Journal of Fish Biology (2002) 61, 987-998
doi:10.1006/jfbi.2002.2114, available online at http://www.idealibrary.com on IDEAL®

Social enhancement and social inhibition of foraging behaviour in hatchery-reared Atlantic salmon

C. BROWN* AND K. LALAND
Sub-Department of Animal Behaviour, University of Cambridge, Madingley, CB3 8AA, Cambridge, U.K.

(*Received 8 April 2002, Accepted 19 August 2002*)

The results of two experiments showed that observation of a trained conspecific Atlantic salmon *Salmo salar* significantly increased the rate at which naïve hatchery-reared fish accepted novel, live prey items, whereas the presence of an untrained conspecific actually decreased learning rates due to social inhibition. Pre-release training involving exposure of hatchery-reared fish to live prey items in the presence of pre-trained demonstrators would probably result in a significant enhancement in their foraging success on release and help prevent starvation, which is thought to be one of the principal causes of post-release mortality.

Key words: social enhancement; inhibition; Atlantic salmon; foraging; hatchery.

INTRODUCTION

In recent years attempts have been made to counteract the decline in marine and freshwater fish populations resulting from habitat destruction and over-exploitation (Huchings, 2000). Alongside management actions, such as tightening quotas and protecting habitats, fishes have also been reared in hatcheries and released into the wild in an attempt to supplement wild stocks (mitigation). Today many countries in the world are engaged in stock enhancement programmes with $>$300 species involved (Welcomme & Bartley, 1998; Brown & Laland, 2001). Some of the better-known examples include flounders, sturgeons and salmonids.

With few exceptions (Eriksson & Eriksson, 1993; Kitada *et al.*, 1992), restocking has made little impact on the number of fishes recruited into fisheries. It is widely known that the survival of hatchery-reared fishes is extremely poor. The number of surviving hatchery-released Pacific salmon (*Oncorhyncus* spp.) across the globe, for example, is estimated to be $<$5% (McNeil, 1991). This figure is especially low if the age and size at which the fishes are released are considered and far lower than wild fishes of similar age (Wales, 1954; Heggberget *et al.*, 1992). Most of the mortality occurs within the first few days after release, which suggests that mortality is principally caused by predation rather than starvation (Brown & Day, 2002). Nevertheless, those fishes that do survive attacks by predators will soon have to begin feeding if they are going to avoid

---

*Author to whom correspondence should be addressed. Present address: Institute of Cell, Animal and Population Biology, University of Edinburgh, Edinburgh, EH9 3JT, U.K. Tel.: + 44 (0) 131 650 8667; fax: + 44 (0) 131 650 6564; email: CulumBrown@Yahoo.com

0022–1112/02/000000+00 $35.00/0

starvation (Ersbak & Haase, 1983). Poor condition due to a lack of foraging success almost certainly contributes to the vulnerability of hatchery-reared fishes to predators, and starvation is often sited as one of the principal causes of mortality in released fishes (Paszkowski & Olla, 1985; Suboski & Templeton, 1989).

Foraging behaviour in fishes is fine-tuned through learning (Hughes *et al.*, 1992; Kiefer & Colgan, 1992). Appropriate early experience is essential if individuals are to learn where to eat, what to eat and how to eat it (handling) and as such learning is intimately connected with ontogeny (Paszkowski & Olla, 1985; Coughlin, 1991). Learning allows fishes to improve their foraging efficiency by adjusting their feeding to match changing circumstances (Hughes *et al.*, 1992). In the hatchery environment, however, many species are fed on a commercial pellet diet that is specifically designed to provide all the nutrients they require. The food is delivered in a highly predicable location, quantity and time of day. Not surprisingly, recognition of novel prey items is a considerable obstacle for hatchery-reared fishes to overcome following release.

Conditioning during early stages of development in the hatchery (Coughlin, 1991) may result in the formation of inappropriate search images or foraging strategies (Ware, 1971; Sosiak *et al.*, 1979; Langley, 1996; Reiriz *et al.*, 1998). In the laboratory juvenile pink salmon *Oncorhynchus gorbuscha* (Walbaum) often show fear responses to novel live prey (Godin, 1978) and in the wild hatchery-reared brook trout (*Salvalinus fontinalis* (Mitchill) tend to prey on items that were similar in appearance to hatchery pellets (Ersbak & Haase, 1983). Moreover, upon release hatchery fishes are slow to start eating and, compared to their wild counterparts, they consume less food, feed on a highly restricted range of prey items and are slow to switch between prey items as they vary in abundance (Sosiak *et al.*, 1979; Ersbak & Haase, 1983).

Recent laboratory experiments investigating the foraging behaviour of hatchery-reared fishes indicate that they can, nonetheless, learn to accept novel, live prey items. Hatchery-reared Atlantic salmon *Salmo salar*, L., for example, were found to accept novel live prey after 16 exposures (Stradmeyer & Thorpe, 1987). The opportunity to observe knowledgeable conspecifics may speed up this learning and it is well established that many fishes forage more efficiently in social groups than alone (Pitcher & House, 1987; Ryer & Olla, 1991; Sundstrom & Johnsson, 2001). Typically, individuals in larger groups find food faster than individuals in smaller groups because the probability of one fish in the group discovering a food patch increases with group size and, once discovered, the foraging behaviour of the finder attracts the remaining fish to the patch. Other studies have found that fishes can learn the route to a food source (Laland & Williams, 1997, 1998), the identity of predators (Magurran & Higham, 1988; Suboski *et al.*, 1990; Krause, 1993), and to escape predators (Sugita, 1980; Brown & Laland, 2002) through social learning processes. Thus the capability of fishes to learn or enhance life-skills through observing or interacting with conspecifics is now well established (Brown & Laland, 2001).

Suboski & Templeton (1989) first suggested the use of social learning as a tool to train hatchery fishes to recognize predators and prey. This view was echoed by a recent review by Brown & Laland (2001). As far as it is known, however, as yet there have been no attempts to utilize social learning protocols in this

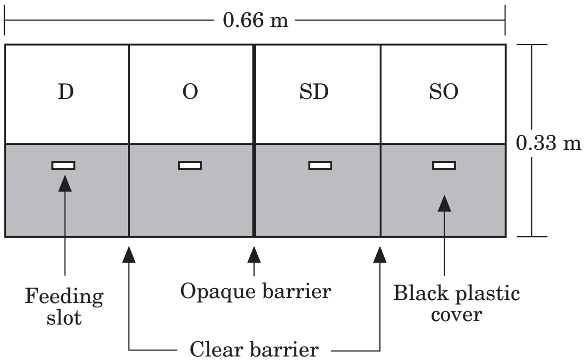

FIG. 1. Overhead plan view of the experimental tanks used in experiment 1. D, pre-trained demonstrator fish; O, naïve observer; SD, sham demonstrator; SO, sham observer. In experiment 2, single naïve fish were placed in the location marked D, and one of each of the pairs of naïve fish were placed in the locations marked SD and SO.

manner. A first step towards the application of social learning methods in hatcheries is to establish that commercial hatchery-reared species, such Atlantic salmon, are capable of social enhancement and to identify the parameters that will determine the effectiveness of social learning procedures.

In the present study two complimentary experiments were undertaken. The aim of the first experiment was to investigate whether hatchery-reared Atlantic salmon learn to accept a novel, live prey item more rapidly when paired with a knowledgeable conspecific (demonstrator) than when paired with another naïve individual (sham demonstrator). If Atlantic salmon do not exhibit this simple form of social enhancement then the opportunities for using social learning protocols to condition life-skills in hatchery fish will be severely curtailed in this species. The second experiment compared the rate of learning of single naïve fish with one member of a pair of naïve fish.

METHODS

SUBJECTS AND APPARATUS

Three-hundred hatchery reared Atlantic salmon parr were purchased from the Environment Agency hatchery at Kielder, Northumberland, U.K. The fish were *c.* 6 months of age at the time of purchase and 7 months old at the time of experimentation. On arrival at the University of Cambridge the fish were sorted by size into four 190 l, round, black plastic tubs, each containing *c.* 75 conspecifics. Fish of intermediate size range (mean ± S.E. standard length, L_S, $=58 \pm 4$ mm) where used for both experiments. Sixty fish were used in experiment 1, and 45 fish in experiment 2. The two experiments were conducted within a week of one another so there was little, if any difference in the age or size of the test subjects between the first and second experiment. The holding tanks were designed to simulate hatchery conditions and were connected to a recirculating, biological filter system. Prior to the experiment the fish were maintained on the same pellet diet as at the hatchery. Room temperature was kept at 14° C and overhead fluorescent globes maintained a 12 L : 12 D photoperiod.

The test tanks consisted of 15 60 cm aquaria that had been divided in half by a black opaque barrier and in half again by a 2 mm sheet of clear perspex (Fig. 1). Water depth was maintained at 150 mm. Each aquarium was surrounded by black plastic on three sides and a black plastic hide was present on the fourth side allowing the experimenter to observe and record the behaviour of the fish without disturbing them. Half of the top of the tank closest to the hide was also covered with black plastic. This cover had a small hole allowing the experimenter to deliver the prey items using a pipette. The remaining open half allowed light to enter the tanks.

EXPERIMENT 1

This experiment compared the foraging performance of naïve fish paired with trained or untrained demonstrator conspecifics.

Fifteen fish were chosen at random from the holding tanks containing fish of intermediate size, and designated as ‘ demonstrators ’. The fish were placed as singletons in an experimental tank in the section labelled ‘ D ’ in Fig. 1, with the adjacent section empty (‘ O ’, Fig. 1). A further 15 fish, chosen at random, were removed from the same holding tank, and designated as ‘ sham demonstrators ’. These fish were also placed as singletons in an experimental tank, but in the ‘ SD ’ section (Fig. 1), with the adjacent section again empty. Demonstrators were fed three live bloodworms *Chironmid* spp. each day at 1600 hours for 10 days. By the end of this training period demonstrators recognized and accepted bloodworms as a prey item. Sham demonstrators were fed with pellet food in an identical manner to the feeding regime for demonstrators. Hence, these fish remained unfamiliar with bloodworms throughout the demonstrator-training period.

On day 11, each demonstrator was paired with a single naïve fish chosen at random from the same holding tank. These fish were designated ‘ observers ’ and each observer was placed in the section of the experimental tank adjacent to a demonstrator. A further 15 naïve individuals from the holding tank were placed as individuals in the empty section of the experimental tank (SO, Fig. 1), adjacent to the sham demonstrators, and designated ‘ sham observers ’. Thus demonstrator-observer and sham demonstrator-sham observer pairs could see each other through a clear perspex partition, but could not see any other individuals.

Experimental feeding occurred once per day for 6 days beginning at 1600 hours. For each pair, the demonstrator and sham-demonstrator fish were offered three bloodworms each separated by a time interval of *c.* 1 min. Following the delivery of the three prey items to the demonstator and sham demonstrator, the observer and sham observer were presented with up to three bloodworms, in an identical manner to demonstrator feeding. If the observer or sham observer did not accept the prey item within a 5 min period, then it was not offered further bloodworms. The number of prey items consumed and the average time to consumption were recorded for all individuals. Where subjects did not feed they were allocated the maximum time score of 300 s. All fish were supplementary fed on standard hatchery pellets at the conclusion of each day in order to control for differences in hunger level that may occur throughout the experiment.

EXPERIMENT 2

Young salmon usually set up small territories and vigorously defend them from intruders. It was expected therefore that the presence of another individual may distract fish from foraging and thus inhibit their ability to learn. Consequently, this experiment compared the foraging performance of singleton naïve fish with naïve fish in pairs. Fifteen naïve fish, designated as ‘ singletons ’, were taken from the holding tanks, and placed into a section of the experimental tank, with the adjacent section empty. A further 30 fish, designated as ‘ naïve-naïve ’ pairs, were placed in adjacent sections of the experimental tank. Naïve-naïve pairs but not singletons could see another fish. Each singleton, and a pre-designated member of each pair, were presented with three live bloodworm for 6 days, in a manner identical to that described in experiment 1, with the same dependent variables recorded.

RESULTS

EXPERIMENT 1

Observers paired with trained demonstrators showed a significantly shorter latency to the first successful strike than naïve fish paired with sham

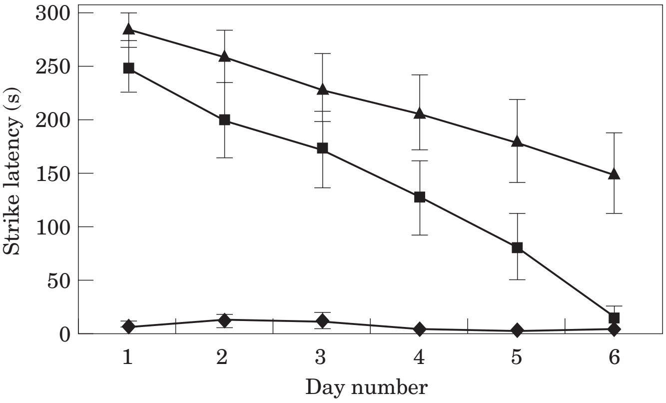

FIG. 2. The mean ± S.E. latency to the first successful strike at a novel, live prey item over 6 days. D (◆), pre-trained demonstrators; O (■), naïve observers paired with demonstrators and SO (▲), sham observers paired with sham demonstrators.

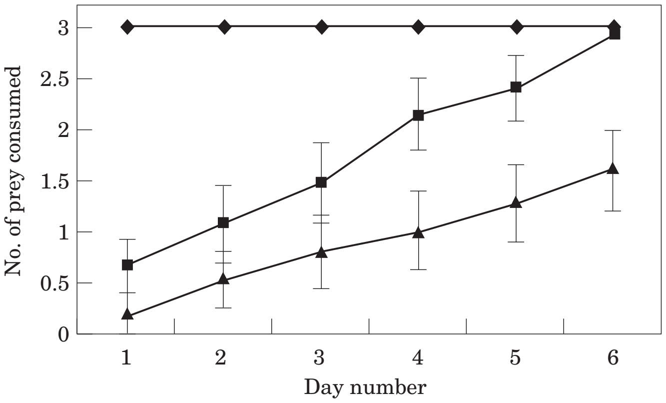

FIG. 3. The mean ± S.E. number of prey items eaten over 6 days. D (◆), pre-trained demonstrators; O (■), naïve observers paired with demonstrators; SO (▲), sham observers paired with sham demonstrators.

demonstrators (repeated measures ANOVA, $F_{1,28}=5{\cdot}020$, $P=0{\cdot}0332$; Fig. 2). All observers exhibited a decreased latency to feed over time, indicative of learning (repeated measures ANOVA, $F_{5,140}=21{\cdot}366$, $P<0{\cdot}0001$) (linear trend test, $F_{1,140}=68{\cdot}892$ and $24{\cdot}410$, $P<0{\cdot}0001$ for observers and sham observers respectively). The rates at which the latency to strike decreased over trials differed for the two treatments, as manifest in a condition by trial interaction that approached significance ($P=0{\cdot}0585$). There was no difference between observers and sham observers on the first day ($P=0{\cdot}4369$). Analysis of the data for the 6th day revealed that observers had a significantly lower latency to strike than sham observers (simple effects, $F_{1,140}=27{\cdot}132$, $P<0{\cdot}0001$). By the 6th day observers with real demonstrators were feeding as quickly as trained demonstrators, while sham observers were significantly slower.

Observers also ate significantly more prey items than sham observers (repeated measures ANOVA, $F_{1,28}=5{\cdot}550$, $P=0{\cdot}0257$; Fig. 3). All observers exhibited a increasing trend in the number of prey items consumed, indicative of learning

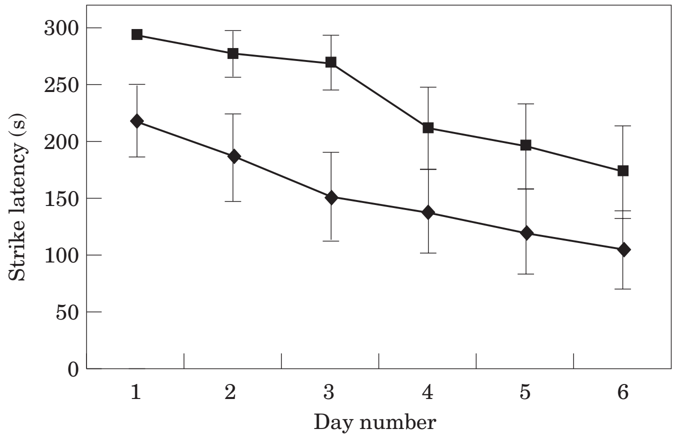

FIG. 4. The mean ± S.E. latency to the first successful strike by single naïve fish (N, ◆) and pairs of naïve fish (NN, ■) over 6 days.

(repeated measures ANOVA, $F_{5,90}=17{\cdot}571$, $P<0{\cdot}0001$) (linear trend test, $F_{1,140}=92{\cdot}264$ and $29{\cdot}854$, $P<0{\cdot}0001$ for observers and sham observers respectively). On the 6th day, observers ate significantly more prey items than sham observers (simple effect, $F_{1,140}=19{\cdot}262$, $P<0{\cdot}0001$), while there was no such difference on the first day ($P=0{\cdot}1268$). There was no significant difference in the rate of learning over trials between the two treatment groups ($P=0{\cdot}3307$). By the 6th day observers consumed a similar number of prey items as trained demonstrators, and in fact ate all of the prey items with which they were presented. Sham observers consumed approximately half of the number of food items as observers throughout the entire test period.

Analyses of the latency data comparing observers and their demonstrators revealed significant treatment, trial and treatment by trial interaction ($P<0{\cdot}0001$ in all cases). Analysis of the data from the first day only shows a highly significant difference between trained demonstrators and observers (ANOVA, $F_{1,140}=99{\cdot}238$, $P<0{\cdot}0001$). By the 6th day, however, there was no significant difference between demonstrators and observers ($P=0{\cdot}1440$) (Fig. 2). Consistent results were obtained for the number of prey items consumed.

EXPERIMENT 2

Singletons showed a significantly shorter latency to the first successful strike than individuals in pairs (repeated measures ANOVA, $F_{1,28}=4{\cdot}831$, $P=0{\cdot}0364$; Fig. 4). All fish exhibited a decreased latency to feed over time, indicative of learning (repeated measures ANOVA, $F_{5,140}=12{\cdot}456$, $P<0{\cdot}0001$) (linear trend test, $F_{1,140}=32{\cdot}079$ and $30{\cdot}036$, $P<0{\cdot}0001$ for singletons and naïve pairs respectively). The rates at which the latency to strike decreased over trials did not differ for the two treatments ($P=0{\cdot}6773$). On the 6th day, however, singletons were significantly quicker to strike than fish in pairs (simple effect, $F_{1,140}=5{\cdot}839$, $P=0{\cdot}017$), while there was no such difference on the first day ($P=0{\cdot}0647$).

Singletons also ate significantly more prey items than individuals in pairs (repeated measures ANOVA, $F_{1,28}=4{\cdot}779$, $P=0{\cdot}0373$; Fig. 5). All fish exhibited an increasing trend in the number of prey items consumed, indicative of learning

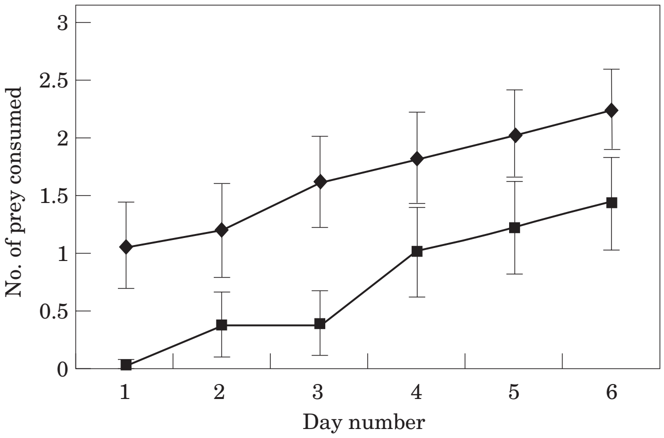

FIG. 5. The mean ± S.E. number of novel, live prey items eaten by single naïve fish (N, ◆) and pairs of naïve fish (NN, ■) over 6 days.

(repeated measures ANOVA, $F_{5,140}=9{\cdot}922$, $P<0{\cdot}0001$) (linear trend test, $F_{1,140}=20{\cdot}852$ and $28{\cdot}869$, $P<0{\cdot}0001$ for singletons and naïve pairs respectively). On the first day, singletons ate significantly more prey items than fish in pairs (simple effect, $F_{1,140}=10{\cdot}683$, $P=0{\cdot}0014$), and this difference remained through to the 6th day (simple effect, $F_{1,140}=6{\cdot}837$, $P=0{\cdot}01$). There was no significant difference in the rate of learning over trials between the two treatment groups ($P=0{\cdot}3307$). Thus, singletons were quicker to strike and ate more prey items than individuals from naïve-naïve pairs throughout the experiment.

COMBINING EXPERIMENT 1 AND 2

By examining the data for the naïve-naïve pairs pooled from both experiments 1 and 2, observers paired with demonstrators from experiment 1 and single naïve fish from experiment 2, a greater insight was provided of the overall outcome of these complimentary experiments. Repeated measures ANOVAs comparing the mean strike latency and the number of items eaten reveal significant treatment effects ($F_{2,285}=4{\cdot}695$, $P=0{\cdot}0130$ and $F_{2,285}=5{\cdot}216$, $P=0{\cdot}0083$ for strike latency and the number of prey eaten respectively). The pattern of results is consistent, with observers learning the foraging task more quickly than singletons and singletons more quickly than individuals in naïve-naïve pairs. The analysis of the strike latency data also yielded a treatment by trial interaction of marginal significance, consistent with a difference in the rate of learning for the three treatments ($F_{10,285}=1{\cdot}789$, $P=0{\cdot}0622$). There was no such difference in the rate of learning for the number of items eaten ($P=0{\cdot}3567$). *Post-hoc* analysis of the data for day 6 revealed that observers foraged significantly more effectively than singletons (studentized range statistic: $q_{2,15}=3{\cdot}325$ and $3{\cdot}782$, $P<0{\cdot}05$ for the number of items eaten and the latency to strike respectively). Similarly, on test day 6 singletons were more effective foragers than pairs of naïve fish (studentized range statistic: $q_{2,15}=7{\cdot}309$ and $9{\cdot}108$, $P<0{\cdot}01$ for the number of items eaten and the latency to strike respectively). There were no differences between treatments on day 1.

DISCUSSION

Despite the fact that Atlantic salmon are not generally regarded as social, it is clear from both experiments that social interaction can influence learning in this species. The first experiment provides evidence that Atlantic salmon are capable of targeting and increasing their rate of feeding on a novel prey item by watching an experienced conspecifics feeding on that prey type. By the 6th test day the behaviour of the naïve observers was indistinguishable from that of the trained demonstrators. All 15 observer fish had accepted the novel, live prey item by the end of the experiment. In contrast to this only 53% of sham observers from naïve-naïve pairs accepted the live prey by test day 6. Observer fish not only had a shorter latency to the first successful strike, but also consumed more prey items compared to sham observers.

Trained demonstrators often attempted to seize the prey items that had been offered to the naïve observers on the other side of the clear partition. These persistent attempts to retrieve the prey by the demonstrators frequently appeared to trigger the observer fish to strike. Whilst striking at prey at the surface (or attempting to strike through the partition), demonstrator fish provide a very strong social cue to the naïve observers. The cue not only informs the naïve fish that food is available, but it also likely to provide some information about its location. Hatchery-reared fishes possess a preference for taking prey from the surface (Reinhardt, 2001), even when this behaviour may not be part of their natural foraging repertoire (Furuta, 1996). This preference is almost certainly brought about by frequent and long-term conditioning in the hatchery environment and may be detrimental following release (Furuta, 1996; Stunz *et al.*, 2001). Further experiments are necessary to determine if the direction of the strike observed by observers can influence their forage location preference (e.g. surface *v.* the benthos).

Given that juvenile Atlantic salmon quickly become territorial and aggressive after hatching and dispersing, it was expected that the presence of a naïve conspecific would interfere with the acquisition of a new behaviour. The results of experiment 2 show that naïve single fish forage more successfully on novel prey items than naïve individuals in pairs even though there is no direct interference. Even on the first test day single fish forage slightly more successfully than the fish in pairs (both naïve-naïve and observers from demonstrator-observer pairs). By the end of experiment 2, 73% of the single fish had accepted the live prey as an alternative prey item compared to only 47% of the individuals from naïve-naïve pairs. It would seem that in experiment 2 the presence of a conspecific inhibited performance in the foraging task.

Two slightly different processes could have been occurring in the naïve pairs that may help to explain the comparatively poor performance of individuals in this treatment. Firstly, naïve fish may have been intimidated by the presence of another fish in the neighbouring compartment. There did not appear, however, to be any signs of aggression between neighbouring fish. Indeed, threat displays were never observed. The second possible explanation is that the naïve pairs were responding to the behaviour of their neighbour (or more specifically, the lack thereof). To begin with all fish tended to hide in a corner of the tank typically under the air-stone provided. It seems likely that the inactivity of both partners inhibited their response to the prey item (Ryer & Olla, 1991), each fish providing negative feedback to the other. The latter situation, ‘ social inhibition ’, may be similar in many respects to the social acquisition of fright responses observed in many fishes including salmonids (Brown & Laland, 2001). In the case of experiment 1, the feeding of demonstrators may not only provide information about the availability, location and characteristics of food, but may also effectively send the message that the novel prey item is a non-threatening stimulus. In experiment 2, on the other hand, paired individuals effectively reinforced each other’s caution.

Further insight into the nature of the social processes that influenced learning can be obtained by comparing the results of the two experiments directly. Singletons initially do comparatively well both in terms of the number of prey consumed and the latency to first successful strike compared to fish in pairs. By test day 4, however, observers paired with demonstrators begin to outperform singletons, and by test day 6 observers forage significantly better than singletons. Whilst naïve-naïve pairs show significant improvement in their foraging behaviour over the 6 test days, they never reach the same level of competence displayed by singletons or observers. Fish in naïve-naïve pairs inhibit one another, whereas observers paired with demonstrators are given strong social cues that encourage them to emerge from hiding and begin feeding.

Several authors have investigated the responses of hatchery-reared juvenile Atlantic salmon to novel prey items, but none using trained demonstrators. Sosiak *et al.* (1979) released hatchery-reared fish into a stream and left them there for 1–3 months. Stomach content analysis on these fish revealed that they ate fewer prey types and had a lower index of stomach fullness than wild fish from the same stream. Reiriz *et al.* (1998) released 72 prey items into an aquarium containing groups of five naïve hatchery-fish after 1 h the remaining prey items were counted. The exposure was repeated every day but data were only collected on days 3 and 7. No attempt was made to track the behaviour of individuals. Groups of naïve fish showed improvements in their foraging skills with repeated exposure and by the 7th day their choice of prey resembled that of wild fish. Stradmeyer & Thorpe (1987) offered pellets and four types of live prey to hatchery-reared juveniles. The fish showed an increase in preference for live prey over 16 exposures. In all of the above cases at least some of the hatchery-reared fish appear to have made the switch from pellet food to live prey, however, few studies report the proportion of fish successfully making the switch. Similar results have been obtained for hatchery-reared coho salmon *Oncorhynchus kisutch* (Walbaum) learning to feed on sand shrimp. Not all fish make the transition from pellet to live food successfully (Paszkowski & Olla, 1985). Paszkowski & Olla (1985) report that 31% of hatchery coho salmon did not accepted live prey during the experimental period, similarly, Gillen *et al.* (1981) report that 27% of tiger muskellunge *Esox masquinongy* Mitchill failed to eat live prey during the course of their study.

The present study suggests that the fishes in the above studies may well have switched to live prey much more rapidly had they been exposed to trained demonstrators. In the current study the range of fish making the change to wild prey was heavily dependent on the social context. On test day 6, fish paired with trained demonstrators showed the greatest propensity to accept live prey (100%), followed by single naïve fish (73%) and then naïve-naïve pairs (53% and 47% for experiments 1 and 2, respectively). The results for the single fish and naïve-naïve pairs closely match the studies mentioned above. These results have compelling implications for the training of hatchery-reared fishes, and although further work is required, it appears likely that the mass training of naïve fish could be achieved by seeding the population with a few ' knowledgeable ' individuals (Suboski & Templeton, 1989; Brown & Laland, 2001; Brown & Day, 2002).

Ryer & Olla (1991) reported a similar social enhancement of feeding for hatchery-reared juvenile chum salmon *Oncorhynchus keta* (Walbaum). Isolated chum salmon ate most when visually exposed to feeding conspecifics compared to non-feeding conspecifics and least of all when exposed to alarmed conspecifics. Templeton (1987) also found that juvenile rock bass *Ambloplites rupestris* (Rafinesque) showed greater consumption of a novel food when given visual access to experienced conspecifics compared to control fish. On the other hand, Sundstom & Johnsson (2001) showed an increase in foraging performance in wild but not hatchery-reared brown trout *Salmo trutta* L. when in visual contact with another conspecific. They tentatively suggest that the high-densities under which hatchery-reared fish are raised are not conducive to social learning. It is conceivable that the densities at which hatchery fishes are reared may interfere with the development of natural social behaviour (Hojesjo *et al.*, 1998; Berejikian *et al.*, 2000). Examination of the interaction between rearing density and the subsequent ability of reared fishes to learn socially, and of the relative proportions of trained and naïve fishes, are likely to be fruitful avenues for future research. Whilst there are numerous other examples of socially enhanced foraging behaviour in many species of fishes (Morgan & Colgan, 1987; Morgan, 1988; Ryer & Olla, 1992; Pitcher & House, 1987; Laland & Williams, 1997), there have been comparatively few studies in commercial species. Comparative analyses of a range of commercial fish species differing in their degree of social cohesiveness would prove interesting both from a theoretical and applied perspective.

This work was funded by BBSRC grant 8/S15529. KNL was supported by a Royal Society University Research Fellowship. Thanks to the Environment Agency hatchery at Kielder for providing the salmon.

References

Berejikian, B. A., Tezak, E. P., Flagg, T. A., LaRae, A. L., Kummerow, E. & Mahnken, C. V. W. (2000). Social dominance, growth, and habitat use of age-0 steelhead (*Oncorhynchus mykiss*) grown in enriched and conventional hatchery rearing environments. *Canadian Journal of Fisheries and Aquatic Science* **57,** 628–636.

Brown, C. & Day, R. (2002). The future of stock enhancements: Bridging the gap between hatchery practice and conservation biology. *Fish and Fisheries* **3,** 79–94.

Brown, C. & Laland, K. N. (2001). Social learning and life skills training for hatchery reared fish. *Journal of Fish Biology* **59,** 471–493.

Brown, C. & Laland, K. N. (2002). Social learning of a novel avoidance task in the Guppy: Conformity and social release. *Animal Behaviour* **63** In press.

Coughlin, D. J. (1991). Ontogeny of feeding-behaviour of 1st-feeding Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Science* **48,** 1896–1904.

Eriksson, T. & Eriksson, L. (1993). The status of wild and hatchery propagated Swedish salmon stocks after 40 years of hatchery releases in the Baltic rivers. *Fisheries Research (Amsterdam)* **18,** 147–159.

Ersbak, K. & Haase, B. (1983). Nutritional deprivation after stocking as a possible mechanism leading to mortality in stream-stocked brook trout. *North American Journal of Fisheries Management* **3,** 142–151.

Furuta, S. (1996). Predation of juvenile Japanese flounder (*Paralichthys olivaceus*) by diurnal piscivorous fish: field observations and laboratory experiments. In *Survival Strategies in Early Life Stages of Marine Resources* (Watanabe, Y., Yamashita, Y. & Oozeki, Y., eds), pp. 285–294. Rotterdam: A.A. Balkema.

Gillen, A. L., Stein, R. A. & Carline, R. F. (1981). Predation by pellet-reared tiger muskellunge and minnows and blue gills in experimental systems. *Transactions of the American Fisheries Society* **110,** 197–209.

Godin, G.-J. J. (1978). Behaviour of juvenile pink salmon (*Oncorhynchus grobuscha* Walbaum) towards novel prey: influence of ontogeny and experience. *Environmental Biology of Fishes* **3,** 261–278.

Heggberget, T., Staurnes, M., Strand, R. & Husby, J. (1992). Smoltification in salmonids. *NINA Norsk Institutt for Naturforskning Forskningsrapport* **0,** 3–42.

Hojesjo, J., Johnsson, J. I., Petersson, E. & T, J. (1998). The importance of being familiar: individual recognition and social behavior in sea trout (*Salmo trutta*). *Behavioral Ecology* **9,** 445–451.

Hughes, R. N., Kaiser, M. J., Mackney, P. A. & Wurburton, K. (1992). Optimizing foraging behaviour through learning. *Journal of Fish Biology* **41,** 77–91.

Hutchings, J. A. (2000). Collapse and recovery of marine fisheres. *Nature* **406,** 882–885.

Kieffer, J. D. & Colgan, P. W. (1992). The role of learning in fish behaviour. *Reviews in Fish Biology and Fisheries* **2,** 125–143.

Kitada, S., Taga, Y. & Kishino, H. (1992). Effectiveness of a stock enhancement program evaluated by a 2-stage sampling survey of commercial landings. *Canadian Journal of Fisheries and Aquatic Sciences* **49,** 1573–1582.

Krause, J. (1993). Transmission of fright reaction between different species of fish. *Behaviour* **127,** 37–48.

Laland, K. & Williams, K. (1997). Shoaling generates social learning of foraging information in guppies. *Animal Behaviour* **53,** 1161–1169.

Laland, K. & Williams, K. (1998). Social transmission of maladaptive information in the guppy. *Behavioural Ecology* **9,** 493–499.

Langley, C. M. (1996). Search images: Selective attention to specific visual features of prey. *Journal of Experimental Psychology: Animal Behavior Processes* **22,** 152–163.

Magurran, A. E. & Higham, A. (1988). Information transfer across shoals under predation threat. *Ethology* **78,** 153–158.

McNeil, W. (1991). Expansion of cultured Pacific salmon into marine ecosystems. *Aquaculture* **98,** 173–183.

Morgan, M. J. (1988). The influence of hunger, shoal size and predator presence on foraging in bluntnose minnows. *Animal Behaviour* **36,** 1317–1322.

Morgan, M. J. & Colgan, P. W. (1987). The effects of predator presence and shoal size on foraging in bluntnose minnows, *Pimephales notatus. Environmental Biology of Fishes* **20,** 105–111.

Paszkowski, C. & Olla, B. (1985). Foraging behaviour of hatchery produced coho salmon (*Oncorhynchus kisutch*) smolts on live prey. *Canadian Journal of Fisheries and Aquatic Sciences* **42,** 1915–1921.

Pitcher, T. J. & House, A. (1987). Foraging rules for group feeders: area copying depends upon density in shoaling goldfish. *Ethology* **76,** 161–167.

Reinhardt, U. G. (2001). Selection for surface feeding in farmed and sea-ranched masu salmon juveniles. *Transactions of the American Fisheries Society* **130,** 155–158.

Reiriz, L., Nicieza, A. G. & Brana, F. (1998). Prey selection by experienced and naive juvenile Atlantic salmon. *Journal of Fish Biology* **53,** 100–114.

Ryer, C. H. & Olla, B. L. (1991). Information transfer and the facilitation and inhibition of feeding in a schooling fish. *Environmental Biology of Fishes* **30,** 317–323.

Ryer, C. H. & Olla, B. L. (1992). Social mechanisms facilitating exploitation of spatially variable ephemeral food patches in a pelagic marine fish. *Animal Behaviour* **44,** 69–74.

Sosiak, A., Randall, R. & McKenzie, J. (1979). Feeding by hatchery-reared and wild Atlantic salmon (*Salmo salar*) parr in streams. *Journal of the Fisheries Research Board of Canada* **36,** 1408–1412.

Stradmeyer, L. & Thorpe, J. (1987). Feeding behaviour of wild Atlantic salmon, *Salmo salar* L., parr in mid- to late summer in a Scottish river. *Aquaculture and Fisheries Management* **18,** 33–49.

Stunz, G. W., Levin, P. S. & TJ, M. (2001). Selection of estuarine nursery habitats by wild-caught and hatchery-reared juvenile red drum in laboratory mesocosms. *Environmental Biology of Fishes* **61,** 305–313.

Suboski, M. D. & Templeton, J. J. (1989). Life skills training for hatchery fish: Social learning and survival. *Fisheries Research (Amsterdam)* **7,** 343–352.

Suboski, M. D., Bain, S., Carty, A. E., McQuoid, L. M., Seelen, M. I. & Seifert, M. (1990). Alarm reaction in acquisition and social transmission of simulated predator recognition by zebra danio fish (*Brachydanio rerio*). *Journal of Comparative Psychology* **104,** 101–112.

Sugita, Y. (1980). Imitative choice behaviour in guppies. *Japanese Psychological Research* **22,** 7–12.

Sundstrom, L. F. & Johnsson, J. I. (2001). Experience and social environment influence the ability of young brown trout to forage on live novel prey. *Animal Behaviour* **61,** 249–255.

Templeton, J. (1987). Individual differences in the behaviour of juvenile rock bass (*Ambloplites rupestris*): Causes and consequences. Masters Thesis, Queens University.

Wales, J. (1954). Relative survival of hatchery and wild trout. *Progressive Fish-Culturist* **16,** 125–127.

Ware, D. M. (1971). Predation by trout (*Salmo gairdneri*): the effect of experience. *Journal of Fisheries Research Board of Canada* **28,** 1847–1852.

Welcomme, R. L. & Bartley, D. M. (1998). An evaluation of present techniques for the enhancement of fisheries. In *Inland Fishery Enhancements*. FAO Fisheries Technical Paper 374, 1–35. Rome: FAO.