Journal of Applied Ichthyology

J. Appl. Ichthyol. (2011), 1–8

ISSN 0175–8659

Received: April 6, 2011
Accepted: July 1, 2011
doi: 10.1111/j.1439-0426.2011.01887.x

Validation of mark-recapture population estimates for invasive common carp, *Cyprinus carpio*, in Lake Crescent, Tasmania

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Summary

A mark-recapture study based on the Petersen method was implemented in 1998 to estimate the abundance of the invasive common carp, *Cyprinus carpio* L., in Lake Crescent, Tasmania. Multiple gear types were employed to minimise capture bias, with multiple capture and recapture events providing an opportunity to compute and compare Petersen and Schnabel estimates. A single Petersen estimate on recapture data and two Schnabel estimates – one each on mark (forward-Schnabel estimate) and recapture (reverse-Schnabel estimate) data – were conducted. An independent long-term double tag study facilitated estimation of the annual natural mortality. Subsequent fish-down of the population suggests that, in all likelihood, the carp have been eradicated from the lake, providing an unprecedented opportunity to verify the forward population estimates carried out in 1998. Results suggest that all three estimates were close to the true population size, with the reverse-Schnabel estimate being the most accurate and within 1% of the true population in this relatively large lake (~2365 ha). Greater accuracy of the reverse-Schnabel approach can be attributed to either minimised fish behavioural (i.e. gear susceptibility or avoidance) or computational bias associated with the forward-Schnabel and Petersen approaches, respectively. While the original estimates served as a guide in eradication of carp from the lake, the ultimate validation provides a reliable framework for abundance estimation of this invasive fish in relatively large water bodies elsewhere.

Introduction

The common carp, *Cyprinus carpio*, is deemed a feral pest fish in Australia, as it is implicated in habitat loss, wetland degradation and decline of native fish (Koehn et al., 2000). This invasive fish was first discovered in Lake Crescent Tasmania (Fig. 1) in 1995. The lake supports a commercial fishery for the native short-finned eel, *Anguilla australis* and a recreational fishery for the exotic brown trout, *Salmo trutta* and rainbow trout *Oncorhynchus mykiss*. It also is a primary habitat for a native fish, *Galaxias auratus*, listed as endangered under the Commonwealth *Environment Protection and Biodiversity Conservation Act* 1999. Early field observations followed by identification of multiple year classes in the Lake Crescent stock (Vilizzi and Walker, 1998) confirmed successful recruitment of the invasive carp in the lake. The threat of its spread to other water bodies with commercial, recreational, conservation and social values triggered a control and/or eradication program, with intensive but selective fishing identified as the most viable option.

To assist the fish-down of carp in the late 1990s, it was important to estimate population abundance. Although population abundance estimation is fundamental to fisheries management, accuracy in estimating absolute population numbers has remained challenging or near impossible in large lakes. This can be attributed to a number of factors ranging from sheer diversity of habitat, limited capture methods adopted, lack of behavioural knowledge of the species such as niche preference and the limitations of population estimation method adopted, among others. According to extensive experiments carried out in European lakes, mark-recapture and hydroacoustic population estimation methods were the most accurate (Dahm et al., 1992) of the currently used

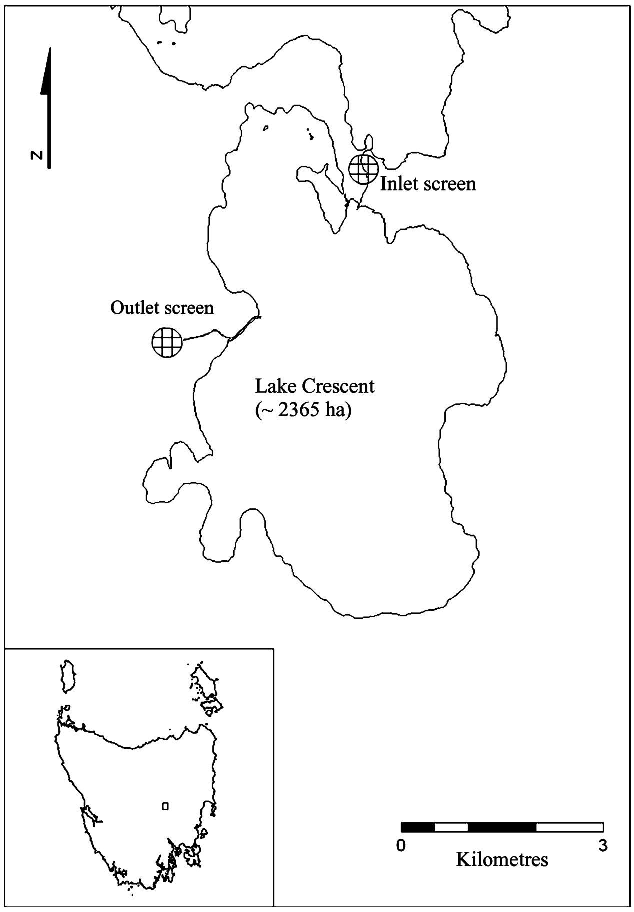

Fig. 1. Map of Lake Crescent, central Tasmania (inset), showing location of containment screens (hatched circles)

techniques in inland lakes, including virtual population, catch per unit effort and filtered volume analyses. Despite recent refinements, hydro-acoustic methods were shown to be unsuitable for estimating fish abundance in large, shallow lakes (Mous and Kemper, 1996).

Mark-recapture methods based on a model developed by Petersen (1896) remain the most often used technique for population estimation in inland waters (Seber, 1982, 1986; Gatz and Loar, 1988; Pollock et al., 1990). In practice, if the Petersen's assumptions (closed population, equal catchability, zero tag loss, tagging does not affect catchability of individuals and all tags are reported in the second sample) are approximately met, useful deductions can be made about the status of fish populations (Ricker, 1975; Pollock, 1991). The assumption of population closure can be addressed through adequate movement barriers. Tag loss can be overcome by using permanent and or multiple markers that are not detrimental to survival of the animals (Oosthuizen et al., 2010). Similarly, random distribution and equal catchability of tagged and untagged fish can be addressed by allowing a sufficient recovery period (Mesa and Schreck, 1989). Multiple fishing gear types are often used to mark and recapture fish to reduce heterogeneity of recapture probability. For example, when common carp (Beukema and De Vos, 1974) and trout (Waters, 1960) were marked and recaptured with different gear types, estimates of population abundance were more accurate than when they were marked and recaptured with the same gear. Although use of multiple fishing gear types to reduce bias in mark-recapture population estimates has been suggested (Rogers et al., 2005), this is rarely implemented. As a result, biases in Petersen estimates even in simulated small pond experiments are not uncommon (Buck and Thoits, 1965; Kitada et al., 2001). More pertinently, validation of fish population estimates in large lake situations where the true population size is unknown has proven difficult or impossible thus far.

The Petersen method is simple but often requires pooling data from multiple capture events, masking biases that may be associated with each capture event. In contrast, the method of Schnabel (forward Schnabel) is designed to account for these biases (Schnabel, 1938). Conceivably, the multiple mark, release and recapture events in a relatively short space of time one associates with the forward Schnabel approach can introduce behavioural bias such as trap happy or trap shy behaviour, resulting in violations of the equal catchability assumption. More significantly, the standard (forward) Schnabel approach is subject to the changing (increasing) proportion of the tagged individuals, only ever reaching the highest proportion on the last sampling event. In contrast, we introduce a simple modification, here referred to as a reverse Schnabel approach that enables (i) maintaining a relatively higher and a near-constant proportion of tagged animals in the population throughout the sampling period, and (ii) also allows adequate time for marked animals to integrate better into the parent population.

Presented here are comparative Petersen, forward- and reverse-Schnabel (weighted mean) population estimates that were used to track the abundance of carp during the 8-year fish-down (eradication) process in Lake Crescent, Tasmania. Radio-transmitter implanted 'Judas' (Taylor and Katahira, 1988) mature male carp were used to identify the locations of carp aggregations and aid in their capture. An independent long-term double tag study facilitated estimation of the annual natural mortality rate and calibration of the removal target (remaining carp in the lake) on an annual basis (1999–2007). To our knowledge the likely eradication of carp from this lake provides the first verification of fish population estimates carried out in a large lake.

Materials and methods

Study area

The study was conducted at Lake Crescent (lat. 42°08′–42°10′S; long. 147°08′–147°11′E) a 2365 ha, shallow (1–2 m), turbid, freshwater lake located at an altitude of 800 m on the eastern edge of the Central Plateau, Tasmania (Fig. 1). Construction of fine mesh screens upstream and downstream of the lake in 1996 effectively rendered it a 'closed' system.

Study period

The mark-recapture study was carried out over a period of 47 days (30 November 1998–15 January 1999). Mark and release of fish occurred over 13 fishing days (30 November–12 December 1998); the marked fish were allowed to disperse and acclimatise for at least 22 days before the recapture process began. Recapture occurred over 12 days (4–15 January 1999).

Capture

To minimise gear bias, multiple fishing gear types were used during both marking and recapture processes. In brief, a combination of eight gillnets (mesh size 3″, 4″, 5″ 6″ and 7″), two seine nets (mesh size 30 mm; 100 m long; 2 m drop), 44 fyke nets, two electro-fishing backpacks (400 V, 4 amps; Smith Root, Vancouver, WA) and one electro-fishing boat (750 V, 6 amps, Smith Root, Vancouver, WA) were used. The fyke nets were deployed around the perimeter of the lake for the duration of the mark-recapture study and checked on a daily basis. On the assumption that transmitter-implanted fish behave similarly to untagged carp, the Judas carp were scouted every morning. When several Judas fish were found in close proximity to each other, one or more gillnets were set around them and the enclosed area electro-fished. Additional gillnets independent of radio-tracking events were deployed randomly about the lake. Soak time averaged 8 h. Backpack electro-fishing was carried out in likely carp habitat such as around fallen timber that was not easily accessible to other fishing techniques. Random seining independent of radio-tracking was also employed when circumstances permitted.

On capture, the sex of adult fish was determined. Those with running milt or ova were recorded as either male or female, respectively, and the remaining deemed as juveniles or undetermined. Adult females were retained and culled to negate future breeding capacity.

Tagging

Running-ripe adult males and juveniles were weighed, measured, anal fin clipped and tagged with a uniquely numbered plastic anchor tag (Hallprint TBF-1 fine T-bar tag inserted using a Dennison 10 312 tagging gun, Miamisburg, OH). The tag was inserted under a scale on the left side of the fish and into the muscle approximately 20 mm below the middle of the dorsal fin. Tags were inserted at a 45° angle to the mid-line and deep enough to ensure that the barb locked behind the pterygiophores (Guy et al., 1996). To detect potential tag loss the anal fin of each of the tagged fish was marked with a hole-punch. A total of 10 adult male carp (Judas) were surgically implanted with unique frequency radio transmitters (Biotel TX2.ICP-1; Biotelemetry Tracking, Adelaide, Australia) inside the body cavity (between the gonad and the inner muscle wall). The procedure was carried out under anaesthesia (AQUI-S; Lower Hutt, New Zealand) 2 months prior to the mark-recapture study. This allowed the radio-tagged fish to recover from the surgical operation and integrate into the population. All radio transmitter implantation activity was carried out either early morning or late evening to minimise stress.

Recapture

The recapture period (4–15 January 1999) utilised the same fishing methods as in the capture period. All caught carp were retained, marks checked (by two independent observers), weighed, length measured and sex recorded. The lake was closed to the fishery and public during the entire eradication period, which ensured that all captures and recaptures were recorded, except for those lost due to natural mortality.

Data analyses

To assess potential gear bias, length frequency distributions of fish caught during both capture and recapture periods were plotted separately. The distribution of the length-frequency data within the sub groups (juveniles or adult males) was subjected to the Skewness–Kurtosis All Normality test using the software DISTRIBUTION ANALYSER 1.2 (Libertyville, IL).

Petersen and Schnabel estimates

Petersen estimates were obtained using the unbiased estimator suggested previously (Chapman, 1951; Seber, 1982) for sampling without replacement:

$$\hat{N} = \frac{(M+1)(C+1)}{(R+1)} - 1 \quad (1)$$

Where M = Number of individuals marked during the tagging period

C = Total number of individuals captured during the recapture period

R = Number of marked individuals caught during the recapture period

The two subgroups (adult males and juveniles) were analysed separately as suggested by Begon (1979). Confidence intervals for the Petersen estimates were calculated using the binomial distribution (Zar, 1996).

Schnabel estimates of the adult male and juvenile population were obtained using the modified formula (Chapman, 1954):

$$\hat{N} = \frac{\sum_t (C_t M_t)}{\sum_t R_t + 1} \quad (2)$$

Where: C_t = Total number of individuals caught in sample t

M_t = Number of individuals marked in the population just before sample t is taken

R_t = Number of individuals already marked when caught in sample t

Multiple marking and recapture events facilitated computation of separate Schnabel estimates for the marking (30 November–16 December 1998) and recapture (4–15 January 1999) periods. Although the same Schnabel formula was used to compute the estimates, the two approaches were distinct in their sampling design, with the former (marking period) involving traditional forward sampling with replacement, wherein the proportion of marked animals in the population increased from zero in the first sampling series with every subsequent sampling series. In contrast, the latter (recapture period) employed a sampling approach without replacement in which the proportion of marked animals remained about the same with each subsequent sampling series. Henceforth these are referred to as forward and reverse Schnabel estimates, respectively. The confidence intervals for the Schnabel estimates were obtained from the Poisson distribution as suggested by Krebs (1999).

As no female carp were tagged and released it was not possible to directly obtain a Petersen or Schnabel estimate of adult female abundance. However, on the assumption that the females are randomly mixed within the general carp population, an indirect estimate of female carp abundance was obtained using the formula:

$$\hat{N}_f = \frac{C_f}{C_m} \times \hat{N}_m \quad (3)$$

Where $\hat{N}_f$ = Estimated number of females

C_f = Number of females captured

C_m = Number of males captured

$\hat{N}_m$ = Petersen / Schnabel estimate of males

Natural mortality

To calibrate and improve the accuracy of the population estimates, we estimated natural mortality rates based on a long-term double tag study. As part of this study a total of 141 adult (3–7 years old) fish ranging from 310 to 535 mm in length were double tagged (one on either side of the fish) with T-bar tags as described above and released in the lake in 2004. Their recapture lasted nearly 4 years, each recaptured fish then removed from the fishery. As proxy to estimate the natural mortality of carp in the lake we used the formula:

$$M = T - (T_c + T_d) \quad (4)$$

Where M = Natural mortality

T = Total number tagged

T_c = Total number recaptured

T_d = Number of fish with double tag loss.

Wherein the number of double tag loss (T_d) was estimated as the estimated number of recaptures, accounting for losses of both tags minus observed recaptures by adopting the equation (Seber, 1982; Krebs, 1999):

$$T_d = c(R_a + R_b + R_{ab}) - (R_a + R_b + R_{ab}) \quad (5)$$

Where

$$c = \frac{1}{1-k} \quad (6)$$

R_a = number of tagged animals in second sample with only an a-tag (i.e. loss of their b-tag)

R_b = number of tagged animals in second sample with only a b-tag (i.e. loss of their a-tag)

R_{ab} = number of tagged animals in second sample with both tags present and

$$k = \frac{R_a R_b}{(R_a + R_{ab}) + (R_a + R_{ab})} \quad (7)$$

Estimation of carp remaining in the lake

To assist the fish-down effort the number of carp remaining in the lake was calculated annually between 1999 and 2007, using each of the three abundance estimators, taking into account the fishing mortality and the natural mortality applying the formula:

$$R_i = R_i - 1 - F_i - N_i \quad (8)$$

Where

R_i = Number of carp remaining in the lake at the end of year i

R_0 = Initial abundance estimate

F_i = Fishing mortality for ith year

N_i = Natural mortality for the ith year.

Results

In general, targeting Judas fish aggregations increased fishing efficiency. The largest proportion of juveniles were caught in the 4″ gillnet (39%), whilst the majority of adult carp were caught in the 5″ or 6″ gillnets (86%). The length-frequency graph of the captured and marked individuals displayed a bimodal distribution broadly corresponding to the juvenile and adult size classes in the population (Fig. 2). Furthermore, the skewness–kurtosis all test results suggests that the length data corresponding to juveniles and adults are normally distributed (P > 0.05). A total of 366 fish were tagged and released (Table 1) – a sample size deemed sufficient to formulate an estimate for management purposes with an accuracy of ±25% for a putative population size of up to 4000 (Krebs, 1999).

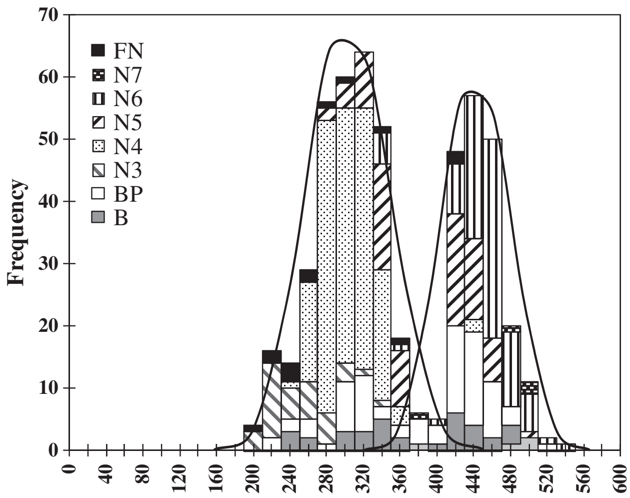

Fig. 2. Gear selectivity and frequency distribution of carp captured during marking period 6 (30 November–16 December 1998). FN, fykenet; N 3–7, 3–7″ gillnet, respectively; BP, backpack seven electrofisher; B, electroboat; S, seine net. Normal distribution of data within sub-groups 8 (juveniles or adult males) tested using software DISTRIBUTION ANALYSER 1.2, with nine Skewness–Kurtosis all, option

Table 1
Number of carp captured, marked and released during tagging period (30 November–16 December 1998)

	Males	Females	Juveniles	Total
No. captured	81	52	298	431
No. released[a]	76	0	290	366

[a]Tagged.

Recapture

During the recapture period (4–15 January 1999) a total of 513 carp were caught: 74 adult females, 124 adult males, and 315 juveniles of which 71 were tagged – 23 males and 48 juveniles (Table 2). The second fishing day yielded 45% of the total fish caught (Table 2). Of the juveniles caught, 55% were in 4″ gillnets whilst 86% of adults were caught in 5″ or 6″ gillnets. Again, the length-frequency graph displayed a bimodal distribution and the skewness–kurtosis all test suggested that the subgroup length data were normally distributed (P > 0.05; Fig. 3).

Abundance estimates

Petersen. Abundances of males and juveniles were estimated separately, as recommended previously (Begon, 1979). As seen in Table 3, the estimated numbers of mature male carp and juveniles were 401 and 1876, respectively. The number of mature females was indirectly estimated to be 239 (Table 3). Post-recapture, all fish caught were removed from the lake.

Table 2
Number of carp caught during recapture period (4–15 January 1999)

Untagged males	Tagged males	Females	Untagged juveniles	Tagged juveniles
101	23	74	267	48

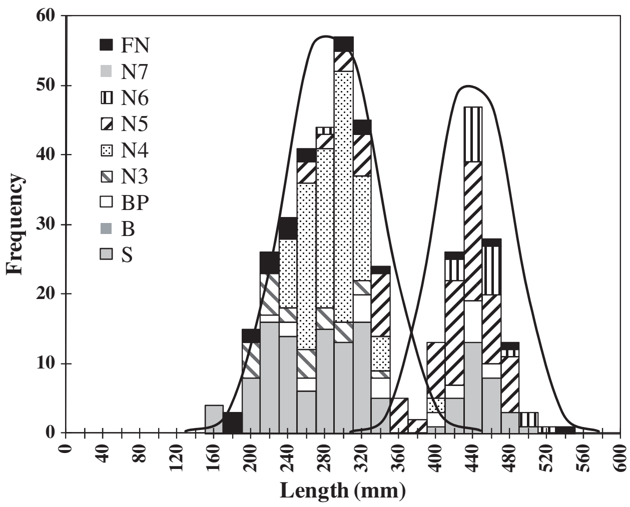

Fig. 3. Gear selectivity and frequency distribution of carp recapture period (4–15 January 17 1999). FN, fykenet; N 3–7, 3–7″ gillnets, respectively; BP, backpack electrofisher; B, 18 electroboat; S, seine net. Normal distribution of data within sub-groups (juveniles or adult 19 males) tested using the software DISTRIBUTION ANALYSER 1.2, with Skewness–Kurtosis all, 20 option

Table 3
Summary of Petersen estimates and estimated number of carp remaining in Lake Crescent, post-mark-recapture study

	Lower 95% CL	Upper 95% CL	Petersen estimate (A)	Number removed (B)	Estimated number remaining (A–B)
Males	281	584	401	124	277
Juveniles	1450	2416	1876	315	1561
Females	167	349	239	74	165
Total			2516	513	2003

Hence, the total juvenile population remaining in the lake at the end of the recapture period was estimated to be 1561 (Table 3). Similarly, adult male and female numbers remaining were estimated at 277 and 165, respectively, with a total of 2003 carp remaining in the lake post recapture (Table 3).

Schnabel. The Schnabel estimator (or weighted mean) was applied to both the marking and recapture periods where the number of marked fish was adjusted on a daily basis. As presented in Table 4, the forward-Schnabel estimates for juveniles, adult males and females were 2073, 581 and 373, respectively. In slight contrast, the reverse-Schnabel estimates for all three subgroups were lower – 1744 juveniles, 356 males and 225 females. Post recapture, the total carp numbers remaining in the lake were estimated to be 2368 and 1811, based on the forward- and reverse-Schnabel estimates, respectively (Table 4).

Natural mortality rate

Of the 141 double-tagged males released in March 2004 a total of 116 (82%) were recaptured by December 2007, as identified by at least a single tag when recaptured. Of these 116 recaptured animals, a total of 25 and 21 individuals had lost only their first or second tags, respectively. In all, 25 of the tagged individuals were unaccounted for. Based on the tag loss frequency it was estimated that a total of seven individuals had lost both tags, leaving the remaining 18 carp presumed to have died due to natural causes, amounting to ≈ 4% annual natural mortality rate.

Table 4
Schnabel estimates for mark (30 November–16 December 1999) and recapture (4–15 January 1999) periods, Lake Crescent

Period	Subgroup	Lower 95% CL	Upper 95% CL	Schnabel estimate (A)	No. removed (B)	Estimated No. remaining (A–B)
Mark (30 November–16 December1998)	Males	303	605	581	124	370
	Juveniles	1420	3524	2073	315	1751
	Females	194	389	373	74	247
	Total					2368
Recapture (4–15 January 1999)	Males	252	574	356	124	230
	Juveniles	1381	2466	1744	315	1429
	Females	159	363	225	74	152
	Total					1811

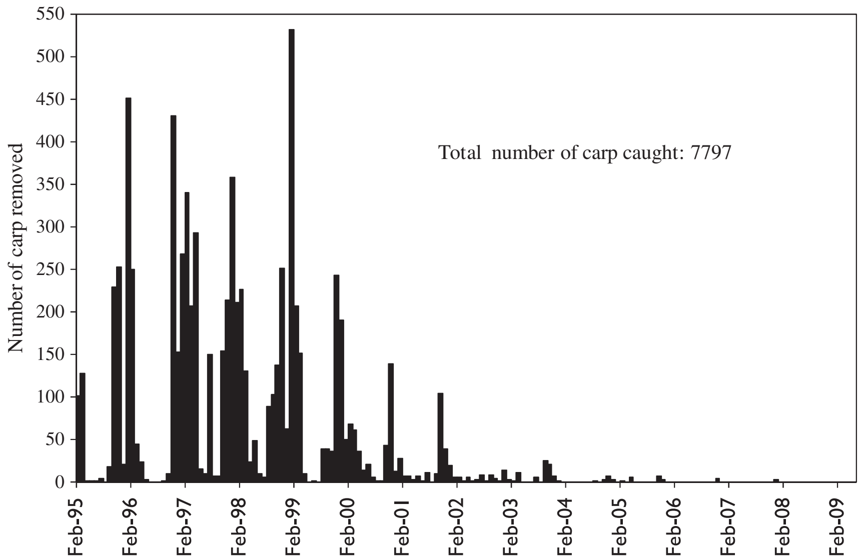

Fig. 4. Monthly carp captures, Lake Crescent, 1995–February 2009

Estimated carp remaining in the lake

A total of 7797 carp were caught in the lake since 1995 (Fig. 4), of which 1809 were caught since completion of the Mark-Recapture study on 15 January 1999. Based on the length–weight and age structure data (not presented), we infer that a total of 67 of these individuals originated from a minor spawning event that occurred in 2001. As is evident from removal data between 1995 and 2009 (Fig. 4), the number of carp caught each month declined over the years, with no carp caught since December 2007, despite continued fishing effort.

Figure 5 presents the predicted number of carp remaining in the lake from 1999 to 2007 based on the three different population estimates, following calibration for annual fishing and natural (4%) mortality. The data suggest that based on the Schnabel estimate on marking and Petersen estimate on recapture period data, a total of 389 (Fig. 5a) and 132 (Fig. 5b) carp, respectively, still remained in the lake at the end of 2007. In contrast, the Schnabel estimate on the recapture period data predicted that only 5 carp remained in the lake in 2007 (Fig. 5c).

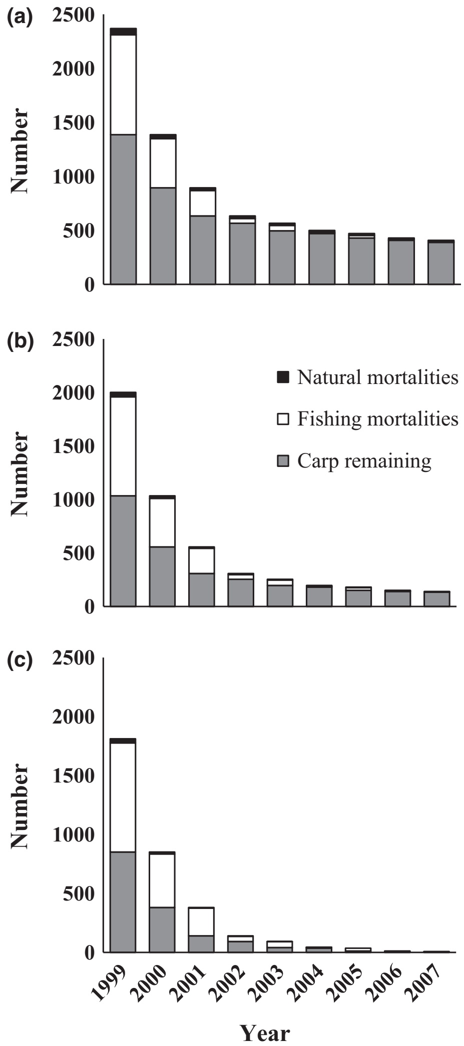

Fig. 5. Estimated number of carp remaining in Lake Crescent following successive seven harvests (fishing mortality), 1999–2007, with annual natural mortality rate ~4%. Projections eight based on Schnabel estimate on marking period data, i.e. Schnabel forward (a) Petersen nine estimate (b) and Schnabel estimate on recapture period data, i.e. Schnabel reverse (c)

Discussion

To meet Petersen's assumptions, the marking and recapture periods need to be completed within a short timeframe (Krebs, 1999) and at the same time attain high sampling proportions to achieve adequate accuracy (Kitada et al., 2001). During the present study, despite the relatively large size of the lake, the entire marking and recapture was carried out with tagging and recapture completed within a 47-day period; marking and sampling was carried out over a period of 13 and 12 days, respectively. This allowed sufficient time (~22 days) for the marked fish to recover post tagging to minimise any behavioural bias between tagged and untagged fish. The 13-day marking period resulted in sufficient carp (366) being caught, tagged and released to formulate an estimate suitable for management purposes, with an accuracy of ±25% for a putative population size of up to 4000 (Krebs, 1999). The proportion of males caught during both marking and recapture periods was significantly higher than the females. This bias was expected in the case of recapture data, as females were retained and killed during the marking period whereas all captured running-ripe males were tagged and released to facilitate the mark-recapture study. However, the observation of biased sex ratios in the marking period data is intriguing. It is possible that this may reflect the true population sex ratio, skewed in favour of males, or that the bias may have crept in as a result of technical limitations of the non-invasive sexing technique adopted, wherein males can be more readily sexed and also reach sexual maturity earlier than females (Alikunhi, 1966; Hume et al., 1983). The latter is more likely, as the cumulative sex ratio of all adults larger in size at first sexual maturity that were obtained post sacrifice suggests the population sex ratio of carp in the lake was nearly equal (50 : 50).

Accuracy of the estimators

In addition to a robust experimental design (Bryant, 2000), a rigorous implementation is required to avoid violation of the assumptions and obtain higher estimation accuracies. Accounting for the female fish removed during the marking period, the Petersen estimate predicted that about 2003 carp were remaining in the lake in 1999. Similarly, the forward- and reverse-Schnabel estimates were 2368 and 1811, respectively. Since then, 1746 carp from the cohorts present at the time of the study were removed from the lake, plus 67 carp from a cohort spawned in 2001. Sustained fishing effort using traps and Judas fish aggregations (25 occasions) from December 2007 to the present has not resulted in capture of any feral carp. Further recent fyke net monitoring of the lake, random electro-fishing and spot rotenone poisoning through most of the Austral spring–summer spawning season of 2009–2010 have resulted in no juvenile or adult carp caught. If any carp were still remaining in the lake one would have expected the population to bounce back, given the very favourable breeding conditions over the last 2 years. Collectively these observations indicate that there are no more carp remaining in the lake. This likely total eradication of carp from the lake provided an opportunity to validate the accuracy of the population estimates carried out in 1999.

Based on the long-term double tag study we estimate a natural mortality rate of 4% per annum. Although a wide range (3–94% per annum) of natural mortality for carp (Clapp et al., 1994; Brown et al., 2005; Balik et al., 2006; Kolaneci et al., 2010) have been reported, typically double digit values correspond to early larval stages. Also these estimates pertain to natural populations, with multiple cohorts typically dominated by zero year classes, unlike the population in Lake Crescent that was restricted to individuals 2 years or older. Further, in the absence of any natural aquatic predator, or known carp diseases in this isolated population, a low mortality rate (4% per annum) is realistic. Assuming that there are no carp remaining in the lake and in retrospect allowing for a 4% natural mortality rate, all three estimates are slightly positively biased but are well within 20% accuracy. The Petersen estimate is approximately 6.6% (Fig. 5a) above the reconstructed number in the original cohorts, whereas the Schnabel marking and recapture period estimates are approximately 16.4% (Fig. 5b) and 0.5% (Fig. 5c) over the reconstructed population number, respectively. The natural mortality estimates make only a small fraction of these reconstructed numbers and do not affect the conclusion of the relative accuracies of the three methods used. The greater accuracy of reverse Schnabel and the Petersen estimates compared to the forward Schnabel suggest that these approaches better satisfy the underlying assumptions. Whilst the forward Schnabel can be achieved at lower cost and shorter time, it compromises accuracy that might lead to increased management costs. We therefore recommend the use of the reverse Schnabel approach perhaps in conjunction with Petersen estimate in any future fish population estimation studies.

Compliance of Petersen's assumptions

The assumption of a closed population appears to have been met by the fine mesh screens that prevented any migration to or from the lake. Also the fishery was closed to the public throughout the eradication programme (1995–2007), mitigating the risks of inadvertent translocation. A combination of management practices and a prolonged period of drought effectively ensured that no new recruitment occurred in the lake. Violation of the closure assumption due to deaths appears minimal, given an estimated annual natural mortality of about 4% (which equates to < 10 fish for the study period).

The assumptions of equal catchability and random distribution of marked and unmarked fish were facilitated by deploying a multitude of gear types in combination with the radio-transmitter Judas carp technique. Equal catchability implies that the population is sampled randomly (Begon, 1979). This is demonstrated by bimodal length-frequency data corresponding to juveniles and adults observed in this study (Figs 2 and 3). Each of these modes exhibits near normal distribution during both mark and recapture periods, suggesting minimal catchability bias. The use of the Judas carp technique to target carp aggregations during both mark and recapture periods greatly assisted this study. During the 13 years of deploying and monitoring Judas carp in the lakes it has been found that neither surgical operations, implantation of radio transmitter nor confinement for long periods away from the lake appear to alter their behaviour. Instead, they quickly mix and mingle with wild carp, as demonstrated by their lake-wide movements and successful betrayal of wild carp locations time and again (to be published elsewhere).

The assumptions of zero tag loss and correct reporting of marks were addressed by fin clipping (second marker) and using a second observer. However, the fin clipping technique used in this study was inadequate, as the fins regenerated during the study period. It is possible that some tag (T-bar tag) losses occurred and were not reported. This is likely to be low, particularly over the relatively short study period as our long term-double tag study suggests – average ~5.25 and 4.5% per annum for tag 1 and tag 2, respectively, and particularly low in the first year. We recommend using a more reliable permanent marker such as an opercular punch or injectable dye in conjunction with a T-bar tag in any future studies.

The greater accuracy of the reverse-Schnabel estimate (~0.5% bias from reconstructed) compared with the forward (mark period) based estimate (~16.5% bias from reconstructed) could be explained by a relatively greater proportion of marked fish (Figure. S1) and a prolonged period (~22 days) between mark and recapture, facilitating adequate acclimation of the marked fish and thus minimising potential bias associated with heterogeneity of capture probability between marked and unmarked fish. Typically, a standard procedure for Schnabel estimates is to base the study on a single series of mark-capture days in which the total daily marked individuals accumulate progressively from zero on the first day. From a capture point of view the forward-Schnabel process could bias the outcome of the estimates in two ways: either (i) negatively as a result of limited opportunity for tagged animals to recover sufficiently, instead rendering them more susceptible for recapture, or (ii) positively as a result of cognitive ability of the animals to learn and evade recapture or insufficient opportunity to reintegrate into the population, or a combination of both. In this study, the standard (forward) Schnabel estimate was positively biased compared to the recapture period (reverse) Schnabel estimate, suggesting that the marked carp were not preferentially susceptible to recapture post marking. The positive bias therefore is likely to have arisen as a result of either insufficient time for the marked animals to reintegrate into the population and/or a proportion of the marked animals had learnt to evade recapture. The reverse-Schnabel estimate was also closer to the reconstructed abundance than the Petersen estimate, suggesting that there is a distinct advantage of greater accuracy in a reverse-Schnabel estimator being used, in preference to a standard forward-Schnabel or a Petersen estimate. While the computational advantage of a standard (forward) Schnabel estimate over the Petersen estimate has been acknowledged (Begon, 1979), this study demonstrates that a greater accuracy can be achieved by adopting a reverse-Schnabel approach.

Conclusion

The present study provides the first practical demonstration that it is possible to accurately estimate fish population abundance in relatively large lakes employing simple computation models as proposed by Petersen in 1896 (Ricker, 1975) and/or Schnabel (1938). The deployment of a combination of gear types effectively minimised the capture bias, and the use of Judas fish technique greatly increased the capture efficiency, thus minimising the duration of capture and recapture whilst achieving required sampling proportions. In a novel approach the present study demonstrates that the reverse-Schnabel estimate without replacement, carried out with separate mark and recapture events interspersed with adequate recovery period, provides a more accurate population estimate. These population estimates assisted in making several informed management decisions throughout the carp eradication programme in the lake (including effort required to eradicate and time to fish-down a cohort) and allowed comparison of routine CPUE data within and between lakes. More significantly, the estimates were central to support the recent management and legislative decisions to declare the lake free of carp and its reopening to the public for fishing and recreational activities. Collectively the methods and results presented here provide a practical and reliable framework for accurate estimation of fish, and more specifically carp populations, in closed water bodies elsewhere.

Acknowledgements

The authors thank members of the Carp Management Programme for the field assistance and input and IFS staff for support. Andrew Taylor assisted in generating the lake map. The Invasive Animal CRC provided funding support over the last year.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Simulated proportion of tagged fish at each sampling event, given a population size of 1000, and 20% tagging and recapture rates.

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