark-recapture programme

In Bangladesh, 581-1013 individuals of each key fish species were tagged between December 1994 and August 1996 (Table 5.5) giving a total of 4,618 releases. Few fish were tagged in the early months, reflecting the low fish availability in the dry season. Many fish were, however, tagged over the high water and drawdown seasons, July to October 1995; and a special effort was made to release tags during the 1996 dry season (January to May) to observe the dispersal patterns of fish with the oncoming flood (Table 5.5).

Tagged fish recaptures averaged 30% in Bangladesh with the smallest *Puntius sophore* and *Glossogobius giurus* having the lowest recapture rates of 7-12%, and the major carp *Catla catla* having the highest recapture rate of 50% (Table 5.6). Most fish were recaptured within only a few months of their release: 79% of all the recaptures were made in either the same or the following calendar month. The average number of days at liberty ranged between 9d for *Puntius sophore* and 46d for *Anabas testudineus*. The highest number of recaptures (99) was made on the day following release, and the longest time between release and recapture was 263d for a *Channa striatus*. Further consideration is given to the implications of such tag recapture rates in section 5.9.

In Bangladesh, fish were released both inside and outside of the FCDI scheme, with slightly more fish released inside (Table 5.7, Figure 5.31). Slightly higher recapture rates were achieved for the inside tag releases for five of the six key species, though the differences were small in all cases.

In general, small fish, particularly *Puntius sophore* and *Glossogobius giurus* were tagged using the lightweight streamer tags (see Section 3.5), while larger fish were tagged with anchor tags (Table 5.8, Figure 5.32). Recapture rates averaged only 7% for the streamer tags, substantially below the overall 47% returns achieved for anchor tags (Table 5.8). These differences may be due to either higher loss rates for streamer tags (see Appendix I), or higher mortalities experienced by small fish, or due to streamer tags.

To achieve a balanced result, all sizes of fish were tagged, as available from the fishery. Following the growth of each season's cohort of fish, smaller fish were generally tagged during the high water period and larger fish during the subsequent dry seasons (Table 5.9). Such fish, however, were randomly selected,

and represented the average stock available in each month. The minimum and maximum sizes of fish tagged ranged from a 3.8cm *A. testudineus* to a 73cm *Wallago attu* (Table 5.9). The fish recaptured were, on average, larger than those released, as expected due to the growth in between release and recapture. Small *C. catla* and *W. attu* appeared to be less recaptured than the other species (Figure 5.32), but in general terms, all but the smallest fish were well represented among the recaptures. The patterns revealed by the mark-recapture data thus represent the overall picture for each key species population as a whole.

5.10.4 Spatio-temporal migration cycles of the key species

Simple mark-recapture data show the positions of fish at their release and recapture, but do not give information about the behaviour pattern of the fish in between those times. For fish recaptured some time after release at a different location, the actual time of their migration cannot be accurately determined. The seasonality of fish migration patterns was therefore examined for the key species by plotting monthly graphs of the movements of only those fish recaptured within the same or the next calendar month. This approach allowed most of the tagging data to be used in the analysis (79% of all the Bangladesh tag recaptures, from 67% for *Anabas testudineus* to 96% for *Puntius sophore*), while excluding those fish whose actual time of migration was least well known. For the Bangladesh analysis, the 1995 and 1996 flood seasonalities were similar (Figures 4.6, 4.7) and both years' data were analysed together to maximise the sample size in each calendar month. This analysis thus assumes that the fish behaved similarly in both the study years, at least within a monthly temporal scale.

As noted earlier, the numbers of fish tagged and released varied between the months (Table 5.5), depending on their availability and the tagging effort applied. The numbers released in different locations was also constrained by fish availability and manpower, though efforts were made to release in as many different locations as possible in each month both inside and outside the embankment. The release locations actually achieved within this intention are shown for each species and month in Figures 5.34 to 5.39.

The following sections examine the temporal and spatial aspects of the migration cycles shown by each key species, by reference to monthly data on the percentages of fish migrating and their migration distances (Figure 5.40), their 'lateral' movements between different habitats (Table 5.10), and the directions of their 'longitudinal' movements (Figures 5.41 to 5.46). Fish were classified as migrants whenever their release and recapture locations differed, or as non-migrants when they were recaptured in the same location as released (see Figure 3.1 for locations used). Migration distances were calculated as the straight line distances between the centres of the release and recapture locations.

- ***Anabas testudineus* migrations (Bangladesh)**

The percentages of *Anabas testudineus* migrating were highest over the high water period between May and November (Figure 5.40), with a peak in July after the waters reached the floodplain level (Figures 4.6, 4.7). Some fish migrated in all months, however, and the distances travelled in the flood season did not appear greater than in the dry season for those fish moving (Figure 5.40).

Fish generally moved on to the floodplain in the early flood, and the many high water migrations were then mostly around the floodplain habitat (Table 5.10). *A. testudineus* then moved off the floodplain at the end of the flood season between September and November to spend the dry season in river and *beel* habitats.

Spatially, the most notable feature about the *A. testudineus* migrations was a consistent upstream migration in the secondary Badai and Atrai rivers by the September releases, coincident with the start of the drawdown in both 1995 and 1996 (Figure 5.41). In the later drawdown, the few small migrations were mostly from the floodplains in to the *beels* and rivers.

- ***Catla catla* migrations**

The major carp *Catla catla* displayed the strongest migratory behaviours with almost all fish migrating over the flood season, covering the largest average distances at the start and the end of the flood (Figures 5.40, 5.42). *C. catla* migrated in and between all habitat types over the flood season, but only resided within the *beel* habitat during the dry season (Table 5.10).

In the early flood, the *C. catla* migrations were all outside the embankment (no fish could be obtained for tagging inside) (Figure 5.42). From July onwards, some fish had entered the FCDI scheme, and *C. catla* were then observed migrating on both sides of the embankment. Flood season migrations were observed in all directions during the early and high water flood period. The largest *C. catla* migrations were, however, observed during the early drawdown period, in a consistently upstream direction along the Atrai river (Figure 5.42, September).

- ***Channa striatus* migrations (Bangladesh)**

The snakehead *Channa striatus* was found to occupy river and *beel* habitats in the dry season (Table 5.10), and to maintain some migratory behaviour at this time (Figure 5.40). Flood season behaviours were not well determined because few fish were released in the early flood (Figure 5.36). Many fish were, however found in floodplain and riverine habitats in the late flood, and particularly returning to the *beels* during the October drawdown (Table 5.10). Most fish were also found to migrate between locations over the full high water season (Figure 5.40).

Spatially, *C. striatus* did not show any strong behavioural patterns except for a consistent migration downstream in the rivers, or into *beels* with the drawdown in October (Figure 5.43).

- ***Glossogobius giurus* migrations**

The goby *Glossogobius giurus* revealed a strong preference for riverine habitats over both the dry and flood seasons, though a few fish did move on to the floodplain with the flood (Table 5.10). Within the riverine habitat, fish were relatively immobile over the dry season, but did migrate during the flood, and most strongly during August and September (Figure 5.40). During both these months, large migrations were observed in both upstream and downstream directions with no overall trend (Figure 5.44).

- ***Puntius sophore* migrations**

Puntius sophore, were, like *G. giurus* particularly found in the riverine habitat over the whole year, with only a few fish in *beels* and floodplains (Table 5.10). In contrast to *G. giurus*, however, *P. sophore* did maintain some migratory behaviour, still within rivers, over the whole year (Figure 5.40). The percentages of fish migrating did not particularly increase during the flood season, though migration distances did appear greater (Figure 5.40).

Spatially, there were too few *P. sophore* recaptures to draw any strong conclusions about longitudinal movement patterns. During the October drawdown, though, the larger *P. sophore* migrations were in a downstream direction (Figure 5.45).

- ***Wallago attu* migrations**

The silurid catfish *Wallago attu* showed strong migratory behaviours with some similarities to *C. catla*. In the dry season, fish resided in both river and *beel* habitats (Table 5.10), with few fish making any movements (Figure 5.40). Migrations were then strong over the flood season, particularly during the middle and late flood (Figure 5.40), with most fish migrating within rivers, and some fish migrating between the rivers, *beels* and floodplains (Table 5.10).

In the middle of the flood season, fish migrated both upstream and downstream (Figure 5.46, August). In the early drawdown, however, fish migrations were consistently upstream (Figure 5.46, September), and then downstream during the late drawdown (Figure 5.46, October).

- **Summary of Bangladesh key species migrations**

The above results for Bangladeshi fish show some similarities between species, and some clear differences, as follows:

- All species showed strong migrations over the flood season.
- AT, CS and PS⁶ maintained some migration over the dry season.
- In the flood season, all fish were found in both river and floodplain habitats. AT showed a preference for floodplains, while GG and PS were more common in rivers.
- In the dry season, fish were found in both river and *beel* habitats. CC were only found in *beels*, while GG and PS were again more common in rivers.
- In the early flood season, June to August, CC, GG and WA migrated actively around the floodplain in both upstream and downstream directions.
- As the drawdown began in September, AT, CC and WA all migrated strongly upstream up the secondary rivers.
- As water levels fell below the floodplain height in October, AT, CS, PS and WA all migrated small distances in a downstream direction or into river and *beel* habitats.

For the Pabna floodplain stock as a whole, these observations describe a general dispersion on to the floodplain with the flood, followed by an upstream migration as the drawdown begins and then a reverse migration back down rivers or into *beels* as the floodplain dries out. The dry season is then spent in those *beels* and rivers which retain water. This general pattern fully supports the active and passive migration phases observed at the sluice gates in sub-project 3 (Appendix E).

5.10.5 Migrations of key species across the PIRDP embankment

Fish migrations across the PIRDP embankment were studied by Sub-Project 3 (Appendix E) which looked at the catches of fish in fishing gears placed at the sluice gates. Such data only show which fish were caught at the sluice gates, not how many were able to migrate through them, though some qualitative conclusions were drawn. The tagging data were thus analysed in relation to the FCDI embankment to clarify whether fish were actually able to penetrate the sluice gates and move in or out of the FCDI scheme.

Of the 1,389 tagged fish recaptured, 14 *Catla catla*, 6 *Channa striatus* and 15 *Wallago attu* were released and then recaptured on opposite sides of the PIRDP embankment. Of these fish, 23 migrated into the PIRDP while 12 migrated outwards (Figure 5.33, Table 5.11). Though the numbers of fish are small, these data confirm the ability of these species to actually penetrate the sluice gates at certain times of year. The other three key species, *Anabas testudineus*, *Glossogobius giurus* and *Puntius sophore* were not observed to cross the embankment, though they were caught in the catches at the sluice gates (see Appendix E).

As noted previously the mark-recapture data do not indicate the exact times of fish migrations, but only reveal the period within which any observed migration must have taken place. Such periods are shown in Table 5.11, for each individual fish which crossed the embankment. These mark-recapture data were examined in comparison with the flood hydrographs (Figures 4.6, 4.7), for each year. Broadly speaking, water flowed in to the FCDI scheme through the sluice gates up until the end of August, and then flowed out from September onwards. For the three species migrating across the embankment, this examination confirmed all four of the migration phases identified in Appendix E. *Channa striatus* showed the simplest migration behaviour, moving passively inwards with the early flood and then passively outwards during the ebb. *Wallago attu* migrated passively outwards during the early ebb season, but then moved back inwards as the ebb became stronger, confirming its attraction for flowing waters at this time of the season. At least six *Catla catla* migrated passively into the PIRDP during the early flood, while another five or six

⁶ Within this summary, AT=*Anabas testudineus*, CC=*Catla catla*, CS=*Channa striatus*, GG=*Glossogobius giurus*, PS=*Puntius sophore*, and WA=*Wallago attu*.

immigrated either during this time or during the early ebb active immigration phase (those fish released outside in June and then recaptured in November or December, Table 5.11). At least one *C. catla* emigrated from the PIRDP during the late flood passive emigration phase.

Though these data provide only a partial picture of the full migration patterns occurring in and out of the Pabna FCDI scheme, they confirm the importance of both of the sluice gates for the access of fish into the system. Based on the release and recapture locations, *Catla catla* and *Channa striatus* were observed to use both sluice gates, while *Wallago attu* only migrated through the larger Talimnagar sluice gate on the main Badai River.

5.10.6 Migration scales

Though many tagged fish were recaptured in their release locations, all six of the Bangladeshi key species showed the ability to migrate significant distances. The maximum straight-line migration distances observed for individual fish of each species ranged between 4.69km for *A. testudineus* and 8.55km for *W. attu* (Figure 5.33). Such figures represent the lower limit for the mobility of each species, as those tagged fish migrating outside of the study area were probably not returned due to the lack of publicity about the tagging programme.

5.11 Spatio-Temporal Migration Cycles - Indonesia

5.11.1 Introduction

The spatio-temporal migration cycles of the Indonesian key species were studied using a combination of data from the catch/effort sampling programme and the mark-recapture programme. Catch data were used for this purpose in Indonesia from the many interceptory barrier gears, which reveal the migrations of fish by their position and orientation. This analysis is equivalent to the 'Sluice Gate' sub-project undertaken at the PIRDP site (see Appendix E), using less complete data, but over a more widespread area. The catch data analysis is presented first as the data are not disaggregated by species: this analysis provides an overview of the migratory seasonality of the multispecies stock. The more detailed analyses of the mark-recapture data are presented after this overview to demonstrate the individual behaviour patterns shown by the different key species.

5.11.2 Seasonality of migration cycles from the catches of barrier gears

As described in chapter 6, four main types of barrier gears are used at the Indonesian study site. *Corong* flume traps and *tuguk* nets are suspended in the *penetak* barriers built across the main River Lempuing. Both gears are suspended from the barriers in such a way as to enable both downstream and upstream migrants to be caught (downstream migrants simply drift in to the gears, while upstream migrants are swept back in to them by the force of the water passing through the aperture in the barrier). The catches from these riverine fishing gears reveal the seasonality of *longitudinal* migrations up and down the main river system.

Empang lalung and *kilung* barrier traps are both fished in positions where the flood waters drain from the floodplains and lakes back into the main rivers. The *empang* traps work like a fyke net, with a *lalung* bamboo box to retain the migrant fish. The larger *kilung* traps have a long suspended bag net in which fish gather while trying to move through the barrier. Both gears may be fished in either direction, but are usually set to catch downstream-moving fish. Unfortunately, neither the direction in which the gears were set nor the water flow direction were recorded for these gears. These data thus reveal the timing of *lateral* fish movements, but not the directions of movements or the detailed responses to currents. Such information was recorded in more detail in the Sluice Gate sub-project in Bangladesh (Appendix E).

Due to the difference in the flood patterns between 1995 and '96 at the Indonesian site, the catch data from the 1995 sampling year are presented first, followed by an examination of the 1996 data. The catch data used are an incomplete record of the total catches taken in each barrier, having been recalled by the respondents for 1-3 days in each half-month sampling period.

- **1995 Migration seasonality**

The 1995 flood was the more extreme of the two study years in Indonesia (see Figure 4.4 and Section 4.4.2). In 1995, the drawdown began in May, but was interrupted in mid-season by a large flood between late June and early July. The dry season then continued until the end of September, before a reasonably steady flood over October and November.

Longitudinal fish migrations along the Lempuing river were shown by large catches in the riverine *tuguk* and *corong* barriers especially during the first half of the drawdown between April and May (Figure 5.47). Fish began moving earlier in the more upstream parts of the river (see the catches in April in upstream waterbodies SKT and SPU in Figure 5.47). Significant longitudinal migrations were also observed during the June/July early reflooding at these upstream sites and at the most downstream ID waterbody, but catches were suspended in between the two phases. After this time, very few fish were caught in the riverine barriers during the second drawdown period. In the early flood season, however, longitudinal migrants were again caught in riverine barriers though in small numbers. As with the drawdown catches, the flood catches were earlier in the more upstream sites (beginning in October) than in the downstream ones (November, see Figure 5.47).

Lateral fish migrations between the floodplains and the river were revealed by large catches in both the *kilung* (Figure 5.48) and the *empang* barriers (Figures 5.49, 5.50). Such catches were observed over both the early and late drawdown phases. Many fish were also caught in the savanna region *kilung* gears during the June/July reflooding (Figure 5.48) when waters rose, but very few fish were caught in these gears during the main flood season in October and November.

Catches in the *kilung* barriers in the Lake region are more difficult to interpret due to the position of the lakes slightly away from the main river (Figure 3.5) and the unknown directions of water flows among the waterbodies. Migrations in this area cannot be so easily classified as either lateral or longitudinal in relation to the main river. Reflecting this unusual hydro-morphology, the catches in the Lake *kilungs* differed significantly from those in the main river. In waterbody DBL, the largest lake furthest from the main river channel, large catches were only taken in the *kilung* at the exit from the lake when waters were rising, not when they were falling. Such migrations were observed in three separate times of the year, in March, June/July and November (Figure 5.51). In contrast, the largest *kilung* catches in waterbodies DBT and LST, closer to the main river, showed the more usual *lateral* seasonality during both the early and late drawdown periods. Waterbody DBT, on the channel leading to the DBL lake also took some large catches in November when the largest DBL catches were taken, but the smaller LST lake did not produce any fish during the flood.

- **1996 Migration seasonality**

In 1996, the waters began falling in the middle of the flood season to give a 'false drawdown' in late February. The real drawdown then began in May with a very sharp fall in water levels. As in 1995, this was again interrupted by a small re-flooding, but this time during June instead of July (see Figure 4.4). The dry season was then short in 1996, lasting only until early August, before the next flood was achieved by September. The 1996 study year was therefore approximately one month ahead of the 1995 study year, and with some differences in the flood pattern.

Longitudinal catches in the riverine *tuguk/corongs* were again taken in the early draw-downs with the largest catches in four of the six riverine waterbodies coincident with the sudden rapid fall in water levels in May 1996 (Figure 5.52). Additional catches were also taken at the end of February in two waterbodies when water levels dropped suddenly in the middle of the flood season. The small re-flooding in June 1996 in the middle of the drawdown did not stimulate the large catches seen in the mid-drawdown flood of 1995, but larger catches were taken in the main re-flooding in August and September, when only small catches were seen in 1995.

Lateral fish migrations were again seen over the whole of the drawdown period (eg Figure 5.53, waterbodies SEB and SA; Figure 5.54, waterbody SPG), continuing at least a month after the longitudinal migrations had stopped. As in 1995, the larger catches were usually taken during the first half of the drawdown. Larger lateral fish migrations were also seen in a few waterbodies in 1996 during the flood season (eg Figure 5.53, LPG; Figure 5.55, LST).

In the Lake region in 1996, large catches were again taken in the DBL and DBT waterbodies at the end of the flood season in September, while few fish were caught during the drawdown (Figure 5.56). The shallower LST waterbody was again more productive during the main ebb season and also during several

small draw-downs within the high water period (Figures 5.55, 5.56).

- **Summary and discussion of migration seasonality observations from catch data**

The catches in the different barrier gears show quite clearly that fish migrations are strongly linked to both rises and falls in water levels. Though the flood patterns varied significantly between the two years, the largest catches were linked to flood events rather than to a particular time of year. In summary, as the drawdown began, fish migrated both along the main river channels and off the floodplains. Towards the end of the ebb season, longitudinal migrations then ceased, and only lateral migrations were seen, presumably off the floodplain. At any time of year, sudden rises in water levels stimulated large catches both in the main river and in the lake region, though usually not in the waterbodies alongside the main river (lateral migrations). At the start of both the ebb and the flood, the earliest movements were observed in the more upstream waterbodies. Comparing the years, the 1996 catches were relatively larger in the flood season in some waterbodies, when few fish were caught in 1995 except in the lake region.

The relative scarcity of longitudinal migrations towards the end of the ebb season (when lateral migrations continued) either imply that riverine migrants are almost fished out during the early drawdown phase, or that they stop moving towards the end of the drawdown. Such migrants may have a very high vulnerability to the riverine barrier gears which particularly increases their mortality rates at this time. The existence of lateral migrations throughout the ebb season also presumably demonstrates the variation in tolerance among different fish species to the worsening conditions on the drying floodplains, and the preference of such fish to stay on the floodplain if possible.

The relative scarcity of fish during the flooding season in the riverine waterbodies emphasises the high mortality which exists over the dry season, though clearly some fish do survive. The larger catches in both the river and in lateral floodplain positions during the 1996 flood are presumed to reflect the shorter and less extreme dry season in that year, which should have allowed more fish to survive over the dry season. The scarcity of lateral migrations during the flood season may be due to the stronger rheotactic response of fish to migrate towards currents within the main river channel, than to migrate with water flows on to the floodplains.

As mentioned earlier, due to the lack of supporting information on the orientation of the gears, these catch data do not give unequivocal evidence on the directions of fish migrations. Discussions with local fishermen, however, confirmed that the main catches in the DBL lake were taken when fresh floodwaters were flowing from the river up the channel into the lake, at which time fish swam from the lake towards the river. The relatively large catches at this time in this largest lake confirm that many fish survive over the dry season in that habitat. The clear differences between the large DBL lake and the smaller non-perennial LST lake demonstrate the significant effect of habitat variations and position relative to the main river, even within waterbodies quite close to each other.

5.11.3 The Indonesian mark-recapture programme

This section provides statistics on the numbers and sizes of fish involved in the tagging programme at the Indonesian study site.

In Indonesia, 91-1,551 individuals of each key fish species were tagged between September 1994 and December 1996 (Table 5.12) giving a total of 3,712 releases. As in Bangladesh, fish were difficult to obtain in certain seasons, and the 1996 sampling year was broadly used to fill in the months with the least tag releases in 1995. The small *Anabas testudineus* was added to the Indonesian tagging programme in the second year, to provide a species comparison with results from Bangladesh, but it proved difficult to obtain enough fish of this species (Table 5.12).

Tagged fish recaptures averaged a lower 18% in Indonesia with the smallest *Anabas testudineus* having the lowest recapture rate of only 4%, and the catfish *Mystus nemurus* having the highest recapture rate of 30% (Table 5.13). Most of the recaptured fish were again taken within only a few months of their release: 74% of all the Indonesian recaptures were made in either the same or the following calendar month. The average number of days at liberty ranged between 10d for *Anabas testudineus* and 50d for *Mystus nemurus*. Many recaptures were taken between one and ten days after their release, and the longest time between release and recapture was 683d for an *Osteochilus hasselti*.

Only 4 tagged *A. testudineus* were returned to the programme, none of which had moved from their release waterbodies. Due to this lack of data, this species is not considered further in the migration analyses for Indonesia.

In Indonesia, it was intended to release fish in all three of the main regions to study the movements between them. However, due to the habitat preferences of the six key species, it proved difficult to achieve a balanced distribution of releases (Table 5.1, Figure 5.57). *Helostoma temmincki* were difficult to obtain in the upstream forest river region, while *Channa striatus*, *Mystus nemurus* and especially *Macrobrachium rosenbergii* all showed an avoidance of the lake habitat. In contrast to the Bangladesh site, recapture rates varied strongly between habitat regions, being consistently highest in the Forest River region, and lowest in the Lake District (Table 5.1). These results are considered further in section 5.9.

As in Bangladesh, it was intended that small fish, particularly *Helostoma temmincki* and *Osteochilus hasselti* would be tagged using the lightweight '12P' streamer tags (see Section 3.5), while larger fish would be tagged with anchor tags (Table 5.15, Figure 5.58). A larger size '7S' streamer tag (Section 3.5) was also supplied to Indonesia for tagging the freshwater prawn *Macrobrachium rosenbergii*, though this proved less suitable than the smaller 12P tag. Again as found in Bangladesh, recapture rates were generally lower for the streamer tags than for the anchor tags (Table 5.15).

All sizes of fish were tagged, as available from the fishery (Table 5.9). Such fish were randomly selected, and represented the average stock available in each month. The minimum and maximum sizes of fish tagged in Indonesia ranged from a 7.3cm *H. temmincki* to a 44.5cm *C. striatus* (Table 5.16). The fish recaptured were, on average, similar in size to those released with little evidence of size-related mortalities or tag losses within the tag types (Figure 5.58).

5.11.4 Spatio-temporal migration cycles of the key species

For the Indonesian analysis of seasonal migration cycles, restriction of the data set to only those recaptures taken within the same or the following calendar month as release enabled 74% of all the Indonesian recaptures to be used in the analysis, from 63% of the *Channa striatus* data to 83% for *M. rosenbergii*. In Indonesia, the flood seasonalities varied significantly between the two study years (see Figure 4.4), and the observed migrations were therefore distinguished between the two years when practical. The locations of tag releases for the Indonesian site are shown for each species and month in Figures 5.60 to 5.64.

As with the Bangladesh analysis, the following sections examine the temporal and spatial aspects of the migration cycles shown by each of the Indonesian key species, by reference to monthly data on the percentages of fish migrating and their migration distances (Figure 5.65), their 'lateral' movements between different habitats (Tables 5.1 and 5.17), and the directions of their 'longitudinal' movements (Figures 5.66 to 5.70).

- ***Anabas testudineus* migrations (Indonesia)**

Since only four tagged *A. testudineus* were recaptured in Indonesia, none of which had moved from their release locations, no conclusions are drawn for this species.

- ***Channa striatus* migrations (Indonesia)**

Channa striatus was the least well recaptured of the other five key species, with only 22 fish available for analysis in the seasonality study (having been recaptured within the same or the next calendar month as released). This small sample size prevents any reliable conclusions on the migratory seasonality of this species (see Figures 5.65, 5.66). The habitats of release and recapture for *C. striatus* do, however, reveal a preference for the floodplain habitat, both in the *lebak* and the *rawang*, with only two fish found in the river habitat in the dry season months (Table 5.17). *C. striatus* was also relatively uncommon in the Lake region, resulting in few tag releases in this area, and no movements were observed between the lake and the riverine regions for this species (Table 5.1, Figure 5.66).

- ***Helostoma temmincki* migrations**

Helostoma temmincki showed the lowest migratory tendency, only moving between waterbodies in the May/June drawdown and the October flood seasons (Figure 5.65). Though conclusions are tentative with only 6 migrations available for the seasonality study, the two largest migrations were downstream in the June drawdown season and upstream in the October flood (Figure 5.67). Most of the tag recaptures were taken in the *lebak* floodplain habitat, although lateral migrations between the floodplain and the river were

also observed at the start and end of the dry season (Table 5.17). No *H. temmincki* were obtained for release or recaptured in the *rawang* flooded forest habitat, suggesting that this surface living species prefers open waters without tree cover.

- ***Mystus nemurus* migrations**

The catfish *Mystus nemurus* maintained some migrations throughout the whole year (Figure 5.65 - percentages migrating), but the largest migrations were observed in May and July 1995 (Figure 5.68, 5.65 - mean distances). These large migrations were nearly all in a downstream direction at this time, in synchrony with the two drawdown phases of 1995 (Figure 4.4): only small migrations were observed during July when the site was reflooded by a temporary flood pulse (Figure 5.68). Outside of this clear pattern, *M. nemurus* showed highly variable migratory behaviour with most months having both upstream and downstream longitudinal migrations. The migrations observed at the start of the flood seasons (August to October) did include some upstream movements, but none of the same magnitude as the earlier downstream migrations.

Mystus nemurus also showed strong lateral migrations to all three habitats, making full use of the floodplain environment (Table 5.17). Though most fish were recaptured in the river system, many fish were also found to migrate to the *lebak* during the early flood and back into the river in the late dry season. However, all such lateral migrations were clearly restricted to the waterbodies close to the main river system - no movements were observed for *M. nemurus* in between the lake and the river system (Table 5.1, Figure 5.68). Indeed, *M. nemurus* were so difficult to obtain for tagging purposes in the Lake region that most of the releases made at that location had to be transported in from their riverine capture location.

- ***Macrobrachium rosenbergii* migrations**

The giant freshwater prawn *M. rosenbergii* showed a clear preference for riverine waters throughout the year, and for rivers and forested floodplain waters during the middle of the flood season (January, Table 5.17). Only one prawn was recaptured in the *lebak* open floodplain habitat, also during the flood. Some movements were observed in all seasons (Figure 5.65), but the largest migrations were seen during the high water and early drawdown period from January to May (Figures 5.65, 5.69). Like *M. nemurus* nearly all of these large longitudinal migrations were in a downstream direction, though they occurred some months before the *M. nemurus* migration. Only two *M. rosenbergii* (both of average lengths) were recaptured upstream of their release locations, in January and May when other prawns were still migrating downstream (Figure 5.69). With these strong longitudinal migrations, *M. rosenbergii* showed the strongest interaction between the Forest and Savanna river regions, but, like *M. nemurus*, showed no movement to or from the Lake region.

The migration pattern observed for *M. rosenbergii* is strongly supported by the length frequency data examined in Section 5.5.3, where fish were observed moving upstream during the course of the early flood and to grow steadily during this time. The combined sources of data indicate an annual life cycle, with spawning in brackish waters (or at least downstream of the study site), an upstream migration in the early flood, and a return downstream migration during the middle and late flood seasons.

- ***Osteochilus hasselti* migrations**

The small cyprinid *Osteochilus hasselti* made the broadest use of the three habitat zones, being found in the rivers all year, moving in to the *rawang* flooded forest in April and May at the end of the flood season, and then in the *lebak/lebung* pools in the dry season in August (Table 5.17). These lateral movements were also accompanied by clear longitudinal migrations in a downstream direction in the April/May drawdown, and back upstream with the August 1996 floods (Figure 5.70). This pattern resulted in *O. hasselti* achieving the largest interaction between the Savanna River and the Lake regions (Figure 5.59, Table 5.1).

- **Summary of Indonesian key species migrations**

As in Bangladesh, the above results for Indonesian fish show some similarities between species, and also several very clear differences, as follows:

- The strongest migrations were observed during the drawdown and flood seasons.
- Only the riverine MN⁷ maintained some migration over the dry season.

⁷ In this section, CS=*Channa striatus*, HT=*Helostoma temmincki*, MN=*Mystus nemurus*,

- Clear habitat preferences were shown by CS for the *lebak* and *rawang* habitats, and by HT which avoided the *rawang*. MN and MR were most common in the riverine habitat, though MN was found everywhere, and MR were common in the *rawang* in the middle of the flood season. OH were found in all habitats, particularly in the *rawang* in the late flood season.
- Only HT and OH migrated between the Lake habitat region and the riverine regions.
- In the dry season, fish occupied river and *lebak/lebung* habitats, but no fish were found in the *rawang* habitat.
- In the early flood season, September/October in 1995 and August in 1996, OH migrated strongly upstream supported by smaller numbers of CS, HT and MN.
- Strong downstream migrations were shown by the riverine MR over the full high water period, January to May; by MN during the May and July 1995 drawdown phases; and by OH during the early drawdown in April/May 1996.

Considering both the catch data from the barrier gears, and the tagging data for the key species, it is clear that the main migrations in Indonesia are the downstream longitudinal migrations (particularly of *Mystus nemurus*) in the early drawdown, as fish try to escape from the drying river catchment. The strong upstream migrations seen in Bangladesh at the start of the *drawdown* were not observed at the Indonesian site.

5.11.5 Migration scales

All five of the Indonesian key species showed significant mobility, with some substantial migrations between different waterbody licensing units. The most migratory species were *Mystus nemurus* and *Macrobrachium rosenbergii*, both of which migrated along the full length of the 36km river section studied, and were also returned from waterbodies outside the study site (Figure 5.59). The longest recorded migration (measured in a straight line) was a downstream movement of over 18km for a *M. rosenbergii* prawn, while the most distant recapture was a *M. nemurus* caught in the *kecamatan* district of Kayuagung (Figure 3.4), at least 5km downstream of the study site boundary.

The least migratory species was *Helostoma temmincki*, most recaptures of which were taken in the same waterbody as their release (only 16% of the 91 recaptures had moved). However, even this species occasionally migrated as far as 9km (Figure 5.59).

In between these extremes, both *Channa striatus* and *Osteochilus hasselti* showed intermediate mobilities at the Indonesian study site, with mostly small movements between waterbodies and maximum migrations of up to 9-11km (Figure 5.59).

5.12 Dry season survival locations

This project's studies on mortality rates showed that natural mortality rates were relatively low at the Bangladesh site, compared to the current total mortality rates, including the effects of fishing (Section 5.9). This suggested that significant gains could be made by restraints on fishing during the dry season period, thereby increasing the numbers of fish contributing to the spawning and recruitment of the next year's cohort.

Having determined *how many* more fish might survive in dry season reserves, this section reports a number of indicative results on *where* such reserves should best be placed.

5.12.1 Indications from catch data

In Bangladesh, some fish catches are taken throughout the dry season in both secondary rivers and *beels*, both inside and outside the PIRD/FCD/I scheme (see Chapter 6, Figures 6.7 and 6.8). Significant catches are also taken, particularly at this time, in the Main River region, though these are largely due to the run of *hilsa* up the main river channels. In contrast, catches are not sustained over the dry season in

MR=*Macrobrachium rosenbergii*, and OH=*Osteochilus hasselti*.

the shallower canals.

At the Indonesian study site, the unusual catch seasonality of the Lake District region suggests that many fish survive over the dry season in that most permanent habitat. In this locality, fish are most caught at the start of the flood season (Figure 5.2) when the new flood waters attract them from the lake system towards the rivers (Section 5.11.2). Similar catch seasonalities have been reported for the Danau Sentarum lake systems on the Kapuas River in West Kalimantan (Dudley, 1996). In contrast, fish in the two Lempuing River regions are most caught in the drawdown and dry seasons, and fewer fish then appear to remain to be caught during the following flooding seasons (Figure 5.2). Within the river system, catches in the downstream Savanna river region in 1996 were least declined from their 1995 levels after the long 1995 drought (Figure 5.2), suggesting that more fish survive in the larger downstream river.

5.12.2 Indications from tag return data

In support of the last section, a lower overall fishing mortality rate is indicated in the Indonesian Lake region by the tag return rates. With tag return rates of only 8%, fish survival in that locality may be more than three times higher than in some of the riverine waterbodies (Table 5.1). Within the riverine habitat, the upstream Forest region produced 50% higher tag recapture rates overall (27%) than the downstream Savanna region (14%). This again suggests that the wider and deeper river sections, as found downstream, produce better conditions for the survival of fish against fishing pressures.

In Bangladesh, overall tag recapture rates were similar both inside and outside the FCD/I scheme, at 29% and 31% respectively (Table 5.7), and both regions would appear to offer similar possibilities for fish survival in dry season waterbodies.

The tagging data also showed that fish occupied secondary river and *beel*/habitats in Bangladesh, with *C. catla* being particularly found in the largest dry season *beels*, and *P. sophore* and *G. giurus* being most common in rivers (Section 5.10, Table 5.10). In the Lempuing River site, *C. striatus* and *H. temmincki* were shown to prefer the floodplain *lebung* waterbodies over the dry season, while *M. nemurus* and *M. rosenbergii* were especially found in the river channel (Section 5.11, Table 5.17).

5.12.3 Indications from length frequency data

The length frequency data (Figure 5.19), supported by the tagging results (Figure 5.69), showed that the Indonesian freshwater prawn *M. rosenbergii* migrated downstream of the study site for the dry season period and then migrated upstream during the early floods, presumably to feed in the upstream areas during the flood season.

In Bangladesh, it is reported that the larvae of this species require brackish water of salinity 12-18ppt for their early development (Roy Jensen, *pers. comm.*, 15 October 1996). Other *Macrobrachium* species require slightly higher salinities of 14-21ppt, and may be found as juveniles further down the estuarine zones (Gamba, 1982). From the available data (restricted to a short, upstream section of the overall River Lempuing), it is assumed that Indonesian *M. rosenbergii* also return to estuarine waters to survive over the dry season, and reproduce.

5.12.4 Indications from Sub-Project 1 (Dry Season Waterbodies) data

Sub-Project 1 in Bangladesh studied the availability of different types of waterbody over the dry season of 1995/96, and the survival of floodplain fish in each type. This study is written up in detail in Appendix C, with a summary of the relevant results provided here.

Sub-Project 1 showed that the many small household *mathe*l ponds produced high catches of fish in the early dry season, but were usually either completely fished out by dewatering, or dried out naturally by the end of the dry season. In contrast, some of the largest, perennial *beels* and the deepest sections of the rivers did retain some water throughout the dry season, and were not dewatered. Based on the rate of decline of their catches, it was estimated that a total of up to 0.6-2.2 tonnes of fish survived over the dry season inside the FCD/I scheme, and 2.9t outside. These very small escapements represent only 0.54-1.9% and 0.6% of the estimated fish populations at the start of the dry season, but do indicate that some fish survive in these larger waterbodies both inside and outside of the FCD/I scheme.

The numbers of fish species in the catches of the perennial *beel* and river waterbodies were also higher, and included more of the larger, valuable species, than in the smaller *kua* waterbodies, with the household

mathel ponds being the least species rich. All the catches were, however, less species rich at the end of the season than at the beginning; the major carps were among those species less common at the end of the season, when catches were dominated by predatory catfish and snakeheads. In five of the six available combinations of waterbody type and season, fish communities were also richer outside the FCD/I scheme than inside. These results suggest that not all species of fish are able to survive over the dry season in floodplain waterbodies, even in the deeper ones, and that more fish do survive outside. It is concluded that the adjacent Main River region is also important for the dry season survival of fish, and that the immigration of fish through the flood control sluice gates does also maintain fish populations inside the PIRDP area.

5.13 Discussion and Conclusions

5.13.1 Age dependent dynamics

This research has shown that virtually all the catches taken at the Bangladeshi site are of fish in their first year of life. Spawning takes place at the beginning of the flood, growth is rapid, and four of the six key species all proved able to spawn at the end of their first year, thereby maintaining the stock to the next year.

An exception to this pattern was the large major carp *Catla catla*, which was *not* mature by the end of its first year, though the catches were still nearly all yearling fish. The Pabna fishery on this species is clearly based on its floodplain nursery grounds. The older *C. catla* were only available in small numbers from the Main River region, and spawning was observed to take place in the main river margins for this species.

This dependence on the yearling stock in Bangladesh was shown to be largely due to its exceptionally high fishing mortality rates, at around 2-4 times higher than natural mortality rates. In Indonesia, in contrast, many more fish survived into their second year of life, and fishing mortality may be up to four times lower for some species, especially those such as *C. striatus* not highly vulnerable to the barrier traps. In contrast to the fish species, the Indonesian giant freshwater prawn *M. rosenbergii* was shown to comprise only a single age class, with annual spawning in the estuarine zone, and growth in the freshwater zone.

Fish stocks effectively based on only single age classes of fish are notoriously vulnerable to overexploitation since the next year's recruitment is entirely dependent on the survival of the one and only cohort present, and its success of spawning in that one year. When environmental conditions cause high mortality rates or overexploitation in a given year, this recruitment and the long-term sustainability of the stock may be seriously threatened. Other species with truly annual life cycles include the majority of squid stocks. To ensure good recruitment for future years, fishing levels on these stocks are generally set at a level which only reduces the end-of-season escapement to 40% of that which would occur without fishing (Beddington *et al*, 1990). With fishing being responsible for most of the mortality at the study sites, this 'proportional escapement' is clearly much lower in these floodplain fish.

Facing this pressure, floodplain fish stocks are clearly adapted to survive in very difficult conditions, and to rebuild stocks rapidly from very low numbers. The stock-recruitment relationship reported for *Puntius sophore* shows that floodplain fish may strongly compensate for reduced abundances by producing extraordinary numbers of recruits in very short periods. This compensation may be even higher when nutrient levels are raised after long dry seasons.

Changes in species compositions have nevertheless been observed at the study sites, and not all species may be as good at surviving as *P. sophore*. Reflecting the mortality rates, fewer large fish were found in Bangladesh than in Indonesia (Hoggarth and Kirkwood, 1996). Reflecting their accessibility, fewer large migratory fish were also found inside FCD/I schemes in Bangladesh than outside. Even since 1993, two of the most valuable species at the Indonesian site appear to have disappeared from local stocks. With such impacts and declines in these highly exploited, almost 'annual' species, it is recommended that a precautionary approach should be applied to the management of both these floodplain stocks. Approaches for precautionary management are discussed in Chapter 7 of this report.

5.13.2 Migratory behaviour

The migratory behaviour of the different key species studied has been shown to be substantially more complicated than a simple movement on and off the floodplains during the flood season. Significant differences were seen between the different key species, between the two study sites, and within the habitat regions of the Indonesian site. These differences largely determine the capture opportunities for fishermen, and the management requirements and opportunities of the two sites.

- **Responses to hydrological stimuli**

In the simplest terms, the fish species generally migrate upstream to spawn at some point around the start of the flood, allowing their eggs to drift back downstream and on to the floodplains with the overspilling waters. The most significant contrast to this pattern was shown by the giant freshwater prawn, *Macrobrachium rosenbergii*, which migrated *downstream* to spawn, probably to estuarine waters, and then returned back upstream into fresh waters over the flood season, to feed and grow as juveniles.

At both sites, fish responded strongly to currents, usually in a positive way, displaying a 'rheophilic' attraction for flowing water. Several migrations were observed linked to sudden changes in water levels, even when these were some months away from the usual seasonality of such events. This suggests that, within limited time windows, fish simply respond to the water conditions in their immediate vicinities, presumably having waited for the appropriate cues. The relative lateness of the migratory responses for fish in downstream parts of the Lempuing River, compared to those upstream, suggests such stimuli arrive in upstream waters first.

While fish may thus have a general perception of their migratory needs and the appropriate responses, some of the observed migrations suggest that fish have little impression of their exact position in the overall river catchments. In the hydrologically complicated PIRDP scheme, when some gates are open and other gates are closed, it must be very difficult for fish to orientate themselves, and be certain about which direction is 'upstream' and which direction 'downstream'.

The Bangladeshi data suggest that the fish in the Pabna study site consider the Badai and Atrai secondary rivers, flowing from the PIRDP scheme out to the Padma/Jamuna, as their 'main' river. The longitudinal migrations in which moved fish up and down these secondary rivers, also took fish on and off the floodplain from the perspective of the main rivers outside and the PIRDP. Their behaviour suggests that they respond only to their immediate rheotropic stimuli, rather than to any wider knowledge of the main river system as a whole. Their behaviour makes sense from the overall catchment perspective, but since so much of the inside floodplains dry out during the drought, movements up the secondary rivers instead of the true main rivers are unlikely to provide many spawning opportunities. Other fish within the main rivers, and not effectively tagged, may of course have shown more ecologically appropriate behaviours. Allowing that some fish do survive inside the PIRDP, up the secondary river catchments, it is possible that each secondary river may contain a partially distinct unit stock, supported by fish moving between secondary rivers in the main river or floodplains outside.

Though these strong migratory behaviours may sometimes produce inappropriate behaviours, they may also be used to increase production on the inside floodplains. By opening sluice gates to appropriate apertures, fish could thus be encouraged to enter the PIRDP over the early ebb period, as well as during the main passive flood season immigration.

- **Catchment influences on migrations**

The strongest migrations at the Indonesian site were observed during the drawdown period in a downstream direction. In contrast, stronger migrations were observed in Bangladesh, earlier in the drawdown period, and in an upstream direction. These differences may be explained by the catchment positions of the two sites (Chapter 4). The Bangladesh site may thus be expected to have fish with a strong tendency of upstream migration as it is located in relatively downstream part of a large river system, with the adjacent main river available year-round for upstream migrations. The Indonesian site may be expected to show more downstream migrations, due to its relatively upstream river position, and to the high mortalities seen in the upstream Forest river region at this site.

The strongest downstream migrations seen in Bangladesh were from the middle to the end of the drawdown season, especially coinciding with the final drying out of the floodplains. In Indonesia, fish were seen to migrate longitudinally downstream only during the early ebb season, but lateral migrations

continued off the floodplains right up until the end of the drawdown, equivalent to the final emigration in Bangladesh.

The 'upstream' migrations in Bangladesh (actually lateral migrations into the PIRDP) included passive movements in the early flood and also strong active migrations as the waters began falling. In Indonesia, upstream movements were seen during freshets (sudden flood events) either during the main ebb or even within the high water or drawdown seasons. Fish also moved strongly from the Lake region towards the river in Indonesia due to the attraction of new flood waters from the adjacent river. Lateral movements on to the floodplain in Indonesia were however not so common, suggesting that these movements are passive tendencies, which fish can resist to avoid capture in the lateral *kilung* and *empang* barrier traps.

The general conclusion from these results is that movements of Bangladeshi fish into the FCD/I schemes such as the PIRDP site are stimulated by the active migratory behaviour of these species, adapted to undertake strong longitudinal migrations in a large river system. Many fish appear to simply respond to the positive attraction for flowing or new water, and may be attracted to the PIRDP site, mistakenly thinking they are moving upstream. Fish at both sites then also take steps to migrate back away from drying conditions when necessary, for example moving off the drying Bangladeshi floodplains, and downstream from the Indonesian Forest river habitat.

- **Fish mobility and accessibility of impounded floodplains**

The mobility of fish at the study sites varied from the virtually sedentary lifestyle of *H. temmincki* in Indonesia to the stronger migratory behaviours shown by *C. catla* and *W. attu* in Bangladesh and *M. nemurus* and *M. rosenbergii* in Indonesia. All fish species were, however, occasionally seen to migrate up to at least 5km, thereby moving between the licensing units of different communities and fishing groups. Such mobility clearly places an incentive on spatially-licensed fishermen to catch as many fish as possible while they remain within their areas of control.

The mobility of fish was also shown to be sufficient to enable some fish to move between the Inside and the Outside regions in Bangladesh, and to penetrate the sluice gates in all of the four migratory phases identified in Sub-Project 3 (Appendix E). Such migration rates were low, however, with only 23 of 1,389 recaptures having moved into the PIRDP, and 12 back out. The three smallest key species, *A. testudineus*, *G. giurus* and *P. sophore* were not observed to cross the PIRDP embankment as tagged fish, though untagged fish of these species were detected in the catches at the sluice gates. As indicated by the species composition studies for Bangladesh as a whole (Appendix J), and for the PIRDP study site, FCD/I schemes do appear to restrain the movement of fish into modified floodplains, but not to completely prevent them. Sluice gates should therefore clearly be recognised as important structures for maintaining the biodiversity and productivity of inside floodplains. Further studies on alternative sluice gate designs could show how this important contribution could be maximised.

5.13.3 Spatio-temporal variability - floodplain modification and inter-annual effects

This research has confirmed that Bangladeshi fish in the Pabna region have the migratory behaviours to move into the PIRDP, and are indeed able to penetrate the sluice gates in small numbers. Modified floodplains are thus *accessible* to outside sources of recruitment, though the embankment undoubtedly limits such accessibility. This section discusses the various results on the comparative population dynamics of fish inside and outside the Bangladesh site to determine whether the *productive capacity* of floodplains is reduced by their hydrological modification. This subject forms the central theme of the PhD thesis supported by this project, and will be addressed more quantitatively in that work.

All the sub-components of the fish population dynamics examined during this project gave no evidence of reduced productive potential inside the PIRDP flood control scheme. Rates of feeding, growth, condition, reproduction, and survival were all thus at least as good inside the FCD/I scheme as outside. In contrast, much greater differences in mortality rates were observed between the Bangladeshi and the Indonesian sites. It is concluded that the productive *potential* of the PIRDP FCD/I scheme *per se* is *not* reduced by its hydrological modification. The almost identical diet compositions of fish inside and outside the PIRDP scheme also show that hydrological modification has not significantly affected resource characteristics or feeding opportunities for floodplain fish. Due to the lower fish abundances inside the PIRDP in the 1995/96 flood year, fish growth rates and condition factors were actually higher in that region than outside. Whether such differences could compensate for the lower fish densities will be addressed elsewhere (Halls, PhD thesis).

Though its productive capacity may be undiminished, the actual production inside the PIRDP scheme was still lower than outside in both the study years. The reduced production is partially explained by agricultural production inside the PIRDP, and the restrictions placed on fishing activities by landowning farmers (see Chapter 6). Since fish abundances and species compositions were both lower inside, especially for the migratory riverine major carps and other larger species, and since migratory access is clearly limited by the flood control scheme, it is concluded that floodplain productivity is also strongly impacted by the partial inaccessibility of the PIRDP and the impact this has on the recruitment of some species. Supporting this conclusion, Inside fish production increased dramatically in the 1996 flood year compared to outside, when the sluice gates were opened due to the lack of local rainfall. It is concluded that fish catches in modified floodplains could be enhanced by increasing recruitment either from internal or external sources. Options for recruitment enhancement are explored further in Chapter 6.

In comparison with the ineffective in/out variations, hydrological conditions also vary significantly between years, and then have stronger impacts on productivity. Such impacts were demonstrated by the consistently higher feeding and growth rates in 1995 for all species in Bangladesh, and the up to two-fold differences in total catches seen between study years in each of the study regions. Such interannual variability is likely to remain as a characteristic of floodplain systems, dependent on complex hydrological features.

5.13.4 Dry season survival and recruitment

The preceding sections have shown that exploited floodplain fish usually only live to spawn once at the end of their first year, and that production in both modified and unmodified floodplains could potentially be enhanced by increasing recruitment rates. The key management issues are then where do pre-spawning fish survive over the high-mortality dry season period?, and how could their survival be increased? Various aspects of this research have indicated, as may have been expected, that fish survive mainly in the deeper and most perennial waterbodies. In Bangladesh, these include the deeper *beels* and river sections, both inside and outside the FCD/I scheme. In Indonesia, key survival locations include the downstream Savanna region of the Lempuing River, and the deepest, largest lakes in the Lake District region. In addition to these locations, some fish are most likely to survive in the main river region in Bangladesh, particularly perhaps the older specimens of the potentially long-lived major carps.

In the modified Bangladesh floodplains, fish populations inside the PIRDP are clearly maintained from sources of recruitment from both inside and outside the FCD/I scheme. From their relative contributions in weight, it was concluded that the majority of inside recruits originate from dry season survival inside the FCD/I scheme. Reasonable production was thus observed in the 1995/96 flood year inside the PIRDP, even though the main Talimnagar sluice gate was closed for almost the whole of the flood season. From the richer species compositions seen outside the PIRDP scheme, and the declines in species richness in dry season waterbodies as the dry season progressed, it was concluded that external sources of production, and immigration through the sluice gates, are likely to be vitally important for maintaining the biodiversity of modified floodplains. Both sources of recruitment are thus likely to be crucial for the overall health and vitality of modified floodplains. Possible management strategies for enhancing the recruitment from these sources are considered in Chapter 7.

5.14 Summary

- This chapter describes the differences in productivity between the two study sites, and their sub-regions, and attempts to explain these differences by examining each stage of the production cycle in detail, including fish recruitment and abundance, feeding and growth, reproduction, migrations and survival. This examination is most thorough for the Bangladesh site, including the extra analyses conducted in four of the Sub-Projects.
- Productivity, measured as catch per unit area, outside the Bangladesh FCD/I scheme (104 and 130kg/ha/yr in 1995 and '96 respectively) was significantly greater than inside (51 and 81kg/ha/yr). This difference may be partially due to a less habitat-rich environment in the inside region selected or to restrictions placed on fishing gears due to agricultural production (see Chapter 6).
- In Indonesia, productivity varied significantly between the two study years, with the 1996 season being only 61% as productive as '95. Catches were particularly reduced to only 51% in both the Lake and Forest regions, but maintained at 75% in the Savanna river region.

- In 1995, fish abundances in Bangladesh, measured as catches per unit effort, averaged across gear types, were up to 20% greater on outside floodplains than inside, and 12-82% greater in the main river. In 1996, in contrast, average CPUEs were higher inside the FCDI scheme than both the outside floodplains and the main river.
- In both years, fish species communities in Bangladesh were richer outside the FCDI scheme with 73-80 species (not including shrimps) in the catches, compared to only 64-74 species inside. In 1995, six species were more than twice as abundant outside the FCDI scheme as inside: the major carps *Catla catla* and *Labeo rohita*, and *Glossogobius giuris*, *Mystus vittatus*, *Wallago attu*, and a mixed group of shrimps; only *Anabas testudineus* was more than twice as abundance inside the scheme. In 1996, *Cirrhinus reba*, *Pseudeutropius atherinoides*, and *Wallago attu* were more abundant outside, while the smaller *Colisa fasciatus*, *Chanda nama*, *Lepidocephalus guntea*, *Mastacembelus pancalus* and *Xenentodon cancila* were more abundant inside. These findings were broadly supported by a nationwide analysis of the FAP17 species composition data, in which the smaller species inside FCD/I schemes had a 20% lower financial value, but a higher nutritional value. It was concluded that the PIRDP embankment reduced the accessibility of the FCD/I scheme, though it did not completely prevent the entry of fish.
- At the Indonesian site, species compositions were richest in the downstream Savanna river region, though this may have been due to the the higher sampling effort. Two of the most valuable River Lempuing species, *Notopterus chitala* and *Osphronemus gurami*, previously recorded as rare in 1993 samples (ODA Project 4791) were not recorded in any of the 1995 or '96 catches.
- Fish recruitment in Bangladesh was observed in the early flood season for the two smallest key species, *P. sophore* and *G. giuris*, and slightly later for the other larger key species. Bangladeshi fish recruited as small as 1-2cm due to the small mesh sizes used in the fishery.
- In Indonesia, fish recruited at larger sizes than in Bangladesh, usually later into the flood season. Both the snakehead *C. striatus* and the freshwater prawn, *M. rosenbergii*, were particularly responsive to flood events, producing recruits shortly after floods even outside the main reflooding season. *M. rosenbergii* were shown to recruit from downstream spawning areas, most likely in estuarine areas, and to grow to adult size in the freshwater river zone in only one year.
- Recruitment was shown to occur in Bangladesh at the same time in the Inside and Outside PIRDP regions, or sometimes even earlier inside for *P. sophore*, which was shown to be highly responsive to the flood cycle. Internal sources of recruitment were identified as most important for supporting the modified floodplain habitats, while external sources of recruitment and immigration through sluice gates were thought to be responsible for maintaining biodiversity.
- Stomach analyses showed that *A. testudineus* was mainly insectivorous, *C. striatus* and *W. attu* were both mainly piscivorous, *G. giuris* ate both fish and crustacea, and *C. catla* and *P. sophore* both ate mainly plankton and algae. Feeding rates and diet compositions were almost identical inside and outside of the Bangladesh study site, for five of the six species investigated. Compared to these minimal spatial differences, slightly greater variation was seen in feeding rates between the two years, with the large '95 flood generally producing higher feeding rates than the '96 one.
- Growth performance, measured as the mean length of the 0+ cohort in November was, with the exception of *G. giuris*, found to be significantly higher during the 95/96 flood year compared to the 96/97 year. During the first flood year, growth performance of four of the six species was also significantly higher inside the FCD/I scheme than outside. The condition (weight at length) of *C. catla*, *G. giuris*, *P. sophore* and *W. attu* was also found to be significantly higher inside the scheme compared to outside, for the 24 month sampling period overall. The observed interannual differences in growth performance were best explained by the flood index and feeding rates, while in/out differences in 1995/96 appeared mostly due to the fish densities, lower inside the PIRDP.
- The density dependence of fish growth was confirmed by controlled experiments on the key species *P. sophore*. At low densities, in fertilised ponds, this species proved capable of growing to sexual maturity and spawning within only 12 weeks of hatching!

- Lengths at maturity of the Bangladeshi key species were shown to vary between the sexes, but to show no differences inside and outside the PIRDP. Fecundity at length was also equal inside and outside the FCD/I scheme, except for *A. testudineus*, where fecundity was higher inside. All the key species except *C. catla* were seen to reach sexual maturity by the end of their first year, and spawning activity reached a peak during the rising-water season for most species. Both *P. sophore* and *G. giurus* had extended spawning seasons and may spawn more than once per flood season. For most species, spawning took place at the same time both inside and outside the FCD/I scheme and fish inside the PIRDP were confirmed to contribute to its recruitment. Fry of the major carp *C. catla* were, however, only caught by *savar* seine nets in the main river during the rising water season, and this species appears to use the floodplain habitats mainly as nursery grounds.
- In Bangladesh, the vast majority of fish were shown to survive no longer than one year, and stocks were nearly always comprised of only a single cohort wholly responsible for the reproduction of the next year's stock. Total mortality rates in Bangladesh are so high that only 0.5-2% of each cohort survive each year - no differences were found in survival rates between the Inside and Outside regions (not including the main river habitat). In Indonesia, far more fish survive beyond their first birthday and mortality rates are correspondingly lower. Very high tag recapture rates suggested that the greatest component of the high overall mortality rates was due to fishing. Fishing mortality rates were particularly high for the most migratory *C. catla* in Bangladesh, and for *M. nemurus* and *M. rosenbergii* in Indonesia. Field and experimental analyses on the natural mortality of *P. sophore* in Bangladesh showed that up to 37% of this species could survive over the dry season in the absence of fishing, depending on fish densities.
- With such high fishing mortality rates increasing the vulnerability of these effectively 'annual' fish species, and observing the declines in some important species, it is recommended that a precautionary approach should be applied to the management of both these floodplain stocks.
- Fish migrating through the sluice gates in Bangladesh displayed four different migration phases, including both passive and active movements in both inward and outward directions. Small fish, such as *Puntius sophore*, *Glossogobius giurus* and shrimps drifted in passively into the PIRDP early in the flood, while the major carps *Labeo rohita*, *Catla catla*, *Cirrhinus reba*, and *Labeo calbasu*, in addition to *Wallago attu* were also attracted in to the PIRDP at the start of the ebb season. The strongest migration was a passive drift out with the ebb, particularly coinciding with the final fall in water levels below the floodplain height. Though many fish were captured at the sluice gates, the ability of some fish to pass through both the gates and the fishing gears was confirmed by the tag recaptures. Since species compositions were depleted inside the PIRDP region, it was concluded that sluice gates should be recognised as important structures for maintaining the biodiversity and productivity of modified floodplains.
- In Indonesia, different migration patterns were observed in the lake and riverine habitats, though both were strongly cued to hydrological events. Only two key species, *H. temmincki* and *O. hasselti* migrated in between the Lake and the riverine regions. Strong longitudinal migrations were also observed at this site, particularly downstream during the ebb, to complement the lateral emigrations off the floodplains also seen in Bangladesh.
- The observed migration patterns were explained by a general 'rheophilic' attraction of floodplain fish for flowing waters, particularly to stimuli within their immediate vicinities, and to the relative catchment positions of the two study sites. The strong downstream migrations in Indonesia during the late drawdown were effective at moving fish away from the high-mortality upstream Forest river region before the dry season. The strong upstream migrations early in the drawdown season seen in Bangladesh were shown to be appropriate for fish moving up such a large river system, and also provided an effective mechanism for the capture of fish moving mistakenly in to the PIRDP floodplains at this time.
- The mobility of all of the key species studied was sufficient to take them in between the licensing units of different fishing groups or communities. The maximum straight-line migrations observed ranged from 4.7km for *A. testudineus* in Bangladesh to over 18km for *M. rosenbergii* in Indonesia. Such mobility clearly stimulates competition between spatially-licensed fishermen, and increases

their incentives to catch as many fish as possible while they remain within their areas of control.

- The key fish species varied in their habitat preferences, with some riverine species and some still-water species at each site. Within these habitats, fish survived over the dry season in the deepest, most perennial waterbodies at each site. In Bangladesh, these included large *beels* and river sections, both inside and outside the FCD/I scheme, but not the smaller household ponds or *kuas*. Species compositions in dry season waterbodies inside the FCD/I scheme were, however, less rich than those outside, and became progressively less rich towards the end of the dry season. In Indonesia, key survival locations included the downstream Savanna region of the Lempuing River, and the deepest, largest lakes in the Lake District region. In addition to these locations, the older specimens of the long-lived major carps survived in the main river region in Bangladesh, and the Indonesian *M. rosenbergii* migrated downstream probably to estuarine zones for the dry season.
- With similar diet compositions in both regions, and rates of feeding, growth, condition, reproduction, and survival all at least as good inside the FCD/I scheme as outside, it was concluded that the productive *potential* of the PIRDP FCD/I scheme is *not* reduced by its hydrological modification. Due to the lower fish abundances inside the PIRDP in the 1995/96 flood year, fish growth rates and condition factors were actually higher in that region than outside. It was concluded that the lower productivity inside the PIRDP must be explained partly by lower fishing efforts (see next chapter), and partly by reduced recruitment inside the scheme, due to the restrictions on access imposed by the FCD/I embankment. Following this result, it was concluded that fish catches in modified floodplains could be enhanced by increasing recruitment either from internal or external sources.

Table 5.1 Fish species recorded at the Bangladesh PIRDP study site with identification codes

ABO	Apocrytes bato	LG	Lepidocephalus guntea
AC	Ailia coila	LGS	Labeo gonius
AM	Amblypharyngodon mola	LN	Labeo nandina
AMR	Aspidoparia morar	LR	Labeo rohita
AP	Aplocheilus panchax	MA	Mystus aor
AT	Anabas testudineus	MAR	Mastacembelus armatus
BB	Badis badis	MAS	Macrognathus aculeatus
BBS	Bagarius bagarius	MB	Mystus bleekeri
BD	Botia dario	MC	Mystus cavasius
BN	Brachygobius nunus	MCA	Mugil cascasia
CA	Crabs	MP	Mastacembelus pancalus
CB	Clarias batrachus	MR	Macrobrachium rosenbergii
CBS	Chanda baculis	MS	Mystus seenghala
CC	Catla catla	MT	Mystus tengra
CCA	Chaca chaca	MV	Mystus vittatus
CCO	Cyprinus carpio	NB	Nemacheilus botia
CCS	Chela cachius	NC	Notopterus chitala
CF	Colisa fasciatus	NN	Notopterus notopterus
CG	Clupisoma garua	OBR	Ophichthyes boro
CGA	Channa gachua	OBS	Opesteron bengalensis
CI	Ctenopharyngodon idella	OM	Oreochromis mossambica
CL	Chela laubua	OP	Ompok pabo
CLA	Colisa lalia	OT	Other species
CLS	Crossocheilus latius	PA	Pseudeutropius atherinoides
CM	Channa marulius	PC	Puntius conchonius
CMA	Cirrhina mrigala	PG	Puntius gelius
CN	Chanda nama	PP	Pangasius pangasius
CP	Channa punctatus	PPA	Pama pama
CR	Cirrhinus reba	PPO	Puntius phutunio
CRA	Chanda ranga	PS	Puntius sophore
CS	Channa striatus	PT	Puntius ticto
CSA	Colisa sota	RC	Rhinomugil corsula
CSN	Corica soborna	RCO	Rohtee cotio
DR	Danio rerio	RD	Rasbora daniconius
ED	Esomus danricus	RR	Rita rita
EV	Eutropiichthys vacha	SA	Scatophagus argus
GC	Gudusia chapra	SB	Salmostoma bacaila
GG	Glossogobius giuris	SF	Salmostoma phulo
GN	Gagata nangra	SG	Securicula gora
GV	Gagata viridescens	SGN	Somileptes gongota
GY	Gagata yousoufi	SH	Shrimp/prawn spp
HF	Heteropneustes fossilis	SP	Setipinna phasa
HI	Hilsa ilisha	SS	Silonia silonia
HM	Hypophthalmichthys molitrix	TC	Tetraodon cutcutia
HT	Hilsa toli	WA	Wallago attu
LB	Labeo bata	XC	Xenentodon cancila
LC	Labeo calbasu		

Table 5.2 Fish species recorded at the Indonesian River Lempuing study site with identification codes

AT	Anabas testudineus	MU	Mastacembelus unicolor
BH	Bagrichthys hypselopterus	MV	Mystus vittatus
BM	Bagroides milopterus	NN	Notopterus notopterus
BS	Barbodes schwanefeldi	O	Osteochilus spp
C	Cryptopterus spp	OH	Osteochilus hasselti
CA	Cyclochelichthys apogon	OM	Oxyleotris marmoratus
CB	Clarias batrachus	OV	Osteochilus vittatus
CD	Clarias melanoderma	P	Palaemon spp
CK	Channa bankanensis	PF	Pristolepis fasciatus
CL	Channa lucius	PG	Puntius gonionotus
CM	Channa micropeltes	PH	Polycanthus hasselti
CN	Cryptopterus apogon	PM	Pangasius micronema
CO	Chela oxygastroides	PP	Pangasius polyuronodon
CS	Channa striatus	PS	Puntius fasciatus
DO	Dangilla ocellata	PT	Puntius tetrazona
HA	Hampala ampalong	R	Mixed small fish
HM	Hampala macrolepidota	RA	Rasbora spp
HT	Helostoma temincki	S	Mixed small cyprinids
L	Others	SL	unknown
LH	Leptobarbus hoeveni	TP	Thynnichthys polylepis
MA	Monopterus albus	TR	Snakeskin gouramy
MN	Mystus nemurus	TT	Trichogaster trichopterus
MR	Macrobrachium rosenbergii	WL	Wallago leeri

Table 5.3 Results of the two-way ANOVA test of differences in mean fork length of the 0+ cohort () inside and outside the Bangladesh FCD/I scheme between flood years

		Mean length (\bar{L}_{Nov})					
	Location	95/96	96/97	Mean	Differ. (cm)	Result	p
<i>A.testudineus</i>	IN	11.9	10.6	11.3	0.1	I > O	0.687
	OUT	12.4	10.1	11.2			
	Mean	12.1	10.3				
	Difference	1.8					
	Result	95/96 > 96/97					
	p	< 0.0001					
<i>C.catla</i>	IN	26.0	27.0	26.5	1.7	O > I	< 0.0001
	OUT	31.5	24.9	28.2			
	Mean	28.8	25.9				
	Difference	2.8					
	Result	95/96 > 96/97					
	p	< 0.0001					
<i>C.striatus</i>	IN	30.3	25.8	28.1	2.3	I > O	< 0.0001
	OUT	25.7	25.8	25.8			
	Mean	28.0	25.8				
	Difference	2.2					
	Result	95/96 > 96/97					
	p	< 0.0001					
<i>G.giuris</i>	IN	5.6	5.9	5.8	0.8	I > O	< 0.0001
	OUT	5.0	4.9	4.9			
	Mean	5.3	5.4				
	Difference	0.1					
	Result	96/97 > 95/96					
	p	0.427					
<i>P.sophore</i>	IN	6.0	5.3	5.6	0.4	I > O	< 0.0001
	OUT	5.1	5.4	5.3			
	Mean	5.5	5.3				
	Difference	0.2					
	Result	95/96 > 96/97					
	p	< 0.0001					
<i>W.attu</i>	IN	47.2	42.5	44.8	7.7	I > O	< 0.0001
	OUT	43.2	31.1	37.1			
	Mean	45.2	36.8				
	Difference	8.4					
	Result	95/96 > 96/97					
	p	< 0.0001					

Table 5.4 Comparison of mean total mortality rate for each species for populations inside & outside the Bangladesh PIRDP study site

Species	\bar{Z}		$\bar{Z}_I \neq \bar{Z}_O$	\bar{Z} combined inside and outside					
	Inside	Outside	<i>p</i>	\bar{Z}	\bar{Z}_{lower}	\bar{Z}_{upper}	\bar{S} (%)	\bar{S}_{lower} (%)	\bar{S}_{upper} (%)
<i>A.testudineus</i>	3.4 (5)	4.5 (1)	NA	3.5	2.7	4.3	3.0	1.3	6.7
<i>C.catla</i>	4.0 (4)	5.7 (3)	0.11	4.7	3.4	6.0	0.9	0.2	3.3
<i>C.striatus</i>	3.6 (4)	4.1 (6)	0.62	3.9	3.0	4.7	2.0	0.9	4.9
<i>P.sophore</i>	2.5 (10)	3.7 (12)	0.06	3.2	2.5	3.9	4.0	2.0	8.2
<i>W.attu</i>	3.5 (3)	3.7 (11)	0.78	3.7	3.1	4.2	2.5	1.5	8.2

Table 5.5 Numbers of fish tagged at the Bangladesh PIRDP study site by species and month

Species	<i>Anabas testudineus</i>	<i>Catla catla</i>	<i>Channa striatus</i>	<i>Glossogobius giurus</i>	<i>Puntius sophore</i>	<i>Wallago attu</i>	Total
1994 December		1	1		2	1	5
1995 February	8	9	9			2	28
March	13	7	6			3	29
April	4		7				11
May	11		16	71	8		106
June	19	84	8	28	58	1	198
July	80	180	25	84	141	110	620
August	95	164	9	184	144	80	676
September	113	77	169	111	156	75	701
October	131	5	249	120	313	83	901
November	4		24			5	33
1996 January				22	16		38
February	66		9	32	76	1	184
March	62	22	27	4	16	29	160
April	56	76	31	5	41	58	267
May	8	8	5	27	39	19	106
June	29			8		20	57
July	191	143	4	7	3	5	353
August	12	33	5	6		89	145
Total released	902	809	604	709	1013	581	4618

Table 5.6 Numbers of fish recaptured at the Bangladesh study site by species and month

Species	<i>Anabas testudineus</i>	<i>Catla catla</i>	<i>Channa striatus</i>	<i>Glossogobius giurus</i>	<i>Puntius sophore</i>	<i>Wallago attu</i>	Total
1995							
February		1	1				2
March	3	9	6			3	21
April	4	1	6			2	13
May	4	1	3				8
June	22	9	3	5	4		43
July	2	43	1	10	4	4	64
August	7	75		21	6	13	122
September	8	47	8	15	2	22	102
October	49	36	88	11	12	38	234
November	10	5	62	2	10	13	102
December	9	11	12			7	39
1996							
January	3	3	7			12	25
February	12	4	10	1	4	3	34
March	32		9	1	1	4	47
April	57	38	32	1	20	29	177
May	12	13	3	3	8	30	69
June	20	1		6	1	10	38
July	41	14	4	7		1	63
August	28	80		5		14	131
September	19	16				2	37
October	12					1	13
November	1					2	3
December	1	1					2
Total recaptured	356	408	255	88	72	210	1389
% recaptured	39%	50%	42%	12%	7%	36%	30%

Table 5.7 Numbers of fish tagged and recaptured at the Bangladesh study site by species and region

Species	<i>Anabas testudineus</i>	<i>Catla catla</i>	<i>Channa striatus</i>	<i>Glossogobius giurus</i>	<i>Puntius sophore</i>	<i>Wallago attu</i>	Total
No. released							
Inside FCDI	778	190	382	375	600	182	2507
Outside FCDI	124	619	222	334	413	399	2111
No. recaptured							
Inside FCDI	308	103	169	49	47	57	733
Outside FCDI	47	301	86	39	25	151	649
Unknown	1	4				2	7
% recaptured							
Inside FCDI	40%	54%	44%	13%	8%	31%	29%
Outside FCDI	38%	49%	39%	12%	7%	38%	31%

Table 5.8 Numbers of fish tagged and recaptured at the Bangladesh study site by species and tag type

Species	<i>Anabas testudineus</i>	<i>Catla catla</i>	<i>Channa striatus</i>	<i>Glossogobius giurus</i>	<i>Puntius sophore</i>	<i>Wallago attu</i>	Total
No. released							
Streamers tag	163	11	31	637	1012	3	1857
Anchor tag	739	798	573	72	1	578	2671
No. recaptured							
Streamers tag	8	1		56	72		137
Anchor tag	348	407	255	32		210	1252
% recaptured							
Streamers tag	5%	9%		9%	7%		7%
Anchor tag	47%	51%	46%	44%		36%	47%

Table 5.9 Mean monthly fork lengths (cm) of fish tagged at the Bangladesh site by species and maximum & minimum lengths of fish tagged by species and tag type

Species	<i>Anabas testudineus</i>	<i>Catla catla</i>	<i>Channa striatus</i>	<i>Glossogobius giurus</i>	<i>Puntius sophore</i>	<i>Wallago attu</i>
Mean Fork-lengths (cm)						
January				7.6	6.0	
February	12.8	21.3	30.4	8.0	6.5	46.2
March	12.8	30.3	34.6	9.4	8.5	51.3
April	12.8	35.5	34.5	8.5	7.6	51.6
May	14.6	31.5	29.5	9.6	7.1	52.7
June	13.3	10.6	25.4	12.1	6.4	52.6
July	10.1	10.1	13.3	10.0	6.4	14.9
August	6.9	12.2	23.0	10.7	6.3	20.0
September	11.1	17.7	19.7	9.6	5.8	32.9
October	11.3	20.7	24.4	8.1	5.6	32.0
November	11.5		26.7			38.3
December			45.0			
Minimum Fork-length (cm)						
Streamers Tag	3.8	4.4	7.1	4.8	4.1	5.7
Anchor Tag	7.3	5.7	8.3	10.1	9.3	7.7
Maximum Fork-length (cm)						
Streamers Tag	9.1	7.8	9.7	24.6	10.0	9.2
Anchor Tag	20.2	45.0	50.2	31.1	9.3	73.7

Table 5.10 The seasonality of fish migrations between rivers (R, including canals), beels (B) and Floodplains (F, including some *Kuas*) at the Bangladesh site as shown by those tagged fish recaptured within the same or next calendar month after their release

Species	Month	No Habitat Change			To Floodplain		From Floodplain		Rivers<->Beels	
		R	B	F	R>F	B>F	F>B	F>R	R>B	B>R
<i>Anabas</i>	2	7	13							1
<i>testudineus</i>	3	20	25							
	4	2	9			1				6
	5	1	3			2				
	6	2	3	5		5	2			
	7	1		55	1			3		
	8	2		3	6	1				
	9	1		19	1	2	2	9		
	10	12		2	4		1	2	1	
	11		2							
<i>Catla</i>	2		5							
<i>catla</i>	3		25	1						
	4		28							
	5									
	6	2		13			4	4		
	7	24	4	44	24	8	4	6	18	1
	8	19	5	12	7	10	2	6	3	9
	9	10		6	7	1	1	3	1	2
	10			1						
	11									
<i>Channa</i>	2	3	3	1						
<i>striatus</i>	3	8	13				1			
	4	12	6						1	
	5	1	3							1
	6		1							
	7	2								
	8	2			1					
	9	2		8	5	2	3	2		
	10	65	1	14	1		37	2	1	
	11	15	1							
<i>Glossogobius</i>	2									
<i>giurus</i>	3	2								
	4									
	5	7								
	6	7			2					
	7	15		2	1	1				
	8	19	1	1	3					
	9	10			2					
	10	10								
	11									
<i>Puntius</i>	2	3	1							
<i>sophore</i>	3	7								
	4	16								
	5	6								
	6		3		1					
	7	4								
	8	5			1					
	9			2						
	10	12	2	1		4	1			
	11									
<i>Wallago</i>	2	1	1							
<i>attu</i>	3	6	12	1						
	4	4	33							
	5		9							
	6		2							
	7	3		2				1		
	8	13	3	5	2	3	1	1	1	3
	9	16		1	3					
	10	35							1	
	11	4								

Table 5.11 Time periods including fish migrations across the PIRDP embankment at the Bangladesh study site, by species, migration direction and sluice gate.

Species	Direction	Sluice Gate	J	F	M	A	M	J	J	A	S	O	N	D
<i>Catla catla</i>	Out > In	Baulikhola												
		Talimnagar												
	In > Out	Baulikhola												
		Talimnagar												
<i>Channa striatus</i>	Out > In	Baulikhola												
		Talimnagar												
	In > Out	Baulikhola												
		Talimnagar												
<i>Wallago attu</i>	Out > In	Talimnagar												
		Talimnagar												
	In > Out	Talimnagar												
		Talimnagar												

Table 5.12 Numbers of fish tagged at the Indonesian study site by species and month							
Species	<i>Anabas testudineus</i>	<i>Channa striatus</i>	<i>Helostoma temmincki</i>	<i>Mystus nemurus</i>	<i>Macrobrachium rosenbergii</i>	<i>Osteochilus hasselti</i>	Total
1994		2	2	23		10	37
September							
October				1			1
November						1	1
December							
1995							
January		35	28	32	48	40	183
February		62	57	11	23	51	204
March		69	58	17	26	23	193
April		40		51		108	199
May		6	47	101	14	123	291
June		36	49	67	4	17	173
July		12		127		14	153
August			79	43		6	128
			1	8			9
September			100	4		58	162
October			1	18	42	31	92
November		1	38	13	10	11	73
December							
1996							
January		10			11		21
February		6	15	4	18	113	156
March	32		8	31	26		97
April				7	4	150	161
May						55	55
June				38		16	54
July	27	5	44		5	100	181
August	20	34	45	25		284	408
	12	27	113	46		80	278
September		3	41	20	51	258	373
October		3		22	1	1	27
November				1		1	2
December							
Total released	91	351	726	710	283	1551	3712

Table 5.13 Numbers of fish recaptured at the Indonesian site by species and month							
Species	<i>Anabas testudineus</i>	<i>Channa striatus</i>	<i>Helostoma temmincki</i>	<i>Mystus nemurus</i>	<i>Macrobrachium rosenbergii</i>	<i>Osteochilus hasselti</i>	Total
1995							
January		2		3	3	2	10
February		4	1		13	1	19
March		1	1	2	3		7
April		5		7	2		14
May		4	2	18	9	57	90
June		3	1	27	4	1	36
July		6	16	32		2	56
August		4	22	27	1	1	55
September		1	4	26		1	32
October		1	14	17			32
November			2	3	1	1	7
December			1		1	1	3
1996							
January			3	1	4	1	9
February		1	1	1	6	9	18
March		1	1	1	7	4	14
April					2	25	27
May			1	5	1	11	18
June			1	4	1	8	14
July	1		1	3	2		7
August	3	1	2	4		15	25
September			7	6		57	70
October			7	13	9	30	59
November		2	3	11	9	24	49
December				1	1	6	8
Total recap'd	4	36	91	212	79	257	679
% recaptured	4%	10%	13%	30%	28%	17%	18%

Table 5.14 Numbers of fish tagged and recaptured at the Indonesian study site, in known locations, by species and region

Species	<i>Anabas testudineus</i>		<i>Channa striatus</i>		<i>Helostoma temminckii</i>		<i>Mystus nemurus</i>		<i>Macrobrachium rosenbergii</i>		<i>Osteochilus hasselti</i>		Total	
No. released														
Forest River				132				282		162			435	1011
Lake District				32		385		24					323	764
Savanna River	91			187		341		404		121			793	1937
Forest River releases recaptured in:	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Forest River			20	15.2			84	29.8	42	25.9	125	28.7	271	26.8
Lake District							6	2.1	14	8.6			20	2.0
Savanna River														
Lake District releases recaptured in:	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Forest River			1	3.1	38	9.9	6	25.0			17	5.3	62	8.1
Lake District					2	0.5					7	2.2	9	1.2
Savanna River														
Savanna River releases recaptured in:	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Forest River			3	1.6	1	0.3	16	4.0	1	0.8	10	1.3	31	1.6
Lake District											3	0.3	3	0.2
Savanna River	4	4.4	11	5.9	49	14.4	93	23.0	21	17.4	93	11.7	271	14.0

Table 5.15 Numbers of fish tagged and recaptured at the Indonesian study site by species and tag type

Species	<i>Anabas testudineus</i>	<i>Channa striatus</i>	<i>Helostoma temminckii</i>	<i>Mystus nemurus</i>	<i>Macrobrachium rosenbergii</i>	<i>Osteochilus hasselti</i>	Total
No. released							
12P Streamer tag		15	25	52	245	203	540
7S Streamer tag	24	6	163	45	38	694	980
Anchor tag	67	330	539	613		653	2192
No. recaptured							
12P Streamer tag				10	66	7	83
7S Streamer tag		1	4	2	13	92	112
Anchor tag	4	35	87	200		158	484
% recaptured							
12P Streamer tag		0%	0%	19%	27%	3%	15%
7S Streamer tag	0%	17%	2%	4%	34%	13%	11%
Anchor tag	6%	11%	16%	33%		24%	22%

Table 5.16 Mean monthly fork-lengths (cm) of fish tagged at the Indonesian study site by species, and maximum and minimum lengths of fish tagged by species and tag type

Species	<i>Anabas testudineus</i>	<i>Channa striatus</i>	<i>Helostoma temmincki</i>	<i>Mystus nemurus</i>	<i>Macrobrachium rosenbergii</i>	<i>Osteochilus hasselti</i>
Mean Fork-lengths (cm)						
January		28.5	17.5	22.1	19.7	15.4
February		23.4	10.7	23.4	21.3	12.1
March	11.9	27.8	10.9	21.9	23.8	12.3
April		28.8		19.9	25.7	11.0
May		29.0	14.0	24.1	25.1	11.3
June		27.9	13.8	21.1	23.8	12.9
July	13.9	26.2	15.8	19.7	25.5	12.6
August	16.3	27.2	14.0	20.0		12.9
September	14.5	20.7	13.6	21.4		12.6
October		28.6	14.9	21.2	19.8	11.7
November		31.7	17.0	25.3	14.6	12.5
December		24.7	14.0	24.7	20.4	12.3
Minimum Fork-length (cm)						
12P Streamer Tag		12.7	7.3	11.2	11.6	9.0
7S Streamer Tag	8.9	13.6	7.2	11.3	10.5	8.0
Anchor Tag	10.0	10.5	9.0	11.6		9.5
Maximum Fork-length (cm)						
12P Streamer Tag		19.7	9.5	24.4	33.0	17.5
7S Streamer Tag	16.5	23.9	23.1	24.3	29.8	19.5
Anchor Tag	17.8	44.5	23.0	39.2		18.5

Table 5.17 The seasonality of fish migrations between rivers (<i>sungei</i> , S), flooded savanna (<i>lebak</i> , L including <i>lebung</i> ponds) and flooded forest (<i>rawang</i> , R) at the Indonesian River Lempuing study site, as shown by those tagged fish recaptured within the same or next calendar month after their release											
Species	Month	No Habitat Change			To Floodplain		From Floodplain		In Floodplain		
		S	L	R	S>L	S>R	L>S	R>S	L>R	R>L	
<i>Channa striatus</i>	1		2	2							
	2								1		
	3			1							
	4		4								
	5										
	6		3				2				
	7		1								
	8		1								
	9										
	10										
	11								1		
	12										
<i>Helostoma temmincki</i>	1										
	2		1								
	3										
	4										
	5	1					1				
	6		16								
	7										
	8		29								
	9		2								
	10	3	3		10						
	11										
	12		3								
<i>Mystus nemurus</i>	1	1			1			1			
	2				1						
	3	1						1			
	4	6			1				3		
	5	13			1	1					
	6	10	3			1	5				
	7	6	20	1			5	5		1	
	8	13			5						
	9	5			1	2					
	10	5			1						
	11	4									
	12										
<i>Machrobrachium rosenbergii</i>	1	4		4		3		4			
	2	6			1	1					
	3	10									
	4	1									
	5	6									
	6	1									
	7	2									
	8										
	9										
	10	4									
	11	1									
	12	1									
<i>Osteochilus hasselti</i>	1	2			1						
	2		2						9		
	3										
	4	2	1	6		18		1	47	1	
	5			6		1		5		1	
	6										
	7	8	1								
	8		36		3		10				
	9	4	2	3				1			
	10	22		2	1					2	
	11										
	12										

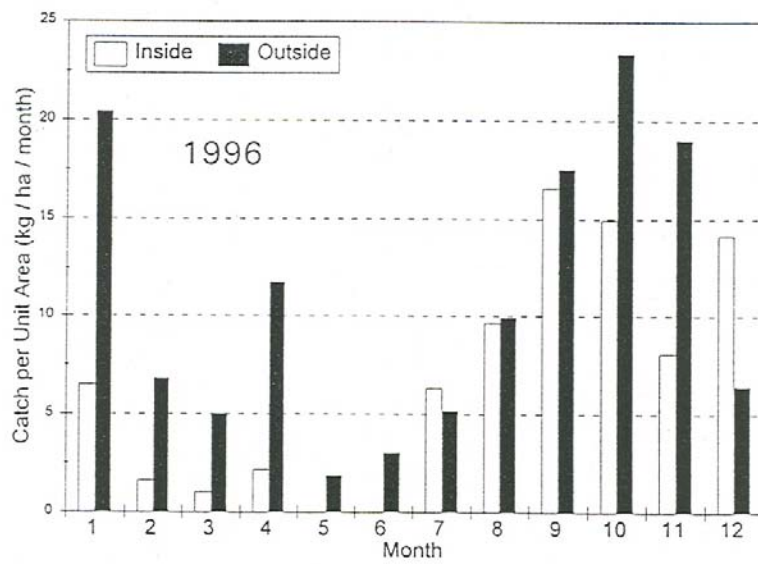
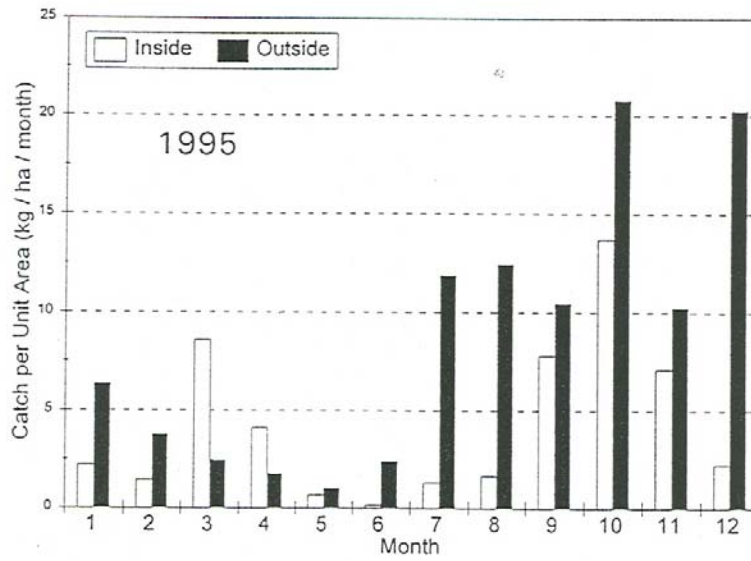


Figure 5.1 Estimated monthly catches-per-unit-area (CPUA, kg/ha/month) during 1995 and 1996, for the Inside and Outside regions at the Bangladesh study site.

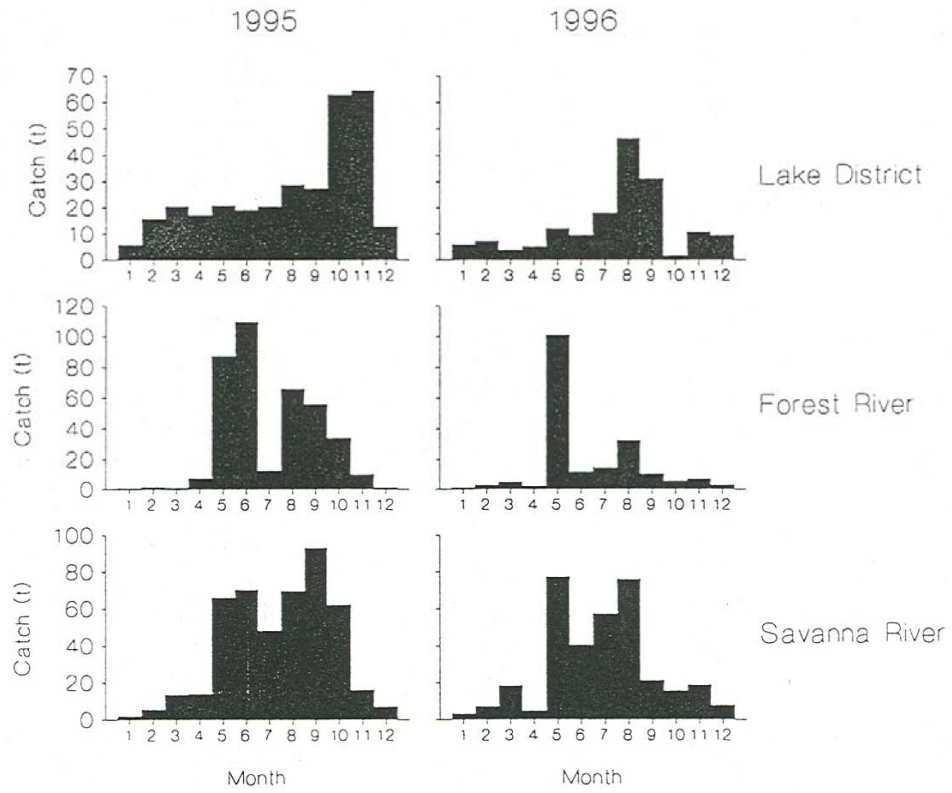


Figure 5.2 Estimated total monthly catches (tonnes) in 1995 and '96, in each of the study region habitat types at the Indonesian River Lempuing study site.

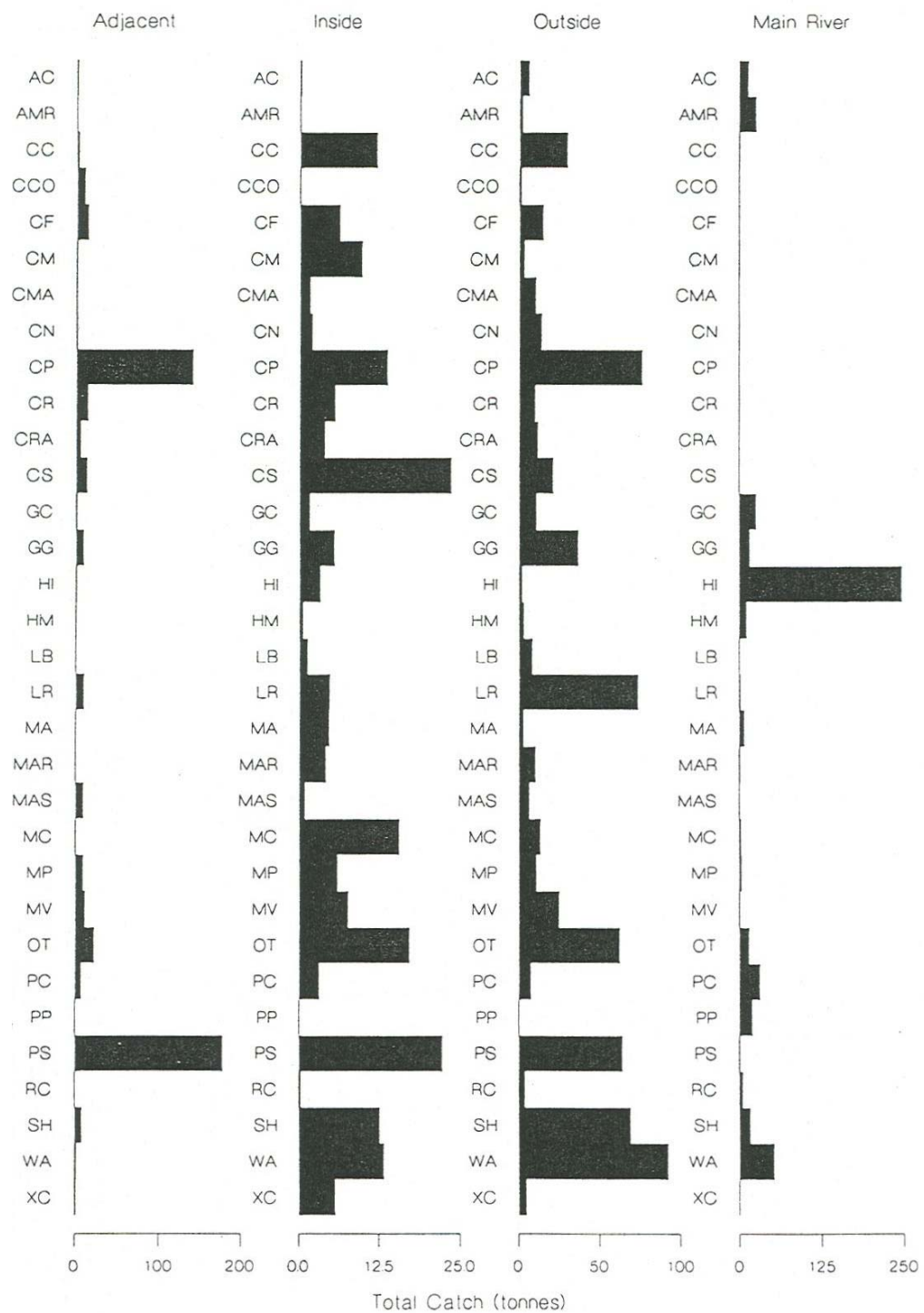


Figure 5.3 Estimated 1995 total catches (tonnes), subdivided by species (species codes given in Table 5.1) and study region, at the Bangladesh study site.

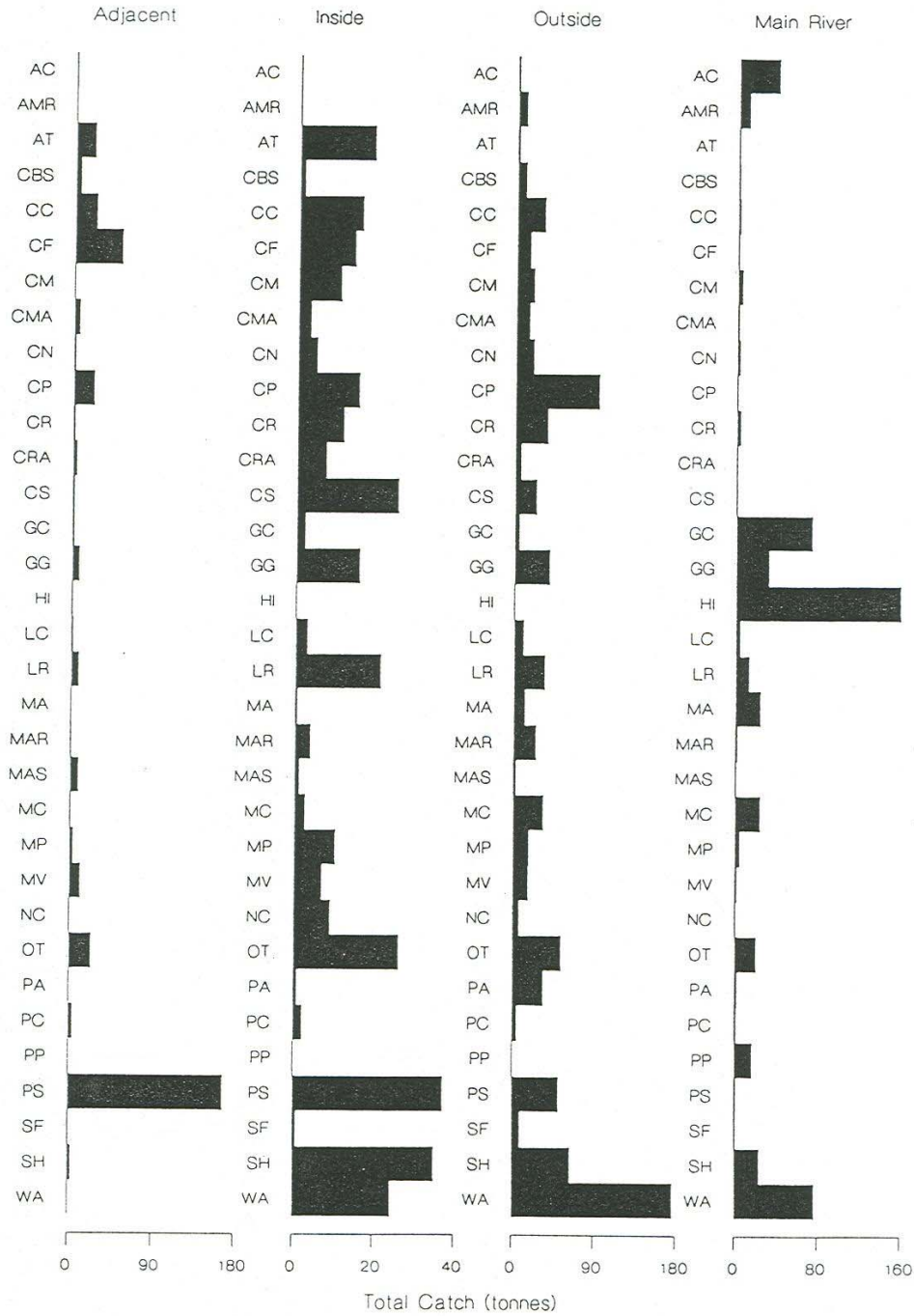


Figure 5.4 Estimated 1996 total catches (tonnes), subdivided by species (species codes defined in Table 5.1) and study region, at the Bangladesh study site.

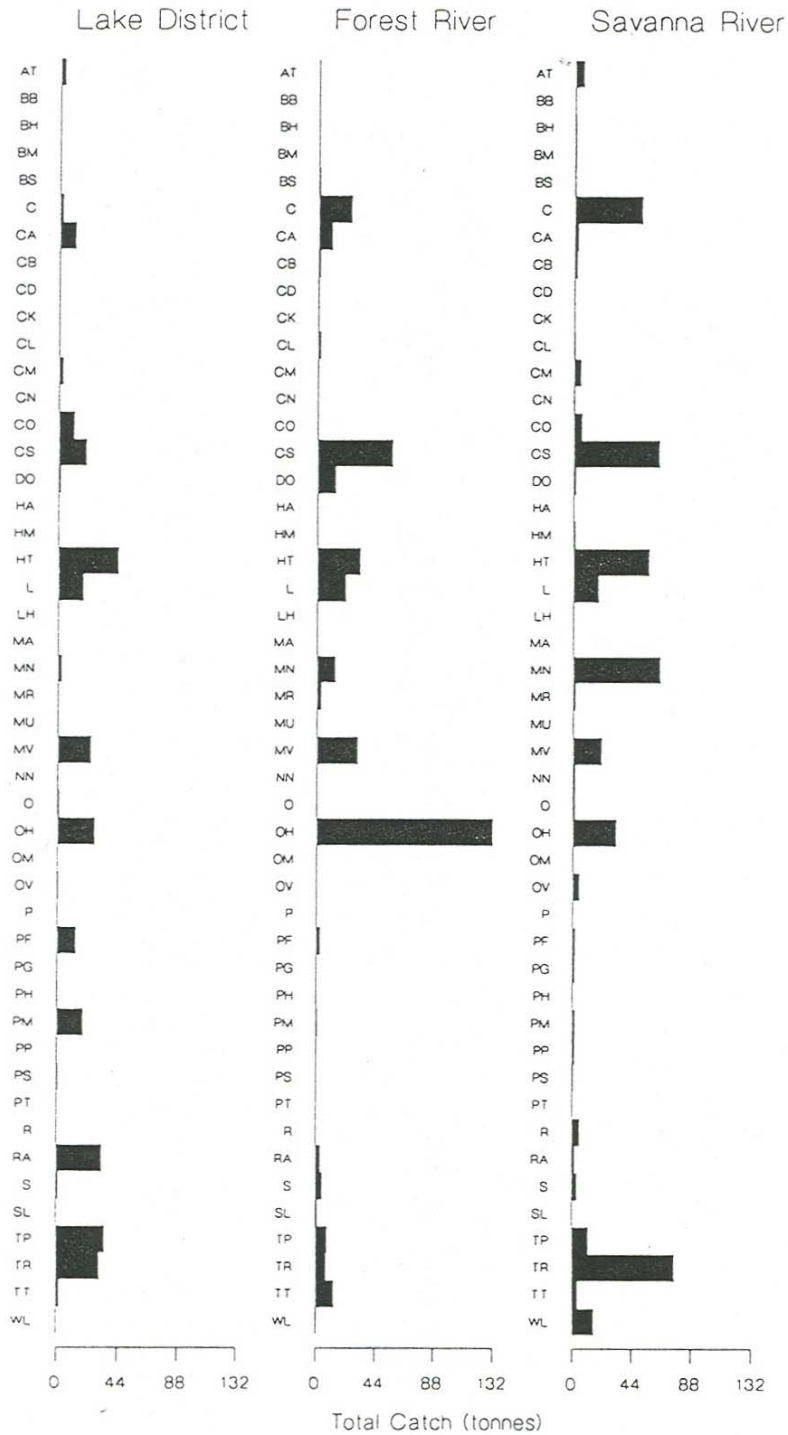


Figure 5.5 Estimated 1995 total catches (tonnes), subdivided by species (species codes given in Table 5.2) and study region, at the Indonesian study site

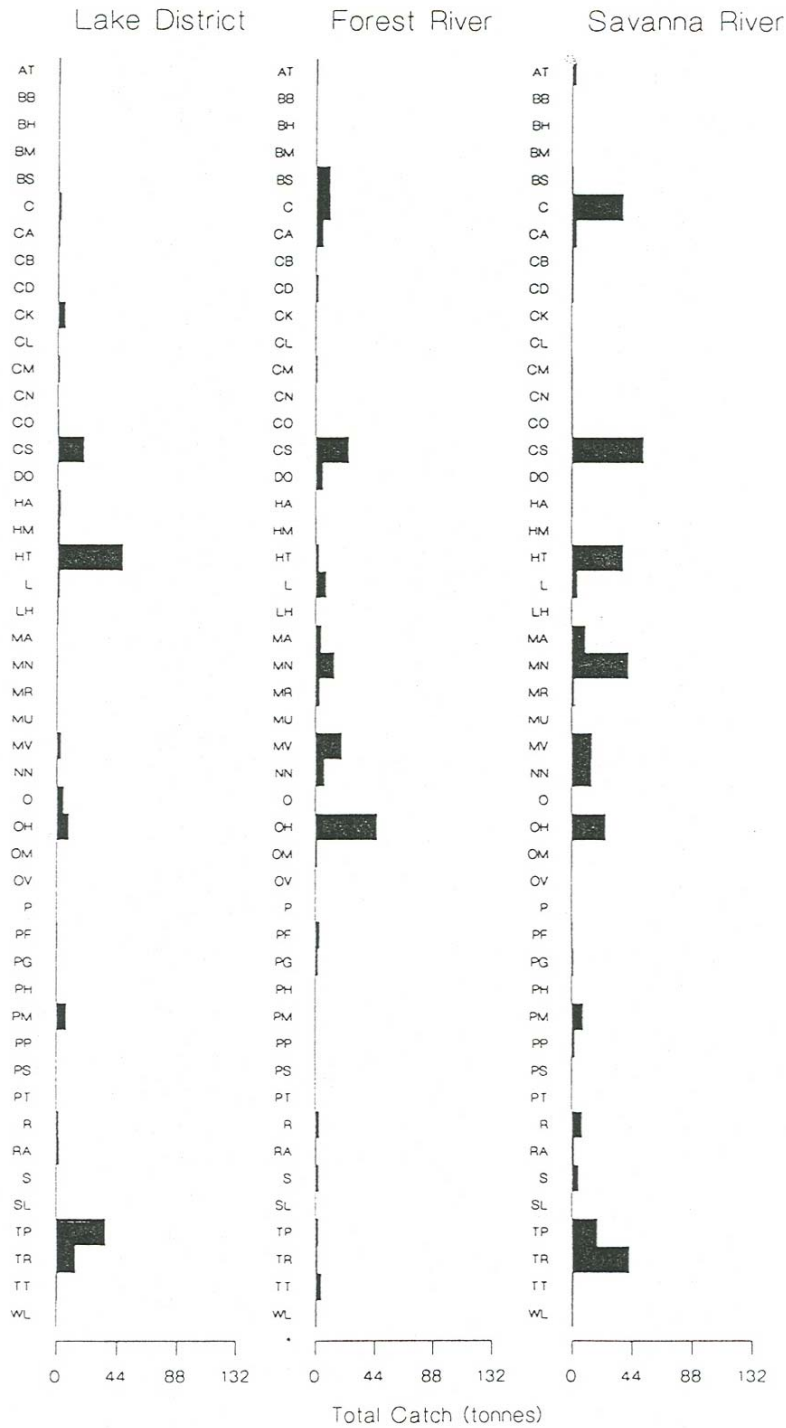


Figure 5.6 Estimated 1996 total catches (tonnes, subdivided by species (species codes given in Table 5.2) and study region, at the Indonesian study site.

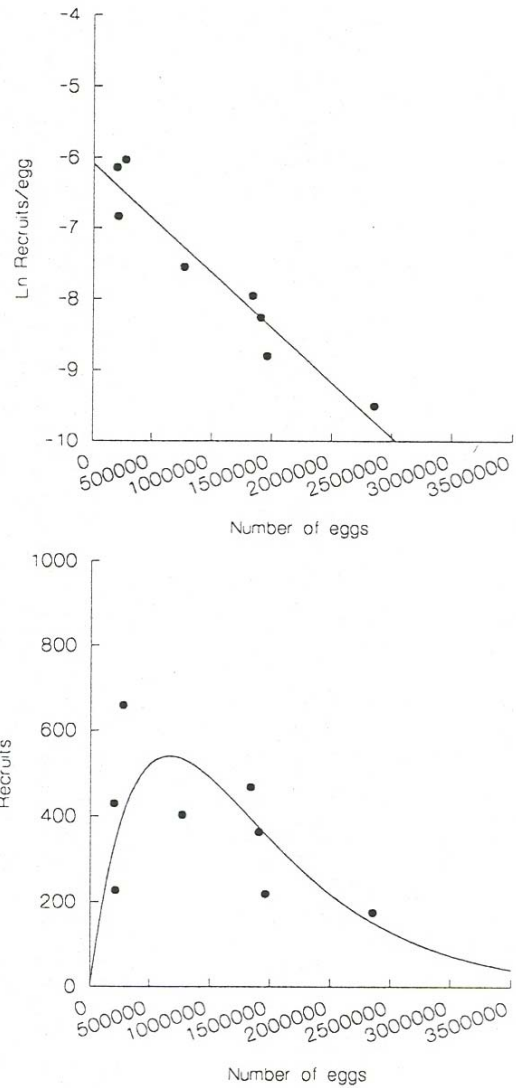


Figure 5.8 Influence of pond fertilisation on the stock-recruit relationship for *Puntius sophore*, in the Ricker-curve fitting model (upper graph), and as recruit/egg plotted against chlorophyll concentrations. See section 5.5.1 for further details.

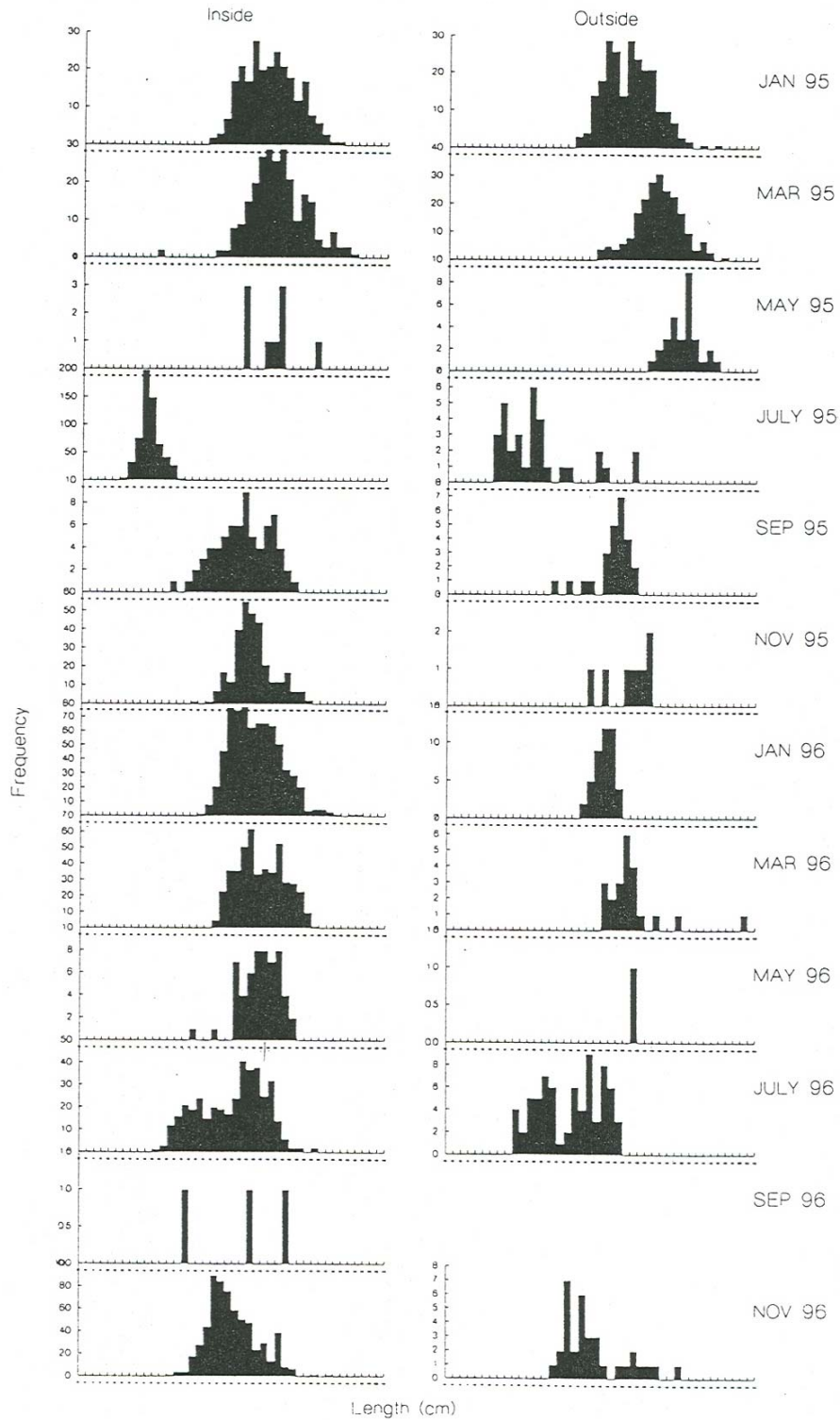


Figure 5.9 Monthly fork length frequencies of *Anabas testudineus*, combined across non-selective gear types, in the Inside (modified) and Outside (pristine) regions of the PIRDP study site. X-Scale = 0.21 cm in 1/2 cm classes.

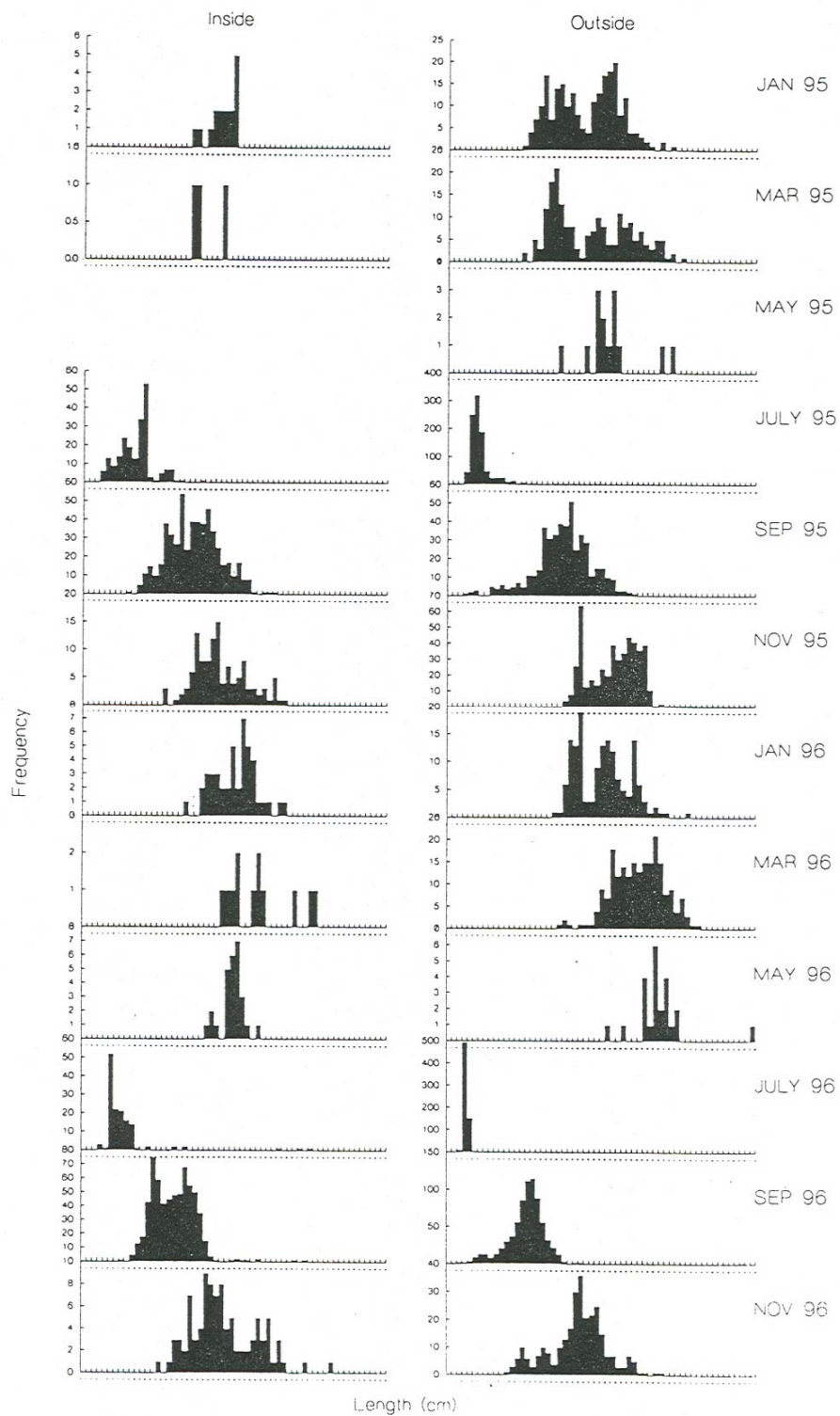


Figure 5.10 Monthly fork length frequencies of *Catla catla*, combined across non-selective gear types, in the Inside (modified) and Outside (pristine) regions of the PIRDP study site. X-scale = 0-57 in 1cm classes.

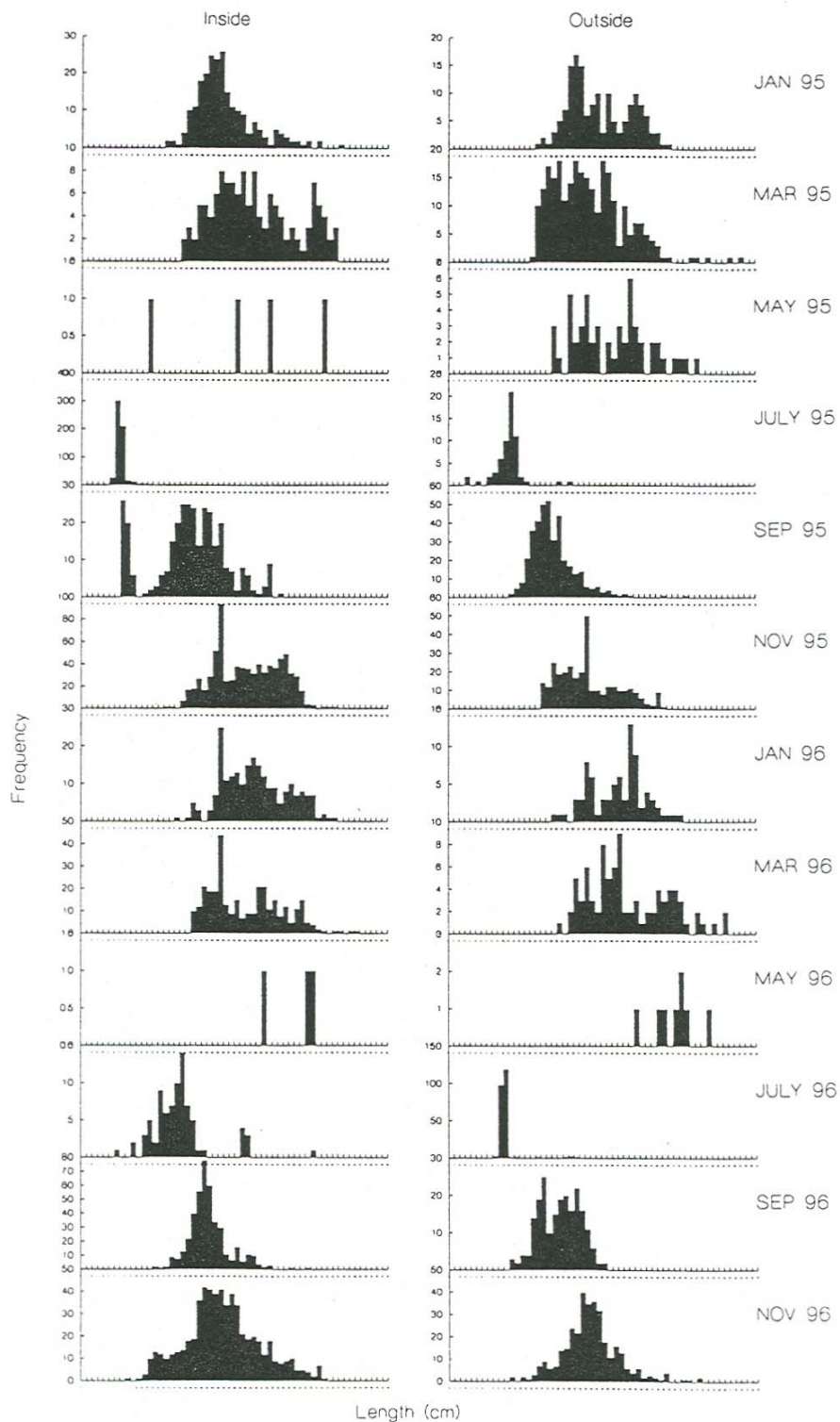


Figure 5.11 Monthly fork length frequencies of *Channa striatus*, combined across non-selective gear types, in the Inside (Modified) and Outside (Pristine) regions of the PIRDP study site. X-scale 0-55cm in 1 cm classes.

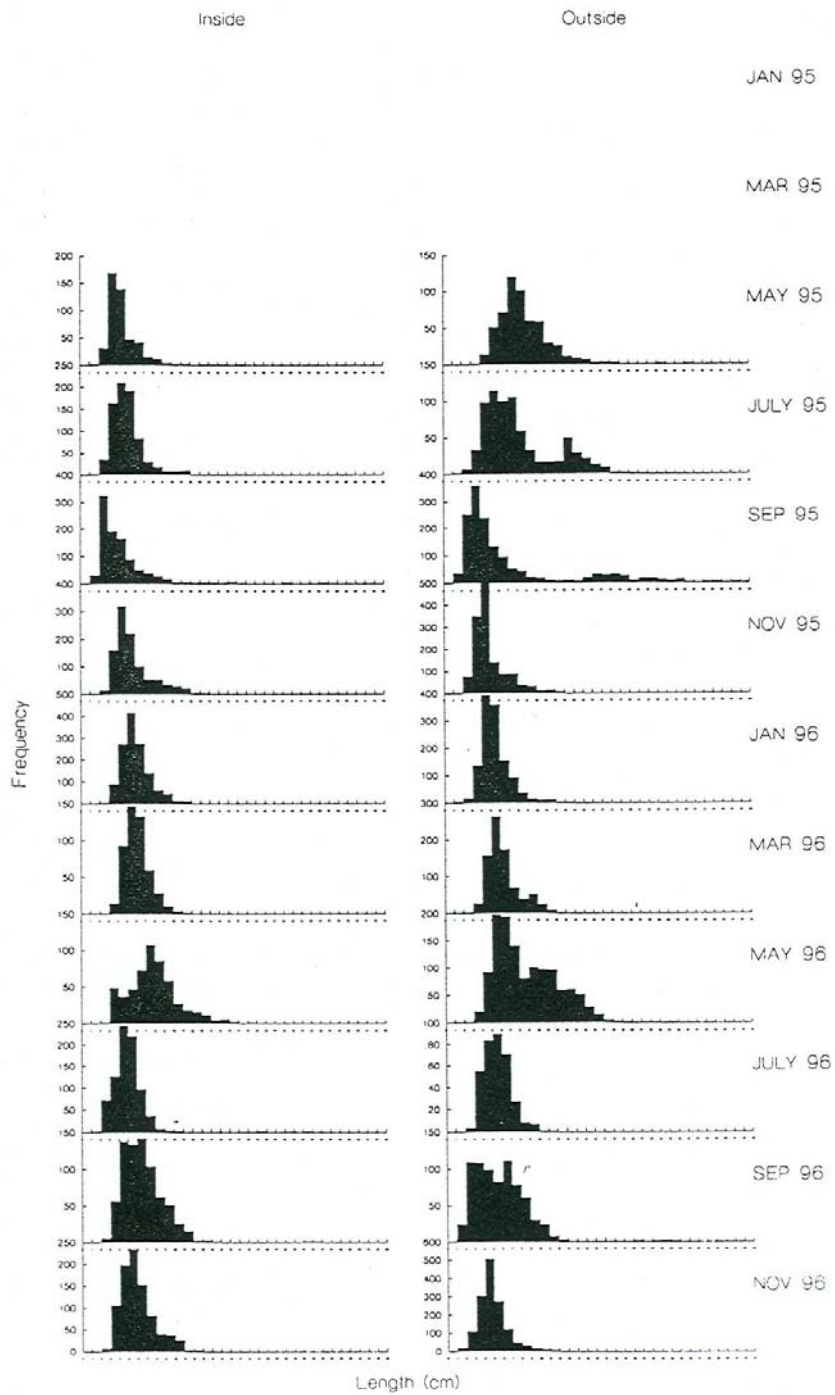


Figure 5.12 Monthly fork length frequencies of *Glossogobius giuris*, combined across non-selective gear types, in the Inside (Modified) and Outside (Pristine) regions of the PIRDP study site. X-scale = 0-33cm in 1cm classes.

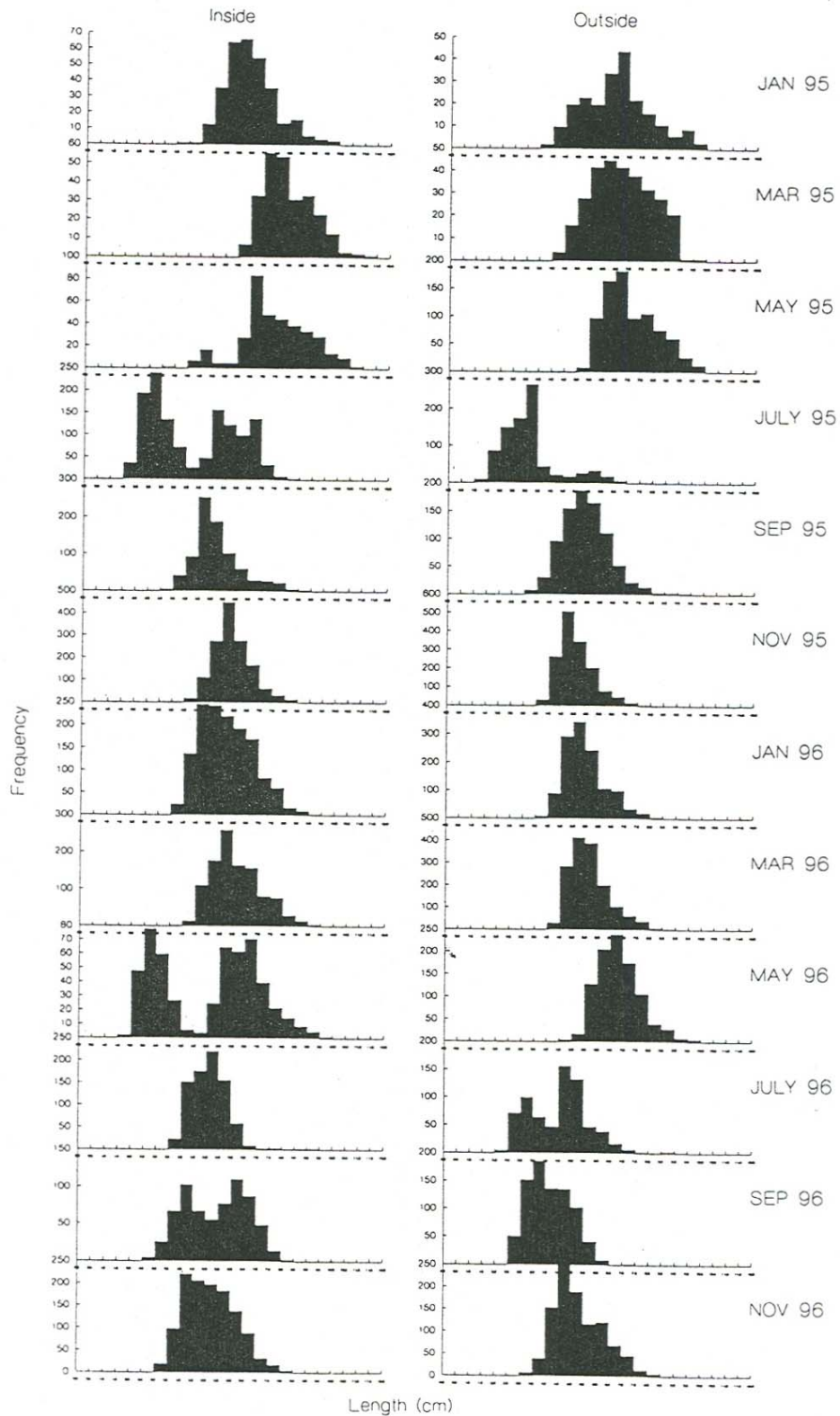


Figure 5.13 Monthly fork length frequencies of *Puntius sophore*, combined across non-selective gear types, in the Inside (Modified) and Outside (Pristine) regions of the PIRDP site. X-scale = 0-12cm in ½cm classes.

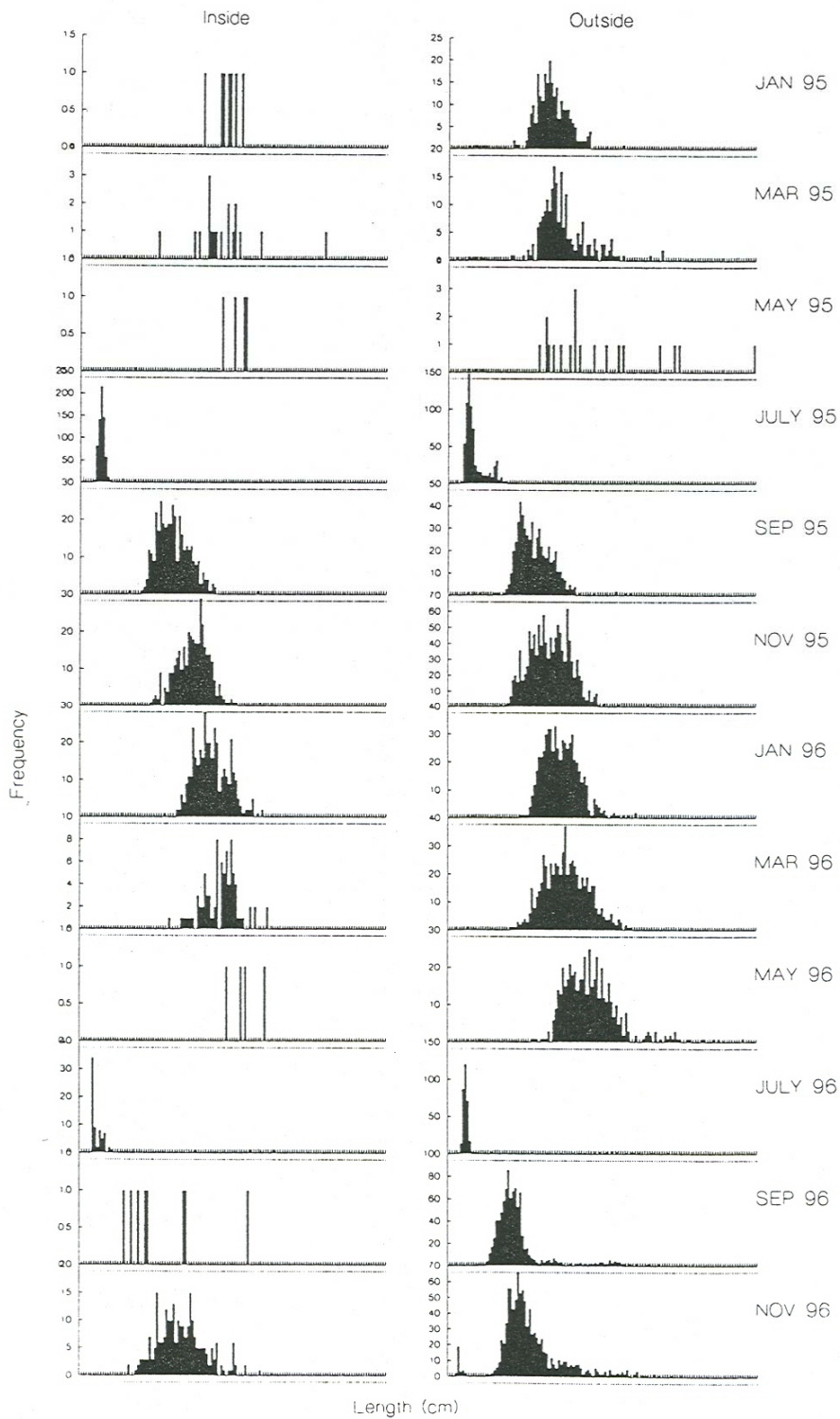


Figure 5.14 Monthly fork length frequencies of *Wallago attu*, combined across non-selective gear types, in the Inside (Modified) and Outside (Pristine) regions of the PIRDP study site. X-scale = 0-127cm in 1cm classes.

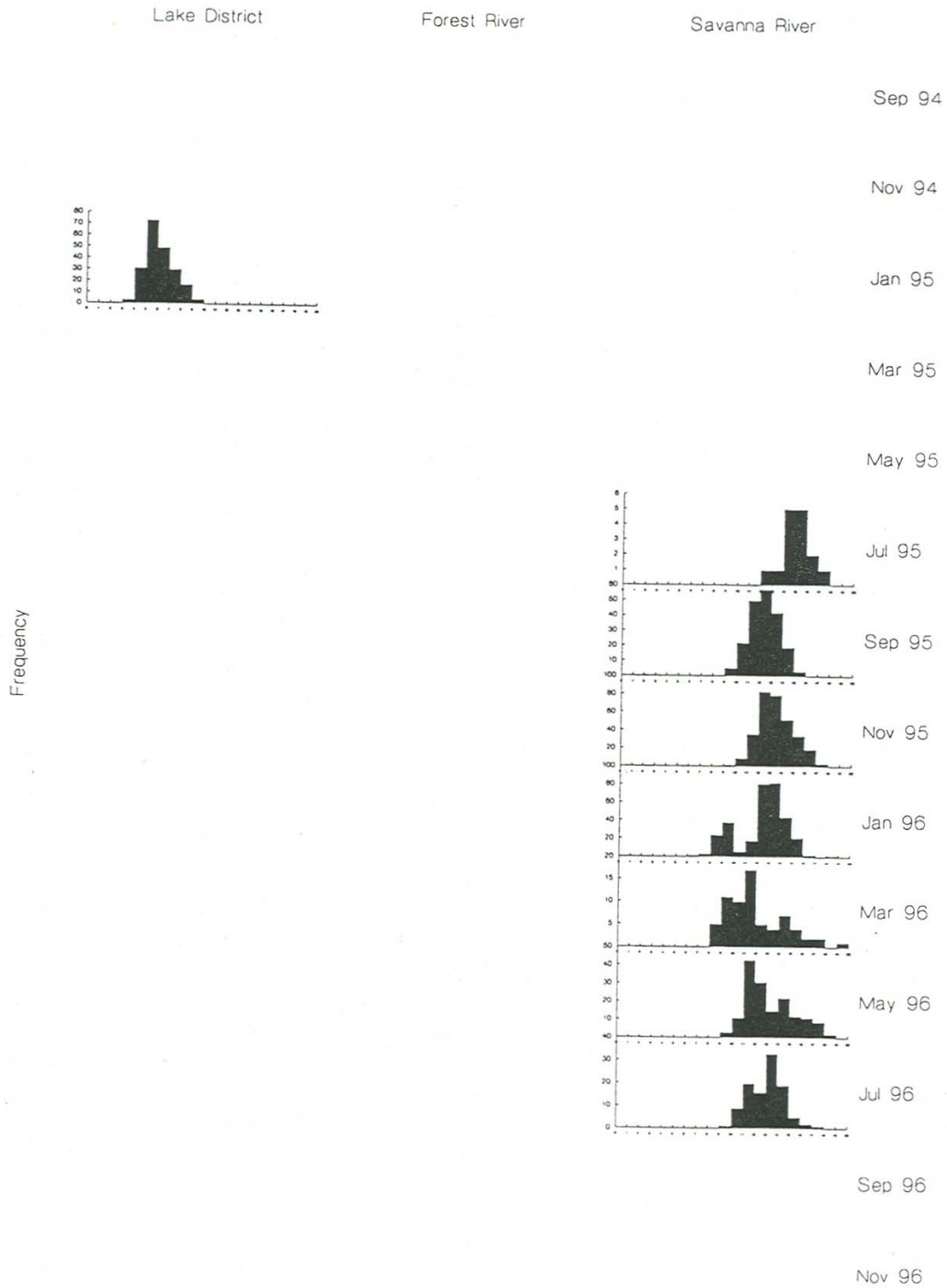


Figure 5.15 Monthly fork length frequencies of *Anabas testudineus* combined across non-selective gear types, in the three habitat regions of the River Lempuing study site. X-scale = 0-20cm in 1cm classes

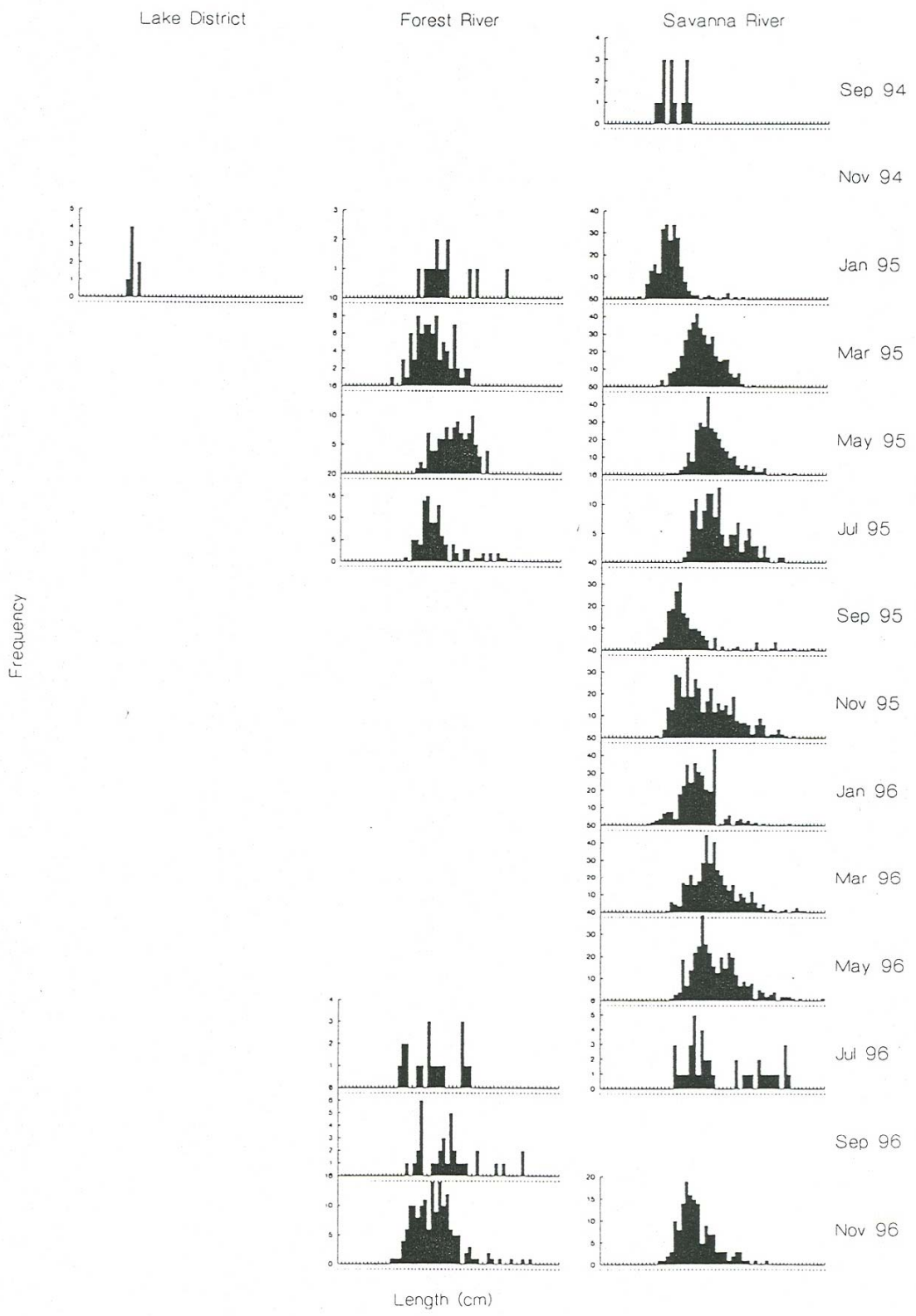


Figure 5.16 Monthly fork length frequencies of *Channa striatus*, combined across non-selective gear types, in the three habitat regions of the River Lempuing study site. X-scale = 0-59cm.

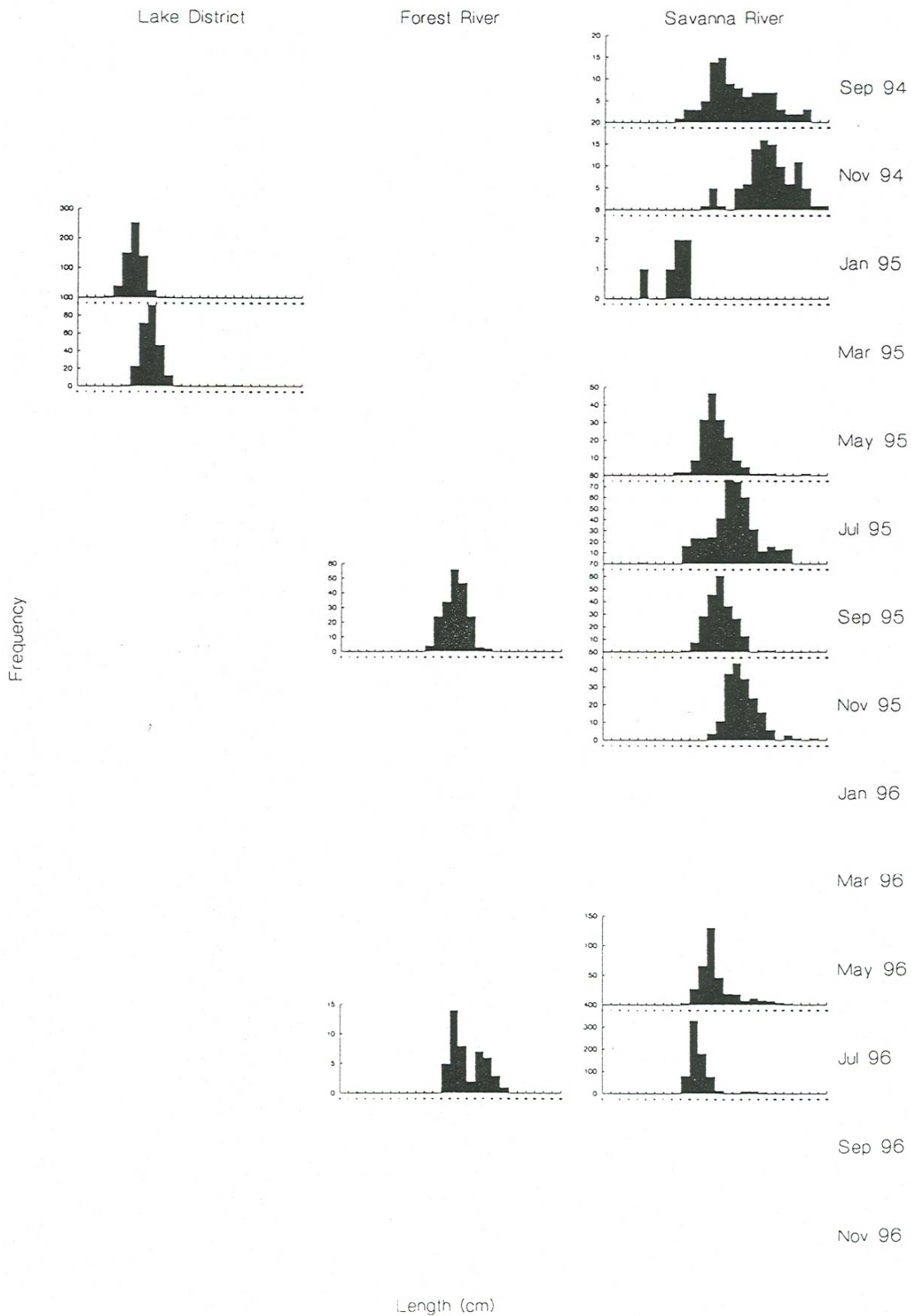


Figure 5.17 Monthly fork length frequencies of *Helostoma temminckii*, combined across non-selective gear types, in the three habitat regions of the River Lempuing study site. X-scale = 0-26cm.

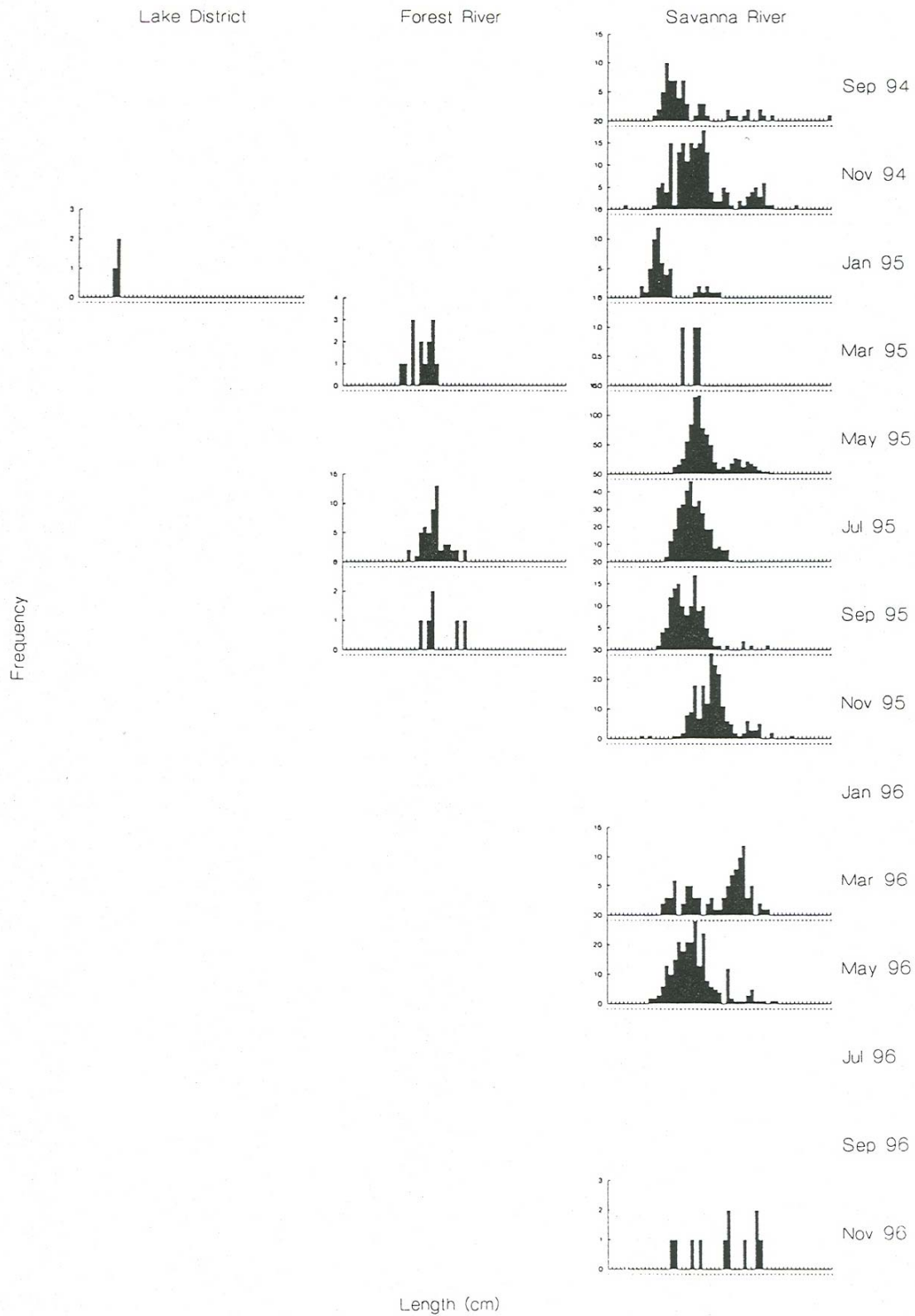


Figure 5.18 Monthly fork length frequencies of *Mystus nemurus*, combined across non-selective gear types, in the three habitat regions of the River Lempuing study site. X-scale = 0-55cm.

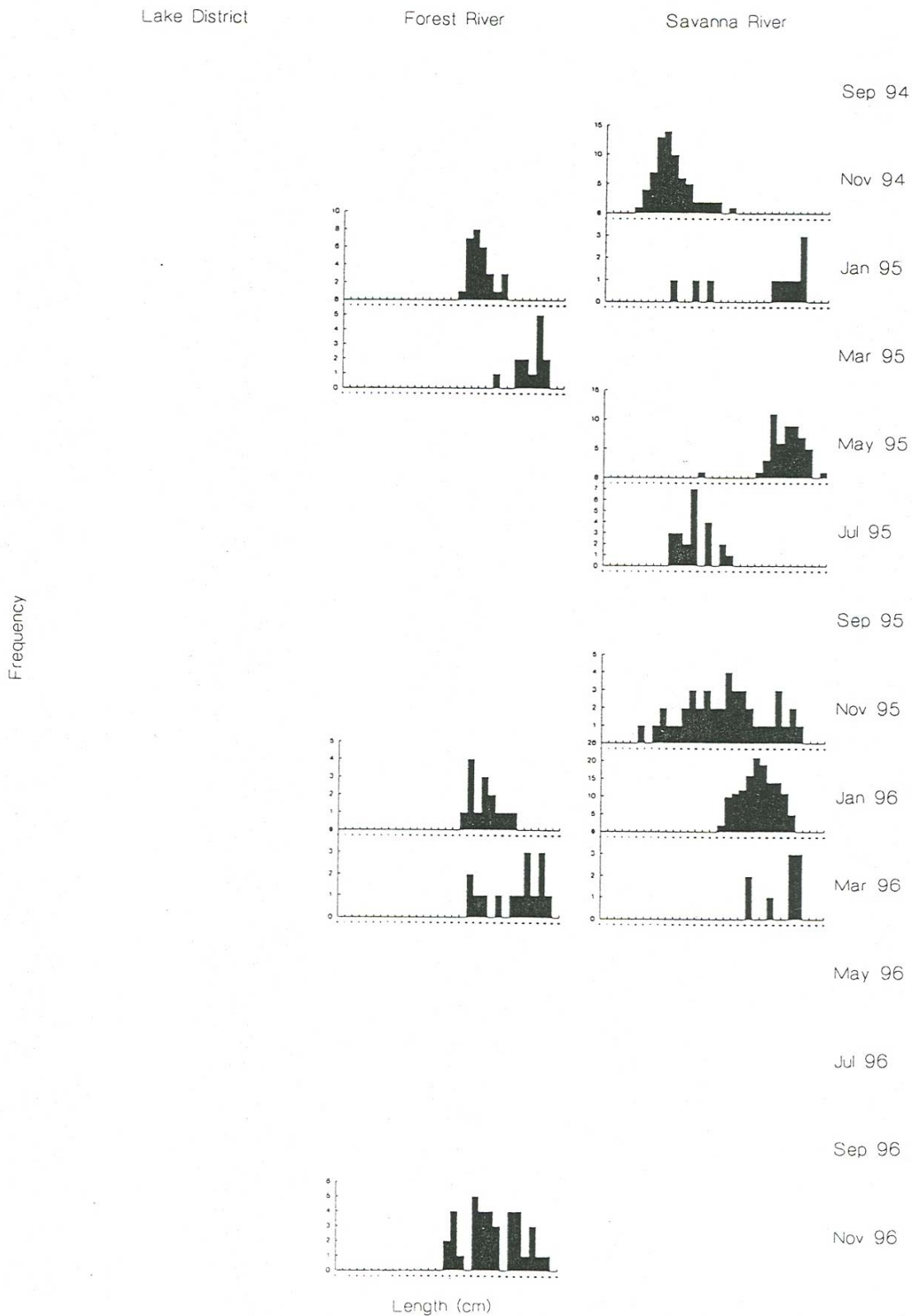


Figure 5.19 Monthly fork length frequencies of *Macrobrachium rosenbergii*, combined across non-selective gear types, in the three habitat regions of the River Lempuing study site. X-scale = 0-31cm.

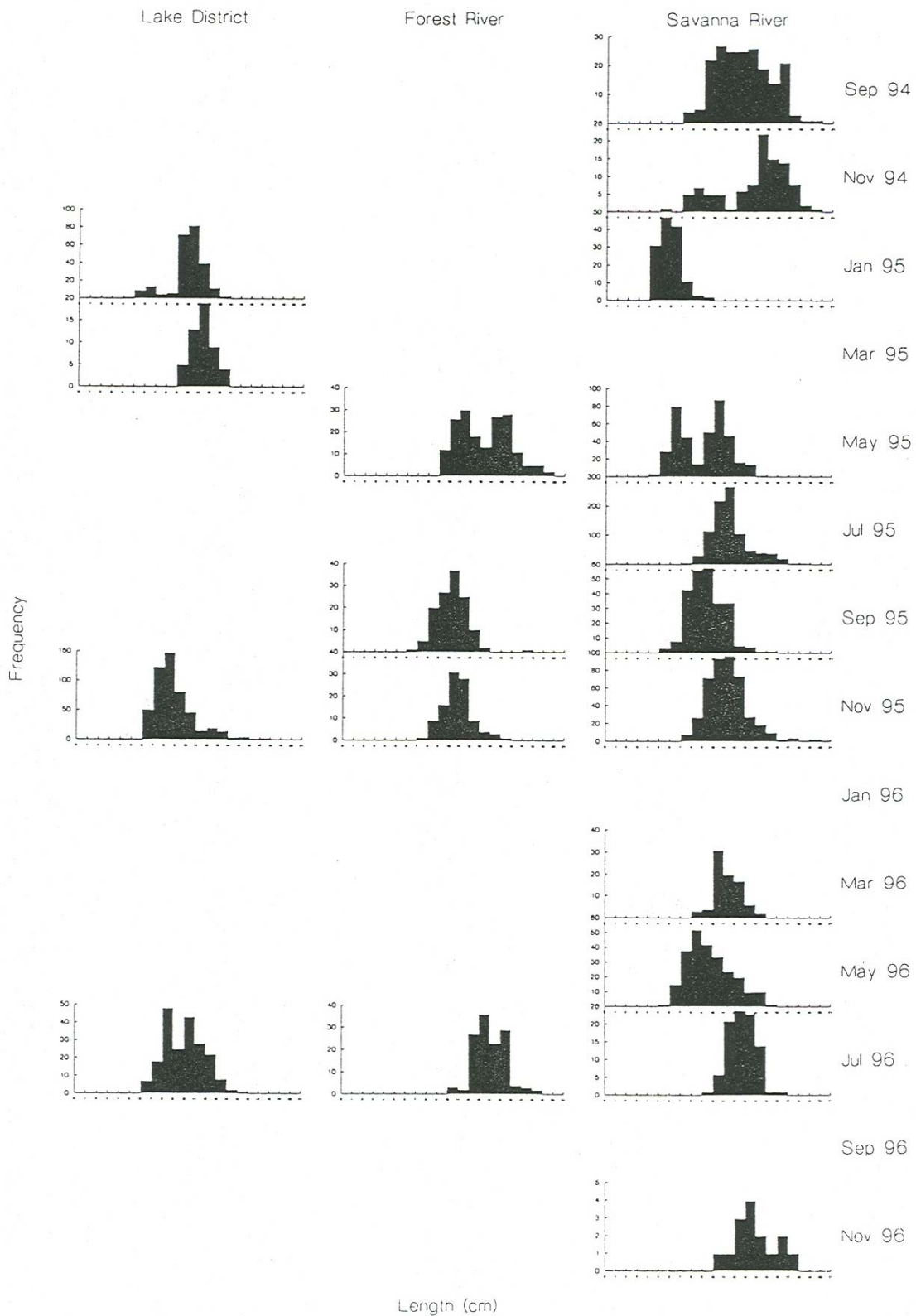


Figure 5.20 Monthly fork length frequencies of *Osteochilus hasselti*, combined across non-selective gear types, in the three habitat regions of the River Lempuing study site. X-scale = 0-21cm.

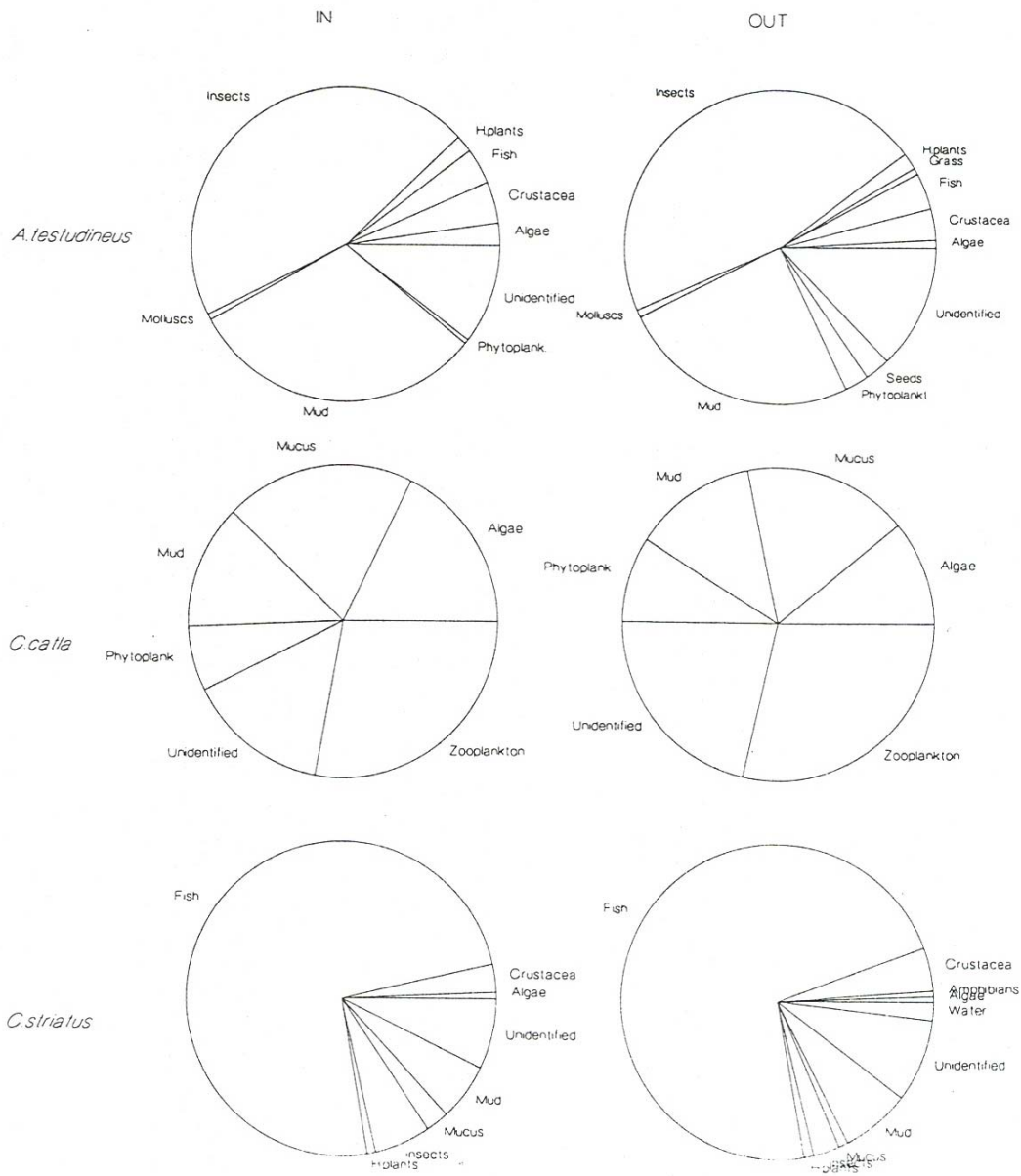


Figure 5.21 Overall diet compositions for *A. testudineus*, *C. catla* and *C. striatus* in the Inside (In) and Outside (Out) regions of the Bangladesh PIRDP study site, in 1995 and '96, expressed as the mean percentage of total stomach volumes.

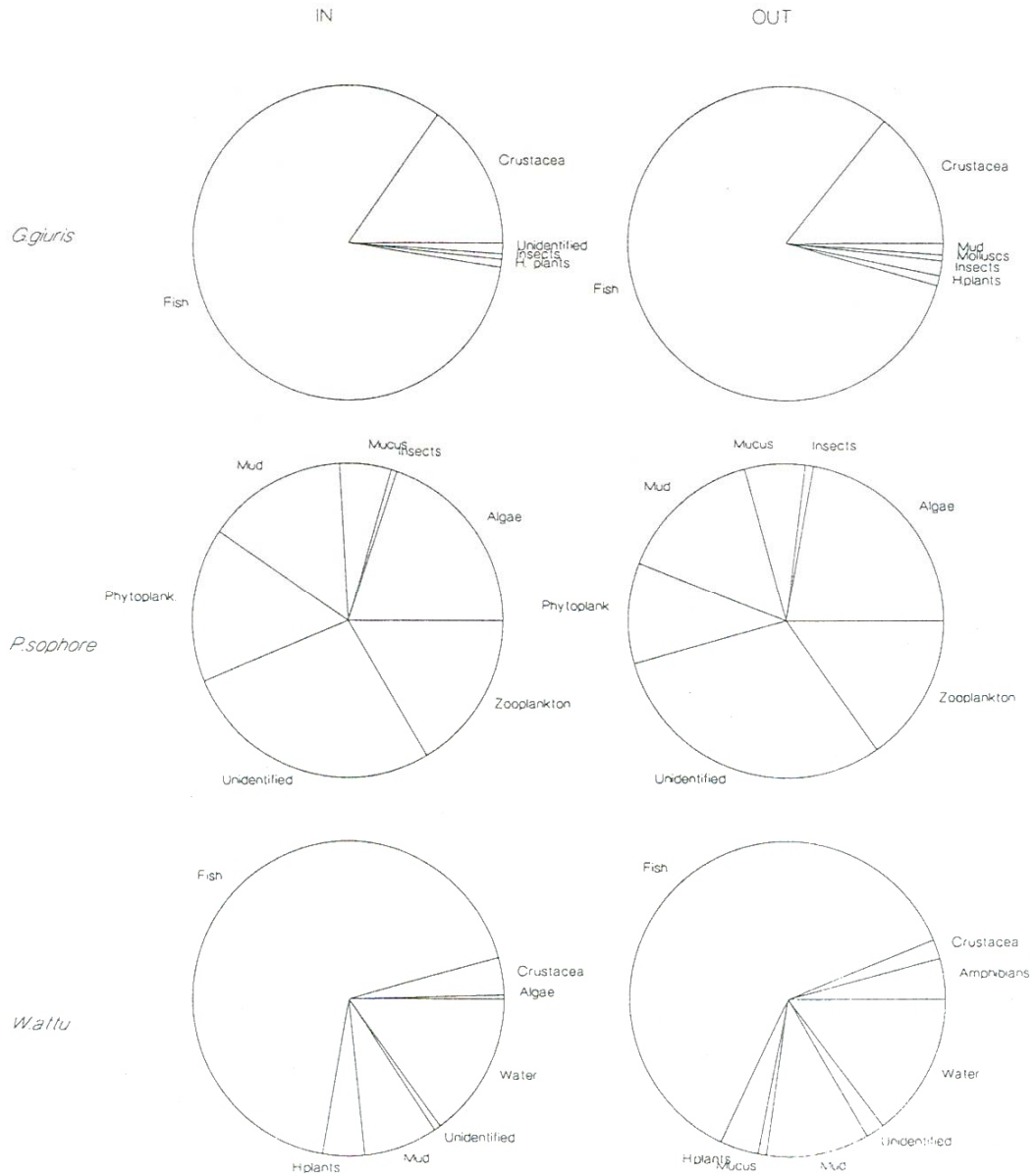


Figure 5.22 Overall diet compositions for *G. giurus*, *P. sophore* and *W. attu* in the Inside (In) and Outside (Out) regions of the Bangladesh PIRDP study site, in 1995 and '96, expressed as a percentage of total stomach volumes

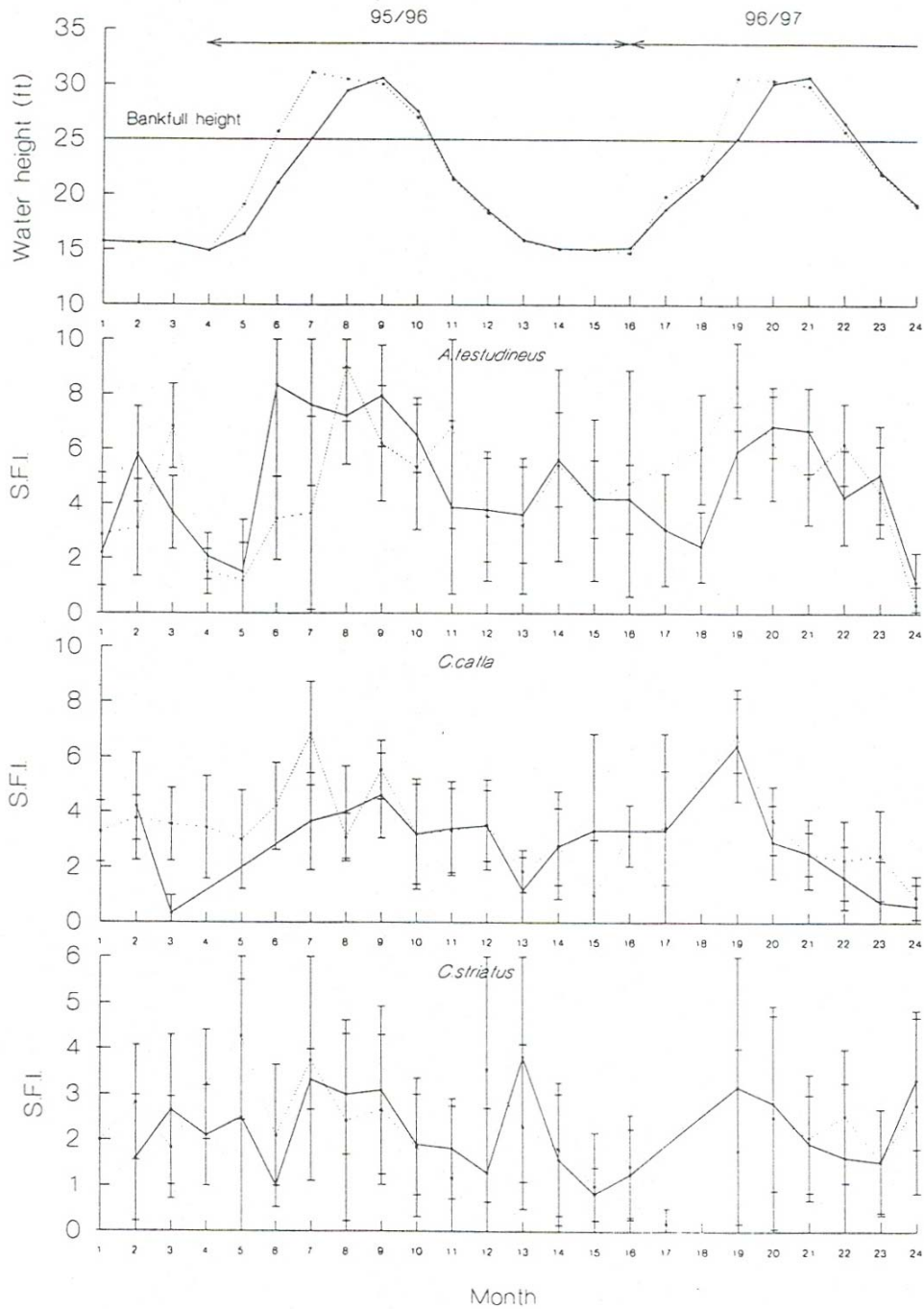


Figure 5.23 Mean monthly stomach fullness indices (SFI) with approximate 95% confidence intervals for *A. testudineus*, *C. catla* and *C. striatus* in the Inside (solid lines) and Outside (broken lines) regions of the Bangladesh PIRDP study site, in 1995 and '96, plotted alongside mean monthly water heights inside (solid lines) and outside (broken lines) the FCD/I scheme.

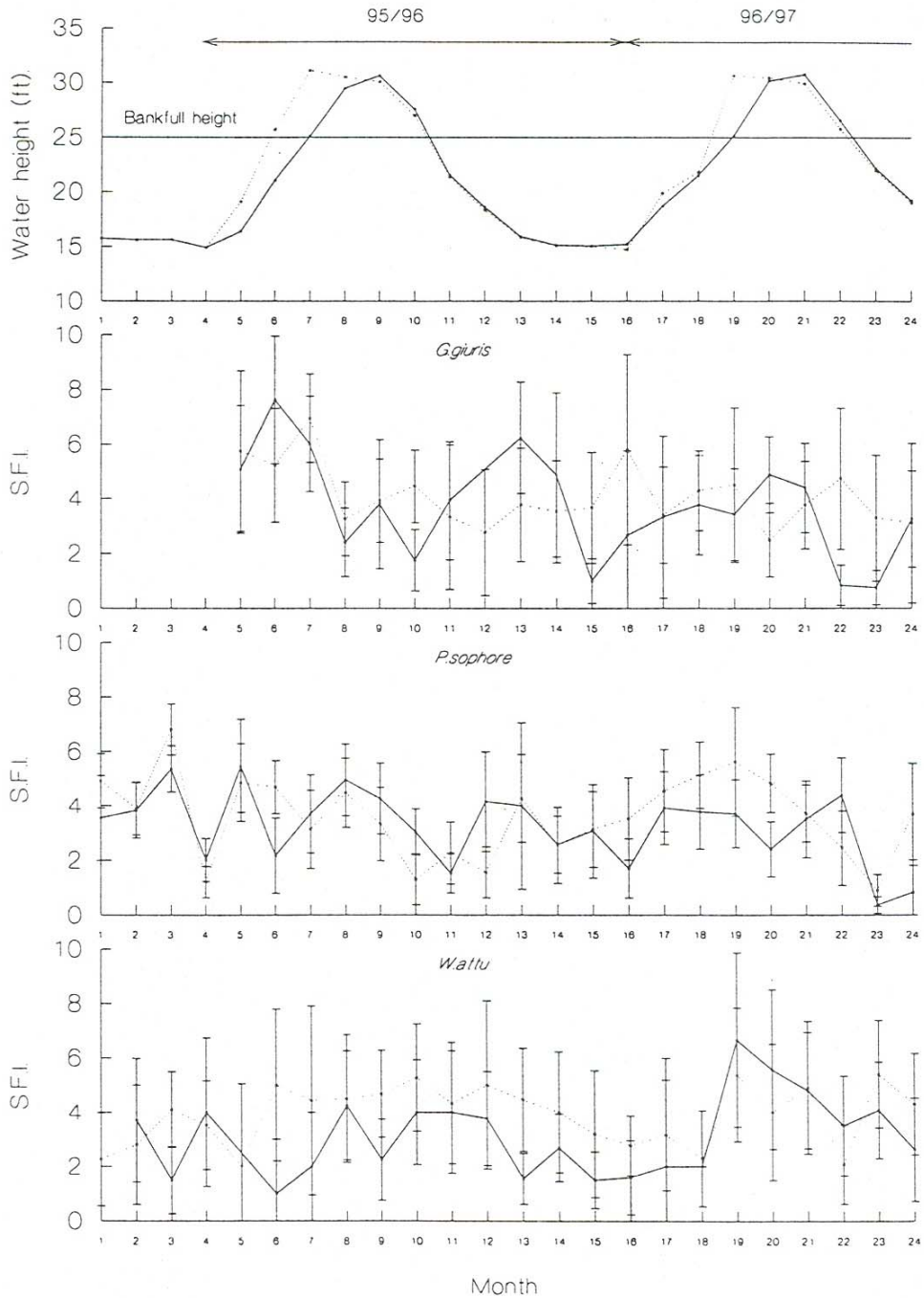


Figure 5.24 Mean monthly stomach fullness indices (SFI) with approximate 95% confidence intervals for *G.giurus*, *P. sophore* and *W. attu* in the Inside (solid lines) and Outside (broken lines) regions of the Bangladesh PIRDP study sire, in 1995, and '96 plotted alongside mean monthly water heights inside (solid lines) and outside (broken lines) the FCD/I scheme.

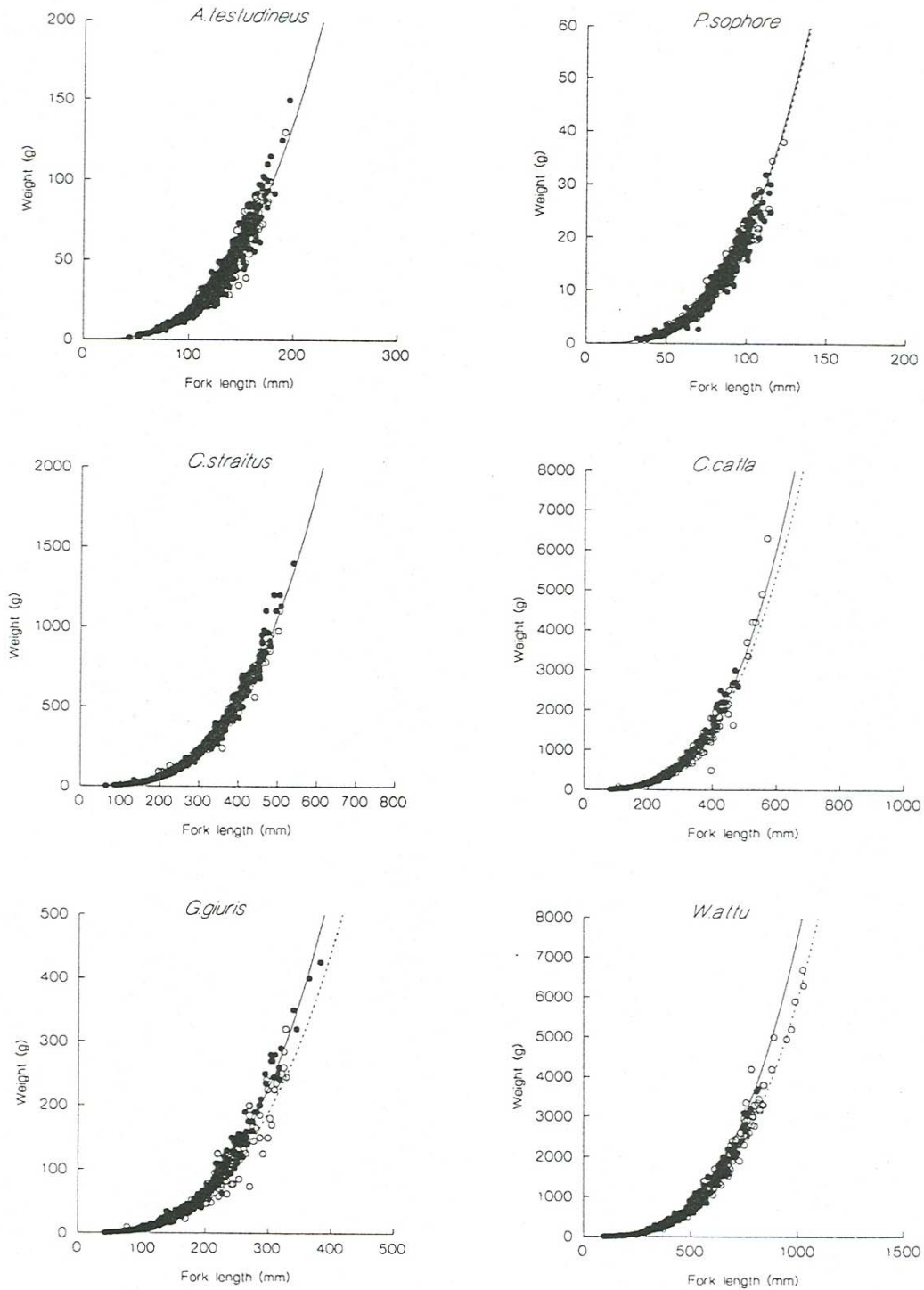


Figure 5.25 Relationships between weight and length for key fish species at the Bangladesh PIRDP study site, sampled in 1995 and '96 inside (solid circles) and outside (open circles, broken line) the FCD/I scheme. A single unbroken line indicates common regression model, when no significant difference existed between the regions.

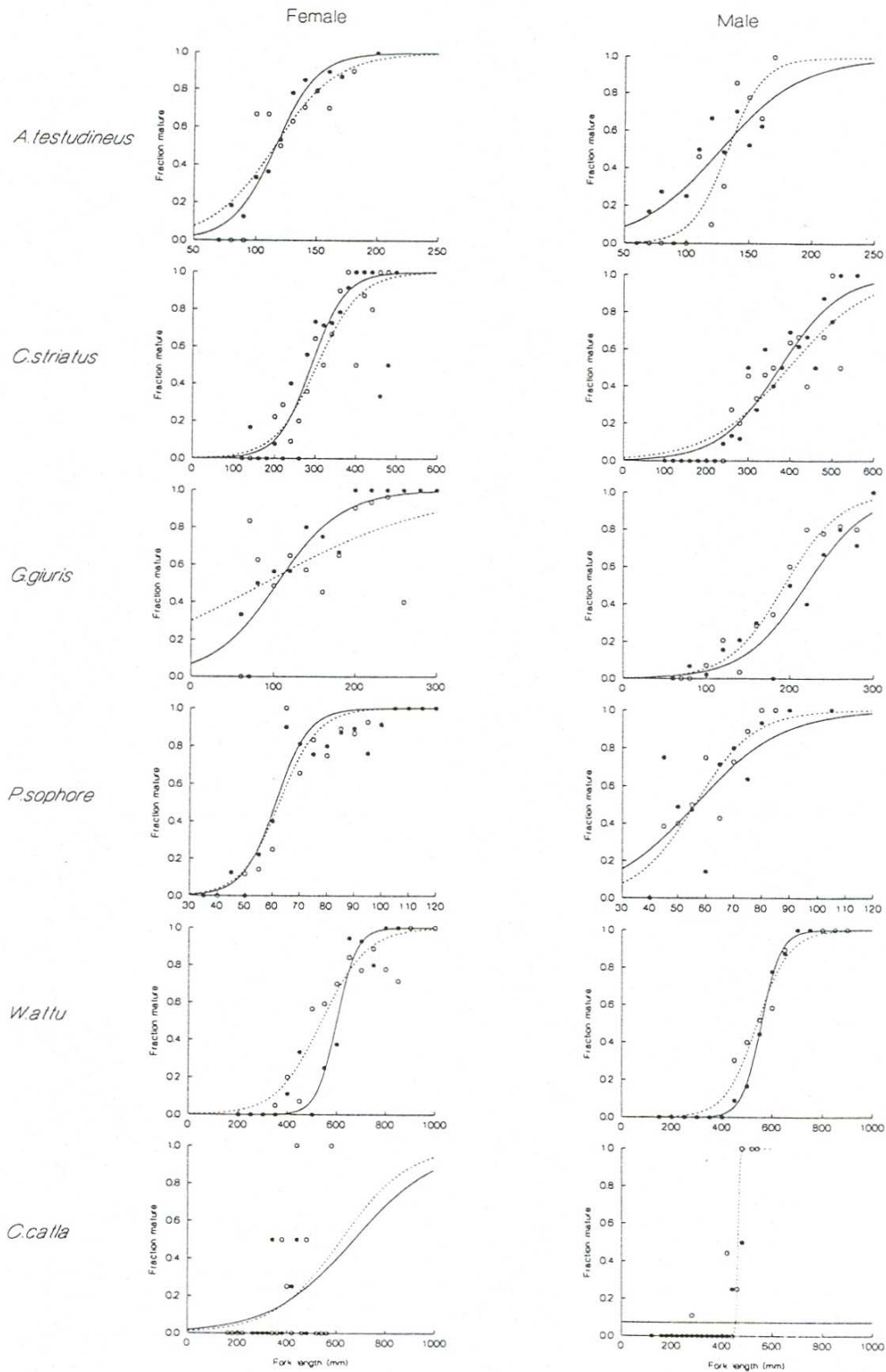


Figure 5.26 Fraction of mature and female key species plotted against their length for estimation of L_{m50} . Solid circles and solid lines, and open circles and broken lines denote data and corresponding logistic model fits for populations sampled from inside and outside the FCDI scheme, respectively.

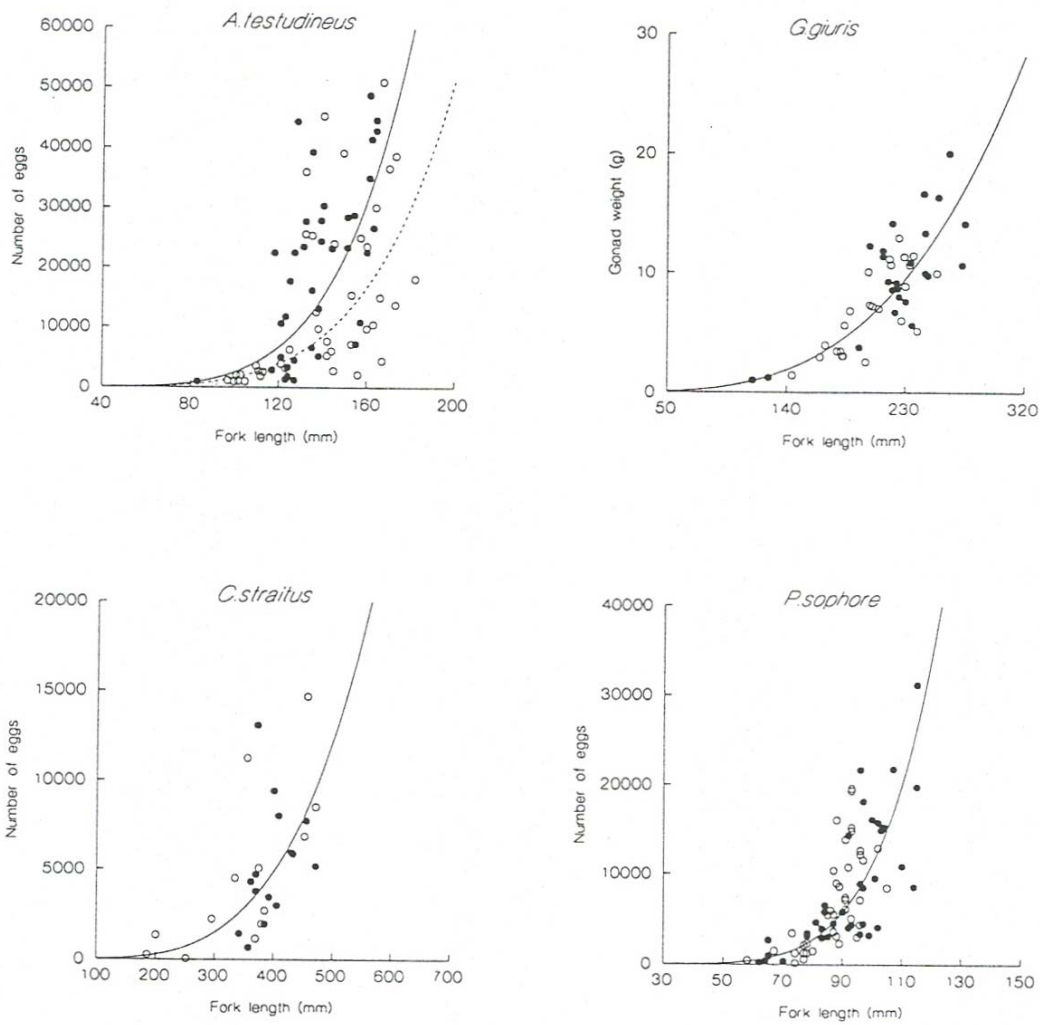


Figure 5.27 Relationships (with fitted regression models) between fecundity (numbers of eggs) or gonad weight and fish lengths for populations caught inside (solid circles, unbroken line) and outside (open circles, broken line) and the PIRDP FCD/I scheme. A single unbroken line denotes a common regression model for both sets of data.

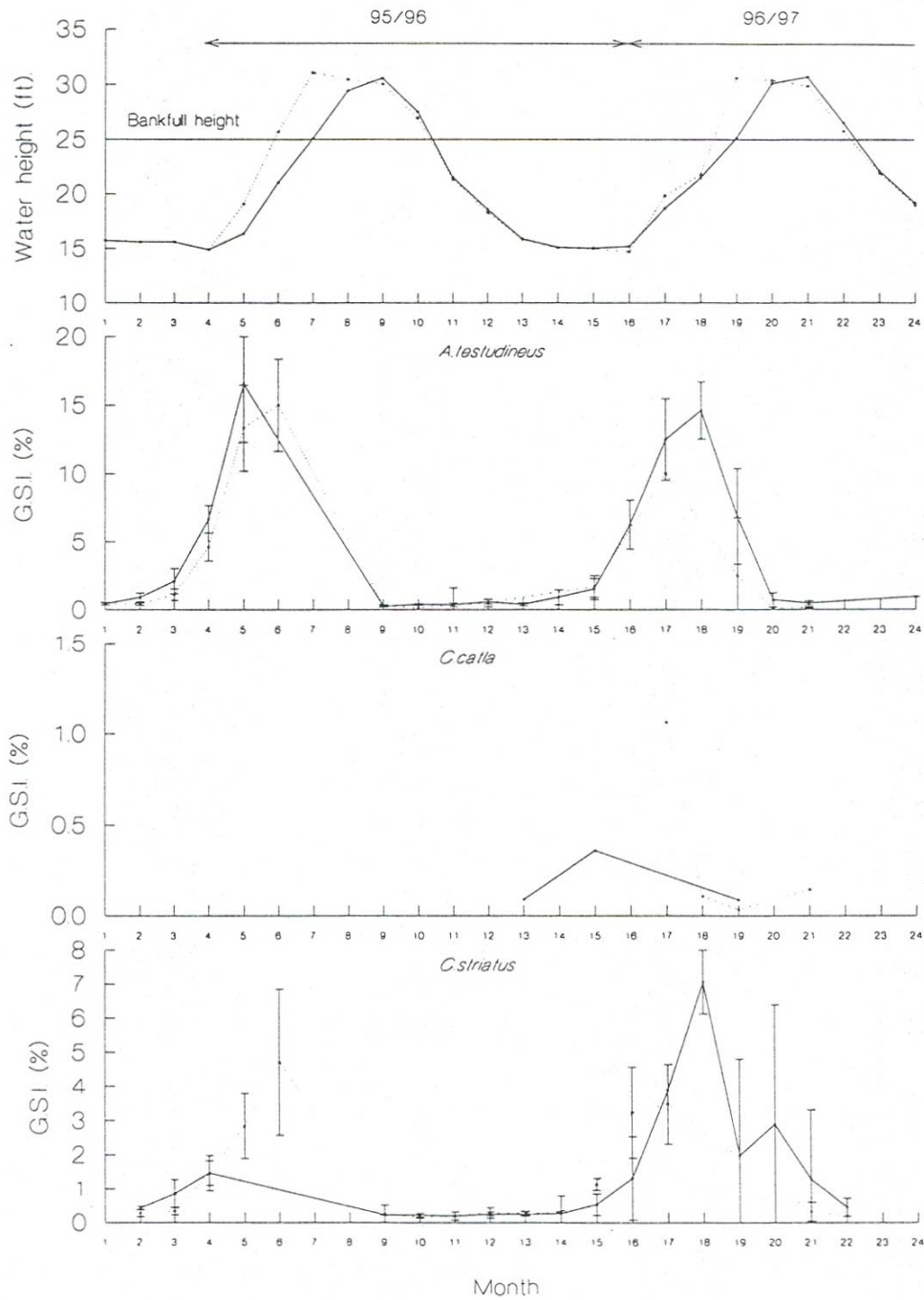


Figure 5.28 Changes in the mean monthly GSI with 95% confidence intervals for populations of *A. testudineus*, *C. catla* and *C. Striatus*

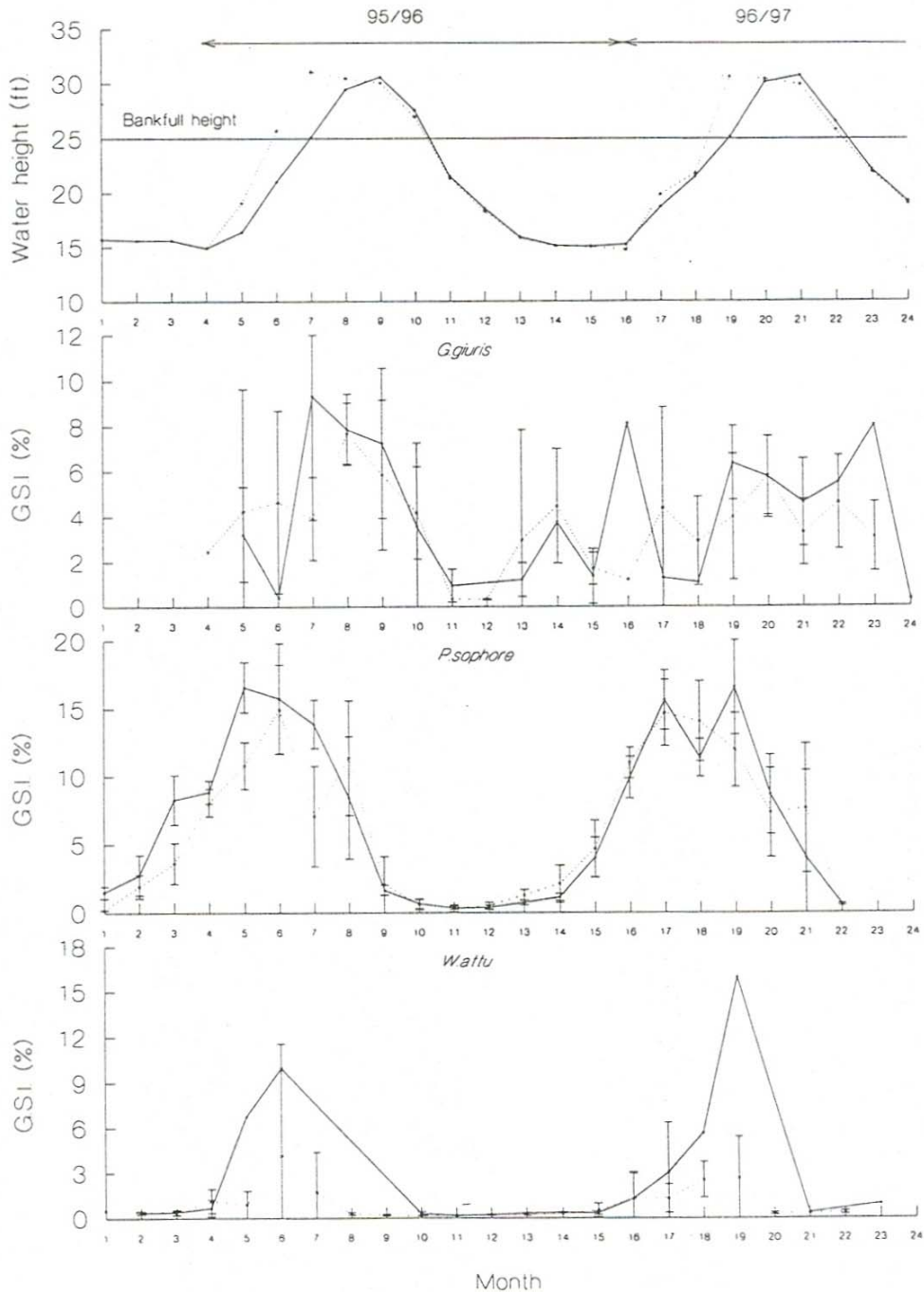


Figure 5.29 Changes in the mean monthly GSI with 95% confidence intervals for populations of *G.giruris*, *P.sophore* and *W.attu* sampled from inside (solid line) and outside (broken line) the PIRD FCDI scheme in 1995 and '96. The uppermost plot shows changes in the mean monthly water height (ft) inside (solid line) and outside (broken line) the scheme.

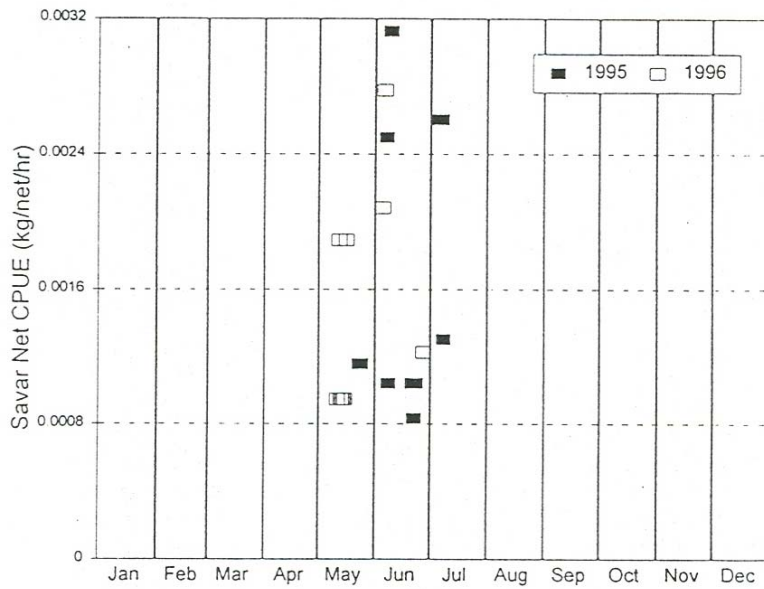


Figure 5.30 Catches per unit effort (kg/net/hour) of major carp fry in saver seine nets in the Jamuna main river at the Bangladesh study site.

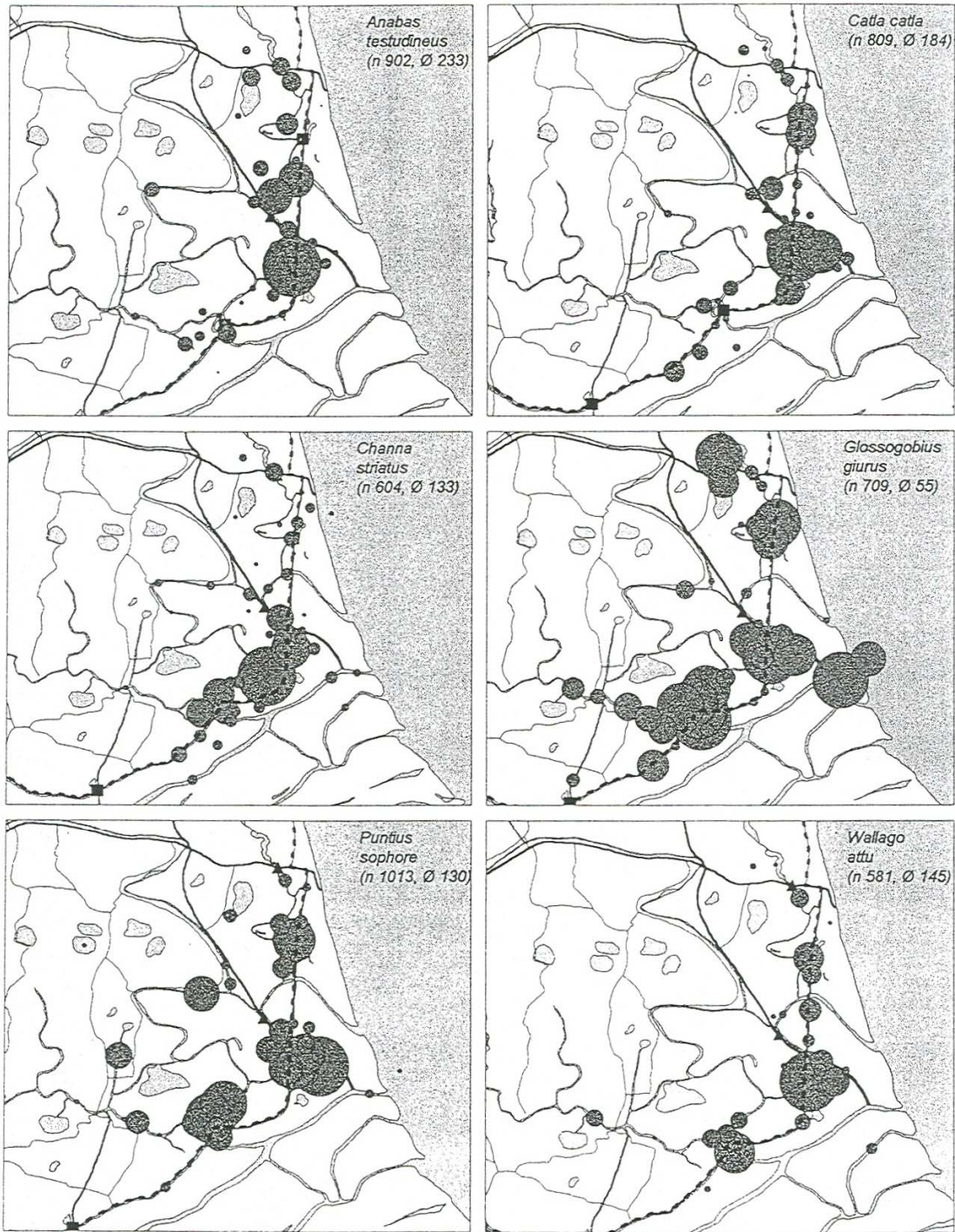


Figure 5.31 Total numbers of fish (*n*) tagged and released at the Bangladesh PIRDP study site, by species and location (Ø indicates the number of fish represented by the largest diameter circle).

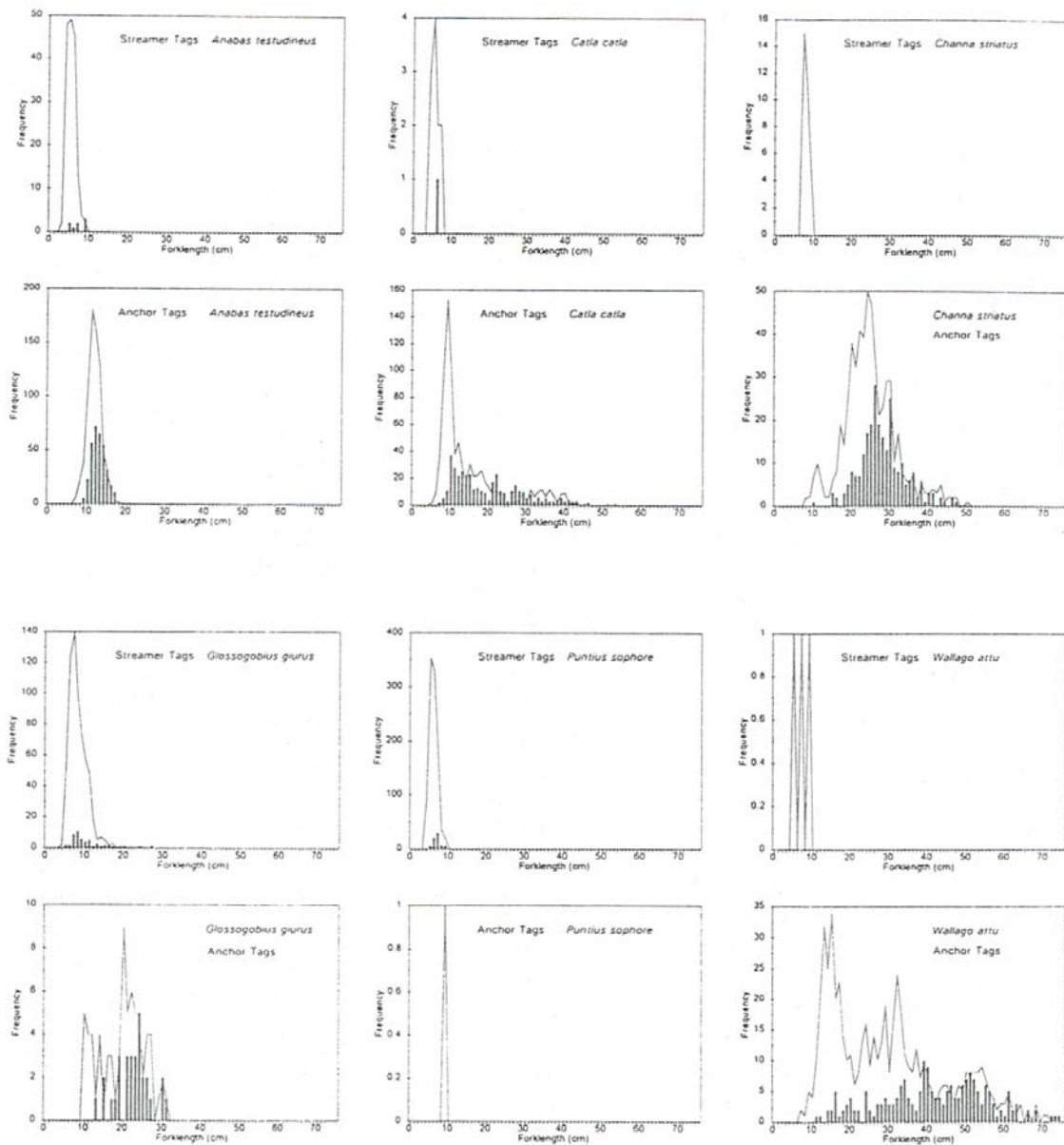


Figure 5.32 Overall fork-length frequencies of fish tagged (lines) and recaptured (bars) at the Bangladesh PIRDP study site, by species and tag type.

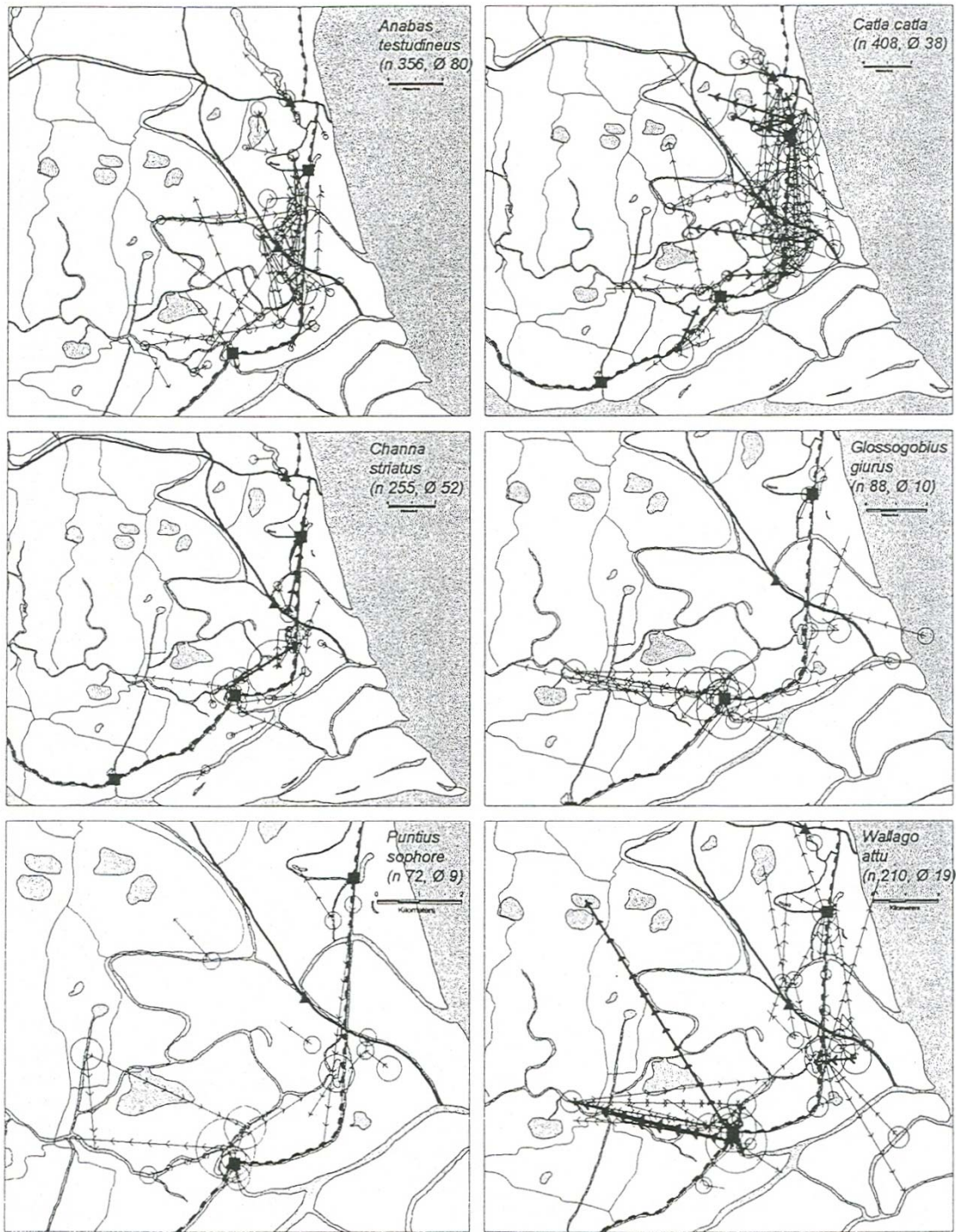


Figure 5.33 Total numbers (n) of each species of tagged fish recaptured at the Bangladesh PIRDP study site, at the same location (circles, with \emptyset indicating the number of fish represented by the largest diameter circle), or at a new location (lines, with arrows indicating the direction of movement, and bold lines indicating migrations across the embankment).

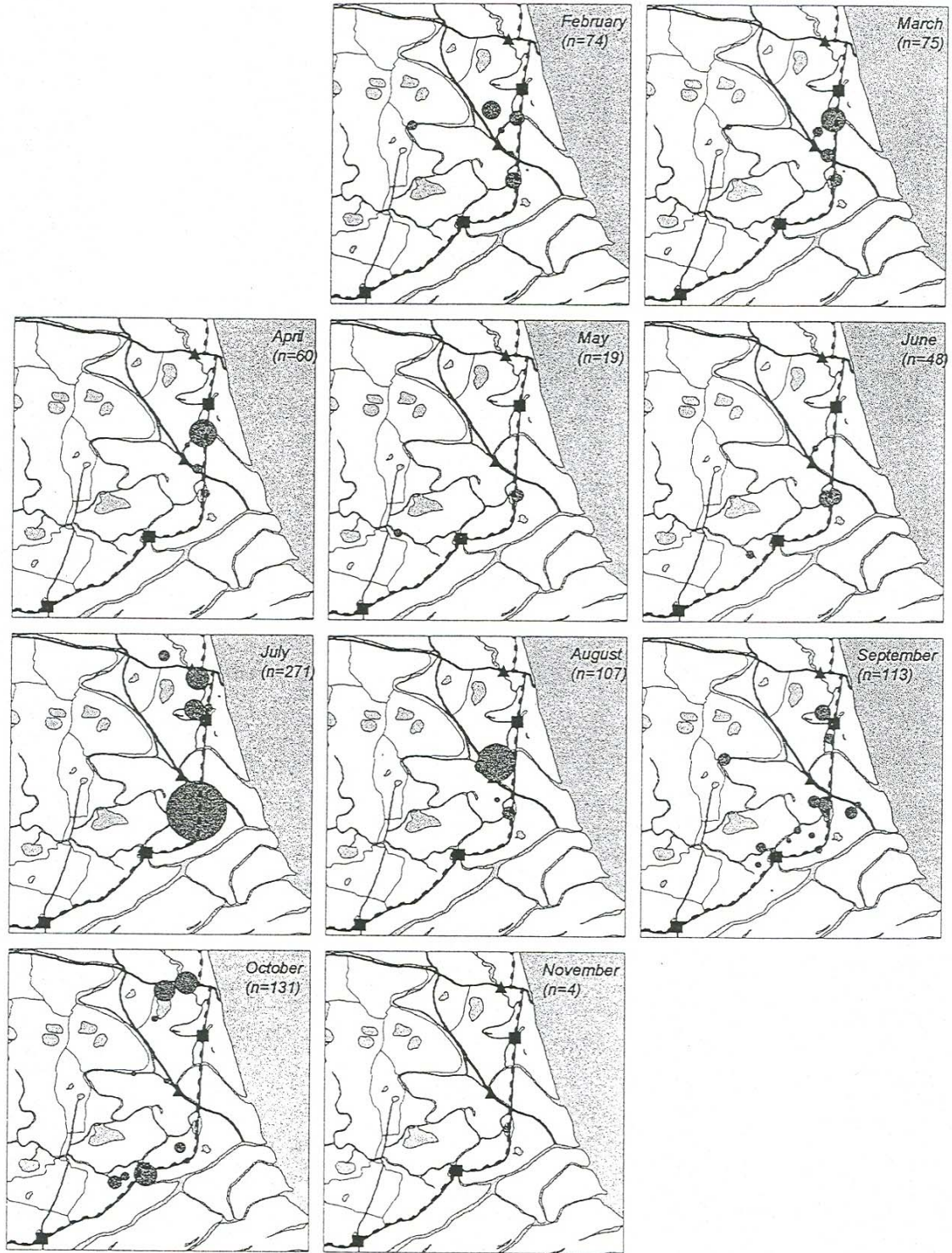


Figure 5.34 Numbers of *Anabas testudineus* (n) tagged and released at the Bangladesh PIRDP study site, by location and month (all years combined). The largest diameter circle represents 178 fish.

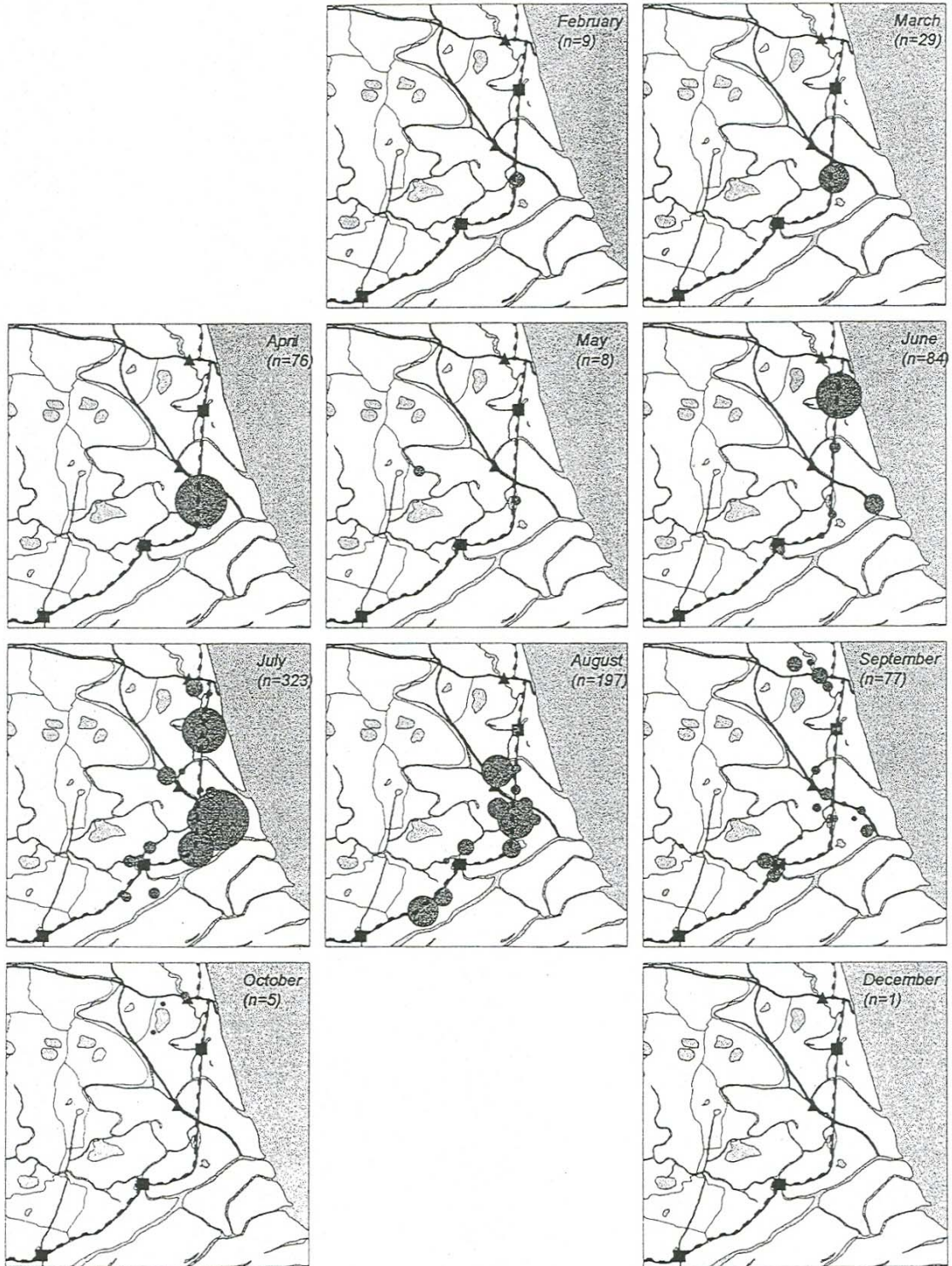


Figure 5.35 Numbers of *Catla catla* (n) tagged and released at the Bangladesh PIRDP study site, by location and month (all years combined). The largest diameter circle represents 96 fish.