

**Fish assemblages of an Australian dryland river: abundance, assemblage structure and recruitment patterns in the Warrego River, Murray-Darling Basin**

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15

**Abstract**

Fish in dryland rivers must cope with extreme variability in hydrology, temperature and other environmental factors that ultimately have a major influence on their patterns of distribution and abundance at the landscape scale. Given that fish persist  
20 in these systems under conditions of high environmental variability, dryland rivers represent ideal systems to investigate the processes contributing to and sustaining fish biodiversity and recruitment in variable environments. Hence, spatial and temporal variation in fish assemblage structure was examined in 15 waterholes of the Warrego River between October 2001 and May 2003. Fish assemblages in isolated waterholes  
25 were differentiated at the end of the dry 2001 winter but were relatively similar

following high summer flows in January 2002 as a consequence of high hydrological connectivity among waterholes. Small, shallow waterholes supported more species and higher abundances than large-deep waterholes. Large, deep waterholes provided important refuge for large-bodied fish species such as adult yellowbelly, *Macquaria* 30 *ambigua*, and the eel-tailed catfish, *Tandanus tandanus*. Recruitment patterns of bony bream (*Nematalosa erebi*), catfish and yellowbelly were associated with high flow events and backwater inundation, however recruitment of yellowbelly and bony bream was also evident following a zero-flow period. Departures from typical flood-induced seasonal spawning patterns may reflect opportunistic spawning behaviours 35 appropriate to the erratic patterns of flooding and dry spells in dryland rivers.

*Extra keywords:* spatial scale, connectivity, geomorphology, hydrology, refugia, alien species

40 Running Head: Fish assemblages and recruitment in an Australian dryland river

## **Introduction**

Most Australian rivers flow through arid or semi-arid regions (Thoms and Sheldon 2000) and are characterised by highly variable and unpredictable flow regimes 45 (Walker *et al.* 1995; Puckridge *et al.* 1998). Typically the fish assemblages of dryland rivers exhibit high variability in assemblage structure, often showing dramatic ‘boom and bust’ patterns of productivity corresponding to periods of flood and drought (Gehrke *et al.* 1995; Puckridge 1997; Arthington *et al.* 2005). During dry periods, fish are confined to isolated floodplain and channel waterholes or ‘refugia’ (Morton *et al.* 50 1995; Magoulick and Kobza 2003), where assemblage structure is typically highly variable from one waterhole and river reach to another, as observed in many of the world’s floodplain rivers (Rodriguez and Lewis 1997; Tejerina-Garro *et al.* 1998; Puckridge *et al.* 2000; Jackson *et al.* 2001; Welcomme 2001; Arthington *et al.* 2005).

During floods, many previously isolated waterholes become connected and fish can  
55 disperse over larger areas and utilise a range of newly inundated habitats (Balcombe  
*et al.* 2005). Thus spatial variability in floodplain fish assemblages is a consequence  
of number of interacting abiotic and biotic factors operating at various spatial scales  
(Arthington *et al.* 2005) such as hydrological and other influences on floodplain  
characteristics, waterhole morphology and connectivity, water quality, habitat  
60 structure and availability, competition for resources and predation (Rodriguez and  
Lewis 1997; Welcomme 2001; Matthews and Marsh-Matthews 2003). Temporal  
variability in fish assemblages is driven by similar processes that impact on fish  
population dynamics via immigration, emigration, spawning, recruitment and  
mortality (Balcombe and Closs 2004; King *et al.*, 2004; Welcomme and Halls 2004).  
65 Studies on spatial and temporal patterns in fish assemblage structure in Cooper Creek,  
a large arid-zone river in the Lake Eyre Basin, have shown that factors affecting fish  
assemblage structure in isolated floodplain waterbodies cannot be fully revealed by  
investigations conducted only at the waterhole scale. A hierarchical, multi-scale  
approach was needed to reveal the influence of antecedent flooding, connectivity of  
70 waterholes and waterhole habitat structure on fish assemblage structure in dry season  
waterholes (Arthington *et al.* 2005). In that study, our temporal frame of reference  
was restricted to a single dry season in 2001 during which temporal patterns in  
waterhole fish assemblages were influenced primarily by water loss and changes in  
habitat structure, and opportunities for recruitment were negligible.  
75 In this paper, we examine spatial and temporal patterns in fish assemblage structure  
within isolated waterholes in the Warrego River catchment (a relatively undisturbed  
catchment of the upper Murray-Darling Basin) between 2001 and 2003. We selected  
this two-year timeframe in order to capture a wider range of temporal variation in

hydrological conditions (channel flows, intermittent flooding, dry spells), waterhole  
80 connectivity and waterhole habitat structure, and to enhance the probability of  
documenting recruitment events and trends. Our aims were: (a) to document the  
range of natural variability in fish populations and assemblage structure in isolated  
waterholes, and the spatial and temporal scales of greatest variation, (b) to determine  
the likely physical and chemical factors that regulate variations in waterhole fish  
85 assemblage structure at scales ranging from the individual waterhole to the river  
reach, and (c) to determine how the recruitment patterns of four common fish species  
contributed to spatial and temporal variations in fish assemblage structure, and the  
potential influence of antecedent flow events on patterns of recruitment. This study  
contributed to the Dryland River Refugia Project, a multidisciplinary investigation of  
90 the processes contributing to and sustaining aquatic biodiversity in dryland rivers of  
Western Queensland (e.g. Bunn *et al.* 2003; Arthington *et al.* 2005; Marshall *et al.*  
2006).

## **Materials and Methods**

### 95 *Study Area*

The Warrego catchment, located in the northwest region of the Murray-Darling Basin,  
has an area of approximately 75,000 km<sup>2</sup>. The headwaters of the Warrego River and  
85 percent of the catchment are located in Queensland with the remainder, 12,500 km<sup>2</sup>  
in New South Wales (Fig. 1). The long-term average annual rainfall in the headwaters  
100 of the Warrego River is 650 mm and this decreases to approximately 250 mm per  
annum in the lower regions of the catchment. Rainfall at Charleville in the upper  
catchment is also highly variable over time, ranging from 220 mm per annum in 1991  
to 10000 per annum in 1950. There is a marked seasonal distribution in rainfall with  
the majority of the catchment receiving 50% of its annual rainfall between December

105 and March, whereas the lower regions of the catchment generally receive only 40% of  
annual rainfall during these summer months. The hydrological regime of the Warrego  
River is also highly variable in time and space. Peak discharges have exceeded  
690,000 ML day<sup>-1</sup> (79,861 m<sup>3</sup>s<sup>-1</sup>) at Fords Bridge Gauge (Fig. 1), and the longest  
period of no flow at this gauging station was 22 months during the late 1950s. Note  
110 that although all discharge figures are expressed in SI units of m<sup>3</sup>s<sup>-1</sup>, they have been  
measured as daily totals.

Streamflow records from the Queensland Department of Natural Resources indicate  
that the mean annual discharge of the Warrego at Wyandra is approximately 640,000  
ML year<sup>-1</sup> (202 m<sup>3</sup>s<sup>-1</sup>). Corresponding values derived from Fords Bridge, 350  
115 kilometres downstream of Wyandra, indicate that nearly 86% of flows diverge into  
Cuttaburra Creek and other distributaries and wetlands downstream of Wyandra.  
The Warrego River displays complex channel morphologies. Its headwaters are  
generally confined within narrow valleys because of regional geological influences.  
Downstream of Cunnamulla, geological influences decrease and this is associated  
120 with marked increases in valley widths. In this region of the catchment the Warrego  
becomes a distributary river system with multiple channels, each channel displaying  
typical meandering characteristics – high sinuosities, low width to depth ratios and  
low bed slopes. Cuttaburra Creek, a relatively large distributary channel, can convey  
up to 40% of the Warrego River's flow (Green, pers. comm. 2005) before returning  
125 flow to Yantabulla Swamp and then joining the Paroo River. The complex systems of  
channels in the lower Warrego system distribute episodic flows to numerous  
permanent and semi-permanent waterholes situated along the various channels. These  
waterholes may contain water for several years after the last flow event. Floodplain  
waterholes also occur in many reaches of the effluent system, however, little is known

130 with respect to their hydrological characteristics, particularly in terms of wetting and  
drying regimes. Both floodplain and in-channel waterholes provide significant  
drought refuge for water birds and native animals during extended periods of no flow  
conditions within the catchment.

Fish assemblage structure was examined in four reaches of the Warrego River located  
135 at Quilberry, Glencoe, Binya and Thurulgoona (Fig. 1). Four waterholes were selected  
at each reach, to represent the natural range of size, shape, connectivity and water  
permanence, except Thurulgoona with only three being readily accessible. All fifteen  
waterholes were sampled for fish twice, in October 2001 and April 2002. The first  
140 sampling trip occurred during a relatively long dry spell when most waterholes had  
been disconnected for at least ten months, when the last significant flow was recorded  
at the Cunnamulla gauge. Four months previous to the first sampling occasion (16-23  
October 2001) a small fresh of 500 ML day<sup>-1</sup> (58 m<sup>3</sup>s<sup>-1</sup>) occurred in the system  
(21/6/2001) and was detected at the Wyandra gauge. This flow would have provided  
some local minor filling of in-stream waterholes upstream of Cunnamulla (the  
145 Quilberry reach), however, as no flow was recorded downstream of Cunnamulla, no  
wetting was achieved at any of the other three reaches.

Prior to the second sampling occasion in April 2002, a flow of 54,000 ML day<sup>-1</sup> (6250  
m<sup>3</sup>s<sup>-1</sup>) was recorded at Cunnamulla on the 14/1/2002. This flow event would have  
provided substantial wetting of the river channel at all fifteen sites. A smaller peak of  
150 3,000 ML day<sup>-1</sup> (347 m<sup>3</sup>s<sup>-1</sup>) was recorded at Cunnamulla on 5/3/2002, providing some  
further wetting and filling of the larger in-channel waterholes on the Warrego River  
and Cuttaburra Creek (see Fig.1). Thus the second sampling occasion followed a  
period of connectivity from channel and backwater flows in the summer of 2001-  
2002.

155 The four waterholes in the Binya reach were sampled on a further two occasions  
(October 2002 and May 2003) to extend our investigation of recruitment patterns in  
relation to flow history and flow events. Following the last recorded flow at  
Cunnamulla in March 2002, the system remained dry with no flow recorded at any of  
the gauges in the Warrego catchment prior to the third sampling occasion (8-10 Oct  
160 2002). On the 16/02/2003 approximately 80,000 ML day<sup>-1</sup> (9,259 m<sup>3</sup>s<sup>-1</sup>) was recorded  
at the Cunnamulla gauge, providing substantial wetting and filling of all Binya  
waterholes prior to the fourth sampling occasion.

### *Methods*

The fish assemblage within each of the fifteen waterholes was primarily sampled  
165 using three fyke nets and a single beach seine. Fyke wing width and sampling  
duration were recorded for each net for the subsequent calculation of catch per unit  
effort (CPUE), where CPUE represents the sum total of individuals collected from  
three fyke nets set for 19h with the wing entrance 10m in width. Fyke nets (13 mm  
mesh) captured both small and large-bodied individuals of all species. Beach seining  
170 (9.5 mm mesh) was used as an additional method to ensure that very small  
individuals, such as juvenile carp gudgeons (*Hypseleotris*) were not missed from  
species richness estimates. Further details of the sampling methods can be found in  
Arthington *et al.* (2005).

Fish were identified, counted and the lengths of the four most abundant species; bony  
175 bream (*Nematalosa erebi*), Hyrtl's tandan (*Neosilurus hyrtlui*), yellowbelly  
(*Macquaria ambigua*) and common carp (*Cyprinus carpio*) were measured on all  
sampling trips. After counting and measurement all native fish were returned alive to  
the water at the point of capture.

Thirty-eight physical floodplain and waterhole variables were measured in October  
180 2001 at three spatial scales (Table 1) using remote aerial photography or on ground  
surveying for each of the fifteen waterholes. The definition and collection of these  
variables was based on methods developed by Parsons *et al.* (2004) and elaborated in  
Arthington *et al.* (2005). Ten water chemistry variables were measured or water  
185 samples collected at each waterhole on all sampling occasions when fish were  
sampled. These included conductivity, N:P, pH, sulphates (SO<sub>4</sub>), silicates (Sil), total  
carbonates (TC), total hardness (ToH), total nitrogen (TN), total suspended solids  
(TSS) and turbidity (Tur). Water samples were collected at the surface and analysed  
using standard methods (APHA 1975).

#### *Data Analysis*

190 Variations in fish assemblage structure and species richness across waterholes and  
sampling times were analysed using CPUE data based on fyke net catches. CPUE data  
were also used as a measure of total fish abundance (all species) and the abundance of  
individual species per waterhole. Species richness for each waterhole was based upon  
the data collected by means of both sampling methods.

195 Assemblage patterns were analysed using ordination based upon hybrid non-metric  
multi-dimensional scaling (MDS). MDS plots were generated from Bray-Curtis  
similarity matrices produced from  $\log_{10}(\text{CPUE} + 1)$  and species presence/absence  
data. One-way analyses of similarities (ANOSIM) based upon the same similarity  
matrices were used to identify assemblage differences among the four sampling  
200 reaches during the October 2001 and April 2002 sampling periods. Two-way crossed  
ANOSIMS were used to examine differences among reaches and sampling times for  
October 2001 and April 2002. One-way ANOSIMS were also used to examine  
differences among waterholes and sampling times in the Binya reach (October 2001,



April and October 2002, May 2003). It was not possible to use two-way ANOSIMS  
205 on this data set due to the low replication of waterholes and sampling times.  
BIO-ENV (Clarke and Warwick 2001) was used to investigate relationships between  
physical characteristics of the landscape (i.e. floodplain features), waterhole  
characteristics, water chemistry and fish assemblage structure/richness. BIO-ENV  
uses generalised Mantel tests to examine associations between faunal datasets and  
210 environmental data expressed as Spearman rank correlation coefficients for the  
association between the two matrices (Clark and Ainsworth 1993). Autocorrelated  
floodplain and waterhole variables were removed prior to the BIO-ENV procedure,  
using Spearman rank correlations ( $r_s > 0.8$ ) to identify redundant variables (see Table  
1). The environmental similarity matrices were based upon normalised Euclidean  
215 distance rather than Bray-Curtis similarity as per Clarke and Warwick (2001). BIO-  
ENV analysis was performed on the October 2001 and April 2002 datasets,  
representing the two sampling occasions where all fifteen waterholes were sampled.  
All multivariate analyses were undertaken in the PRIMER version 5 software package  
(Clarke and Gorley 2001).  
220 To examine patterns of body length structure and possible recruitment in relation to  
sampling time and antecedent hydrological events, size frequency histograms were  
constructed for the four most common and abundant fish species. Recruitment  
patterns were examined only at the Binya reach (Fig. 1) over the period October 2001  
to May 2003 (i.e. at the end of the dry season of 2001, after the wet season of 2002,  
225 after the dry season of 2002 and after the wet season of 2003).

## **Results**

### *Fish assemblage patterns across four reaches on two sampling occasions*

The fish fauna was composed of 10 indigenous species from eight families and three  
230 alien species from two families (Table 2). Considerable variation in total fish  
abundance was observed among waterholes and sampling times (Fig. 2). The most  
abundant and widespread species on the two sampling occasions when all fifteen  
waterholes were sampled, October 2001 (post dry) and April 2002 (post wet), was the  
bony bream, *Nematalosa erebi*. This species accounted for at least 40% of the catch  
235 on those occasions and was found in 14 of the 15 waterholes (Table 2). Other  
widespread species were yellowbelly (*Macquaria ambigua*) and Hyrtl's tandan  
(*Neosilurus hyrtl*) the latter also being the most abundant species in April 2002,  
accounting for 41% of the total catch at that time. The exotic common carp (*Cyprinus  
carpio*) was also widespread and abundant, particularly in October 2001 when it was  
240 caught in 11 of the 15 waterholes and accounted for 16% of the total catch. The  
goldfish (*Carassius auratus*) was also found in 11 waterholes in October 2001 but  
comprised only 5% of total catch at that time.

Some waterholes had notably low fish catches, particularly Quilberry and Sandford  
Park waterholes in the Quilberry reach, and Noorama in the Thurulgoona reach (Fig.  
245 2). Catches varied considerably between October 2001 and April 2002 at most  
waterholes, however, there was no consistent temporal pattern within any one reach  
(Fig. 2). The main species contributing to large increases in abundance over this  
period (e.g. at Key, Rocky and Red waterholes) was Hyrtl's tandan (*N. hyrtl*)  
(4,150% increase across the three waterholes). Observed decreases in fish abundance  
250 between October 2001 and April 2002 generally occurred in the medium-sized  
waterholes (e.g. Clear, Glencoe, Woggannorah and Thurulgoona Homestead). These  
were largely due to the reduced numbers of bony bream (*N. erebi*) in the three former  
waterholes (300%), while at Thurulgoona Homestead there was a large reduction in

the number of native spangled perch (*Leiopotherapon unicolour*) and the exotic carp  
255 and goldfish (8,500% decrease combined across the three species).

Multivariate patterns of fish assemblage structure based on abundance (CPUE) and  
species richness showed no clear separation among waterholes with the exception of  
Sandford Park and Quilberry waterholes in the Quilberry reach (Fig. 3). Noorama  
waterhole in the Thurulgoona reach was also differentiated from the other waterholes  
260 in terms of fish assemblage structure but to a lesser extent than the two large  
Quilberry waterholes. There were significant differences in fish assemblage structure  
among some reaches in October 2001 based upon CPUE data (Table 3).

In addition, reach differences were also apparent for patterns of both richness and  
CPUE based on the combined April and October dataset, particularly between  
265 Quilberry and Binya reaches (Table 3, Fig. 3). In contrast, fish assemblages could not  
be differentiated between the two sampling times across all reaches for either CPUE  
or richness (Table 3).

No significant variation in multivariate patterns of fish CPUE or species richness  
across all waterholes could be explained by water chemistry. However, waterhole  
270 geomorphology and habitat structure explained some of the variability of CPUE and  
species richness patterns in both October 2001 and April 2002 (Table 4). The variable  
most commonly associated with these assemblage patterns was waterhole cross  
sectional area (CSA). In combination with snags (SN) and overhanging vegetation  
(OV), CSA explained up to 45% of variation in the spatial patterns of waterhole fish  
275 assemblages expressed in terms of CPUE and species richness (Table 4). The strong  
association between fish relative abundance and species richness with CSA is  
consistent with the distributional data showing very low fish numbers and species at  
waterholes with the highest CSA values (Quilberry, Sandford Park waterhole and

Noorama). Conversely, waterholes with the smallest CSA values (Rocky and Red)  
280 had the highest fish abundances (Fig. 2).

Associations between individual species and geomorphological and habitat variables  
measured at three spatial scales revealed that landscape-scale factors were not in  
general correlated with the abundance of individual fish species (Table 5). The one  
exception to this was a significant negative association between total floodplain width  
285 and goldfish abundance in October 2001.

The variables most commonly associated with the abundance of each fish species  
were those measured at the waterhole scale. For example, a significant amount of the  
variation in eel-tailed catfish (*Tandanus tandanus*) abundance on both sampling  
occasions was explained by waterhole shape. The positive correlation for this catfish  
290 with cross sectional area (CSA) and depth of cross section (DCS) and negative  
association with width to depth ratio (WD) suggest that this species was more likely  
to be found in higher abundance in large, deeply incised waterholes (Table 5). In  
contrast, the abundances of bony bream (*N. erebi*) and Hyrtl's tandan (*N. hyrtlii*) were  
negatively associated with CSA, suggesting that large, deeply incised waterholes were  
295 unlikely to support high numbers of these species. Apart from CSA, DCS and WD,  
other waterhole features correlated with individual species abundances were surface  
area (A) and wetted perimeter (WP) (Table 5).

Within waterholes, geomorphological factors associated with species abundances  
were off-take channels (OC), mid-channel bars (MCB) and anabranches (AN). These  
300 associations were only evident in April 2002 following summer rains and subsequent  
river runs when off-take channels would have provided additional wetted habitat for  
*T. tandanus*, whereas bony bream and Hyrtl's tandan showed a negative association  
with mid-channel bars and anabranches. When water levels are low to moderate, the

presence of bars within the channel and shallow anabranches may act to reduce the  
305 amount of wetted habitat for some species.

*Fish assemblage patterns at Binya reach on four sampling occasions*

The longer term fish data collected from the most downstream (Binya) reach, showed  
that fish assemblages in the four waterholes were consistently similar to each other on  
all four sampling occasions, with no significant influence of waterhole characteristics  
310 on the multivariate patterns of CPUE and richness (Table 3). There was, however,  
significant variation in assemblage structure among sampling occasions for both  
CPUE and richness (Table 3, Fig. 4). Fish assemblages were most different on the  
fourth and final sampling occasion, May 2003, as shown by the position of May fish  
assemblages in the lower right areas of ordination space in Figure 4a and 4b.

315 Length-frequency data indicate some periods of recruitment by the three most  
abundant indigenous species and common carp. There was, however, a lack of  
consistency in the recruitment patterns among the four species and across the Binya  
waterholes, and to a lesser extent in relation to the time of sampling.

Bony bream (*N. erebi*) showed likely periods of recruitment in three of the four  
320 waterholes, particularly in Red Hole in April 2002 and Mirage Plains and Tinnenburra  
holes in May 2003 (Fig. 5). A large proportion of the fish collected were in size  
classes  $\leq 60$ mm S.L. at these times suggesting successful spawning leading to  
juvenile recruitment by late summer. Similar to the temporal patterns in size structure  
observed in bony bream, Hyrtl's tandan (*N. hyrtl*) also showed some definite periods  
325 of recruitment in the same three waterholes, although these were most obvious in  
April 2002 (Fig. 6) and coincided with the highest catches of this species in the Binya  
reach across all sampling times. There was also obvious recruitment of juvenile

tandans in May 2003, however, the numbers caught were very low suggesting a very weak spawning response or low survival of larvae and juveniles of *N. hyrtlii*.

330 Yellowbelly (*Macquaria ambigua*) also appeared to have a number of juvenile recruitment periods, particularly in Mirage Plains and Red holes in October 2002 and May 2003 (Fig. 7). There was also some obvious recruitment by May 2003 in the other waterholes, as evidenced by the dominance of fish  $\leq 30$  mm S.L. (Fig. 7). The size structure plots for carp (*C. carpio*) indicate that larger-bodied individuals  
335 tended to dominate fish assemblages within the Binya waterhole group with only a few juveniles present (Fig. 8). Juvenile carp (<100mm S.L.) were collected in May 2003 following the largest flood recorded during the Warrego study period. However, our data suggest a weak juvenile recruitment event.

#### 340 **Discussion**

Fish assemblage structure in the Warrego River catchment reflected a number of processes operating across a range of spatial scales. There was a high degree of similarity in fish assemblages among waterholes and reaches with the only significant pairwise reach differences apparent in October 2001 and no evidence of  
345 differentiation from then until April 2002. This finding suggests that there was high connectivity potential among all waterholes and reaches between October and April, i.e. the early to late summer of 2001-2002. Flow events during this period included an overland flood in January 2002, three months prior to the second sampling occasion (April 2002) and an in-channel flood pulse two months following this flood.  
350 This degree of hydrological connectivity among waterholes during the wet summer months of 2002 appears to underpin the spatial patterns found in the fish assemblage. By the end of a wet period fish assemblages would tend to show low differentiation in terms of species composition and relative abundances, providing the most common

fish species present have high vagility, which is likely (Bishop *et al.* 1995; Pusey *et al.* 2004; Arthington *et al.* 2005). Summer flooding in the Warrego study area appears to have ameliorated the influence of biophysical processes that typically operate within individual, isolated waterhole during dry periods, and drive fish assemblages along independent trajectories of change (Bishop and Forbes 1991; Bishop *et al.* 1995; Magoulick and Kobza 2003; Arthington *et al.* 2005).

In the context of rivers in the Murray-Darling Basin (MDB) the role of hydrological connectivity is an important factor to consider given the poor current condition of MDB fish assemblages (Schiller and Harris 2001; Koehn and Nicol 2004). Much of the impact on fish stocks in the MDB has been attributed to hydrological and associated land management changes to support agriculture, changes that ultimately impact on connectivity among waterbodies, reaches and even sub-catchments. Factors that threaten connectivity include: river regulation and associated construction of weirs and levee banks, the release of water from dams to accommodate irrigation demands thereby disrupting natural seasonal flow patterns, and floodplain alteration to facilitate the capture of flood flows in off-channel storages, often severing natural pathways of connection between floodplains and river channels (Walker *et al.* 1997; Balcombe and Closs 2004; Koehn and Nicol 2004). The Warrego generally does not suffer from these disturbances to natural patterns of stream flow and connectivity and this relative lack of disturbance appears to be reflected in the condition of the fish fauna. Compared to other Murray-Darling rivers, Warrego catchment waterholes support higher abundances and richer assemblages than other sub-catchments of this river system (Gehrke *et al.* 1995). Furthermore, in the Warrego study, the low proportion of alien fish relative to total fish abundance (100 native to alien ratio) contrasts with the findings of Gehrke *et al.* (1995) in two Upper Murray-Darling

380 rivers - the Paroo (~ 1.6) and the Darling River (~13). Given its present condition, the Warrego River may serve as a model dryland river for the further investigation of ecological processes sustaining fish in variable environments in both the Murray-Darling Basin and other similar systems.

The average number of species and fish abundances in Warrego waterholes were somewhat lower than those found by Arthington *et al.* (2005) in another dryland river, 385 Cooper Creek, within the Lake Eyre basin. Differences in species richness must be a reflection, to some extent, of the smaller fish species pool in the Warrego catchment (total of 10 indigenous species in 8 families) compared to the Cooper Creek system (total of 12 indigenous species in 8 families). The reasons for marked differences in fish abundance per waterhole are unclear, but could be associated with higher rates of 390 primary production in Cooper Creek waterholes compared to the Warrego River (Bunn *et al.* 2003; 2005). The higher fish abundances recorded in Cooper Creek waterholes in 2001 could also be related to the energy subsidies provided by extensive antecedent flooding in the summer of 2000 (Arthington *et al.* 2005; Balcombe *et al.* 2005).

395 October 2001 and April 2002 datasets revealed Quilberry reach to be most differentiated from the Binya reach in both fish abundance and species richness. These two reaches are the most distant in the catchment (see Fig. 1) which could suggest that physical distance may influence fish assemblage characteristics or even that the Cunnamulla Weir may impede fish movement between Quilberry and Binya 400 reach. However, two distance measures were used in the BIO-ENV analyses (channel and straight line distance to nearest waterholes) and neither influenced fish abundance and species richness among waterholes. A better explanation of the observed pattern is the major influence of having the two largest and most deeply incised waterholes in



the study area - Quilberry and Sandford Park waterholes in the Quilberry reach.

405 These two waterholes supported the lowest numbers of individuals and species on  
both sampling occasions. It must also be noted that the other Quilberry waterholes,  
Clear and Sandford Park Lagoon, supported average abundances and no fewer species  
than downstream waterholes. This suggests that patterns of waterhole morphology  
and habitat structure at the landscape scale are more important drivers of fish  
410 assemblage structure than physical distance and degree of separation *per se*. This is  
consistent with evidence that waterhole scale factors exerted a strong influence on fish  
diversity and abundance in the Warrego catchment, particularly cross-sectional area  
(CSA) and the presence of woody material (snags) derived from riparian vegetation.  
Thus at the waterhole scale, geomorphology and habitat structure largely explain  
415 variations in fish assemblage structure. Large deep waterholes supported fewer fish  
species and lower abundances, yet may act as key refugia for large-bodied fish such as  
adult yellowbelly and the catfish, *T. tandanus*. This could be particularly important  
under conditions of extended drought (up to 22 months in the Warrego catchment)  
when smaller waterholes may dry completely and large waterholes provide the only  
420 habitat sustaining aquatic species during dry spells between wet periods. Small  
populations of maturing and adult fish would be significant sources for juvenile  
recruitment when flows replenish and rejoin isolated waterholes.

Conversely, small shallow waterholes of the Warrego River supported more species  
and higher abundances per unit area than large-deep waterholes, a pattern that could  
425 be driven largely by a greater amount of productive littoral zone and hence,  
significant potential for increased production of aquatic food resources (Bunn *et al.*  
2003, 2005; Balcombe and Closs 2004; Medeiros 2005). Evidence of the importance  
of snags as a waterhole feature associated with variations in fish assemblage structure

is also not surprising given that undercut root masses, large fallen logs and smaller  
430 woody material represent one of the few ubiquitous aspects of structural heterogeneity  
in these waterholes. These structural features probably provide significant sites for the  
production of food resources for fish and also predator refuges for smaller-bodied fish  
(Wright and Flecker 2004; Crook *et al.* 1999). The low abundance of small-bodied  
fish in the large, deeply incised waterholes may also be explained in part by higher  
435 rates of predation from larger predators (fish and birds) due to the relative lack of  
physical refugia per unit area. Riparian protection to achieve natural delivery of  
timber and small woody material to waterholes should be an important consideration  
in the management of this catchment.

Temporal data for Binya reach waterholes showed a high degree of similarity in fish  
440 assemblage structure among the four waterholes in both October 2001 and May 2003.  
In contrast there was little concordance in the fish assemblages among the four  
waterholes in both April and October 2002. The large difference between April and  
October 2002 can be explained by the high numbers of juvenile tandans (*N. hyrtlii*) in  
Red Hole, Mirage Plains and Tinnenburra waterholes in April, with only a few  
445 individuals of this species captured in October. In Red Hole, there was also a large  
decrease in the abundance of bony bream (*N. erebi*) between April and October 2002.  
Hence, stochastic patterns of juvenile recruitment among the four waterholes largely  
influenced temporal variations in fish assemblage structure in the Binya reach. This  
suggests that non-uniform processes of recruitment operated across these three  
450 waterholes. Such variability could be driven primarily by subtle differences in  
hydrology within this waterhole group, given that within the Binya reach the  
waterholes we studied were located in three sub-catchments - Mirage Plains Ck,  
Cuttaburra Ck and Warrego R (see Fig. 1).

Recruitment of *N. hyrtlii* was particularly variable among waterholes, with high  
455 numbers of juveniles found only in Rocky, Red and to a lesser extent, Tinnenburra  
waterholes in April 2002. There is no obvious explanation for this result, apart from  
the similarity between Red and Rocky holes in that they are small in area, but  
relatively deep with very hard substrata. Little is known about the breeding biology of  
this tandan, particularly in the MDB (Pusey *et al.* 2004). Hence, it is not known  
460 whether this species spawns preferentially in these peculiar waterholes, or whether  
larvae/juveniles preferentially move into them during periods of flow, or achieve  
higher survivorship in such habitats. Recruitment of yellowbelly (*M. ambigua*)  
appeared to be associated with summer flows given that juveniles were found mostly  
following summer flow events, although only in small numbers. However, juvenile  
465 yellowbelly were also present in Mirage Plains and Red Hole in October 2002 after a  
dry winter/spring period without any channel flows. Thus it would appear that  
spawning of this species is not solely dependent upon flow events as proposed by  
King *et al.* (2003) in the Ovens River (a River Murray tributary) but has a much more  
opportunistic breeding strategy (see Mallen-Cooper and Stewart 2003 and Pusey *et al.*  
470 2004 for review and discussion). Bony bream (*N. erebi*) recruitment also appeared to  
be linked to flow events, especially given the high numbers of smaller size classes  
caught in April 2002 and May 2003 following high flows (see Fig. 5). It seems that  
the bony bream is also not an obligate flood spawner in this catchment as juveniles  
were also present in October 2001 and 2002 (at the end of dry spells) in at least two  
475 waterholes, albeit in low abundance.

Known as flood spawners, carp (*C. carpio*) did not produce the huge numbers of  
juveniles following floods that are often reported in more southern reaches of the  
Murray-Darling Basin (King *et al.* 2003; Driver *et al.* 2005). Floods tend to occur

between late winter and spring in the lower MDB, whereas floods occur later in the  
480 northern parts of the basin, principally in the summer and early autumn. Juvenile carp  
( $<100\text{mm S.L.}$ ) were collected in May 2003 following the largest flows recorded  
during the Warrego study period ( $80,000\text{ML/day}$   $\{9,259\text{ m}^3\text{s}^{-1}\}$  at the Cunnamulla  
gauge). It is possible that only the February 2003 flood was sufficient in magnitude  
and duration to produce successful recruitment of carp through to juvenile stages.  
485 Brown *et al.* (2005) suggested that although increased river flow in the mid-Murray  
River resulted in carp spawning, it had to be of a great enough magnitude and  
duration to inundate wetlands to result in successful juvenile recruitment. Although  
the later flows in the Warrego system may not inhibit spawning impacts on juvenile  
carp recruitment and/or survival could be felt as temperatures fall in late autumn.  
490 King (2005) found early stage larval carp fed on algae and small-bodied cladocerans,  
moving on to more epibenthic prey (such as chironomids, chydorid cladocerans and  
hemipterans) as juveniles. These prey resources could become limited as  
temperatures fall in late autumn and early winter resulting in low net juvenile carp  
recruitment. To examine the role of flood timing on carp recruitment we would have  
495 needed to measure larval recruitment of the species, a requirement beyond the scope  
of this study.

High flows occurred during the summer months of 2002 and 2003 and the recruitment  
patterns of common and abundant species (bony bream, *N. erebi*, catfish, *N. hyrtlii*,  
and yellowbelly, *M. ambigua*) were associated with these events and backwater  
500 inundation, particularly after the high summer flows recorded in February 2003.

However, recruitment levels were typically low for species known to respond to high  
flows and floodplain inundation (e.g. yellowbelly) and did not achieve levels recorded  
in the southern MDB. Furthermore, yellowbelly and bony bream showed evidence of

recruitment in October 2002 following a winter period without any channel flows. We  
505 suggest that these departures from typical flood-induced seasonal spawning patterns  
may reflect opportunistic spawning behaviours appropriate to life in a dryland river  
system that only occasionally experiences high summer flows and extensive  
floodplain inundation, and one that may on occasion experience elevated flows during  
normally dry, winter months (e.g. June 2001). Conjecture still surrounds the stimuli  
510 required for spawning and the roles of flow and other factors in juvenile recruitment  
of the yellowbelly, as discussed in Humphries *et al.* (1999), Mallen-Cooper and  
Stewart (2003) and Pusey *et al.* (2004). Further work on spawning and recruitment of  
*Macquaria ambigua*, and the ambiguities of its breeding biology in relation to flow, is  
clearly warranted to protect this iconic species and to inform land and water  
515 management planning in the Warrego catchment.

## **Conclusions**

The management of rivers with highly variable flow regimes is a particular challenge  
in dryland areas of Australia (Boulton *et al.* 2000). This paper contributes new  
520 information and insight into the factors influencing the structure and diversity of  
Warrego River fish assemblages, and importantly, the influence of intermittent  
channel flows and minor flooding on patterns of recruitment during a relative dry  
period between October 2001 and May 2003. We have shown that fish assemblages in  
isolated waterholes at the end of the 2001 dry season were differentiated in terms of  
525 species richness, total abundance and the abundance of individual species but tended  
towards similarity of composition after summer channel flows and flooding of low  
level backwaters had restored connectivity among isolated reaches and waterholes.  
Connectivity fosters fish movement, colonisation of previously isolated waterholes,

and processes associated with ‘boom and bust’ cycles of recruitment and productivity  
530 (Junk *et al.* 1989; Closs and Lake 1996; Puckridge *et al.* 1998; Amoros and Bornette  
2002; Fausch *et al.* 2002; Sheldon *et al.* 2002; Arthington *et al.* 2005). We conclude  
that it will be particularly important to maintain the natural quantities and timing of  
channel freshes and higher flow events that inundate backwaters, as these flows  
evidently achieve hydrological connectivity and drive ecological processes that  
535 sustain the diversity, recruitment and population dynamics of native fish species in the  
Warrego catchment. Furthermore, as it is part of a relatively undisturbed catchment,  
the Warrego River may serve as a model for further investigation of ecological  
processes sustaining native fish in variable environments.

540

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700 **Tables**

**Table 1** Warrego River waterhole geomorphology and habitat variables (and abbreviations) measured at three scales for BIO-ENV analysis. Highlighted variables were removed following redundancy analysis.

<b>Landscape</b>	<b>Entire waterhole</b>	<b>Within waterhole</b>
Total floodplain width (TFW)	Area (A)	Hydraulic radius (HR)
<b>Effective floodplain width (EFW)</b>	Cross sectional area (CSA)	Depth of cross section (DCS)
Channel distance to nearest waterhole (CD)	Width to depth ratio (WD)	Mid-channel bars (MCB)
Straight line distance to nearest waterhole (SLD)	Wetted perimeter (WP)	Backwater (BAW)
Bifurcation ratio (BR)	<b>Shape index (SI)</b>	Off-take channels (OC)
<b>Number of channels (NOC)</b>	Fetch length (FL)	Bench 0 - 1/3 (B1)
	<b>Perimeter (P)</b>	Bench 1/3 - 2/3 (B2)
	<b>Length (L)</b>	Bench 2/3-3/3 (B3)
	<b>Circularity ©</b>	Side bars (SB)
	<b>Elongation ratio (ER)</b>	Backwater (BAW)
	<b>Length to width ratio (LW)</b>	Anabranches (AN)
	<b>Volume (V)</b>	<b>Bed and bank complexity (BBC)</b>
		Eroding banks (EB)
		Snags (SN)
		Anabranches (AN)
		Boulders (BOU)
		Fringing vegetation (FV)



705 **Table 2** Fish species found in 15 waterholes of the Warrego River catchment in October 2001 and April 2002.

<b>Family/species</b>	<b>Common name</b>	<b>% of total CPUE Oct 2001 (maximum no. of waterholes where present)</b>	<b>% of total CPUE Apr 2002 (maximum no. of waterholes where present)</b>
<b>Indigenous species</b>			
<b>Ambassidae</b>			
<i>Ambassis agasizzii</i> Steindachner, 1867	olive perchlet	5 (2)	2 (1)
<b>Clupeidae</b>			
<i>Nematalosa erebi</i> (Günther, 1868)	bony bream	53 (14)	40 (14)
<b>Gobiidae</b>			
<i>Hypseleotris</i> spp.	carp gudgeons	<1 (9)	<1 (5)
<b>Melanotaeniidae</b>			
<i>Melanotaenia fluviatilis</i> (Castelnau, 1878)	crimson-spotted rainbowfish	<1 (2)	<1 (4)
<b>Percichthyidae</b>			
<i>Macquaria ambigua</i> (Richardson, 1845)	golden perch	7 (12)	6 (14)
<b>Plotosidae</b>			
<i>Neosilurus hyrtl</i> i (Steindachner, 1867)	Hyrtl's tandan	6 (9)	41 (12)
<i>Tandanus tandanus</i> Mitchell, 1838	eel-tailed catfish	3 (7)	1 (6)
<b>Retropinnidae</b>			
<i>Retropinna semoni</i> (Weber, 1895)	Australian smelt	<1 (3)	<1 (2)
<b>Terapontidae</b>			
<i>Bidyanus bidyanus</i> (Mitchell, 1838)	silver perch	<1 (1)	<1 (2)
<i>Leiopotherapon unicolor</i> (Günther, 1859)	spangled perch	4 (6)	5 (14)
<b>Alien species</b>			
<b>Cyprinidae</b>			

<i>Carassius auratus</i> (Linnaeus, 1758)	goldfish	5 (11)	1 (5)
<i>Cyprinus carpio</i> (Linnaeus, 1758)	common carp	16 (11)	4 (7)
<b>Poeciliidae</b>			
<i>Gambusia holbrooki</i> (Girard, 1859)	mosquitofish	0 (0)	<1 (1)

**Table 3** Summary of ANOSIM results comparing Warrego River fish assemblages

based upon CPUE and presence/absence among reaches, times and waterholes. Note:

710 Reaches and waterholes: B=Binya, G=Glencoe, Q=Quilberry, T=Thurulgoona. Sampling times: 1 = October 2001, 2 = April 2002, 3 = October 2002, 4 = May 2003.

Sampling time	Transformation	Factor	Global R	P	Significant pairwise tests
1	Log (CPUE +1)	Reach	0.283	0.009	Q-B (0.03), G-B (0.03) G-T (0.03)
1	Pres/abs	Reach	0.162	n.s.	
2	Log (CPUE +1)	Reach	0.121	n.s.	
2	Pres/abs	Reach	0.154	n.s.	
1&2 combined	Log (CPUE +1)	Reach	0.202	0.003	Q-B (0.005), G-T (0.01)
1&2 combined	Log (CPUE +1)	Time	0.094	n.s.	
1&2 combined	Pres/abs	Reach	0.158	0.02	Q-B (0.005), Q-T (0.02)
1&2 combined	Pres/abs	Time	0.102	n.s.	
1,2,3,4 Binya	Log (CPUE +1)	Waterhole	-0.028	n.s.	
1,2,3,4 Binya	Log (CPUE +1)	Time	0.51	0.001	1-4 (0.03), 2-4 (0.03), 3-4 (0.03)
1,2,3,4 Binya	Pres/abs	Waterhole	0.06	n.s.	
1,2,3,4 Binya	Pres/abs	Time	0.439	0.001	1-2 (0.03), 1-4 (0.03), 3-4



**Table 4** Summary of BIO-ENV results based on Spearman rank correlations ( $r_s$ )

715 between fish assemblage structure (CPUE and richness) and geomorphological and  
water chemistry variables. Note: Results only presented for best possible solution.

Sampling time	Transformation	Best variable combination
1	Log (CPUE +1)	CSA, SN, OV (0.68)
1	Pres/abs	CSA, SN, (0.60)
2	Log (CPUE +1)	CSA, SN, OV (0.68)
2	Pres/abs	CSA, OC, B2, OV (0.42)
		CSA, B2, BOU, OV (0.42)

**Table 5** Significant Spearman rank correlations ( $r_s$ ) between fish species

720 abundance/diversity with geomorphological (codes given in Table I) and water  
chemistry variables (Tur = turbidity, ToH = total hardness, Sil = silicates, TC = total  
carbon, TSS = total suspended solids, N:P = nitrogen:phosphorus ratio).

Sampling time	Factor	Fish species, $r_s$ (p)
Geomorphology		
1	TFW	<i>C. auratus</i> , -0.66 (0.007)
1	A	<i>N. erebi</i> , -0.73 (0.002)
1	CSA	<i>T. tandanus</i> , 0.86 (0.00004)
1	DCS	<i>T. tandanus</i> , 0.89 (0.00001)
2	A	<i>N. hyrtlui</i> , -0.74 (0.002)

2	CSA	<i>N. erebi</i> , -0.74 (0.002) <i>N. hyrtlii</i> , -0.70 (0.004)
2	WD	<i>T. tandanus</i> , -0.65 (0.009)
2	WP	<i>N. erebi</i> , -0.66 (0.007)
2	OC	<i>T. tandanus</i> , 0.66 (0.007)
2	AN	<i>N. hyrtlii</i> , -0.82 (0.0002)
2	MCB	<i>N. erebi</i> , -0.78 (0.0007)
Water chemistry		
1	Tur	<i>T. tandanus</i> , 0.80 (0.0005)
1	ToH	<i>N. erebi</i> , 0.65 (0.009)
1	Sil	<i>N. erebi</i> , -0.74 (0.002)
1	TC	<i>N. erebi</i> , -0.83 (0.0001)
1	TSS	<i>T. tandanus</i> , -0.70 (0.003)
1	N:P	<i>N. erebi</i> , 0.81 (0.0003)
1	NO <sub>3</sub>	<i>T. tandanus</i> , -0.67 (0.006)
2	Tur	<i>N. hyrtlii</i> , -0.67 (0.006)
2	ToH	<i>N. erebi</i> , 0.57 (0.03)
2	TN	<i>N. erebi</i> , -0.66 (0.008)

725 **Figures**

**Figure 1.** The Warrego River catchment and four study reaches with insets showing waterhole configurations within each reach.

730 **Figure 2.** Total fish abundance based upon catch per unit effort (CPUE) derived from three standardized fyke nets per waterhole summed across four reaches and four sampling trips, October 2001 to April 2003.

**Figure 3.** Non-metric multi-dimensional scaling plots based upon  $\log_{10}(x+1)$  transformed CPUE data for sampling times 1 and 2 (a) and for presence/absence of species richness for sampling times 1 and 2 (b). Open shapes = October 2001, closed = April 2002. Reaches and waterholes: Q=Quilberry: Quilberry (Qu), Clear (Ch), Sandford Park Lagoon (Sl), Sandford Park waterhole (Sh), G=Glencoe: Glencoe (Gw), Key (Kh), Rocky (Rw), Wogganorah (Ww), B=Binya: Binya (Bw), Red (Rh), Mirage Plains (Mp), Tinnenburra (Ti), T=Thurulgoona: 740 Thurulgoona Homestead (Th), Thurulgoona waterhole (Tw), Noorama (Nw).

**Figure 4.** Non-metric multidimensional scaling plots based upon  $\log_{10}(x+1)$  transformed CPUE data for the Binya reach on sampling dates 1, 2, 3 and 4 (a) and for presence/absence of species richness for sampling dates 1, 2, 3 and 4 (b). See Table 745 three caption for sampling date and reach codes.

**Figure 5.** Size-frequency distributions for *Nematalosa erebi* in four waterholes in the Binya reach of the Warrego River catchment on four sampling occasions. Note 1: Schematic of flow events provided at the top of figure, where wide arrows = overland flood events,

750 dashed arrows = flow pulses, horizontal lines = periods of no flow. Note 2: Numbers of fish  
(approximately equal to total CPUE) measured for each plot appear at the top right of each individual  
plot.

**Figure 6.** Size-frequency distributions for *Neosilurus hyrtlui* in four waterholes in the  
755 Binya reach of the Warrego River catchment on four sampling occasions. Note: See  
caption for Fig. 5.

**Figure 7.** Size-frequency distributions of *Macquaria ambigua* in four waterholes in  
the Binya reach of the Warrego River catchment on four sampling occasions. Note:  
760 See caption for Fig. 5.

**Figure 8.** Size-frequency distributions of *Cyprinus carpio* in four waterholes in the  
Binya reach of the Warrego River catchment on four sampling occasions. Note: See  
caption for Fig. 5.

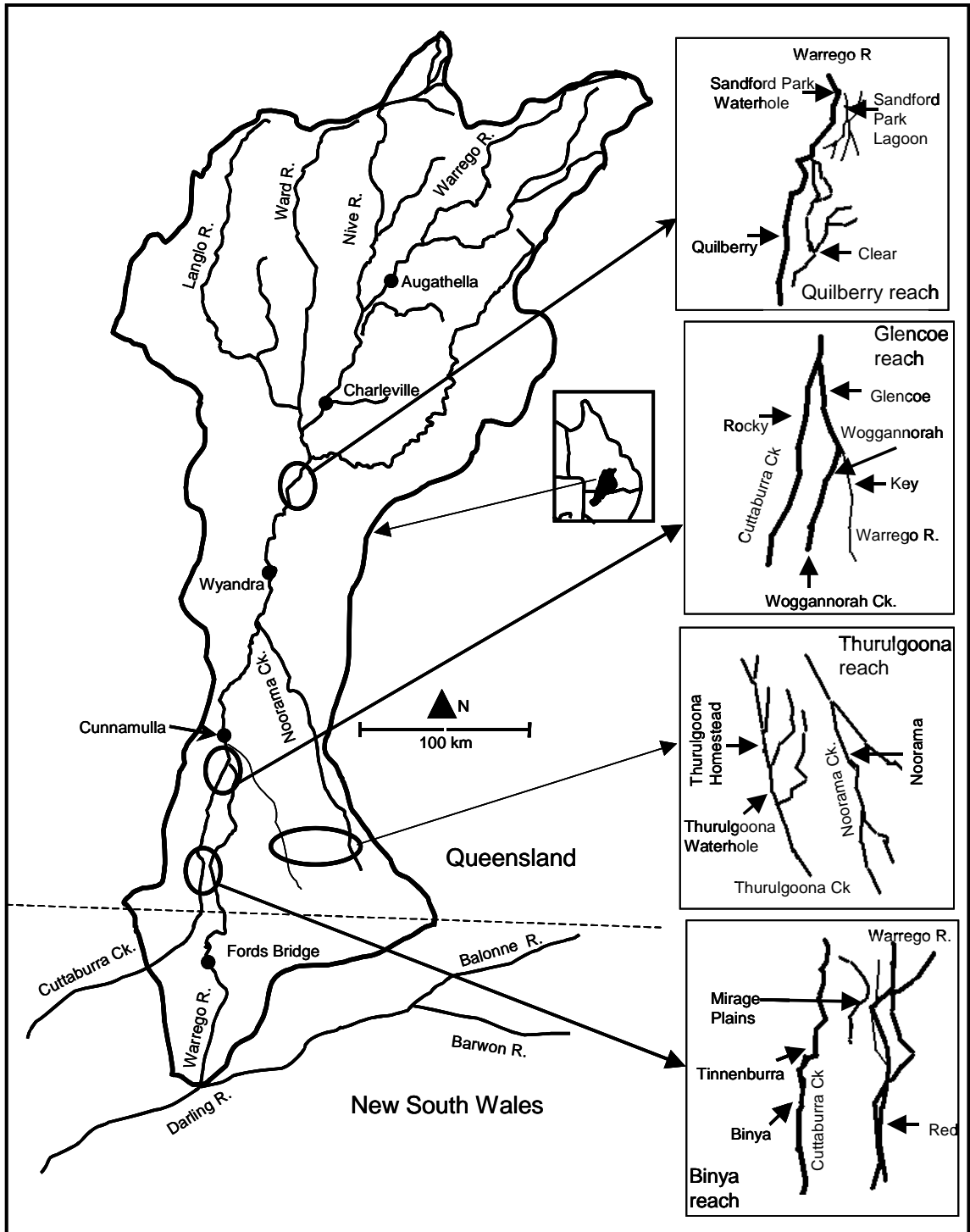


Fig. 1

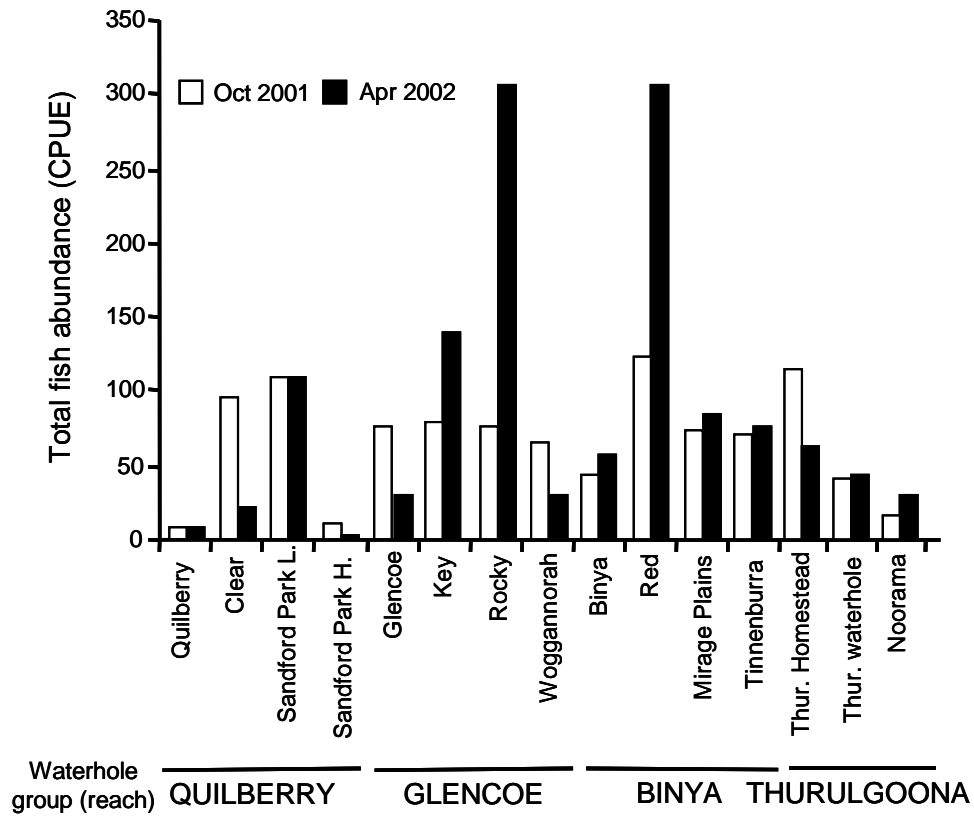


Fig. 2

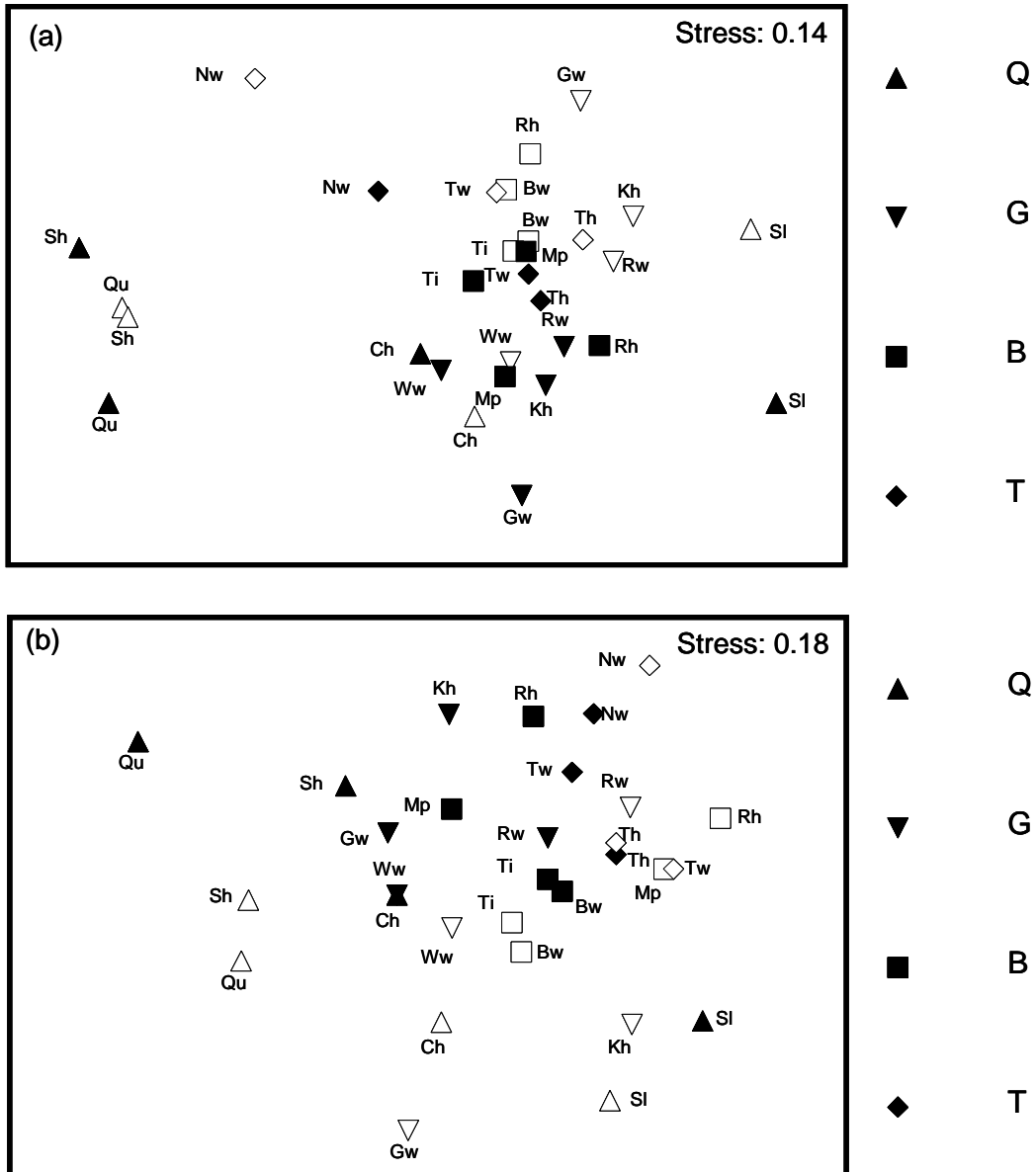


Fig. 3

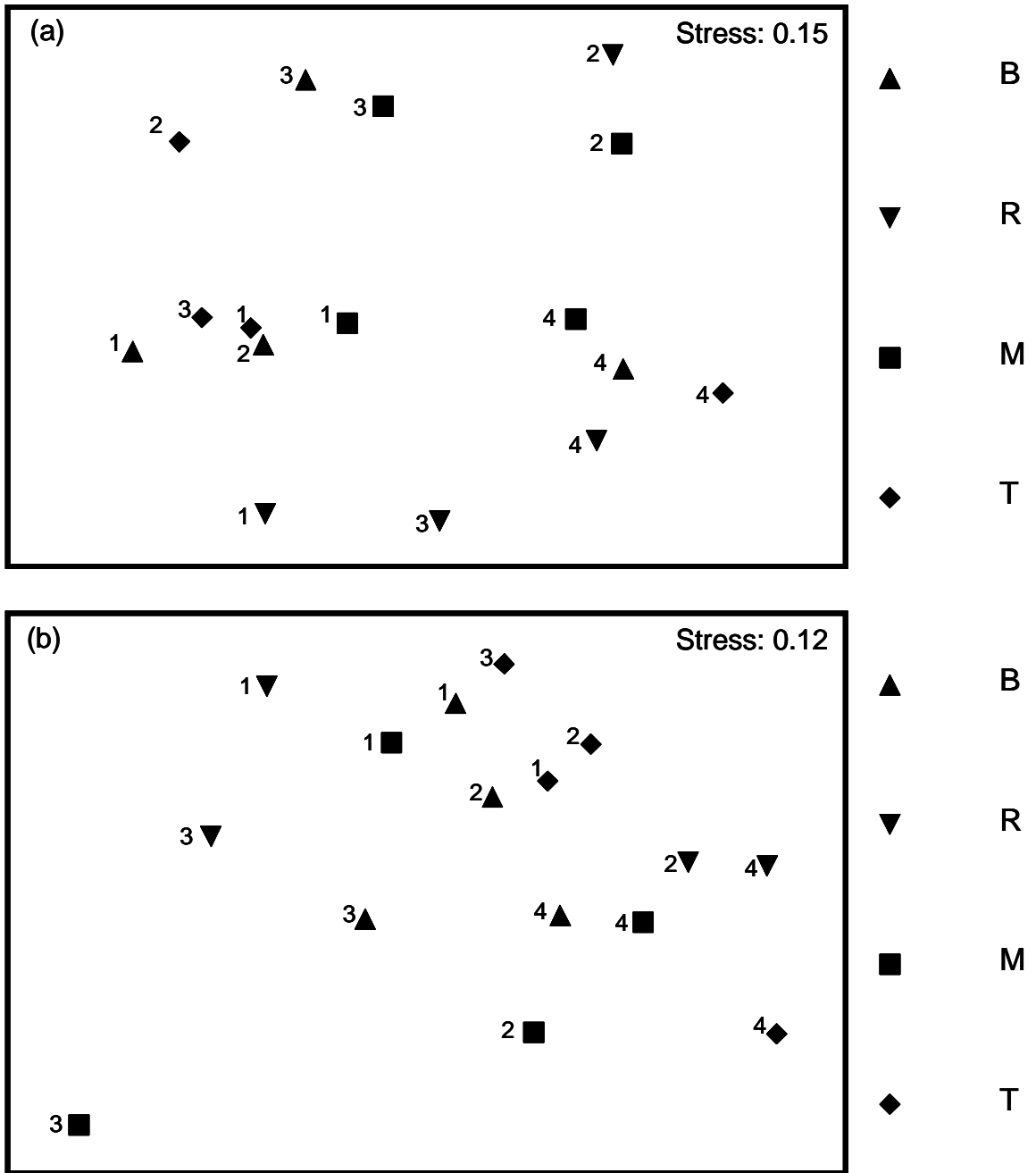


Fig. 4



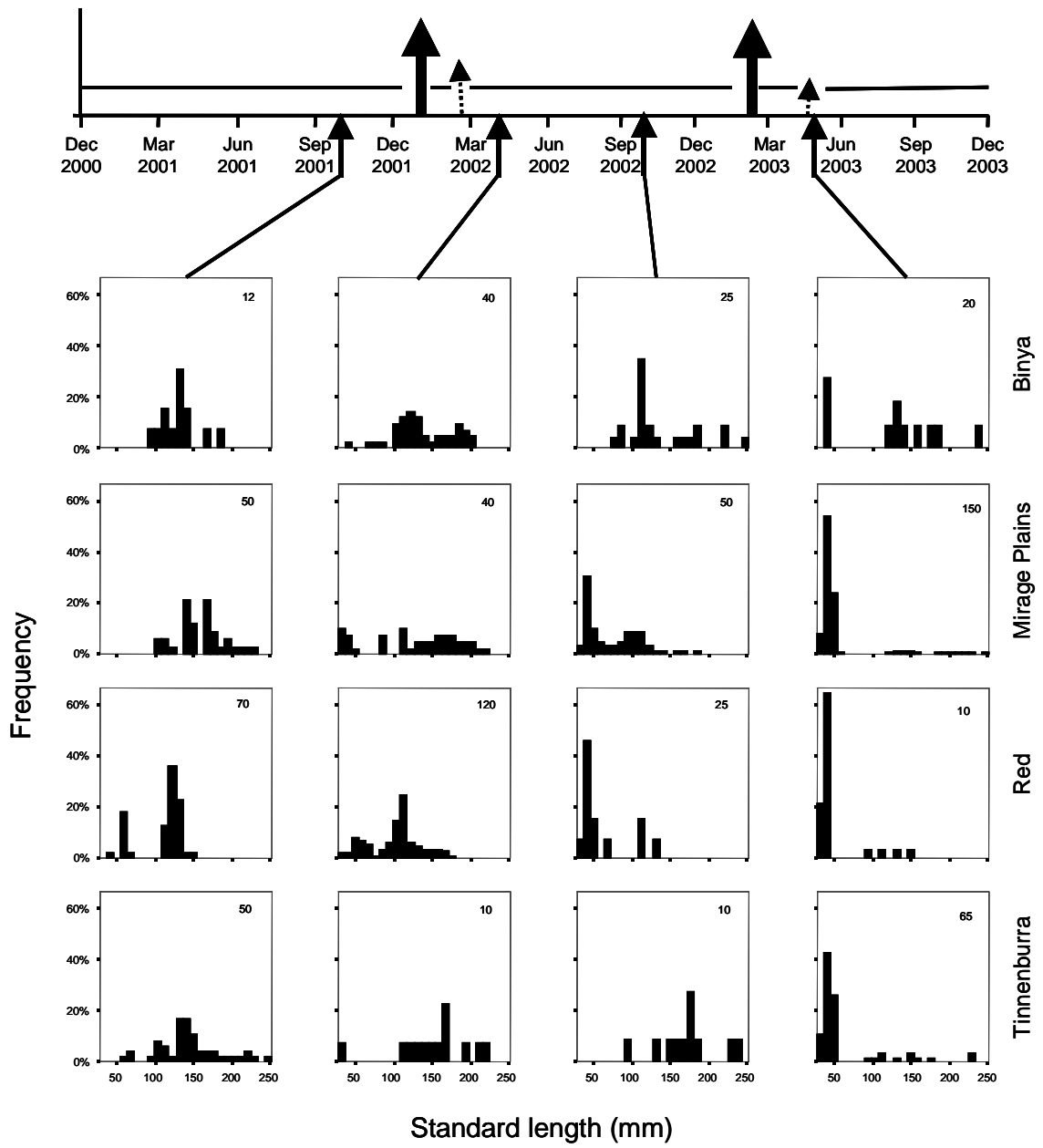


Fig. 5

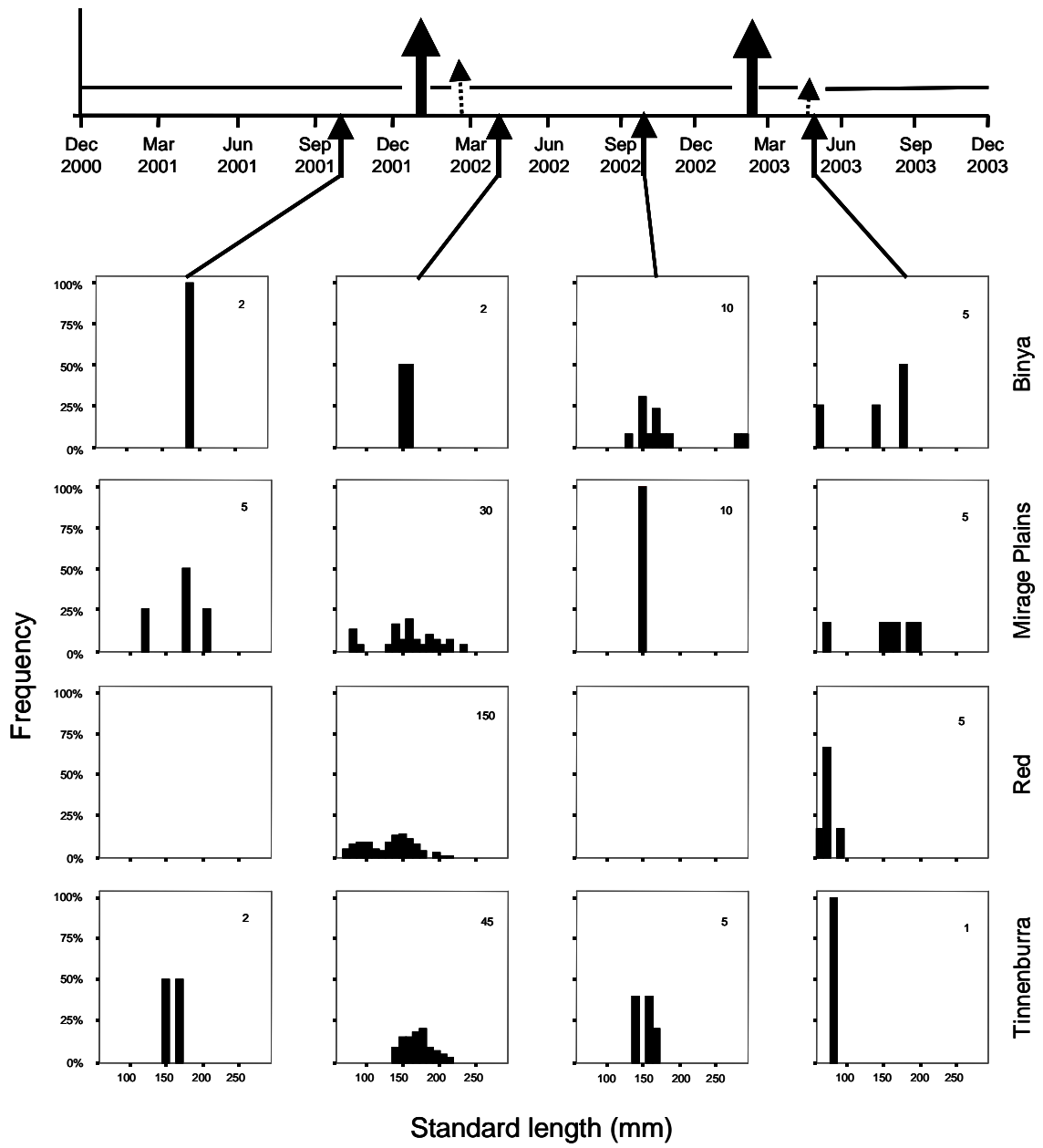


Fig. 6

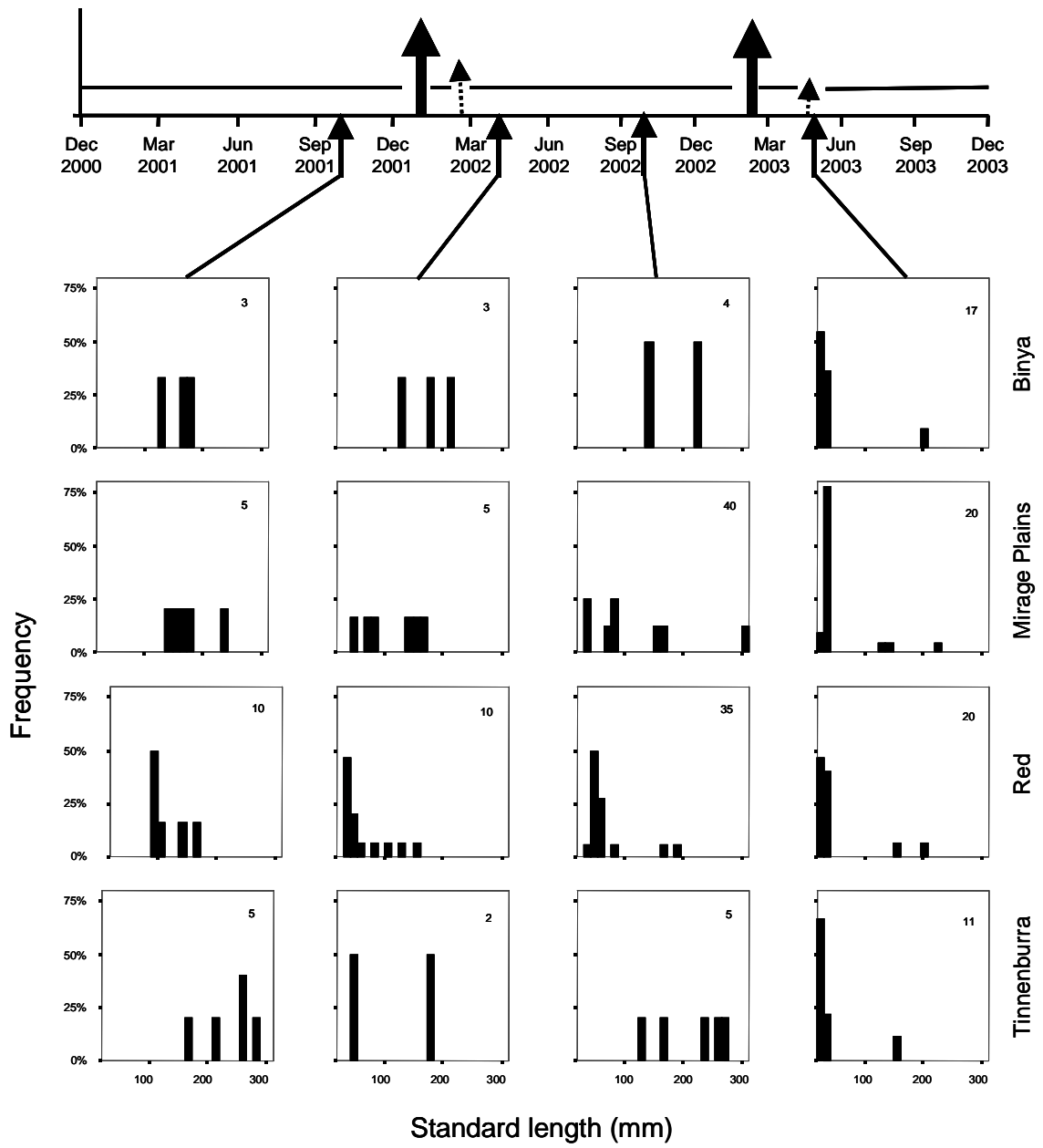


Fig. 7

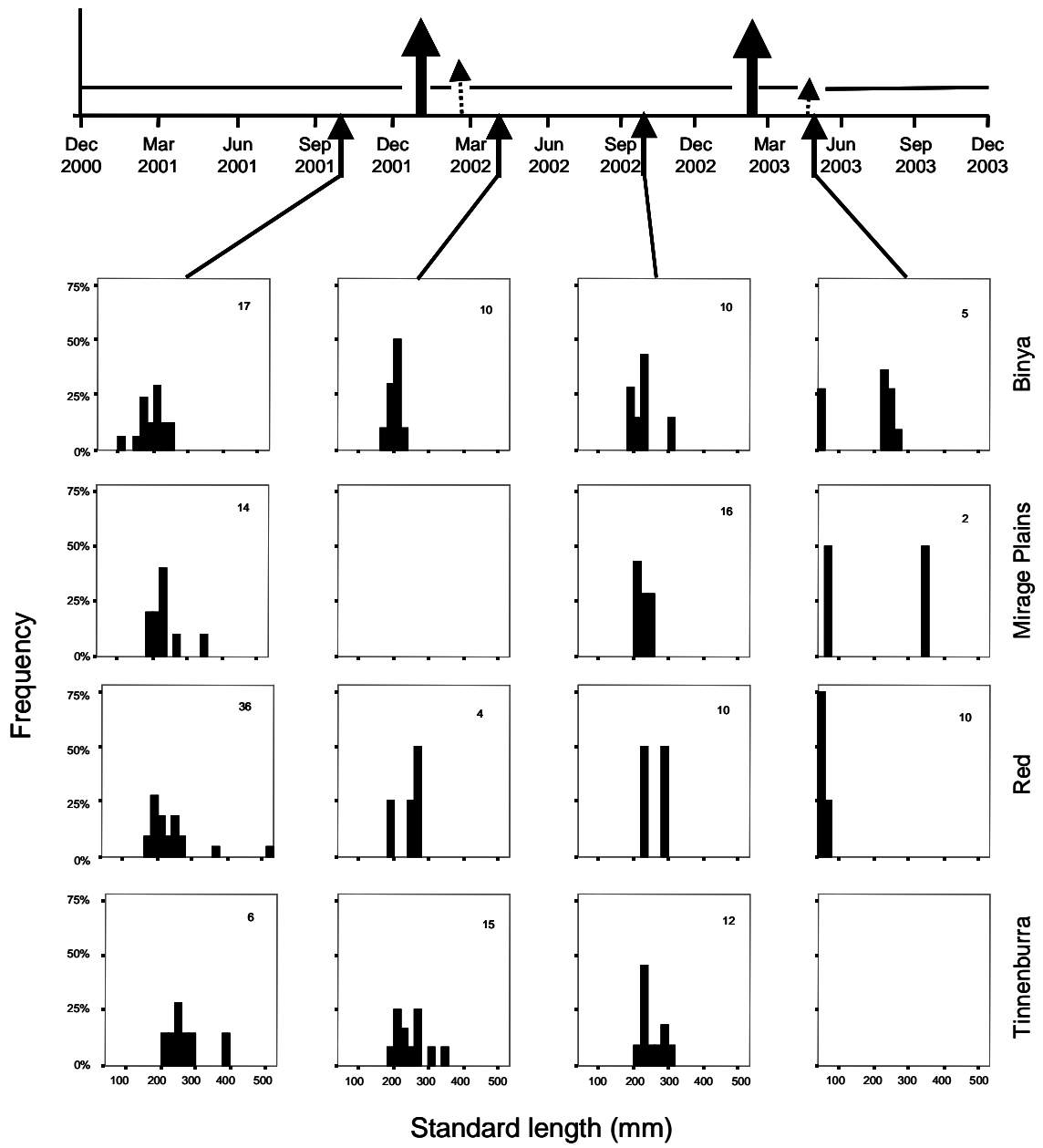


Fig. 8