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Restoring depleted coral-reef fish populations through recruitment enhancement: a proof of concept

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To determine whether enhancing the survival of new recruits is a sensible target for the restorative management of depleted coral-reef fish populations, settlement-stage ambon damsel fish *Pomacentrus amboinensis* were captured, tagged and then either released immediately onto small artificial reefs or held in aquaria for 1 week prior to release. Holding conditions were varied to determine whether they affected survival of fish: half the fish were held in bare tanks (non-enriched) and the other half in tanks containing coral and sand (enriched). Holding fish for this short period had a significantly positive effect on survivorship relative to the settlement-stage treatment group that were released immediately. The enrichment of holding conditions made no appreciable difference on the survival of fish once released onto the reef. It did, however, have a positive effect on the survival of fish while in captivity, thus supporting the case for the provision of simple environmental enrichment in fish husbandry. Collecting and holding settlement-stage fish for at least a week before release appear to increase the short-term survival of released fish; whether it is an effective method for longer-term enhancement of locally depleted coral-reef fish populations will require further study.

Key words: behaviour; enrichment; *Pomacentrus amboinensis*; recruitment; restorative management; settlement-stage coral-reef fishes.

INTRODUCTION

Worldwide, coral reefs are in decline (Carpenter *et al*., 2008), one consequence of which is the decrease in abundance and diversity of fishes (Wilson *et al*., 2006). Most susceptible are fish species that have obligate coral associations, particularly those whose larvae settle onto live coral (Jones *et al*., 2004). There are two general

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responses to managing this demise. The first is the use of zoning plans and marine protected areas, which provides the opportunity for natural ecosystem regeneration by restricting access and decreasing anthropogenic activities on reefs. The second is a more interventionist approach, by attempting to restore the communities that inhabit reefs. This has included efforts to repair or replace the coral matrix through transplants and the provision of artificial settlement sites (Rinkevich, 2005; Shaish *et al*., 2008) and attempts to enhance depleted populations through the release of individuals into the wild. This technique is referred to as stock enhancement, which in the context of reefs, has thus far largely focused on invertebrate species (giant clam, subfamily Tridacninae, Gomez & Mingoa-Licuanan, 2006; sea cucumber, *e.g. Holothuria scabra*, Purcell & Simutoga, 2008). The few examples of attempts to repopulate fish communities have used species that associate with corals only transitorily, for example, the Pacific threadfin *Polydactylus sexfilis* (Valenciennes) and the red snapper *Lutjanus campechanus* (Poey) (Friedlander & Ziemann, 2003). Despite being an integral part of their ecosystem, there are no data on enhancement programmes for obligate coral-reef fishes.

There are reservations over active management approaches such as this because they do not directly address the primary causes of degradation, *e.g.* habitat and live coral loss through climate change induced warming, pollution and over-fishing (Jameson *et al*., 2002; Graham *et al*., 2006; Newton *et al*., 2007). Stock enhancement, like reef restoration, however, may be a useful supplementary management tool (Edwards, 2008; Mumby & Steneck, 2008). Empirical studies are required to determine whether this is the case, particularly because it remains a practiced yet unproven technique (Sadovy, 2005).

Coral-reef fishes have a pelagic larval and benthic adult stage, experiencing an estimated mortality rate of *c.* 60% during settlement (Doherty *et al*., 2004; Almany & Webster, 2006). The release of juveniles from cultured wild-caught or hatchery-reared larvae into recruitment limited populations (as many coral-reef fish populations are) can bypass or reduce this mortality bottleneck that occurs at settlement (Bell *et al*., 2008). This, in combination with the highly effective methods available for collecting coral-reef fishes from a great variety of families during or just prior to settlement, *e.g.* light traps, crest nets and hoa nets (Doherty, 1987; Dufour & Galzin, 1993), makes settlement larvae an ideal life-history stage on which to focus attempts to enhance depleted fish communities.

As predation is the main threat to settlement-stage fish survival (Planes & Lecaillon, 2001), simply using light-attracting devices to increase the recruitment rate of settlement-stage fishes to localized patches on a reef will not necessarily lead to a sustained increase in population size (Munday *et al*., 1998). Indeed, an increase in recruitment of fishes at this stage may well result in higher abundance of their gape-limited predators and, therefore, increase recruit mortality (Munday *et al*., 1998). In temperate stock-enhancement programmes, predation is the main cause of the high mortality experienced by released fishes (Olla *et al*., 1994; Brown & Laland, 2001; Salvanes & Braithwaite, 2006). Survival of released fish can be significantly increased by holding fish in conditions that stimulate their behavioural development, *e.g.* exposure to predators, altering the spatial or temporal distribution of food, manipulation of the social environment and the provision of natural habitat refugia (Olla *et al*., 1998; Brown & Laland, 2001).

The aim of this study was to determine whether enhancing recruitment could be used to assist depleted populations of obligate coral-reef fish species. To examine whether the high level of settlement-stage mortality could be alleviated, wild-caught larvae were held captive for a short period and then released onto the reef. If holding fishes captive during the vulnerable stage around metamorphosis makes them less susceptible to predation, then the prediction would be for higher survival rates in the fishes that were held prior to release, relative to those released immediately. The conditions in which fishes were held captive were manipulated, to determine whether tank variability leads to increased survival in released fishes, as it does for the North Sea cod *Gadus morhua* L. (Braithwaite & Salvanes, 2005). If being held in phsycosensorily deprived conditions leads to behaviourally deficient animals (Olla *et al*., 1998), then the prediction would be for higher survival rates in fishes that were held in tanks enriched with habitat refugia relative to those held in bare tanks.

MATERIALS AND METHODS

The ambon damsel *Pomacentrus amboinensis* Bleeker was the study subject. These fish can be caught in abundance during their summer breeding period in light traps, which can be used to collect fish just prior to settlement on the reef (Meekan *et al*., 2001). *Pomacentrus amboinensis* is common to the Great Barrier Reef, where like most Pomacentridae, it represents an important part of the total fish biomass (Ackerman & Bellwood, 2000). As a protogynous hermaphroditic species (Jones, 1987), males guard the nest in which females lay demersal eggs. The eggs hatch 4–5 days later and the larvae then spend 15–23 days off the reef in pelagic water, after which time they return to the reef to settle, typically to small reef patches on the reef base or slope where there is a mixture of live coral, sand and rubble (Kerrigan, 1996; McCormick & Makey, 1997). This species undergoes a high mortality bottleneck in the days immediately following settlement, when up to 75% of young fish may be removed by predators (Almany, 2004). Their main predators are the dusky dottyback *Pseudochromis fuscus* Müller & Troschel, the rockcod *Cephalopholis boenak* (Bloch), moonwrasse *Thalassoma lunare* (L.) and two species of lizardfish *Synodus variegatus* (Lacépède) and *Synodus dermatogenys* Fowler. All are either site-attached or home ranging (Holmes & McCormick, 2006; McCormick & Holmes, 2006). A further useful feature of the *P. amboinensis* is that it remains attached to the site once settled (McCormick & Makey, 1997), allowing for the assumption that once fish were released onto patch reefs they would remain in place, unless eaten.

Settlement-stage *P. amboinensis* were caught using light traps deployed before dusk (1830 hours) and collected after dawn (0600 hours) from permanent moorings in 10–15 m depth over a sandy substratum, in the near-shore waters of Lizard Island Research Station (14° 14′ S; 145° 26′ E) from the 22 to 27 November and the 8 to 12 December 2007. Settlement-stage *P. amboinensis* were separated from the rest of the catch and placed in shaded outdoor aquaria supplied with aerated flowing sea water at an estimated density of 200 fish per 40 l tank.

A pilot study carried out in November 2007 was used to determine the release protocol, and the frequency and duration of visual counts needed to assess post-release survival. Mixed species groups of *P. amboinensis* and the lemon damsel *Pomacentrus molucensis* Bleeker were used, as too few *P. amboinensis* were available for these trials. *Pomacentrus molucensis* are similar in size at settlement to *P. amboinensis* (mean standard length, L_S, *P. amboinensis*: 11·5 mm and *P. molucensis*: 11·3 mm; McCormick *et al*., 2002). At settlement, *P. molucensis* will only settle on live coral, typically on areas of continuous reef (Booth, 2002) but also isolated coral bommies (Figuira *et al*., 2008). *Pomacentrus amboinensis* is more of a settlement generalist, settling to live coral and rubble on continuous reef and patches (McCormick & Makey, 1997; Booth, 2002). These broad similarities at settlement made *P. molucensis* a sufficient substitute for the purposes of a pilot study. In this 12 day pilot trial, the greatest rate of mortality occurred during the first 2 days following release (on average 25% loss). The rate of mortality then reached a plateau, decreasing by 2% (of the original number released) over the remaining 10 days. Based on this information, survival of *P. amboinensis* in the full experiment was measured on days 1 and 2 by three visual surveys (at 0600, 1200 and 1700 hours), on day 3 by two surveys (0600 and 1700 hours) and then once daily (0600 hours) for a further 5 days, for a total of 8 days.

In December 2007, single species experimental trials using *P. amboinensis* were conducted. On the morning of capture (day 0), fish were randomly allocated to one of three treatment groups, then tagged and photographed for measurement as follows. Each fish was placed into a plastic click-seal bag (size: 9 cm × 12 cm) containing aerated sea water and placed flat on its side on top of a laminated piece of graph paper. Fish were digitally photographed using an Olympus Camedia C-5000. The camera was positioned *c*. 30 cm above the fish with both the fish and the graph paper in focus. The $L_S (\pm 0{\cdot}01$ mm) were measured from the photographs using Image-J (Rasband, 1997–2009; http://rsb.info.nih.gov/ij). The same observer measured fish throughout the experiment to reduce between-observer variation. Using a 29-gauge hypodermic needle, fish were tagged through the plastic bag with a subcutaneous fluorescent elastomer tattoo (Northwest Marine Technology; www.nmt-inc.com). Tag colours (blue, orange, pink and yellow) were alternated among treatment groups to reduce any potential interaction between predation rate and colour. Tagging of fish allowed any movement between neighbouring patches to be detected and enabled the identification of released fish.

Settlement-stage fish selected for the experiment were randomly allocated to three treatment groups: (1) released the day after capture and referred to as settlement-stage, (2) held for 7 days in enriched tanks and (3) held for 7 days in non-enriched tanks, together referred to as captive held. There were four replicates per treatment group, each containing 30 fish (360 fish in total). Four aquaria were modified so that they could each house one enriched and one non-enriched replicate group separately. Silicone sealant was used to fix a single opaque Perspex divider, creating two separate holding areas per aquarium (dimensions 30 cm × 15 cm × 20 cm). Each half had an independent supply of fresh aquarium-supplied sea water and an outflow standpipe which maintained the water at 15 cm depth. On the enriched side, the aquarium was lined with sand and had a live cauliflower coral *Pocillopora damicornis* coral head (*c*. 8 cm × 8 cm × 8 cm) positioned in the centre of the tank, while the non-enriched side of the aquaria was left bare.

Settlement-stage fish were not fed during the time they spent in the laboratory and were released the day after capture (day 1). Fish held for >24 h (captive-held) received their first feed the day after capture (day 1) and were fed twice daily (0600 and 1800 hours), receiving their last laboratory meal at 0600 hours on the day of their release (day 8). They were fed 40 ml of 12–16 h old *Artemia* sp. nauplii (density: *c*. 2000 individuals per 1 ml sea water).

The release protocol was identical for all three treatment groups. The exception to this was that the captive-held fish were photographed again *c*. 4 h prior to release on day 8. At 12 h before fish were released, the patch reefs were cleared of existing *P. amboinensis* using an anaesthetic consisting of a mixture of clove oil (eugenol 85–95%), alcohol (98% ethanol, 2% methanol) and fresh sea water (ratio 0·005: 0·05:1) (Munday & Wilson, 1997). On the day of release, fish were placed in open 8·5 l plastic click-seal bags (one bag per replicate group containing 30 fish) filled with aerated water. Bags were sealed for transport and taken to the patch reef site and fish were released between 1600 and 1700 hours. Fish were released onto small artificial patch reefs that had been built on a 4–5 m depth sandy bottom in the Lizard Island lagoon (14° 41′ S; 145° 28′ E). One treatment replicate group was released per patch. Reefs consisted of a coral rubble base (60 cm × 40 cm × 20 cm) with a live *P. damicornis* coral head (*c*. 20 cm × 20 cm × 20 cm) positioned on top. For 1 h following release, wire cages (100 cm × 100 cm × 100 cm, mesh size: 5 mm) were positioned over each patch reef to exclude predators, after which the cages were removed (McCormick & Meekan, 2007).

Patches were arranged in rows with 5 m within and between rows. As newly settled *P. amboinensis* tend not to move >0·5 m in the first week following settlement (McCormick & Makey, 1997), the 5 m separation was assumed sufficient to prevent between-patch migration, and tagging of fish allowed this to be tested. Each treatment group was represented on every row away from the reef edge (distance 20, 25, 30 and 35 m), except 30 m where there was a settlement-stage group alone. The final number of treatment group replicates was: settlement-stage = 4, enriched = 3 and non-enriched = 3. This was due to the loss of one enriched and non-enriched replicate group during the captive period, as the tank was inadequately sealed allowing fish to pass between the enriched and non-enriched sides of the tank.

Released fish were surveyed for 8 days as described above. On the final day, survivors were collected using clove oil and transported back to the aquarium in 8·5 l click-seal bags where they were photographed again.

The treatment effect on fish survivorship was examined using survival analysis. Data were right-hand censored, as some individuals outlived the study, and interval-censored as survival of released fish was recorded at set time increments, *i.e.* the time of death was unknown but was bounded between observation periods. To obtain the significance levels for the explanatory variables, deviance statistics generated from models with and without the explanatory variables were compared using χ^2-tests. Survivorship is not a linear function of age, as the risk of mortality decreases with time after settlement. This was assessed in a preliminary model comparison, where the Weibull error distribution (non-constant survivorship) had a greater explanatory power for the variance in the data than an exponential (constant survivorship) error distribution (χ^2, d.f. $= 1$, $P \leq 0{\cdot}01$). A *post hoc* assessment of the within-tank mortality of the captive-held fish was made, where the proportion of fish remaining alive after 7 days in captivity in the different tank treatments (enriched or non-enriched) was compared using a Kruskal–Wallis test.

Differences in L_S among treatments were compared using one-way ANOVA at the different experimental stages (capture, release and recapture). Significant effects were further explored using *post hoc* Tukey's HSD tests to determine which treatment groups differed in L_S. All analyses were implemented in the R environment (R; http://www.r-project.org), using the R package survival (S original by Terry Therneau and ported by Thomas Lumley).

RESULTS

Irrespective of holding conditions, the survival of fish from the combined captive-held treatment groups was higher than that of the settlement-stage treatment group that were released immediately onto patch reefs [Survival analysis (Weibull error distribution), $P < 0{\cdot}01$; Fig. 1]. After 8 days on the patch reefs, 24% of the settlement-stage treatment fish had survived, while 40% of the non-enriched and 60% of the enriched individuals survived (inclusive of any within-tank mortality experienced during the 7 day holding period). This difference in survival on the patch reefs between fish held in the enriched or non-enriched conditions was not significant (χ^2, d.f. $= 1$, $P > 0{\cdot}05$); however, a comparison of their survival during the 7 days spent in captivity showed that fish held in non-enriched tanks suffered greater mortality than those held in the enriched tanks (Kruskal–Wallis, d.f. $= 1$, $P < 0{\cdot}05$). There was no effect of tag colour (χ^2, d.f. $= 1, 3$, $P > 0{\cdot}05$), and the distance of experimental patch from the lagoon reef edge (χ^2, d.f. $= 1, 3$, $P > 0{\cdot}05$) also did not affect the survival of released individuals for all three treatment groups. No between-patch movement was detected from the coloured tags present on the fish.

There was no difference in the mean L_S of fish at the start of the experiment when they were allocated to different treatment groups [one-way ANOVA, d.f. $= 2, 7$, $P > 0{\cdot}05$; Fig. 2 (capture, day 0 for all treatment groups)]. A test for normality showed that the non-homogeneity in variance of size distribution of fish at the release stage was not significant (Bartlett test K-squared, d.f. $= 2$, $P > 0{\cdot}05$). At the point of release, after 7 days in captivity, there was a main effect of treatment group on the L_S of fish [one-way ANOVA, d.f. $= 2, 7$, $P < 0{\cdot}01$; Fig. 2 (release, day 1 for the settlement-stage fish and day 8 for the captive-held fish)]. The settlement-stage fish that were 7 days younger at the time of release were smaller than fish

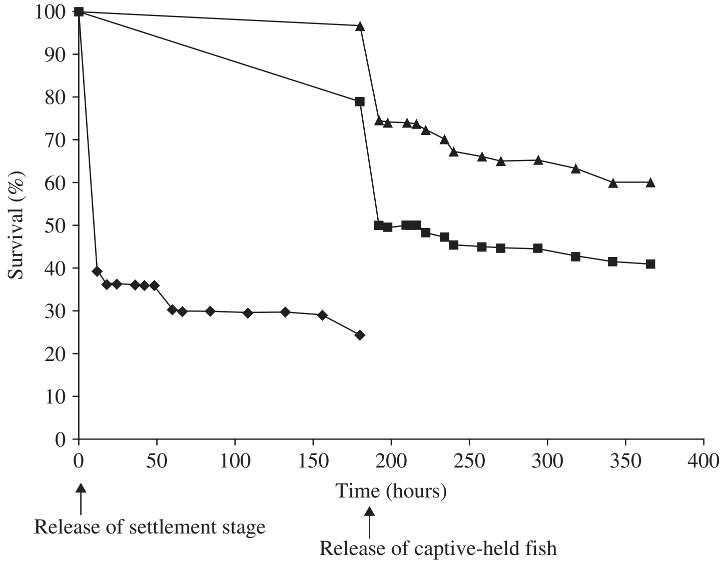

FIG. 1. Percentage survival per treatment group. The settlement-stage *Pomacentrus amboinensis* (—◆—) were released within 36 h of capture, while the non-enriched (—■—) and enriched (—▲—) treatment groups were released after 7 days captivity in aquaria (↑, release times). The total number of individuals captured and released per treatment group: settlement-stage (131 at capture, 130 at release), non-enriched (90 at capture, 71 at release), enriched (90 at capture, 87 at release).

held in captivity (Tukey's HSD, $P < 0{\cdot}05$). Enriched and non-enriched fish did not differ in size (Tukey's HSD, $P > 0{\cdot}05$). At recapture, after 8 days on the patch reefs, the captive-held fish (enriched and non-enriched) were significantly larger than the settlement-stage fish (one-way ANOVA, d.f = 1, 6, $P < 0{\cdot}05$; Fig. 2). Recapture was 8 days after initial capture for the settlement-stage and 15 days for the captive-held fish.

DISCUSSION

Fish that were held for 7 days in captivity prior to release had significantly increased survival when released onto patch reefs in comparison with fish released immediately after capture. Survivorship was improved by 16–36%. This major effect on survivorship following the relatively minor intervention of holding fish captive for a week led to increased survival of *P. amboinensis*. Artificial enhancement is a common technique for commercially fished species. This study demonstrates that by assisting fishes through vulnerable settlement and metamorphosis processes, the immediate survival of new recruits can be increased, and hence enhancement may be a useful tool for the conservation of coral-reef fishes. Holding conditions had no effect on survival once released onto the reef; however, during captivity fish kept in bare tanks survived less well than fish kept in tanks containing pieces of coral. This suggests there is merit in including psychosensory enrichment in the holding conditions in fish husbandry.

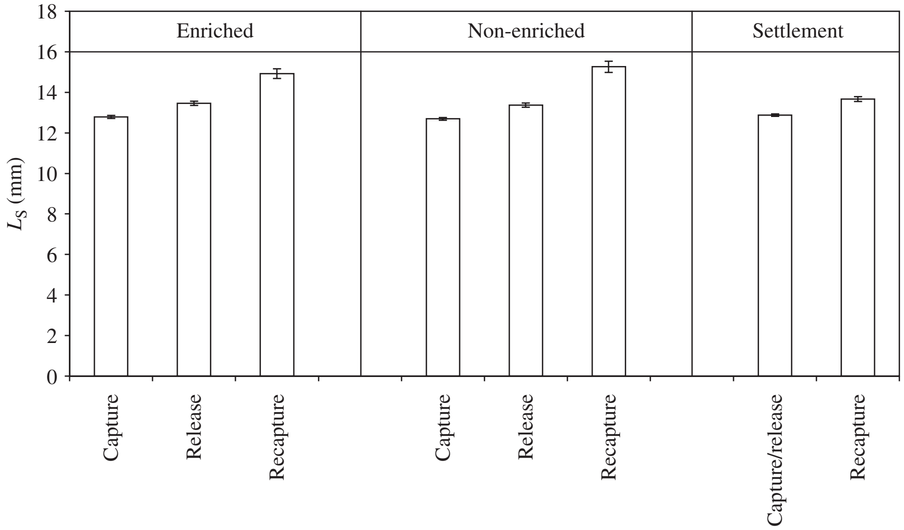

FIG. 2. The size of *Pomacentrus amboinensis* measured in standard length (L_S) with a panel per treatment group. Fish were either held for 7 days in tanks with enriched or non-enriched conditions, or released straight after capture (settlement-stage). The L_S measurements were taken at three stages, at the time of collection from the light traps (capture), at release onto the patch reefs (release) and at recapture after 7 days on the patch reefs (recapture). As the settlement-stage treatment group were released immediately after capture, the capture and release measurements are the same (capture–release); therefore, the age of the settlement-stage fish at this stage is equivalent to the tank-held fish at the release stage.

The chief advantage of holding fishes is that it confers higher survival once they are released onto the reef, potentially through a reduction in vulnerability to predation. This is inferred from a predator-exclusion experiment that identified predation on metamorphosing fishes as the major cause of mortality in settlement-stage pomacentrids when fishes were released into cages containing patch reefs with or without natural predators (Planes & Lecaillon, 2001). Over a period of 48 h, fishes released onto predator-free patches experienced a 14% mortality rate in contrast to fishes released on to the patches containing predators, where mortality ranged from 29 to 76%.

Releasing fishes immediately after capture directly onto a particular area (Munday *et al*., 1998), led in this experiment at least, to poorer survival in the immediately released fishes relative to fish held captive for a week. In order to enhance recruitment artificially on a small scale, it is better to hold fish captive for a short period, as *P. amboinensis* experiences its highest mortality risk at settlement (Almany, 2004; McCormick & Hoey, 2004). Fish were held in captivity beyond that peak (2 days following settlement; Almany & Webster, 2006) and those that survive through this critical period are likely to persist in the long-term.

Irrespective of whether fish were released immediately or were held in captivity, average L_S increased during the first 8 days following initial capture. Hence, by the time of release the captive-held fish were larger than the settlement-stage fish. *Pomacentrus amboinensis* undergoes size-selective mortality at settlement. The direction (positive and negative) of this process can vary (Hoey & McCormick, 2004;

Gagliano & McCormick, 2007) and is thought to be driven by predation. Whether settlement mortality is selective for smaller individuals can depend on physiological and morphological traits, *i.e.* the individual fish condition (Hoey & McCormick, 2004) and also on the predator conditions into which fish recruit (Holmes & McCormick, 2006). It would appear that a period of alleviated predator-stress in captivity allowed fish to increase in size, allowing the captive-held fish to successfully evade predation once released onto the reefs.

The possibility cannot be excluded that the greater mortality suffered by the immediate-release group was a result of these fish still recovering from a stress response to the handling and tagging procedure. Although this may have had an effect, these fish experienced similar levels of mortality (76%) as those previously reported during the natural settlement of damselfish (Pomacentridae) onto patch reefs in the presence of predators (*c*. 75%; Almany, 2004). If handling and tagging were detrimental, this should have resulted in an increase in mortality over and above this level.

It is not clear whether less common larger fish, which are not as site-attached immediately after settlement, would respond as positively to the experimental protocol. Furthermore, it is also not clear how the tank environment contributed to enhanced survival on release. During this study, rough weather conditions led to low larval catch rates, preventing the further replication needed to test whether the tendency for higher survivorship in the enriched holding conditions was biologically significant. As the within-tank mortality of fish held in enriched tanks was lower in comparison with the non-enriched tanks; this demonstrates that there is merit in providing fish with structure while in captivity. One theory is that artificial rearing conditions cause the production of behaviourally deficient or modified animals (Olla *et al*., 1998; Brown & Laland, 2001; Hawkins *et al*., 2008). This has been demonstrated for behavioural traits likely to affect survival in the wild such as foraging behaviour in *G. morhua* (Braithwaite & Salvanes, 2005). It seems plausible that providing some structure to the tank allowed fish to hide from conspecifics, leading to lower stress levels and therefore lower levels of mortality while in captivity and possibly to lower predation upon release.

Pomacentrus amboinensis was used in this study because it can be readily caught at the settlement-stage and is amenable to experimentation. Although they do not form part of commercial food fisheries, in many countries they are an important ecological component of the reef fish assemblage, being the second most abundant family and making the greatest contribution to biomass production (Depczynski *et al*., 2007). Pomacentrids also represent 47% of the global export of marine ornamental fishes for the aquarium trade (Wabnitz *et al*., 2003). These findings are therefore relevant for the conservation of reef fishes by providing a management model that may be relevant to commercially harvested fishes, and a demonstrated tool for less commercially exploited, but ecologically important, species.

Attempts to restore and enhance natural recruitment have proved successful for corals (Heyward *et al*., 2002; Amar & Rinkevich, 2007), but have rarely been trialled for reef fishes (Sadovy, 2005). This study has demonstrated that holding settlement-stage coral-reef fishes for as little as a week leads to a significant increase in survival. Therefore, this may be a promising method for use in attempts to increase population numbers in commercially important or endangered reef fish species.

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