

Variability in the growth, feeding and condition of barramundi (*Lates calcarifer* Bloch) in a northern Australian coastal river and impoundment

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Abstract. *Lates calcarifer* supports important fisheries throughout tropical Australia. Community-driven fish stocking has resulted in the creation of impoundment fisheries and supplemental stocking of selected wild riverine populations. Using predominantly tag–recapture methods, condition assessment and stomach flushing techniques, this study compared the growth of stocked and wild *L. calcarifer* in a tropical Australian river (Johnstone River) and stocked fish in a nearby impoundment (Lake Tinaroo). Growth of *L. calcarifer* in the Johnstone River appeared resource-limited, with juvenile fish in its lower freshwater reaches feeding mainly on small aytid shrimp and limited quantities of fish. Growth was probably greatest in estuarine and coastal areas than in the lower freshwater river. Fish in Lake Tinaroo, where prey availability was greater, grew faster than either wild or stocked fish in the lower freshwater areas of the Johnstone River. Growth of *L. calcarifer* was highly seasonal with marked declines in the cooler months. This was reflected in both stomach fullness and the percentage of fish with empty stomachs but the condition of *L. calcarifer* was similar across most sites. In areas where food resources appear stretched, adverse effects on resident *L. calcarifer* populations and their attendant prey species should be minimised through cessation of, or more conservative, stocking practices.

Additional keywords: condition factor, feeding intensity, habitat fidelity, movement, von Bertalanffy.

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Introduction

Lates calcarifer is a euryhaline species of the family Centropomidae with a pan-tropical distribution extending throughout much of the Indo-west Pacific, including northern Australia (Greenwood 1976). Throughout its Australian range, *L. calcarifer* is considered a valuable commercial and recreational species as well as a major aquaculture species (Garrett *et al.* 1987; Barlow *et al.* 1996; Tucker *et al.* 2006). The life cycle of *L. calcarifer* in Australia generally involves recruitment of juveniles into rivers after having been spawned in high-salinity coastal environments. Juveniles remain in these freshwater and tidal habitats until maturity, when most move permanently downstream into higher-salinity coastal areas or estuaries (Dunstan 1959; Russell and Garrett 1983, 1985; Davis 1986; Russell 1987; Pender and Griffin 1996; McCulloch *et al.* 2005).

Concerns have been raised following past declines in existing commercial and recreational wild *L. calcarifer* fisheries in coastal Queensland. Coincidentally, demands have been made by anglers to create new recreational fisheries in many of the water supply and irrigation impoundments throughout much of the State. To address these issues, hatchery-produced *L. calcarifer* were stocked from the mid-1980s to supplement wild

riverine stocks as well as to create new fisheries in impoundments (McKinnon and Cooper 1987; Pearson 1987; Rimmer and Russell 1998; Hollaway and Hamlyn 2001). As *L. calcarifer* requires high salinity to reproduce, its introduction into freshwater impoundments is seen as reversible over time. These ‘put and take’ fisheries, despite their need for constant restocking, have proven to be highly popular with recreational freshwater anglers (Hollaway and Hamlyn 2001; Russell *et al.* 2004).

Lake Tinaroo, on the Atherton Tablelands in north Queensland, is one of the most successful and popular ‘put and take’ *L. calcarifer* fisheries in Australia. Stocking in this impoundment began in 1985 and by the early 2000s, over half a million *L. calcarifer* had been released (Burrows 2004). Annual stockings have continued in Lake Tinaroo until the present day. Assessment of the stocked population during the early 2000s found that older age classes of *L. calcarifer* dominated the fishery. McDougall *et al.* (2008) suggested that this was due primarily to cannibalism of smaller, newly stocked *L. calcarifer*, thereby skewing the population towards older, larger fish. These authors speculated that stocking bigger fish (~300 mm total length (TL, mm)) and encouraging anglers not to release larger *L. calcarifer*, were ways of restoring balance to the population.

As a result, most of the more recent stockings (including in this study) into the impoundment have involved the release of larger-sized (~200–300 mm TL) hatchery fish (Queensland Department of Agriculture, Fisheries and Forestry, unpubl. data).

Enhancement of the wild population in the Johnstone River on the north-east Queensland coast has been undertaken almost annually since 1992 (e.g. Russell and Rimmer 2004; Russell *et al.* 2004, 2013). Many of these cohorts of hatchery-produced *L. calcarifer* were subsequently monitored through both fisheries-dependent and -independent surveys (Russell *et al.* 2004; Russell and Rimmer 2002, 2004). The identification of stocked fish was facilitated by marking all individuals at release with either a coded-wire tag or, in the case of a small number of larger fish, a plastic dart or anchor tag (Russell *et al.* 1991, 2004; Russell and Hales 1992; Russell and Rimmer 1997, 2000; Rimmer and Russell 1998, 2001; Russell 2006). Wild individuals in this population were also monitored concurrently with the stocked fish by tagging these individuals with plastic dart or anchor tags upon first capture (Russell *et al.* 2013).

There have been several detailed studies on the age and growth of *L. calcarifer*, particularly in Australia (Dunstan 1959; Davis 1984; Davis and Kirkwood 1984; McDougall 2004; Robins *et al.* 2006), in Papua New Guinea (Dunstan 1962; Reynolds and Moore 1982) and in Asia (Jhingran and Natarajan 1969). Several of these, particularly those undertaken in Australia and Papua New Guinea, have attempted to examine the influence of various environmental and seasonal factors on the growth of *L. calcarifer* stocks (e.g. Reynolds and Moore 1982; Davis and Kirkwood 1984; Sawynok 1998; Robins *et al.* 2005, 2006). A recent Australian study identified that population (and thus stocking) density was a major factor influencing growth of stocked and wild *L. calcarifer* (Russell *et al.* 2013).

Globally, studies have shown fish stocking to have effects on the growth of the stocked species, as well as on the growth of conspecifics, and prey and competitors present in the receiving habitats. Baer and Brinker (2008) noted that the growth rate of stocked and resident wild fish may decrease with increased stocking density and stocking may also influence the growth rates of competing species (Shemai *et al.* 2007). In another study, Jonsson and Jonsson (2011) cited stocking of brown trout as a cause of density-dependent growth reduction in native Atlantic salmon that was noticeable, even at low population densities.

This current study aims to expand on earlier research by examining the factors underpinning growth and condition of both stocked and wild *L. calcarifer* resident in the Johnstone River and of the stocked Lake Tinaroo fishery. Possible factors influencing growth of *L. calcarifer* at the various study sites, including feeding intensity, diet and competition, are discussed.

Methods

Study areas

Johnstone River

This river system is made up of the North and South Johnstone Rivers which merge to form the main Johnstone River ~5 km upstream of its mouth near the township of Innisfail (~17°32'S, 146°02'E) in north-east Queensland. Both the North and South Johnstone Rivers originate on an inland

tableland and flow in an easterly direction before draining into the Coral Sea. The rivers cross a narrow, but fertile, coastal plain (<30 km wide) where sugarcane farming is the dominant agricultural activity. At 1630 km², its total catchment is relatively small when compared with other Australian rivers. The freshwater reaches of both rivers are characterised by mostly good 'dry'-season water quality, perennial flows, a high gradient in some areas, and rocky, coarse or sandy substrates. Elevated water velocity with high turbidity predominates during the 'wet'-season peaks in the Austral summer (Russell and Hales 1993). The river currently supports a multispecies recreational line fishery and a small, seasonal commercial gill-net fishery that is restricted by State government regulation to the lower estuary and adjacent coastal foreshores. *L. calcarifer* is a major component of both of these fisheries. A steep escarpment prevents the upstream movement of most fish, including *L. calcarifer*, from the coastal plain to upland tableland areas. For the purposes of this study, the coastal, freshwater sections of the Johnstone River were further subdivided into five individual sampling zones on the basis of river habitat and hydrology. These were the lower freshwater reaches of the North (NJL) and South (SJL) Johnstone rivers, the middle coastal reaches of the North (NJM) and South (SJM) Johnstone rivers and the upper coastal reaches of the North Johnstone River (NJU). The upper coastal reaches of the South Johnstone River were inaccessible and therefore not sampled. A map showing the location of these zones is given in Russell *et al.* (2013).

Lake Tinaroo

This large impoundment (~17°10'S, 145°33'E) is situated on the easterly flowing Barron River, which is arguably the most heavily regulated of all northern Australian streams (Russell *et al.* 2000). It is the largest impoundment in the region and has a storage capacity of 436.5 GL, a surface area of 33.7 km², a shoreline of ~209 km and a surface elevation of 670 m. It is primarily used to supply irrigation water to the surrounding agricultural district and is also used for electricity generation, recreation and as a source of domestic water. The perimeter of Lake Tinaroo is characterised by a dendritic-like system of inlets or arms and their associated feeder tributaries, most of which are smaller creeks. The lake is bounded on the northern and eastern sides by a national park and a forestry reserve whereas on the southern and western sides there are mainly dairy farms, crops and residential acreage developments.

No extensive water temperature data are available for either the Johnstone River or Lake Tinaroo for the period of the study. However, using air temperature as a proxy, the 4-year (2006–09) monthly average air temperature for July taken from a location close to Lake Tinaroo was 21.6°C while, for the same period in the coastal reaches of the Mulgrave River (immediately adjacent to the Johnstone River), it was 25.9°C.

Stocking with *L. calcarifer*

The Johnstone River, as well as containing a natural population of wild *L. calcarifer*, was stocked from 1992 until 2005 and then again in 2009. As part of the current study, 9423 ~50-mm-TL fish were released into the system during November and December 2009. Most ($n = 7386$) of these fish were stocked at

two sites in the North Johnstone River: an upstream site (NJU) and a downstream site (NJL) near the limit of tidal influence. A smaller number ($n = 2037$) were also stocked into the South Johnstone River (SJM). All stocked fish were purchased from two commercial hatcheries and were from several different spawnings. Prior to their release, TL measurements were made from 192 fish randomly sampled from across both the November and December stocking cohorts. Stocked fish were marked with a coded-wire tag for ease of identification at later recapture.

In Lake Tinaroo, 2996 \sim 200-mm-TL *L. calcarifer* were released in February 2010. All individuals were measured (TL, mm) and were large enough to be marked with a plastic anchor tag before release to facilitate later identification. Fish were stocked into the Severin and Kauri Creek arms on the north and eastern sides of the lake, near to where the creeks flowed into the impoundment. These sites were chosen primarily because they contained extensive fish refugia, mainly in the form of macrophytes and aquatic grasses and afforded the fish an easy pathway (if needed) further upstream into the flowing reaches of the creeks. Details of fish sizes, stocking locations and strategies, and hatchery origins are given in Russell *et al.* (2013).

Tagging methodologies

Coded-wire tags

All *L. calcarifer* released into the Johnstone River as part of this study were marked with coded-wire tags (North-west Marine Technologies Inc. (NMT), Shaw Island, WA, USA, www.nmt.us) before release. This allowed them, upon recapture, to be identified and distinguished from similarly sized wild fish. Details of tagging procedures are given in Russell *et al.* (2013). Earlier work had demonstrated that using this technique to mark similarly size (\sim 50 mm TL) juvenile *L. calcarifer* resulted in very high survival and tag retention rates (Russell and Hales 1992). Stocked fish were tagged only in the cheek muscle, as past studies showed that this tagging position was readily checked using an NMT wand detector and allowed the tag to be easily applied using an NMT MKIV automatic injector (Russell and Hales 1992). Depending on the release location, the current cohort of fish was tagged in one (left or right side) or both cheek muscles. In earlier releases, fish were also tagged in additional body locations, including the base of the pectoral or pelvic fins and in the tail. Such flexibility in placing the tags enabled a more exact means of non-destructively determining where and when a recaptured fish was originally stocked.

Other tagging methods

For *L. calcarifer* (mean length = 194.6 mm (s.d. = 10.7 mm) TL) stocked into Lake Tinaroo, a Hallprint type TBF-2 (45 mm) fine anchor T-Bar tag (Hallprint Pty Ltd, Hindmarsh Valley, South Australia; www.hallprint.com) was inserted between the pterygiophores of the secondary soft dorsal fin rays using an Avery Dennison Mark III tag applicator (Avery Dennison Corporation, Miamisburg, OH, USA; www.monarch.averydennison.com). In the Johnstone River, wild fish and subsequently recaptured stocked (coded-wire tagged) fish between \sim 160 and 300 mm TL were all marked using this technique and tag type. For wild or recaptured fish $>$ 300 mm TL, a Hallprint type PDT (85 mm) dart tag was inserted between

the posterior pterygiophores of the second dorsal fin using a hollow (\sim 2 mm bore) tagging needle. To correctly position the tag, a scale was lifted from the insertion location and the needle was pushed into the muscle until the tip passed between the pterygiophores of the dorsal rays. After insertion, the tag was then pushed a short distance into the flesh and slightly turned before being gently tugged to ensure it was securely anchored. Where the first tag was either not placed correctly or was damaged, it was then either cut off or otherwise removed and a second tag inserted to the rear of the first location. The flag end of the tag contained a unique number and a brief message requesting fishers to measure the fish and report the recapture to a freecall phone number. Alternatively, the recapture information could be directly entered into the online database at www.info-fish.net/suntag/ (accessed 26 November 2014). This state-wide recreational fishing tag-and-release database is managed by SUNTAG, which is a program of the Australian National Sportfishing Association.

Sampling techniques

Some information on recaptures of wild and stocked fish was obtained by periodically monitoring the catches of local commercial and recreational fishers. However, in this study most data were obtained from fisheries-independent research sampling using different types of boat-mounted electrofishers.

Fisheries-independent research sampling

A 4.3-m electrofishing boat equipped with a Smith-Root Model 7.5 GPP electrofisher (Smith-Root Inc., Vancouver, WA, USA, www.smith-root.com) was used as the main river and impoundment survey vessel. This vessel was manned by three crew: the coxswain and two persons netting fish. If site access or stream size (stream order ≤ 3), were unsuitable for launching the 4.3-m vessel, a smaller 3.5-m aluminium boat mounted with a Smith-Root 2.5 GPP electrofisher with a coxswain and only one person netting stunned fish was used. Prior to the commencement of each survey, the conductivity at the site was measured to determine the approximate settings required for efficient electrofisher operations. Generally, a pulsed DC current was used with voltages of 135–1000 V depending on local conditions. At each site, the vessel was manoeuvred so as to either slowly cover the area immediately adjacent to the bank or close to potential *L. calcarifer* habitat. Potential habitat targeted included snags, overhangs, macrophyte or grass beds and rocky structures.

After capture, all fish were placed into a portable aerated fish-bin (60 L) or into an onboard live fish well (90 L). Periodically during sampling at each site, fish were anaesthetised using AQUI-S (Aqui-S NZ Ltd, Lower Hutt, New Zealand; www.aqui-s.com) with dosages ranging between 20 and 40 mg L⁻¹. Fish, once anaesthetised, were measured to the nearest millimetre (TL) and weighed to the nearest gram using Arlec digital scales (Arlec Australia Pty Ltd, Melbourne, Australia; www.arlec.com.au). They were then scanned for the presence of tags: coded-wire tags and anchor or dart tags in the Johnstone River and anchor or dart tags in Lake Tinaroo. In the Johnstone River, an NMT wand detector was used to determine whether captured individuals were marked with a coded-wire tag. The position of the coded-wire tag in stocked

fish (e.g. left, right or both cheek muscles) was also noted. Tag numbers were recorded for all recaptured dart- or anchor-tagged individuals. Before release, most fish were stomach flushed using the gastric lavage techniques described in Russell *et al.* (2013) and any contents were preserved in vials containing 70% ethanol for subsequent laboratory examination. In the laboratory, stomach contents were identified to the lowest possible taxonomic level and the number of items in each taxonomic group was counted. After being blotted dry, the taxonomic groups were weighed (nearest 0.1 g) and volumetrically measured by determining the quantity of water that they displaced using a graduated cylinder.

Commercial and recreational fisheries sampling

During the study, commercial catches from gill-net fishers were also regularly examined. This occurred generally at local fish-processing businesses or at the premises of commercial fishers. Sampling involved measuring (TL, to the nearest 1 mm) and scanning *L. calcarifer* for the presence of CWTs using the NMT wand detector. The coded-wire tag was excised from any stocked fish that were so identified. Fish that were marked with a plastic dart or anchor tag were measured (TL, to the nearest 1 mm) and the tag number recorded for later determination of that individual's release or recapture history. Stomach contents were not collected from commercially caught individuals.

Opportunistic use was also made of available historical tag and recapture data from other sources including the SUNTAG recreational fishing database mentioned above. This provided information on recaptures of fish marked with plastic dart- or anchor-tags by recreational anglers from the Johnstone River and Lake Tinaroo.

Data analyses

Recapture data from *L. calcarifer* stockings were sourced as far back as June 1994 for the Johnstone River fish and October 2004 for Lake Tinaroo. Initially, these data were filtered by recapture interval and growth where fish at liberty for less than 31 days or where the overall length increase between successive recaptures was <1 mm were discarded from the datasets.

The ages of stocked fish were obtained using an estimated birth date and time-at-liberty as calculated from recovered coded-wire tags. Ages for juvenile wild fish were obtained by estimating age-at-size (using both the age-size estimates in the literature (e.g. Davis and Kirkwood 1984) or known-ages of similarly sized tagged stocked fish as a guide) together with, where appropriate, the time-at-liberty for any recaptured tagged fish. The latter method becomes unreliable with increasing size of fish so no attempt was made to estimate the ages of untagged, wild fish greater than ~500 mm TL. The exception to this were wild *L. calcarifer* that had been caught at a smaller size where their age could be accurately estimated and then marked with a conventional dart- or anchor-tag before their release. As the spawning season for *L. calcarifer* occurs over several months (Russell and Garrett 1985), 1 December was used as a nominal birth date for all wild-fish ageing estimates.

Traditional asymmetric growth functions were fitted to data for both wild and stocked *L. calcarifer* from the Johnstone River and to stocked fish from Lake Tinaroo. Research electrofishing

accounted for most fish sampled in the freshwater and upper tidal areas. As this technique could not be effectively used in higher-salinity areas, *L. calcarifer* caught in the lower reaches of the Johnstone River and adjacent coastal areas were mostly sourced from commercial and recreational fishers. In the Johnstone River, this resulted in a bias towards sampling juvenile *L. calcarifer*, which were mostly found in freshwater and upper tidal habitats. As a further complication, the fisheries-dependent samples were also subject to a maximum (1200 mm TL) and minimum (550 mm TL) size restriction limit. This heavy bias towards younger fish in the Johnstone River dataset made the estimation of the von Bertalanffy growth parameter using only length-age data problematic. Instead, the Fabens method (Fabens 1965; Ogle 2012) using available mark-recapture data (see above) was used to calculate mean estimates of asymptotic length and the Brody growth coefficient for the von Bertalanffy growth formula, which is:

$$L_t = L_\infty \{1 - e^{-K(t-t_0)}\}$$

where L_t is the total length (TL) at age t ; L_∞ , asymptotic length; K , Brody growth coefficient; and t_0 , hypothetical age at TL = 0.

In the Johnstone River, seasonality in growth was measured using the seasonal form of the von Bertalanffy equation:

$$L_t = L_{t-\delta} + (L_\infty - L_{t-\delta})(1 - e^{-K\delta/365+S(t-\delta)-S(t)})$$

where L_t is the length at recapture, t is the day of recapture, δ is the time at liberty (days), $L_{t-\delta}$ is length at release, L_∞ is the asymptotic length, K is the average exponential growth parameter and

$$S(i) = 0.5(CK \sin[2\pi(i - t_s)])\pi^{-1}$$

where C measures the magnitude of the seasonal oscillation and t_s is the time shift for the annual cycle (Somers 1988; Robins *et al.* 2006). Parameters to be estimated were L_∞ , K , C and t_s . This equation incorporates the effects of time at liberty, seasonality and length-at-release. Only fish at liberty for between 30 and 365 days were used and median size at release was 347 mm TL. Individual growth curves, assuming the same responses, were compared using regression analysis.

Fulton's condition factor (K) for individual fish was calculated using the formula:

$$K = \frac{100w}{l^3}$$

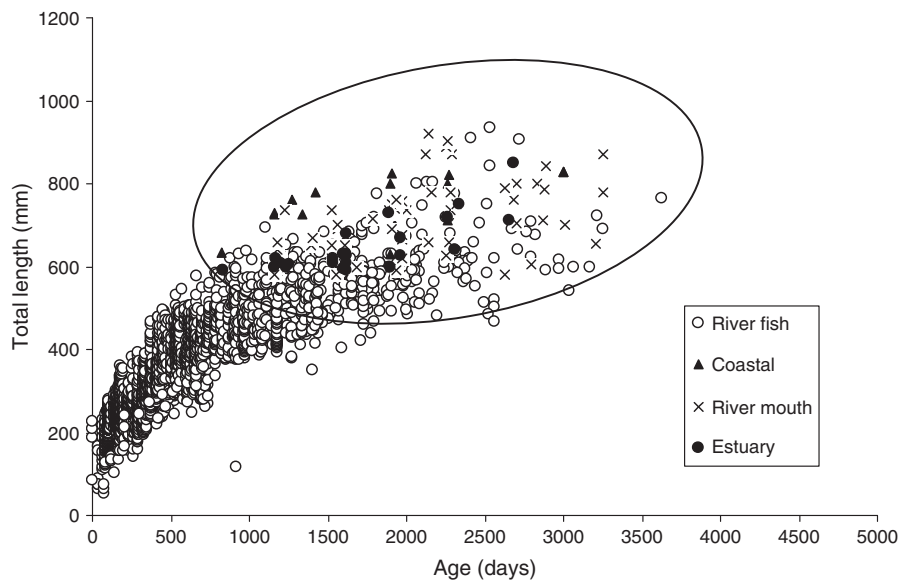
where w and l are the observed total weight and total length of the fish respectively. Condition factors were compared using ANOVA. The average monthly stomach fullness index was calculated as a measure of the wet weight (g) of the food consumed divided by its volume (mL). An arcsine-transformation was then applied to normalise the indices. A G^2 test was used to compare the proportion of fish with empty stomachs in both wild and stocked fish.

All statistical analyses were undertaken using the GENSTAT 14.1 statistical package (VSN International: www.vsn.co.uk/genstat, accessed 1 November 2011).

Table 1. Recapture locations in the Johnstone River and adjacent environs of stocked and wild *L. calcarifer* from this study

Average age (days) at recapture is given in parentheses

Recapture location	Stocked fish	Wild fish	Total
Johnstone River (Freshwater)	2907 (470.7)	1984 (590.5)	4891 (519.3)
Johnstone River (Estuary)	24 (1702.5)	1	25 (1710.0)
Johnstone River (Mouth)	61 (2023.9)	5 (2132.6)	66 (2032.1)
Adjacent coastal rivers and foreshores	14 (1862.9)	2	16 (1868.6)
Unknown	4 (1629.3)	0	4 (1629.3)
Total	3010	1992	5002

**Fig. 1.** Length-at-age plot of stocked and wild fish captured from the Johnstone River and adjacent environs. Most of the fish in the larger size classes (see circled area) were caught in the estuary, river mouth and coastal habitats rather than in the freshwater reaches of the river.

Results

Two separate age–length recapture datasets were available for wild and stocked fish in the Johnstone River and the nearby coastal regions (Table 1; Fig. 1). These were caught between 1993 and 2005 ($n = 3781$) and between 2009 and 2011 ($n = 1221$). From the more recent dataset, mark–recapture data were obtained for 2612 wild and 802 stocked fish from the Johnstone River and 191 stocked *L. calcarifer* (including 25 multiple recaptures) from Lake Tinaroo. Most recapture data for the Johnstone River fish caught as part of this current study were from the period between October 2009 and December 2011. Recaptures of Lake Tinaroo *L. calcarifer* were between March 2010 and October 2011.

A major difference between the two Johnstone River datasets was that the earlier, longer-term dataset contained only age–length data whereas the more recent dataset also included additional information on condition factor and stomach fullness. The methods used for estimating the ages of these fish are described in the Growth section below. The Lake Tinaroo dataset also included fish of known age, together with data on their condition and stomach fullness.

Growth

Ages were estimated for 5002 *L. calcarifer* from the Johnstone River. Of these, ~60% were stocked and ~40% were wild; their growth is shown in Fig. 1. All *L. calcarifer* from the Johnstone River were caught between February 1993 and December 2011. Most of these fish (~97%) were juveniles (less than the minimum legal size of 580 mm TL) and were caught almost entirely in the lower, freshwater and upper tidal reaches of the river. Of the remaining fish ($n = 237$), 107 were caught in the estuary, river mouth or in adjacent coastal areas (Fig. 1). Most of these *L. calcarifer* were older than 3 years (1095 days) (Table 2).

Estimates of the von Bertalanffy growth parameters using the Fabens method were made for stocked and wild *L. calcarifer* in the Johnstone River and for stocked fish in Lake Tinaroo. The estimates of L_{∞} for stocked *L. calcarifer* in Lake Tinaroo were significantly greater than the L_{∞} obtained for either wild or stocked fish in the Johnstone River ($P < 0.05$) (Table 3). Similarly, the L_{∞} for wild fish was greater than that for stocked fish in the Johnstone River ($P < 0.05$) (Table 3). The estimates of K for both stocked fish in the Johnstone River and Lake Tinaroo

were both significantly greater than that for wild *L. calcarifer* in the Johnstone River ($P < 0.05$).

Juvenile growth

Fig. 2 shows the average monthly total lengths over a 24-month period for young-of-the-year wild and stocked *L. calcarifer* in the Johnstone River and for fish stocked into Lake Tinaroo in 2010. Average size (\pm s.d.) of *L. calcarifer* released into the Johnstone River in November and December 2009 was 60.9 ± 4.8 mm TL and 52.3 ± 9.5 mm TL respectively. By March 2010, their average size (\pm s.d.) had increased to 241.6 ± 27.1 mm TL ($n = 20$). Although there were only

small numbers ($n = 4$) of wild fish caught in these same locations in March 2010, their average size was 244 mm TL.

The mean size (\pm s.d.) of *L. calcarifer* stocked into Lake Tinaroo in February 2010 was 194.0 ± 12.53 mm TL ($n = 2996$). Fig. 2 suggests that in 2011, the growth rates of both stocked and wild fish in the Johnstone River were similar and both were relatively slow when compared with the *L. calcarifer* in Lake Tinaroo. The mean monthly total lengths of Lake Tinaroo *L. calcarifer* increased rapidly during the warmer months from c. November 2010 to March 2011. Corresponding increases in the mean monthly total lengths of either the wild or stocked fish in the Johnstone River was less pronounced. At the completion of sampling in October 2011, the mean monthly total lengths of *L. calcarifer* in Lake Tinaroo was at least 177 mm more than either the wild or stocked fish in the Johnstone River.

Table 2. Number of *L. calcarifer* (wild and stocked) in the Johnstone River and local environs caught in each habitat type
Capture location was not known for four fish

Habitat type	Age >1095 days	Age \leq 1095 days	All fish
River	472	4419	4891
River mouth	66	0	66
Estuary (middle)	24	1	25
Coastal foreshore	15	1	16
Total	577	4421	4998

Table 3. Estimates of von Bertalanffy growth parameters L_∞ and K for stocked and wild *L. calcarifer* from the Johnstone River and from stocked *L. calcarifer* in Lake Tinaroo
Asymmetric 95% confidence limits are shown in parentheses. All estimates are significant at $P < 0.001$

Cohort	n	L_∞ (mm)	K (year^{-1})
Johnstone River (wild)	2612	1059 (1003–1116)	0.13 (0.12–0.14)
Johnstone River (stocked)	802	829 (778–879)	0.19 (0.16–0.22)
Lake Tinaroo (stocked)	191	1322 (1206–1438)	0.21 (0.18–0.24)

Growth of fish caught in different habitats

Most of the *L. calcarifer* caught in this study from habitats characterised by high salinities (i.e. estuary, coastal areas, and the river mouth) were generally aged >3 years (1095 days). Therefore, statistical comparisons of the growth of fish from different habitats were restricted to this age group (Table 2; Fig. 3). This reduced the sample size and a high degree of scatter decreased the precision obtained when fitting exponential curves to data from each habitat type. Assuming that each of the individual datasets had the same response shape for this age range (>1095 days), individual parallel curves when compared using non-linear regression analyses were all found to be significantly different ($P < 0.001$) (Fig. 3). Fish caught in river habitats grew significantly less than fish captured in any of the other areas whereas the coastal fish grew the fastest. No comparable data were available for Lake Tinaroo.

Seasonal growth

The seasonal von Bertalanffy growth equations for *L. calcarifer* in the Johnstone River suggest that growth of both wild and

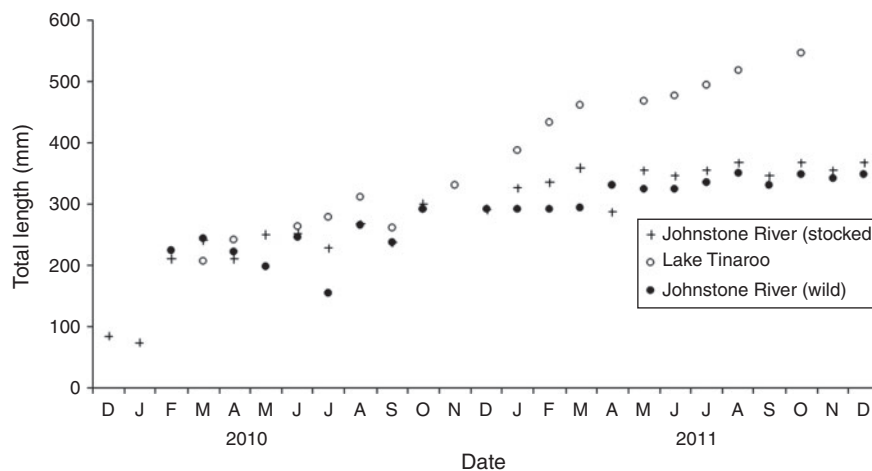


Fig. 2. Mean monthly sizes of stocked and similarly aged wild *L. calcarifer* in the Johnstone River and stocked *L. calcarifer* in Lake Tinaroo. Johnstone River fish were stocked in late 2009 and Lake Tinaroo fish were stocked in early 2010.

stocked fish peaked *c.* early January in the Austral summer, before declining and then temporarily ceasing between *c.* Days 160–210 in the Austral winter (Fig. 4). During the warmer months, these data suggest that the growth of stocked fish is slower than that of wild *L. calcarifer* in this river system. There were insufficient data to construct a seasonal growth curve for Lake Tinaroo fish.

Age and site fidelity

The average ages of stocked *L. calcarifer* caught in the downstream, freshwater and upper tidal reaches of the North

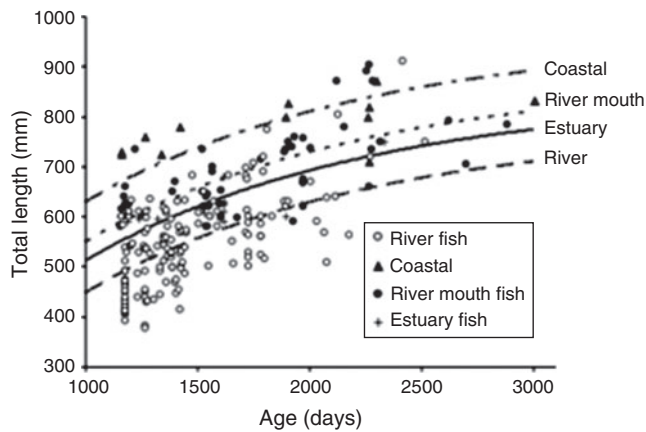


Fig. 3. Length-at-age plot for stocked *L. calcarifer* from four habitat types either in the Johnstone River or in adjacent coastal foreshore areas. Exponential same-shape curves were fitted to data from each habitat type for fish >1095 days old.

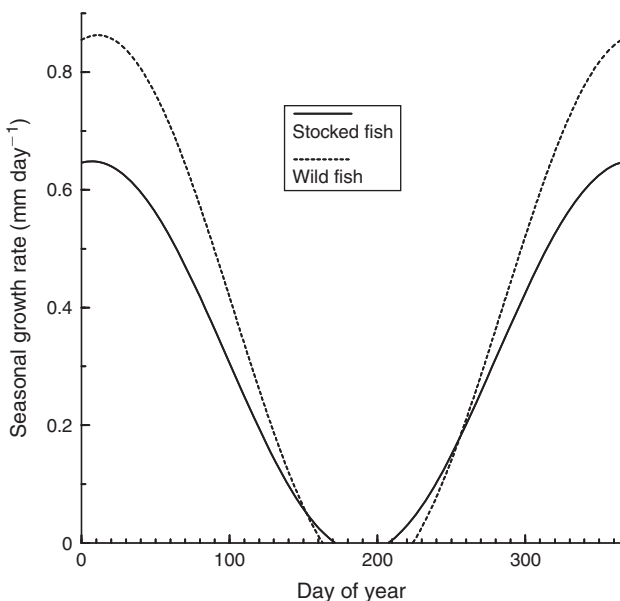


Fig. 4. Somers seasonal growth model for both stocked and wild *L. calcarifer* in the Johnstone River. An overall median release value of 347 mm was used for constructing the curves. Day 0 on the *x*-axis is 1 January.

Johnstone and South Johnstone rivers were 0.96 and 1.41 years respectively. The average age (and size) of stocked fish caught progressively decreased with increasing distance from the river mouth. Those fish captured in freshwater areas were younger (and smaller) than those from the river estuary. Young-of-the-year *L. calcarifer* stocked into the North Johnstone River in November and December 2009 began to appear in the freshwater areas of the South Johnstone River from *c.* March 2010 onwards. Earlier sampling in 2005 (Fig. 5) showed the presence of small numbers of young-of-the-year wild *L. calcarifer* in freshwater areas of both the North and South Johnstone rivers from as early as January (Fig. 5).

Most recaptured stocked fish were juveniles caught at the lower freshwater tidal sampling location (NJL) in the North Johnstone River. The average age of fish caught at this sampling site was ~ 1 year and the maximum age was just over 6 years old. Similarly, in the freshwater sampling site (SJL) in the lower South Johnstone River, stocked fish were an average of 1.4 years old with a maximum age of 7.7 years. Smaller numbers of stocked fish were caught here; however, most had dispersed from the release sites in the North Johnstone River to this location. Only three of the *L. calcarifer* originally stocked into the South Johnstone River in 2009 were known to have been recaptured. None of these three had made substantial movements from their original release location, suggesting a low survival rate for this stocking cohort.

In this study, mostly juvenile fish were caught in the lower, freshwater reaches of the North and South Johnstone rivers, although small numbers of larger stocked and wild *L. calcarifer* were also recovered from freshwater sampling locations upstream in both the North (maximum TL = 1189 mm) and South (maximum TL = 1240 mm) Johnstone Rivers. No age estimates were made for these individuals because of the inherent difficulty in estimating the age of large fish using only length data.

Seasonal variation in feeding

In the Johnstone River (North and South), sampling of stomach contents of juvenile *L. calcarifer* was undertaken in the period from October 2010 to September 2011. During this time, the overall proportion of fish with empty stomachs was significantly higher in stocked *L. calcarifer* than in wild fish of the same age class ($G^2 = 61.1$, *d.f.* = 1, $P < 0.001$). Overall, there was a high proportion (>50%) of both wild and stocked fish in the Johnstone River with empty stomachs. In most cases, both the proportions of stocked and wild juvenile *L. calcarifer* with empty stomachs and the stomach fullness indices of juvenile *L. calcarifer* varied seasonally (Fig. 6). For example, in December 2010 the percentage of both wild (41%) and stocked (33%) *L. calcarifer* with empty stomachs was quite low but this increased in the cooler months in 2011. From April to July 2011, the percentage of Johnstone River fish with empty stomachs increased, with 100% of stocked fish sampled in July having empty stomachs. The fullness index for both wild and stocked *L. calcarifer* was highest in December and then generally declined as water temperatures fell in winter (Fig. 6).

Over the same period in Lake Tinaroo, the percentage of monthly samples with empty stomachs was lowest in October

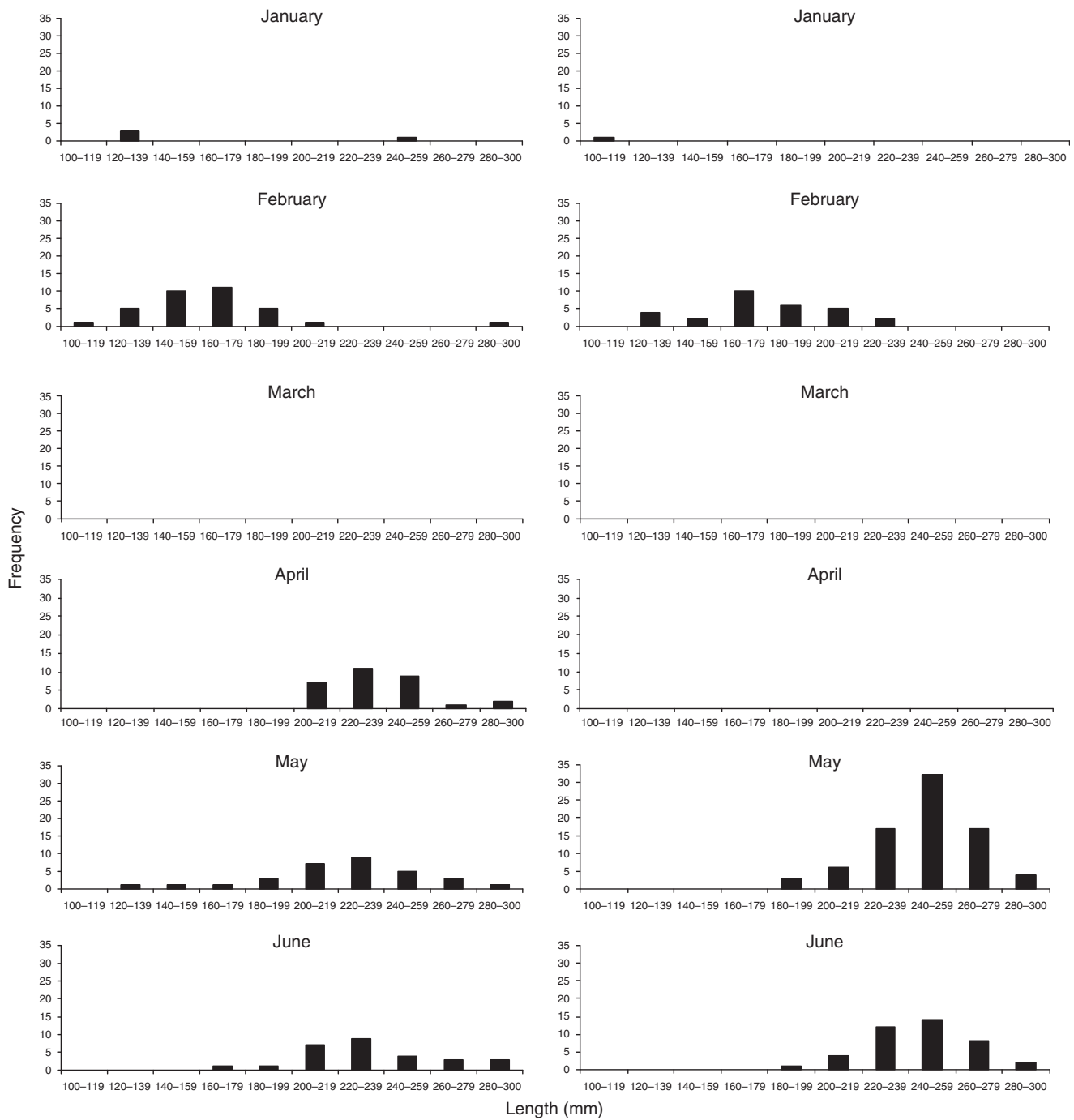


Fig. 5. Monthly length–frequency of wild juvenile *L. calcarifer* <300 mm TL sampled in the North (left) and South (right) Johnstone rivers in 2005. Sampling was not carried out in March in either river and in April only in the North Johnstone River.

and increased to *c.* March and then slowly declined (Fig. 6). The proportions of empty stomachs in monthly samples was generally less than in the same age class fish in the Johnstone River and the mean fullness index was significantly higher in Lake Tinaroo than in the Johnstone River ($t = 3.90$, d.f. = 196, $P < 0.001$).

Condition factor

When both wild and stocked *L. calcarifer* from the 2009 cohort were compared across all the Johnstone River zones and in Lake Tinaroo, there was a significant difference in condition factors ($F_{6,1372} = 7.4$, $P < 0.05$). Least-significant-difference (l.s.d.) pair-wise multiple comparisons suggest that there

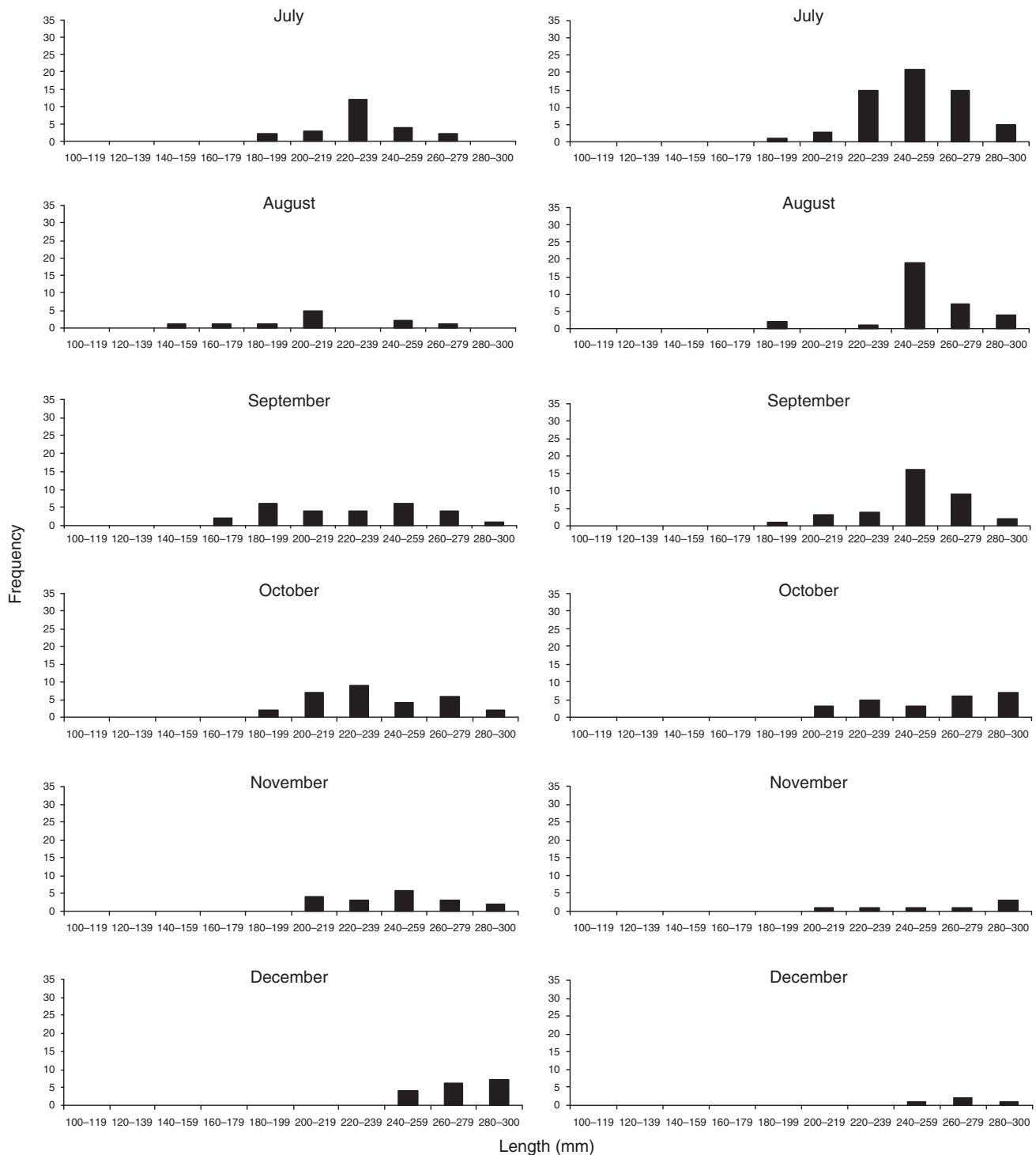


Fig. 5. (Continued).

were no significant differences ($P > 0.05$) between stocked and wild fish in either the lower North and South Johnstone zones (NJL and SJL) or between stocked fish in Lake Tinaroo and the North Johnstone middle zone (NJM). The condition factor of wild fish caught in the North Johnstone middle zone (NJM) was similar to that of stocked fish

($P > 0.05$) in that zone but significantly different from condition factors for both wild and stocked *L. calcarifer* in all other zones ($P < 0.05$).

When the condition factors of wild fish (2007, 2008 and 2009 cohorts combined) and the 2009 stocked cohort were compared, there was no significant difference ($F_{1,1579} = 1.3$, $P > 0.05$).

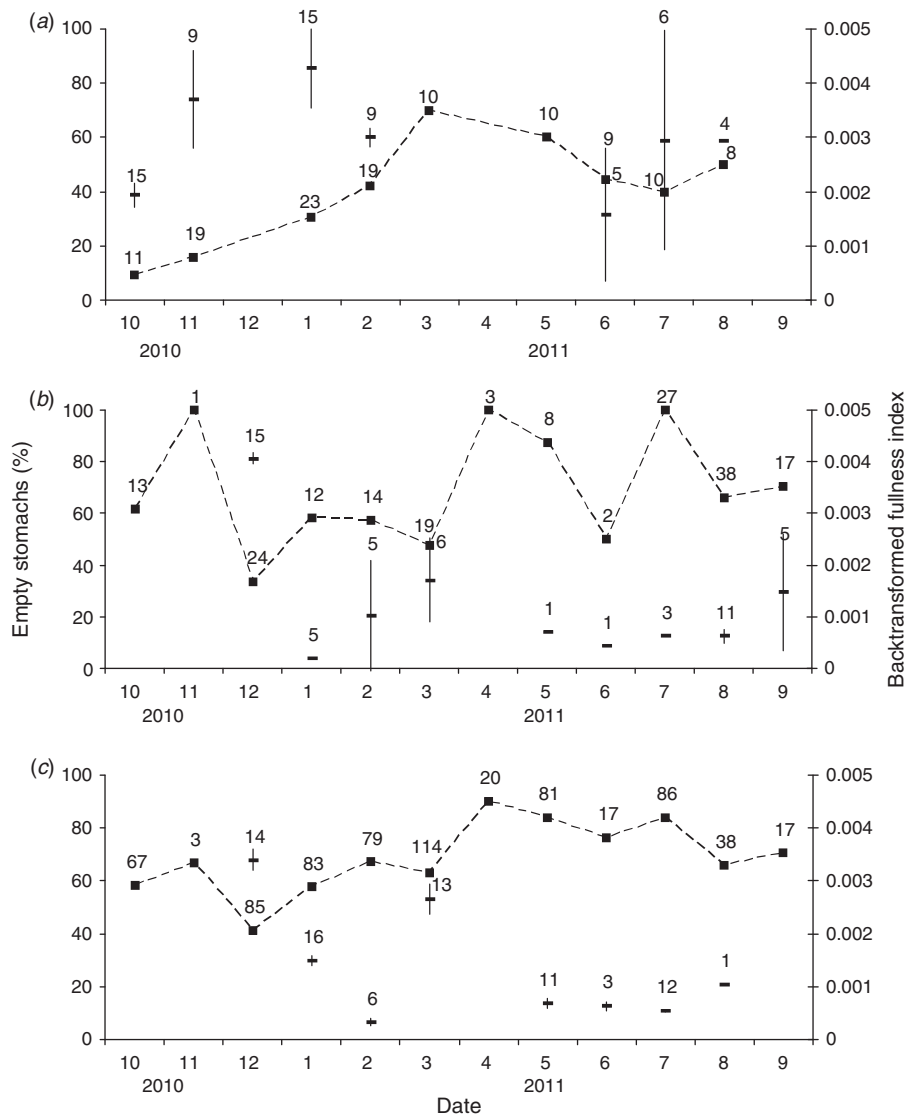


Fig. 6. Monthly variation in percentage of fish with empty stomachs (closed squares) and monthly stomach fullness indices (–) from (a) Lake Tinaroo and both (b) stocked (2009–10 cohort) and (c) wild Johnstone River *L. calcarifer*. Numbers above markers indicate sample size and vertical bars around the stomach fullness indices are standard errors.

Further, there were no significant differences between the individual year classes (2007, 2008 and 2009 cohorts) of wild and stocked (2009 cohort) fish ($F_{3,1372} = 1.0, P > 0.05$).

Discussion

The growth of the *L. calcarifer* populations examined in this study were highly variable and probably driven largely by local environmental conditions. Overall, the growth of wild and stocked fish in the Johnstone River was slower than that of similarly aged fish in Lake Tinaroo. There was also differential growth between stocked and wild cohorts of *L. calcarifer* at the Johnstone River sites. Differences in average growth parameters for *L. calcarifer* have been observed for populations in Australia (Dunstan 1959; Davis and Kirkwood 1984; Russell 1990;

Robins *et al.* 2006) and in Papua New Guinea (Reynolds and Moore 1982). The calculated asymptotic lengths (L_{∞}) for populations in these studies ranged from 868 mm TL (Davis and Kirkwood 1984) to 1829 mm TL (Robins *et al.* 2006). Variable average asymptotic lengths for *L. calcarifer* were obtained in this current study for Johnstone River wild (1059 mm TL) and stocked (829 mm TL) and Lake Tinaroo (1322 mm TL) fish. These values were mostly within, or close to, the range identified in the literature but were considerably lower than the 1829 mm TL calculated by Robins *et al.* (2006). Several factors need to be considered when looking at these variations in the growth parameters, not the least of which is any inherent biases introduced through the sampling methodology. In the current study, much of the data used for the Johnstone River L_{∞} estimates were from individuals caught in freshwater and upper

tidal habitats as part of targeted fisheries-independent research sampling; this resulted in the inclusion of only a few older, larger fish in the calculation of the growth parameters. Similarly, due to the sampling methodology (primarily electrofishing), few juvenile fish from the lower estuary, river mouth and coastal areas were included in the analyses. Given that the maximum sizes of wild and stocked *L. calcarifer* caught in the river during this study were 1300 mm TL and 1220 mm TL respectively and 1280 mm TL from Lake Tinaroo, the sampling techniques used could have contributed to the apparently low estimates of L_{∞} . These sizes are similar to results obtained using a method developed by Froese and Binohlan (2000) that estimated the L_{∞} values at 1331 mm TL and 1251 mm TL for wild and stocked Johnstone River fish respectively and 1264 mm TL for *L. calcarifer* in Lake Tinaroo. Another consideration may be that the calculated growth function(s) do not reach an asymptote (Knight 1968; Roff 1980). Further, when using tagging data to estimate growth, L_{∞} may not be estimated properly because the model would predict negative growth for fish whose initial length was greater than the asymptotic length (Somers 1988; Francis 1988). Because of these uncertainties, some degree of caution should also be exercised when interpreting the comparisons made between the calculated von Bertalanffy parameters for fish from the Johnstone River and Lake Tinaroo.

Several factors may influence the growth of *L. calcarifer* resident in the Johnstone River and in Lake Tinaroo. These include the quality and quantity of available food, water temperatures and the energetic requirements and expenses associated with living in variable habitat types. For example, under riverine conditions a euryhaline species such as *L. calcarifer* may need to expend energy that could have otherwise been used for growth on osmoregulation (Robins *et al.* 2006) or to deal with swift tidal currents or seasonal flooding. In a freshwater impoundment, however, conditions are often more benign, potentially allowing individuals to expend more energy for growth. This may be the case in the current study, whereby fish stocked into Lake Tinaroo grew faster than both stocked and wild fish in the Johnstone River.

However, food quality and quantity are likely to be the major factors affecting the growth of *L. calcarifer* in the Johnstone River and these are influenced primarily by the productivity of the available habitat types in the system. A major driver for determining productivity in the Johnstone River is likely to be its hydrology. It is a short, shallow, fast-flowing coastal stream that is subject to heavy seasonal flooding, which probably, temporally at least, makes its freshwater habitats somewhat unproductive (Russell and Hales 1993). This would explain why fish in the Johnstone River that were caught in its lower freshwater reaches and upper tidal habitats grew significantly more slowly than *L. calcarifer* captured in either the estuary or river mouth, whereas those resident in coastal habitats grew the fastest.

Juvenile *L. calcarifer* resident in the lower freshwater reaches of both the North and South Johnstone Rivers were often associated with aquatic macrophytes, in particular, with the extensive beds of *Vallisneria* spp. present in this system (Russell *et al.* 2013). These macrophyte beds performed the dual functions of providing cover, as well as harbouring abundant prey in the form of small atyid shrimps and other similar-sized species (Russell *et al.* 2013). It is this abundance of suitably

sized prey at key release locations that was likely responsible for the more than doubling in size of juvenile stocked *L. calcarifer* between the time of their release in November and December 2009 and February–March 2010. However, after this initial spurt, the growth of fish resident in these macrophyte beds decreased, probably due to a lack of suitably sized prey species for larger size classes of *L. calcarifer*. This particular location in the lower North Johnstone River (NJL) had been regularly stocked with *L. calcarifer* since the early 1990s, and it may have been the cumulative result of these activities that caused the depletion of stocks of larger prey species or a possible increase in cannibalism. However, a parallel study of the diet of *L. calcarifer* in the same river found little evidence of cannibalism (Russell *et al.* 2013). It would appear more likely that lower productivity in these reaches of the Johnstone River resulted in a lack of these larger-sized prey species.

Although most mature *L. calcarifer* eventually move to saline environments to spawn (Dunstan 1959), an absence of quality food resources could potentially hasten this movement into the more productive coastal or estuarine environments or into adjacent, perhaps more favourable river systems. However, whereas food availability may be limiting growth of larger juvenile *L. calcarifer* in the Johnstone River, the considerable number of multiple tag–recaptures (some over several years) from river locations (particularly the North Johnstone River) suggests that this is apparently not resulting in many unexpected or premature movements of either stocked or wild juvenile fish.

In Lake Tinaroo, where there is an apparent surfeit of suitable foods in the form of fish and crustaceans (Russell *et al.* 2013), growth in the first 2 years after stocking easily outpaced that of similar-aged *L. calcarifer* in the Johnstone River. This was despite lower water temperatures in the impoundment as a result of a higher altitude (670 m above sea level) that should have considerably slowed growth during winter. In the Johnstone River, there was also a decrease in growth in both stocked and wild *L. calcarifer* over the cooler winter months. In *L. calcarifer* populations in the Johnstone River and in Lake Tinaroo, there was evidence of both higher stomach fullness values and fewer empty stomachs during warmer periods than in the cooler months. However, the mean stomach fullness index was significantly higher in *L. calcarifer* from Lake Tinaroo than in the Johnstone River fish, suggesting higher food consumption in Lake Tinaroo fish throughout the year (Fig. 6), possibly because of higher prey abundance.

It is possible that, during the capture process, an unknown level of autoregurgitation may have confounded the stomach contents results. On one occasion there was evidence of regurgitation of prey noted immediately after capture when a partially digested juvenile *L. calcarifer* was observed with other fish awaiting processing in the boat's holding tank (Russell *et al.* 2013). However, there were no other similar observations, suggesting that autoregurgitation was probably an uncommon occurrence.

Given the apparent high level of site fidelity of juvenile *L. calcarifer* in the Johnstone River, food availability could be expected to affect not only the growth but also the condition of captured fish. Ribeiro *et al.* (2004) noted the usefulness of using condition factor and growth rates for assessing the importance of different habitats to the life history of fish. They further noted

that habitat was not uniform and food resources were sometimes patchy, resulting in some areas being more favourable for fish growth than others and that physical conditions can also change with time. In the current study, the condition data from 2009 wild fish resident in the middle zone of the North Johnstone River were different from both stocked fish in that zone and from stocked and wild fish in all other zones. However, when a larger dataset that included all of the wild fish from the 2007–09 year classes were analysed, there were no significant differences, suggesting that habitat differences by themselves at the river and impoundment sites were having only a minor influence on fish condition.

Although the condition factors of *L. calcarifer* sampled from these various habitats were not necessarily significantly different, it was evident from this study that the fish that resided in these habitats types did have differential growth rates. In coastal and estuarine areas, and in Lake Tinaroo where there appears to be more available food (especially for the larger juvenile fish), similarly aged fish grew faster than individuals from the freshwater reaches of the Johnstone River, where productivity appeared somewhat limited. Furthermore, *L. calcarifer* that had undertaken a seaward migration or those that were caught in coastal environs generally had a higher L_{∞} ; what was not evident was what caused the apparent differences in growth between the stocked fish and wild fish from the Johnstone River that co-occupy the same habitats. Although stocked fish may take some time to switch from a high-protein dry-pellet hatchery diet to a wild diet, this should not affect growth for more than a few weeks. Alternately, it may be that having been domesticated, these *L. calcarifer* lost many of their innate hunting skills and other competitive advantages and therefore were outperformed by their wild conspecifics. There is evidence of this in other species; for example, stocked trout (*Salmo trutta*) have been shown to have poor performance and lower fitness when compared with wild counterparts (Hansen 2002).

Several studies have linked differences in growth of *L. calcarifer* to variations in environmental conditions. The conditions to which an individual is exposed over its lifetime, some of which may be transient, can increase the probability of highly variable growth as a result of adaptive phenotypic plasticity (Morita and Morita 2002). In *L. calcarifer*, Davis and Kirkwood (1984) suggested that variable growth rates were most likely a reflection of different environmental and seasonal conditions experienced by the fish in the different river systems, rather than intrinsic differences in growth. They also noted that growth achieved in different years within the same river varied for the same reasons. The growth of sexually precocious *L. calcarifer* present in streams in the north-eastern Gulf of Carpentaria was considerably slower than that of fish in other parts of northern Australia (Davis 1984). Davis (1984) regarded these fish as being 'stunted' and suggested that their sexual precocity may be linked to local environmental conditions. In a more recent study, Robins *et al.* (2006) suggested that environmental conditions, particularly freshwater flows, influenced growth of *L. calcarifer*. They found that growth rates of *L. calcarifer* in the Fitzroy River varied seasonally and were significantly and positively correlated with fresh water flowing into the estuary. Robins *et al.* (2006) regarded this as evidence to support the hypothesis that freshwater flows are important in

driving the productivity of estuaries and can improve growth of species higher up in the trophic chain. Environmentally driven variability in the growth of *L. calcarifer* has probable management implications for the fishery, including regional variations in both the size- and age-at-first-maturity and therefore both minimum and maximum legal catch sizes (Davis and Kirkwood 1984).

Although the stocking of low densities of *L. calcarifer* into the habitats examined during this study appears to have minimal effect on species of conservation importance (Russell *et al.* 2013), there may be consequences for stocking higher numbers of fish into apparently prey-limited areas such as the Johnstone River. In such habitats, growth of *L. calcarifer* (particularly juveniles) appears to be constrained and any increases in population size, particularly substantial increases, may further adversely affect the growth of resident wild fish. In all locations where such concerns have been identified, more conservative stocking practices need to be adopted or even a complete cessation of stocking activities.

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