CSIRO PUBLISHING

Australian Journal of Zoology, 2015, **63**, 245–252
http://dx.doi.org/10.1071/ZO15034

Distribution, abundance and population structure of the threatened western saw-shelled turtle, *Myuchelys bellii*, in New South Wales, Australia

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Abstract. The western saw-shelled turtle is listed as threatened globally, nationally, and within the Australian state of New South Wales. Although nearly all of the geographic range of the species lies within New South Wales, little information has been available on the distribution, abundance and structure of New South Wales populations. Through a survey of 60 sites in 2012–15, I established that *M. bellii* is much more widely distributed in New South Wales than has previously been recognised, comprising four disjunct populations, including two in the New South Wales portion of the Border Rivers basin. It occurs mainly in larger, cooler rivers upstream of barriers to dispersal of the Macquarie turtle, *Emydura macquarii macquarii*. Although *M. bellii* is locally abundant, its populations are greatly dominated by large adults and recruitment appears to be low. Eye abnormalities are common in some populations but do not necessarily impair body condition or preclude long-term survival. The species is threatened by competition with *E. macquarii*, which appears to be expanding its range through translocation by humans, and possibly by predation, disease and drought. Long-term monitoring of *M. bellii* is needed to assess population trends and responses to threats, and active management to restrict the further spread of *E. macquarii* is probably required to ensure the persistence of *M. bellii* throughout its current range.

Received 14 June 2015, accepted 31 August 2015, published online 23 September 2015

Introduction

Globally, turtles and tortoises are one of the most imperilled vertebrate groups, with ~60% of all modern species either extinct or threatened (van Dijk *et al*. 2014). Their characteristic life-history traits of late maturation, modest fecundity and high mortality of eggs and hatchlings make population persistence reliant on great adult longevity (Klemens 2000). If the mortality of adults increases, population reduction may be rapid, but if adult mortality remains low yet recruitment falls, adult longevity may disguise impending population decline. Causes of diminishing turtle populations and threats to those that remain are varied and include overharvesting, as either target species or by-catch, habitat loss or degradation, disease, effects of introduced species and climate change (Turtle Conservation Fund 2002; Ihlow *et al*. 2012).

Coastal Australia has been identified as a global priority area for turtle conservation (Buhlmann *et al*. 2009). One of the species inhabiting this area is the western saw-shelled turtle, *Myuchelys bellii* (Gray, 1844), also known as Bell's turtle and the Namoi River snapping turtle, a riverine species endemic to the New England region of north-eastern New South Wales and the Darling Downs region of southern Queensland. In Queensland it is probably confined to 8 km of a single stream but in New South Wales it is distributed more widely (Fielder *et al*. 2014). It is listed as endangered on the International Union for Conservation of Nature's Red List of Threatened Species (under the name *Elseya bellii*: www.iucnredlist.org/details/40758/0), as nationally vulnerable under Australia's *Environment Protection and Biodiversity Conservation Act* (under the name *Wollumbinia belli*: www.environment.gov.au/cgi-bin/sprat/public/publicspecies.pl?taxon_id=86071) and as vulnerable in New South Wales under that state's *Threatened Species Conservation Act* (under the name *Elseya belli*: www.environment.nsw.gov.au/threatenedspeciesapp/profile.aspx?id=10266).

The distribution and abundance of *M. bellii* in Queensland have been thoroughly assessed (Fielder *et al*. 2014), but comparable information has not hitherto been available for New South Wales. Consequently, the status of the species in New South Wales and its vulnerability to threatening processes are poorly understood. Here I report the results of an extensive survey for *M. bellii* in New South Wales, undertaken in the years 2012–15. My aims were to establish the current geographic range, local abundance and population structure of the species in New South Wales, and relate its distribution and abundance to abiotic environmental variation and the occurrence of other turtle species. I hoped to thereby gain some insight into its population status, the factors limiting its distribution, and its susceptibility to threats.

Materials and methods

Study species

M. bellii is a medium-sized, short-necked chelid turtle with a maximum straight-line carapace length of ~230 mm in males and ~300 mm in females. Males take ~9 years to reach sexual maturity and females ~19 years, mean fecundity is low (14 eggs per female per annum) and longevity is estimated to exceed 40 years (Fielder *et al*. 2014). The species appears to be confined to running waters and is well adapted for aquatic respiration, enabling it to remain submerged in deep water for long periods, especially in winter (Fielder 2012). It has an omnivorous diet, including algae and aquatic and terrestrial plant material and invertebrates (Fielder *et al*. 2014). In New South Wales it has been regarded as being confined to the upper reaches of the Namoi and Gwydir River drainages (e.g. Georges and Thomson 2010; Cogger 2014).

Study area

Sixty sampling sites in the New England region were selected with the aim of broad geographic coverage, concentrated within and surrounding the previously reported distribution of *M. belli* in New South Wales and including a few outlying locations (Fig. 1). Sites were chosen primarily on the basis of availability of road access for transport of equipment, occurrence of pools deeper than 1 m, and permission from land owners and managers. One site was in a reservoir but the remainder were in streams.

The study region comprises flat and undulating terrain on the New England Plateau and steeper slopes to the east and west. Much of it has been cleared of its original vegetation to support livestock grazing and cropping, but substantial areas of native forest remain. The climate is temperate with cold winters (mean daily minimum of –2 to 3°C in July) and warm–hot summers (mean daily maximum of 25 to 34°C in January). Mean annual rainfall ranges from 650 to 900 mm with the highest monthly average falls in summer. The Great Dividing Range runs across the region from north to south, dividing the river systems into those that flow west within the Murray–Darling Drainage Division and those that flow eastward to the Pacific Ocean (Fig. 1). The larger western streams have been impounded by major dams to support downstream irrigation development.

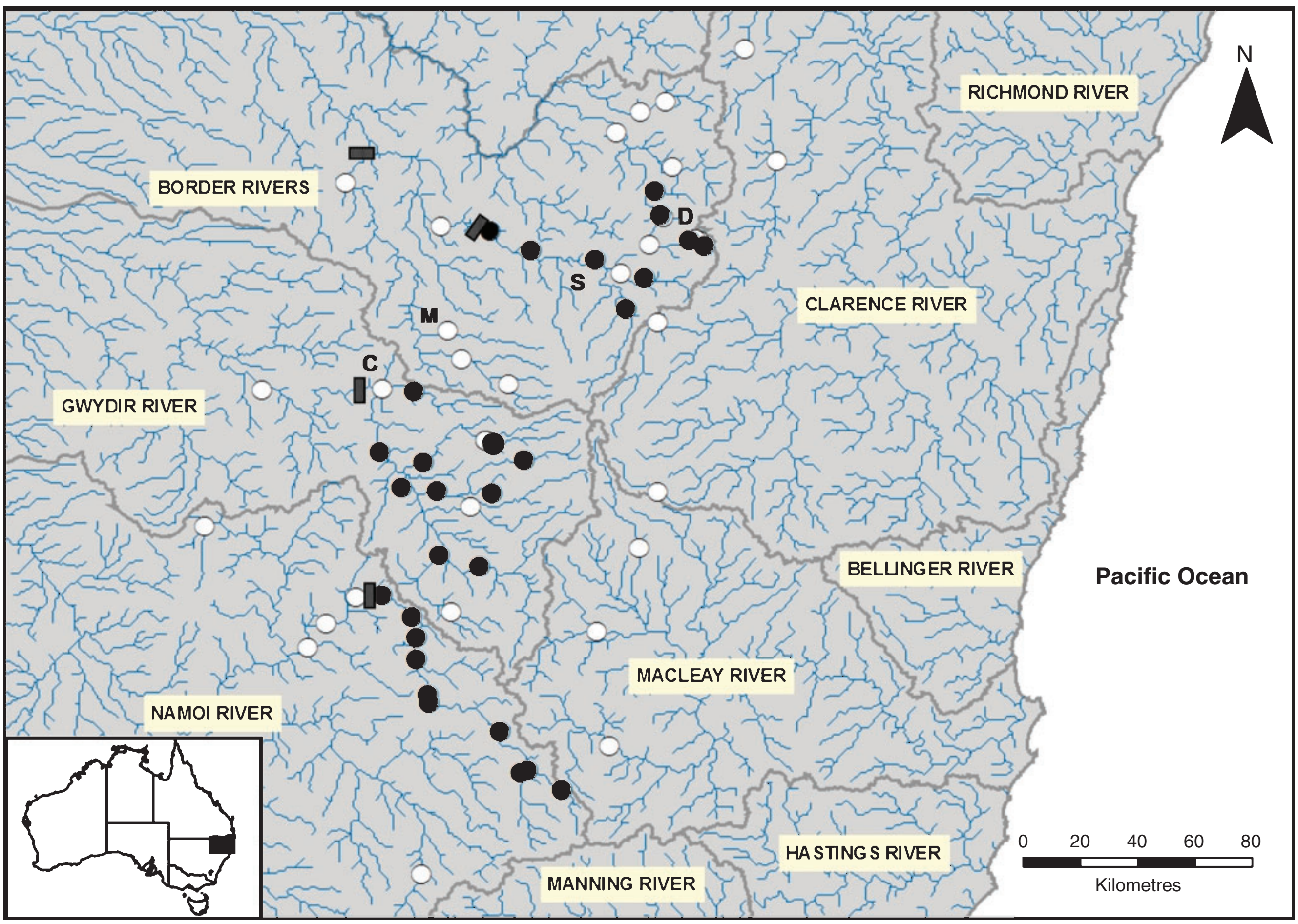

Fig. 1. Map of river basins in north-eastern New South Wales (bounded by thick lines) and major streams (thin lines) showing survey sites where *Myuchelys bellii* was recorded (black circles) and not recorded (white circles). Some site symbols overlap. Symbols D, S and M indicate the Deepwater, Severn and Macintyre rivers and symbol C shows the location of Copeton Dam and Lake Copeton. Stippled bars show the locations of potential barriers to turtle dispersal created by large cascades and waterfalls.

Turtle sampling and environmental data

Sampling was undertaken in the warmer months from November to March, when the species is active and feeding. Turtles were captured primarily in 'cathedral' traps – telescoping vertical cylindrical nets 1 m wide and 2 m high when fully extended, constructed of 13- and 25-mm mesh, with three entrance funnels near the base measuring 300 mm wide and 40 mm high at their centres. These traps were baited with beef or sheep liver and deployed in still or slowly flowing water 1–2 m deep, with their bases resting on the stream bed and their tops floating so that captured animals could breathe air. Unbaited fyke nets (13-mm mesh; 1 m high and 3 m long, with two wings 10 m long) were also used at some sites where bedform, substrata and current velocity were suitable, placed at a depth of ~0.8 m to allow breathing by captured animals. Nets were placed ~15 m or farther apart and were cleared at a mean interval of ~3 h during daylight hours but left for ~12 h overnight. Intersite variation in the total length of stream over which traps were distributed (mean = 264 m; range = 20–1140 m) and trapping effort (mean = 5.9 trap-days; range = 0.3–21.8 trap-days; >1 trap-day at 92% of sites) resulted from access limitations (private property boundaries; cliffs), logistical factors (time constraints; availability of equipment), limited pool areas for placing traps at some sites, and more protracted or repeated sampling at some locations to boost sample sizes. A few additional turtles were captured opportunistically by hand, including by diving. The number of days between first and last sampling at a site ranged from <1 to 1120 (mean 303).

Captured turtles were identified and sexed by external examination unless smaller than the threshold of sexual dimorphism, as expressed by differences in tail morphology and, for *Chelodina longicollis*, plastron shape (Chessman 1978). They were examined for external abnormalities, measured with vernier calipers for straight-line medial carapace length, weighed with digital scales in most cases, marked with varying combinations of notches in marginal scutes so that they could be identified if recaptured, and released as soon as possible near the point of capture.

Three variables describing the physical environment of the sampling sites were extracted from the Australian stream and nested catchment database (Stein *et al*. 2014). This database associates numerous environmental attributes with defined stream segments, mostly bounded by tributary or distributary junctions and having a mean length of 2.4 km. This spatial scale was considered the appropriate order of magnitude at which to characterise habitat of *M. bellii*, because individuals range over stream lengths of up to ~8 km (Fielder *et al*. 2014). The chosen variables were the mean annual air temperature of the stream segment and its immediate environs, the modelled mean annual runoff at the stream segment, and the segment's average slope (Table 1). Temperature was selected because of its importance to ectothermic animals and because *M. bellii* is a high-elevation species and hence possibly intolerant of high temperatures. Air temperature was used as a surrogate for water temperature because of insufficient data on the latter and the strong relationship between the two (Webb *et al*. 2003). Runoff and slope were considered important as predictors of in-stream physical habitat (Hubert and Kozel 1993; Buffington *et al*. 2002). In some cases the sampling site overlapped two segments in the database, in which case values of the environmental variables for the two segments were averaged.

Data analysis

Relative body condition of *M. bellii* was calculated by dividing observed mass by the mass predicted from a regression of mass (M) on carapace length (L) for all weighed individuals ($n = 531$), of the form $M = aL^b$, where a and b are constants. A condition value >1 thus signified a mass higher than expected for the turtle's carapace length.

Routine statistical tests were applied to compare mean values (t-test; analysis of variance; Tukey's test) and proportions (Chi-square tests) for various attributes of turtle populations. Separate-variance t-tests were used if variances were significantly different between the two groups being compared (F-test, $P < 0.05$); otherwise, pooled-variance tests were employed. In the interests of independence of observations, recaptures were excluded from these tests, except for comparisons of recapture rates.

A general linear model (GLM) was used to test whether the site-specific catch per unit effort (CPUE) of *M. bellii* could be related to environmental variables – both physical (temperature, runoff and slope) and biotic (CPUE of other turtle species). CPUE of each species was calculated as the number of specimens caught in traps (including recaptures) divided by the number of trap-days. Trap-days with cathedral and fyke nets were considered equivalent and combined, because the two methods had similar average returns of 4.7 and 4.2 turtles per trap-day respectively. Hand captures were excluded from the calculation. All variables in the model except temperature had strong positive skew (>1), which was removed by logarithmic (runoff, slope) or fourth root (CPUE) transformation before analysis. Model residuals were examined to see whether they were normally distributed.

Table 1. Ranges of values of abiotic and biotic variables for sites west and east of the Great Dividing Range

Variable	Units	Range (western sites)	Range (eastern sites)
Mean annual air temperature	°C	11.8–17.6	11.6–16.7
Stream segment slope	%	0.02–1.65	0.08–1.11
Mean annual runoff	ML	745–187984	9205–76783
CPUE of *C. expansa*	No. trap-day^{-1}	0–0.5	0–0
CPUE of *C. longicollis*	No. trap-day^{-1}	0–18.0	0–19.0
CPUE of *E. macquarii*	No. trap-day^{-1}	0–9.5	0–17.0
CPUE of *M. bellii*	No. trap-day^{-1}	0–15.3	0–0

Results

Altogether, the survey yielded 1656 captures (including recaptures) from 1443 individual turtles, 88% of which were effected with cathedral traps, 11% with fyke nets and <1% by hand. The captures comprised four species: the broad-shelled turtle, *Chelodina expansa* Gray, 1857 (7% of sites; <1% of captures); the eastern long-necked turtle, *Chelodina longicollis* (Shaw, 1794) (77% of sites; 37% of captures); the Macquarie turtle, *Emydura macquarii macquarii* (Gray, 1830) (33% of sites; 24% of captures); and *M. bellii* (48% of sites; 39% of captures). *M. bellii* was represented by four separate populations in the Namoi, Gwydir, Severn and Deepwater river systems, the last two being within Border Rivers basin (Fig. 1). It was not recorded at any site east of the Great Dividing Range or in the most downstream sites on the western rivers.

Among sites at which *M. bellii* was recorded, its CPUE varied substantially (mean 2.8 turtles per trap-day; range = 0.2–15.3), as did the proportion of the total turtle catch that it represented (mean 58%; range = 2–100%). *M. bellii* was frequently recorded as coexisting with *C. longicollis* but never with *C. expansa* and only rarely with *E. macquarii*. The distributions of *M. bellii* and *E. macquarii* were sharply demarcated in the Namoi River, with *E. macquarii* found only downstream of a steep river section with large cascades in Warrabah National Park, whereas *M. bellii* was found only upstream of this section (Fig. 1). A similar segregation occurred in the Severn River, with *E. macquarii* not recorded upstream of a steep, cascading reach in the Severn River Nature Reserve, whereas *M. bellii* was not recorded downstream of this reach. In the Gwydir River, a steep river section containing large cascades lies immediately downstream of Copeton Dam, and *M. bellii* was not recorded downstream of this section (Fig. 1). However, in this case *E. macquarii* was found above the cascades, but only immediately upstream in Lake Copeton and not at any other upstream site. Individuals of *E. macquarii* sampled from the lake were mostly juveniles, suggesting a population that is rapidly increasing and possibly derived from a recent translocation such as a release of unwanted pet turtles. In the Deepwater River, *E. macquarii* was apparently absent from the most upstream reaches sampled, but its range substantially overlapped that of *M. bellii*. The Deepwater River lacks a section with large cascades but is somewhat isolated because the Mole River, which is formed by the junction of the Deepwater and Bluff rivers, is mostly a shallow, braided, sandy river with few deep pools. The Macintyre River, within the Border Rivers Basin, has a steep section, including the Macintyre Falls, immediately upstream of its junction with the Severn River (Fig. 1). However, *E. macquarii* was recorded at three of four sites sampled upstream from the falls whereas *M. bellii* was not found at any site in the Macintyre River system.

The frequency distribution of carapace length of *M. bellii* was bimodal because of the substantial size difference between adult males and females in this species (Fig. 2). Excluding recaptures, 4% of *M. bellii* were below the size at which sexual dimorphism develops, compared with 6% of the *C. longicollis* and 10% of the *E. macquarii* caught at sites west of the Great Dividing Range (Fig. 2). The difference from *M. bellii* was highly significant for *E. macquarii* (Chi-square test, $P < 0.001$) but not for *C. longicollis* ($P = 0.11$). The proportion of *M. bellii* below the size of sexual

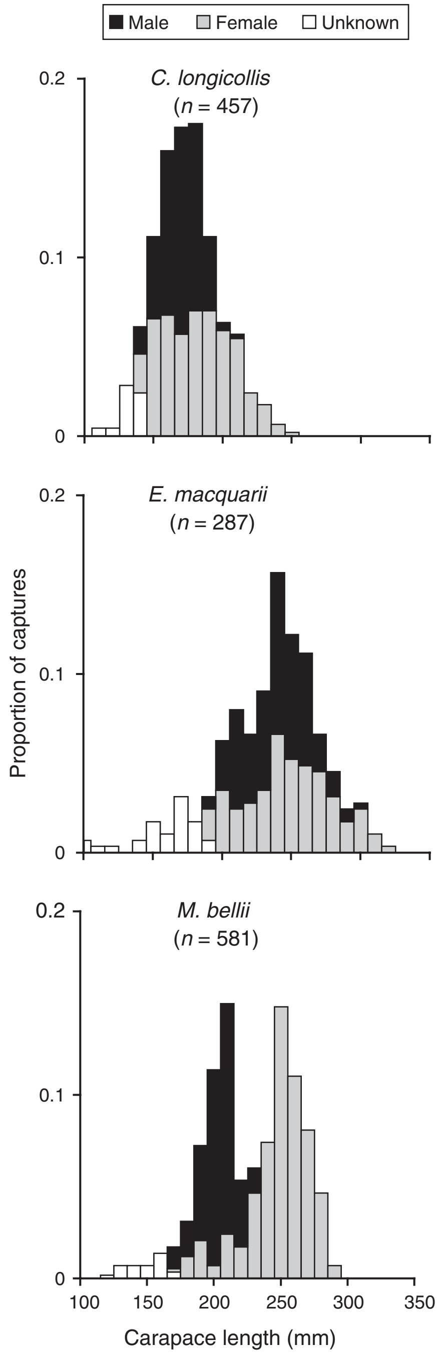

Fig. 2. Frequency distributions of carapace lengths (rounded to the nearest 10 mm) of *Chelodina longicollis*, *Emydura macquarii* and *Myuchelys bellii* captured from all sites west of the Great Dividing Range, excluding recaptures.

dimorphism differed significantly among river systems (Chi-square test, $P = 0.003$), being highest in the Deepwater (9%), followed by the Severn (8%), Gwydir (6%) and Namoi (1%).

Of those *M. bellii* larger than the threshold of dimorphism, 62% were females – a highly significant departure from a 1 : 1 sex ratio (Chi-square test, $P < 0.001$). This skew may have been a consequence of unequal capture probability because the recapture rate (% of all captures that were recaptures) was significantly higher for females (12%) than for males (6%) (Chi-square test, $P = 0.02$). The recapture rate for turtles smaller than the threshold of dimorphism was intermediate (7%), and not significantly different from the rate for larger turtles with both sexes combined (Chi-square test, $P = 0.65$). The proportion of females differed significantly among river systems (Chi-square test, $P = 0.01$), being highest in the Namoi (67%), followed by the Gwydir (60%), Severn (41%) and Deepwater (40%).

The size distribution of *M. bellii* differed significantly among the four river systems in which the species occurred for both males (ANOVA, $P < 0.001$) and females ($P = 0.002$) larger than the threshold of dimorphism (Fig. 3). Males from the Severn River system were significantly larger than those from each of the other river systems (Tukey's tests, $P < 0.001$), and females from the Deepwater River were significantly smaller than those from each other system (Tukey's tests, $P < 0.01$).

Excluding recaptures, 8% of *M. bellii* had visible abnormalities in one or both eyes, including cataracts, darkening, swelling, shrunken pupils and missing eyes. These abnormalities were not observed in turtles smaller than the threshold of sexual dimorphism, and above the threshold were significantly and substantially more frequent in females (12%) than in males (3%) (Chi-square test, $P < 0.001$). The incidence of eye abnormalities differed significantly among river systems (Chi-square test, $P < 0.001$), being greatest in the Namoi (15%), followed by the Severn (8%), Gwydir (2%) and Deepwater (0%). Carapace length and body condition did not differ significantly between turtles with and without eye abnormalities for either females (*t*-tests, $P = 0.15$ and 0.13 respectively) or males ($P = 0.51$ and 0.15). Turtles with ocular abnormalities may survive for many years, because a female *M. bellii* captured and marked in 2006 (Fielder *et al*. 2014), when it was apparently blind in both eyes (D. Fielder, pers. comm.), was recaptured in the present study in 2015 in the same state. Obvious disease other than eye problems was rare, but several individuals had varying degrees of healed shell damage.

The GLM of CPUE of *M. bellii* was restricted to the 53 sites west of the Great Dividing Range because eastern sites appeared to be beyond the potential range of the species. The CPUE of *C. expansa* was not included as a predictor in the model because that species was so rarely captured. The overall model explained a substantial proportion of variation in CPUE of *M. bellii* ($R^2 = 0.48$) and was highly significant ($P < 0.001$). Mean annual air temperature and abundance of *E. macquarii* had significantly negative effects on abundance of *M. bellii*, while mean annual runoff had a significantly positive effect (Table 2). The distribution of model residuals was not significantly different from normal (Shapiro–Wilk test, $P = 0.43$).

The typical reach from which *M. bellii* was collected consisted of deep pools (maximum depth >2 m) separated by shallow sections with dry beds (for less perennial rivers in drier climatic periods) or riffles (for more perennial rivers and in wetter periods). The pools typically contained abundant underwater cover in the form of boulders, logs and macrophyte beds. *M. bellii* was never observed in shallow water during the day, but overnight captures and recaptures indicated that it often moved into shallows and between pools overnight, presumably while foraging. During dry periods, many long reaches of the study rivers lacked any

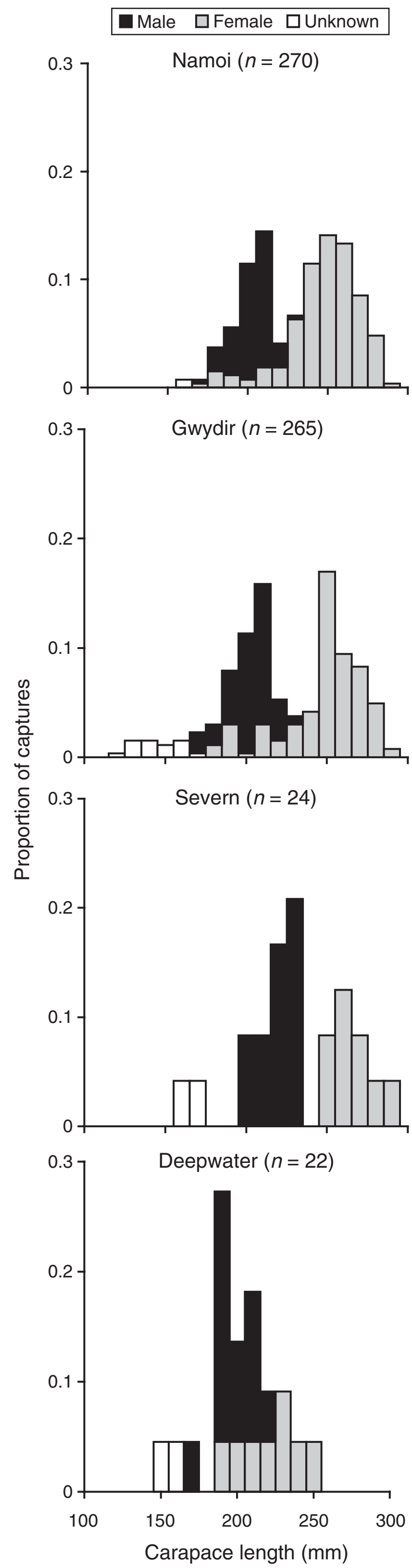

Fig. 3. Frequency distributions of carapace lengths (rounded to the nearest 10 mm) of *Myuchelys bellii* captured from the Namoi, Gwydir, Severn and Deepwater river systems, excluding recaptures.

Table 2. Results of the GLM of CPUE of *Myuchelys bellii* for all sites west of the Great Dividing Range

Effect	Coefficient	s.e. of coefficient	Tolerance	*t*	*P*
Constant	0.850	0.902		0.942	0.351
Mean annual air temperature	–0.154	0.070	0.500	–2.208	0.032
$\log_e$(segment slope)	–0.103	0.072	0.872	–1.441	0.156
$\log_e$(mean annual runoff)	0.200	0.068	0.670	2.929	0.005
4th root CPUE of *Chelodina longicollis*	0.008	0.127	0.866	0.065	0.949
4th root CPUE of *Emydura macquarii*	–0.360	0.129	0.580	–2.793	0.008

suitable daytime habitat and *M. bellii* was confined to the remaining deep pools.

Discussion

This study has clarified the geographic range of *M. bellii* in the Namoi and Gwydir river systems, establishing its downstream limits and showing that it is widely distributed in larger waterways upstream of those limits. It has also increased the number of recognised populations of the species from three (Fielder *et al.* 2014) to five, and narrowed the apparent gap between the New South Wales and Queensland ranges of the species (Cogger 2014; Fielder *et al.* 2014), by demonstrating the widespread occurrence of *M. bellii* in the New South Wales portion of the Border Rivers basin.

M. bellii was the turtle species most commonly captured at sites west of the Great Dividing Range and, on average, made up the majority of catches at those sites where it was recorded. However, the current distribution of *M. bellii* in New South Wales and Queensland is fragmented. Its five populations in separate river systems seem unlikely to interchange by terrestrial dispersal across drainage divides, because *M. bellii* was never observed on land apart from one female on a river bank that was probably preparing to nest. In addition, *M. bellii* was not found in any river east of the Great Dividing Range, even where suitable habitat was present and *E. macquarii* was absent, although some eastern and western river systems on the New England Plateau are separated by only a few kilometres of gently sloping or undulating terrain.

Captures of *M. bellii* in New South Wales were greatly dominated by large adults, suggesting a low rate of recruitment, possibly due to losses of eggs and hatchlings to a variety of terrestrial and aquatic predators (Fielder *et al*. 2014). Sampling predominantly with baited traps may have biased against the capture of juveniles (Ream and Ream 1966), but any such bias appeared to be limited because the recapture rate did not differ significantly between turtles smaller and larger than the threshold of sexual dimorphism. A low proportion of juveniles may not signal population decline if adult survivorship is very high, but any rise in mortality could threaten population persistence because of infrequent recruitment and the long time taken by *M. bellii* to reach maturity. No dead individual or remains of *M. bellii* was found during the present study, but Fielder *et al.* (2014) reported some deaths in New South Wales due to recreational fishing. Eye abnormalities have been reported previously for *M. bellii* with a comparable incidence to that found in the present study (Fielder *et al*. 2014), and may contribute to adult mortality, but the current results suggest that they do not impair body condition or preclude long-term survival.

Statistically significant differences among rivers systems were found for the proportion of *M. bellii* below the threshold of sexual dimorphism, the sex ratio of *M. bellii* above this threshold, the mean body sizes of males and females, and the incidence of eye abnormalities. However, values for the Deepwater and Severn River systems may be unreliable because of low sample sizes. The population in the Namoi River system stands out for its high incidence of eye abnormalities, as also reported by Fielder *et al*. (2014), and low proportion of small individuals, attributes that may signify an ageing population. A significantly biased sex ratio has been reported previously for the Namoi River system (Fielder *et al*. 2014) but, as noted above, may be an artefact of unequal capture probabilities.

M. bellii was captured in large numbers at several sites whereas elsewhere it appeared to be quite rare. The GLM results indicated that it was more abundant in river reaches with lower mean annual air temperatures and greater mean annual flow. The former relationship reflects its high-elevation distribution and the latter is probably due to the tendency for rivers with greater flow to have larger and deeper pools (Hubert and Kozel 1993; Buffington *et al*. 2002), which provide daytime and refuge habitat for the species. The reduction in availability of deepwater habitat that occurs during drought could have adverse effects on *M. bellii*, particularly if drought becomes more prevalent in the future as climatic modelling suggests (Wanders and Wada 2015; Zhao and Dai 2015).

The strong negative association between *M. bellii* and *E. macquarii* could conceivably reflect either different habitat requirements or interspecific competition. However, the observed distribution of the two species in relation to natural physical barriers to turtle dispersal (large cascades and waterfalls) suggests that competition has played a major role, likely resulting from dietary overlap between the two genera (Spencer *et al*. 2014). The fragmented current distribution of *M. bellii*, and the lack of strong genetic differentiation between northern and southern populations (Fielder *et al*. 2012), suggest that it was formerly more widely and continuously distributed and has suffered range contraction, most likely caused by range expansion of *E. macquarii*. Three of the four *M. bellii* populations in New South Wales are confined to higher elevations where barriers appear to have naturally prevented access by *E. macquarii* (those in the Namoi, Gwydir and Severn River systems). In the Macintyre River system, *E. macquarii* has somehow been able to reach areas upstream of Macintyre Falls, and *M. bellii* is apparently absent from the entire system, even though it contains suitable habitat and lies between other rivers inhabited by *M. bellii*. The two species do coexist in the Deepwater River, where upstream dispersal of *E. macquarii* is not prevented by any major barrier although it is perhaps constrained by the shallowness of the Mole River. However, *E. macquarii* is numerically dominant over *M. bellii* in the Deepwater River except in the farthest upstream section, and may still be in the process of displacing *M. bellii*. Range expansion of *E. macquarii* has possibly been facilitated by anthropogenic habitat alteration (Spencer *et al*. 2014) and by climatic warming since the last glacial period.

E. macquarii may be a superior competitor because of greater fecundity than *M. bellii*, faster maturation and larger maximum size. Populations of *E. macquarii macquarii* within the Murray–Darling drainage division have a mean clutch size of ~20, with some females producing two and possibly three clutches per annum (Chessman 1978; Thompson 1983; Judge 2001; Spencer 2002), thereby exceeding the reproductive output of *M. bellii* reported by Fielder *et al*. (2014). In addition, female *E. macquarii* mature at ~10 years (Chessman 1978; Spencer 2002), about half the maturation age of *M. bellii* (Fielder *et al*. 2014). Continued range expansion by *E. macquarii*, facilitated by translocation, is likely to be a serious risk to *M. bellii* populations, although low temperatures might perhaps exclude *E. macquarii* from the most elevated areas where *M. bellii* occurs.

In summary, *M. bellii* is more widely distributed and abundant in New South Wales than has previously been appreciated, but nevertheless faces several potential threats. While its geographic range is now well established, additional studies are necessary to assess its status against IUCN Red List criteria relating to population size and trend (IUCN 2012). No data exist on past trends for New South Wales populations but the present study and that of Fielder *et al*. (2014) can form a baseline for future monitoring. Research on population dynamics is needed to assess recruitment and mortality rates and develop demographic models of New South Wales populations, while the risks imposed by competition, predation, disease and drought need to be better understood. Molecular genetic analysis would probably shed further light on the origin of the population of *E. macquarii* in Lake Copeton. If this population is left unchecked, it is highly likely that *E. macquarii* will eventually invade the entire upper Gwydir River system, reducing or even eliminating the *M. bellii* population.

Acknowledgements

Early stages of this work took place while I was employed by the New South Wales Office of Environment and Heritage (OEH). I am grateful to Matthew Adams, Gillian Dunkerley, Darren Fielder, Hugh Jones and Erin Roger for assistance with fieldwork and to numerous landowners and managers for permitting access. Turtle capture and handling procedures were authorised by the New South Wales Department of Primaries Industries Scientific Collection Permit No. P09/0079, OEH Scientific Licence No. SL 100532, OEH Animal Ethics Committee approval No. 110912/05 and University of New South Wales Animal Care and Ethics Committee approval No. 13/123B. I thank two anonymous referees for helpful comments on the manuscript.

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Handling Editor: Paul Cooper