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REVIEW PAPER

Social learning and life skills training for hatchery reared fish

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With the stress placed on our natural resources, many fisheries increasingly rely on restocking from hatchery-reared sources in an attempt to maintain commercially viable populations. However, the mortality rates of hatchery-reared fishes during the period directly following release are very high. The successful development of restocking programs is consequently dependent upon production and release strategies that lead to improved migratory, anti-predator and feeding behaviour in hatchery fish. While relevant individual experience prior to release might improve performance, social learning potentially provides a process whereby fish can acquire locally adaptive behaviour rapidly and efficiently. It is now well over a decade since Suboski & Templeton (1989) raised the possibility of using social learning processes to improve the post-release survival of hatchery-reared fishes. This period has witnessed considerable progress in the understanding of how social learning operates in fish populations. We review new methods and recent findings that suggest how social learning protocols could realistically be applied on a large scale to enhance the viability of hatchery fish prior to their release into the wild. We also suggest a practical pre-release training protocol that may be applied at the hatchery level.

Key words: social learning; restocking; hatchery; life skills; training.

INTRODUCTION

Restocking was first considered for the cod (*Gadus morhua*, L.) by the Americans in the 19th Century following a dramatic decline in the wild population (Kurlansky, 1999). Today many heavily targeted fish populations are artificially bolstered by the release of hatchery-reared fingerlings in an attempt to restore or maintain fish numbers. Stocking is an extremely widespread fisheries management tool particularly in inland fisheries but is also common in marine and coastal areas involving species such as salmon (*Oncorhynchus* and *Salmo* spp.), sturgeon (*Acipenser* spp.) and flounder (e.g. *Paralichthys* spp.) (Welcomme & Bartley, 1998). Table I provides a brief list of some of the species that have been the subject of restocking programs, but it is by no means complete. Welcomme & Bartley (1998) estimate that most countries in the world participate in restocking to some extent and that there are well over 250 species involved. They

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Table I. A brief list of some of the species and countries involved with restocking programs around the world

Common name	Species name	Stocking locations
Arctic char	*Salvelinus alpinus* (Linnaeus)	France, U.S.A.
Atlantic cod	*Gadus morhua* (Linnaeus)	Iceland, Norway, Newfoundland, U.S.A.
Atlantic salmon	*Salmo salar* (Linnaeus)	Widespread
Atlantic sturgeon	*Acipenser oxyrinchus* (Mitchill)	U.S.A., Iran
Ayu	*Plecoglossus altivelis* (Temminck & Schlegel)	Japan
Barfin flounder	*Verasper moser* (Jordan & Gilbert)	Japan
Barramundi	*Lates calcarifer* (Bloch)	Australasia
Beluga	*Huso huso* (Linnaeus)	Iran
Bitterling	*Rhodeus sericeus* (Pallas)	Italy
Black sea bream	*Brama brama* (Bonnaterre)	Japan
Border barb	*Barbus trevelyani* (Gunther)	South Africa
Brown trout	*Salmo trutta* (Linnaeus)	Widespread
Chinook salmon	*Oncorhynchus tshawytscha* (Walbaum)	Australia, Canada, Chile, New Zealand, U.S.A.
Chub	*Leuciscus cephalus* (Linnaeus)	Europe
Chum salmon	*Oncorhynchus keta* (Walbaum)	Japan
Common barbel	*Barbus barbus* (Linnaeus)	Belgium
Common carp	*Cyprinus carpio* (Linnaeus)	Widespread
Common snook	*Centropomus undecimalis* (Bloch)	U.S.A.
European eel	*Anguilla anguilla* (Linnaeus)	Widespread
Golden perch	*Macquaria ambigua* (Richardson)	Australia
Grass Carp	*Ctenopharyngodon idellus* (Valenciennes)	Widespread
Japanese flounder	*Paralichthys olivaceus* (Temminck & Schlegel)	Japan
Lake trout	*Salvelinus namaycush* (Walbaum)	Canada
Largemouth bass	*Micropterus salmoides* (Lacepède)	South America, Mexico
Masu salmon	*Oncorhynchus masou masou* (Brevoort)	Japan
Murray cod	*Maccullochella peelii peelii* (Mitchell)	Australia
Nassau grouper	*Epinephelus striatus* (Bloch)	Indonesia
Northern pike	*Esox lucius* (Linnaeus)	Europe

Table I. *Continued*

Common name	Species name	Stocking locations
Pacific threadfin	*Polydactylus sexfilis* (Cuvier)	U.S.A.
Perch	*Perca fluviatilis* (Linnaeus)	Europe
Rainbow trout	*Oncorrhyncus mykiss* (Walbaum)	Australia, Canada, Chile, New Zealand, U.S.A.
Red drum	*Sciaenops ocellatus* (Linnaeus)	U.S.A.
Red sea bream	*Pagrus major* (Temminck & Schlegel)	Japan
Short finned eel	*Anguilla australis* (Richardson)	Australia
Shortnose sturgeons	*Acipenser brevirostrum* (Lesueur)	U.S.A.
Silver carp	*Hypophthalmichthys molitrix* (Valenciennes)	Widespread
Silver hake	*Merluccius bilinearis* (Mitchell)	U.S.A.
Silver perch	*Bidyanus bidyanus* (Mitchell)	Australia
Sneep	*Chondrostoma nasus* (Linnaeus)	Czech Republic
Sockeye salmon	*Oncorhynchus nerka* (Walbaum)	U.S.A.
Southern flounder	*Paralichthys lethostigma* (Jordan & Gilbert)	U.S.A.
Striped jack	*Pseudocaranx dentex* (Bloch & Schneider)	Japan
Striped mullet	*Mugil cephalus* (Linnaeus)	U.S.A.
Summer flounder	*Paralichthys dentatus* (Linnaeus)	U.S.A.
Sunapee char	*Salvelinus alpinus oquassa* (Girard)	U.S.A.
Tench	*Tinca tinca* (Linnaeus)	Europe
Tilapia	*Oreochromis* species	Widespread
Whitefish	*Barbus andrewi* (Barnard)	South Africa
Whitefish	*Coregonus lavaretus* (Linnaeus)	France, Greece
Zander	*Stizostedion lucioperca* (Linnaeus)	Europe

TABLE II. Stocking types and their associated principal aims (after Welcomme & Bartley, 1998)

Stocking type	Principal aim
Compensation	To mitigate a disturbance to the environment by human activities
Maintenance	To compensate for overfishing
Enhancement	To increase or maintain productivity at the highest possible level
Conservation	To maintain biodiversity

suggest that several different types of stocking programme may be identified and grouped according to their principal aims (Table II) (see Cowx, 1999 for a slightly different categorization).

Throughout Europe and North America the number of salmonids released from culture for restocking purposes now matches or exceeds natural production (Petersson *et al.*, 1996; Hilborn & Eggers, 2000). The U.S.A. alone releases over 2 billion Pacific salmon (*Oncorhyncus* spp.) every year. Similar levels of stocking occurs across the Baltic countries. Stocks of Atlantic Salmon in the Baltic Sea for example are now almost entirely comprised of fish released from hatcheries (Ericksson & Ericksson, 1993). Similarly, 90% of the Japanese catch of chum and pink salmon are derived from stocked fish (Kitada, 1996). Fisheries in the Caspian Sea are almost entirely dependent upon hatchery-released fish. The number of fish stocked into the Caspian Sea by Iran alone is astronomical. In 1996 it was estimated that over 12 million sturgeon (*Acipenser oxyrinchus,* Mitchill) fingerlings were released, 2·5 million perch (*Perca fluviatilis*), 100 million bream (*Abramis brama*, L.) and 140 million mahi sephid (*Rutilus frisii*, Nordmann) (Abdolhay, 1996).

While restocking is widely used as a fisheries management tool, it is also been used for the conservation and management of threatened species (e.g. Flagg *et al.*, 1995). Nehlsen *et al.* (1991) found that 214 stocks of salmonids across the U.S.A. where significantly depleted and almost half where on the verge of extinction. A similar story can be told for the majority of freshwater fish species across the world (IUCN, 2000). In light of the substantial role restocking plays in both fisheries management and conservation biology, there is wide agreement that well planned and properly managed hatchery-based programs will continue to play an important role in bolstering fish stocks in the foreseeable future (Andrews & Kaufman, 1994; Unwin & Glova, 1997).

One of the major problems with the viability of restocking is the dramatic level of mortality of newly released individuals (Suboski & Templeton, 1989; Olla *et al.*, 1998). On a world-wide basis around 5×10^9 hatchery reared salmon are released annually but less than 5% survive to adulthood (McNeil, 1991). Studies from around the world have shown that hatchery reared fish have lower survival rates and provide lower returns to anglers than wild fish (Wales, 1954; Heggberget *et al.*, 1992). The difference in mortality levels between hatchery reared and wild fish is especially large if one considers the size or age classes at which hatchery fish are typically released (Maynard *et al.*, 1995). The relatively poor success rate of restocking and a number of other environmental issues (e.g. loss of genetic integrity) have lead to a fierce debate regarding the value of hatchery supplementation programs (for example see Winton & Hilborn, 1994). Hatchery rearing practice in terms of total production improved dramatically for both marine and freshwater fishes over the latter half of the 20th century, however, methods for reducing post-release mortality have not kept pace with these advances. While the number of hatchery-released fish continues to increase, the proportion of individuals surviving to adulthood is actually decreasing (Pearcy, 1992).

Poor survival in hatchery-reared fish is a major concern as it greatly reduces the efficiency of using hatchery stocks to supplement wild production (Mesa, 1981; Sproul & Tominaga, 1992; Maynard *et al.*, 1995; Olla *et al.*, 1998). While behavioural differences between hatchery and wild fish are likely to provide some of the reasons for the differences in mortality, the basis for these differences is often not clear (Suboski & Templeton, 1989). Fisheries biologists have attempted to explain the deficiencies in the behaviour of hatchery reared fish and counteract them (Jarvi & Uglem, 1993; Berejikian *et al.*, 1996, 2000; Maynard *et al.*, 1995). To date, however, attempts to address those deficiencies have been disappointing. With a few exceptions, efforts to improve the annual production in both freshwater and marine fisheries have met with little success (e.g. Griffin, 1993; Hilborn & Winton, 1993; Cowx, 1998, 1999).

It appears that in most instances mortality is highest during and immediately after release into the wild (Heggberget *et al.*, 1992; Olla *et al.*, 1994, 1998). The highest levels of mortality occur in the first few days post-release rather than over the following weeks (Howell, 1994). In salmon, however, there is some agreement that if a smolt can survive the first 3 weeks of life in the wild then its chances of survival are substantially improved. This finding suggests that it may be possible to improve survivorship through research directed at reducing mortality for the periods during and immediately following release (Heggberget *et al.*, 1992; Sproul & Tominaga, 1992).

It is clear that many commercial fish species are not able to cope with the transition from life in captivity to life in the wild. When hatchery reared fish are released into the wild they are immediately placed in a novel, and variable environment and are exposed to predatory risk. In addition to appropriate osmoregulatory ability, an animal that is released from captivity must have, or quickly acquire, appropriate migratory, feeding and anti-predator behaviours (Heggberget *et al.*, 1992). Hatchery-reared fish show deficits in virtually all aspects of behaviour owing to the impoverished conditions in which they are raised.

It is well known that foraging (Reiriz *et al.*, 1998), anti-predator (Yamaoka *et al.*, 1994) and migratory behaviour (Dodson, 1988; Dittman *et al.*, 1996), while frequently based on unlearned predispositions, are to a large extent acquired through learning during a fish's lifetime (Magurran, 1990; Kieffer & Colgan, 1992). Juveniles destined for release into the wild must, therefore, be raised under conditions that enable them to gain the necessary experience to ready them for life in the real world. Ideally, hatcheries would produce juveniles that have the same physiological and behavioural characteristics as their wild counterparts.

It would seem, however, that the production of ecologically viable fry is not part of the production equation because the production of large quantities of fish, rather than natural history and ecology, largely guides hatchery practices (Johnsson, 1993). There is also evidence that the process of artificial breeding has not only resulted in behavioural changes (e.g. Berejikian *et al.*, 1996; Johnsson *et al.*, 2000), but also resulted in a genetic divergence of the hatchery strains from the wild type (Petersson *et al.*, 1996). The reason for such a divergence is that both natural and sexual selection pressures are altered or relaxed during the process of artificial breeding. It may be possible to overcome the differences in behaviour by enriching the environment in which the fish are raised including the provision of anti-predator and foraging training before being released into the wild (Wiley *et al.*, 1993). Genetic differentiation between captive and wild stocks may also be overcome by a frequent turn over of the spawning stock as is the case with the Mary River Cod, *Maccullochella peelii mariensis* (Rowland) recovery program in Australia (Simpson & Jackson, 1996) and the lake trout rehabilitation project in the Great Lakes (Eshenroder *et al.*, 1999) (see Carvalho & Cross, 1998 for a discussion).

As with other behaviours, anti-predator responses have both inherent and learned components, and most behaviour patterns should be viewed as lying somewhere on the continuum between these two extremes (Keifer & Colgan, 1992). The characteristic C-start or fast-start startle response in fish is a classic example of a comparatively ‘ hard-wired ’ behaviour. C-starts are initiated by the mauthner neurone-lateral line system and are a largely closed circuit system with little allowance for altering the response with repeated exposure or practise (Eaton *et al.*, 1977). However, other behavioural components of anti-predator behaviour are more dependent on experience. Predator-naive populations of fish do occur naturally in the wild, but are typically found above natural barriers such as waterfalls. Although predator naive fish have poor anti-predator skills compared to fish that live sympatrically with predators (Magurran, 1986), it has been found that naive fish can rapidly improve their response with experience (Olla & Davis, 1989; Magurran, 1990; Kieffer & Colgan, 1992; Berejikian, 1995; Brown & Warburton, 1999*a*). For instance Magurran (1990) found that when predator naive and wary minnows were brought into the lab and bred under captive conditions, the first generation of predator-wary fish still showed superior anti-predator responses compared with their naive counterparts. However, both populations showed rapid improvements in their responses with experience.

Anti-predator behaviour is, more often than not, an energetically costly exercise because it must be traded off against other activities. Time and energy spent avoiding predators might be better spent on foraging and mating (Ryer & Olla, 1998). For this reason anti-predator behaviour often degrades once prey are no longer subjected to predation pressure. This secondary loss of behaviour may be partial or almost complete depending on the length of time since isolation from the selective force (e.g. predators; Griffin *et al.*, 2000). Separation from selection for many generations (on an evolutionary time-scale) is more likely to result in large-scale loss of responses compared with separation during an individual’s lifetime. Recent work on guppies suggests that genetic responses to adverse selection pressures can be extremely fast, occurring over just a few generations (Endler, 1995; Carvalho *et al*., 1996; Reznick *et al*., 1997). While the subsequent loss of a behaviour following the removal of a strong selective force may not occur so rapidly, nevertheless, the number of generations since a hatchery stock was removed from the wild is likely to have major repercussions when it comes to the development of life skills training protocols. Hatchery fish that are many generations removed from their wild counterparts are likely to have more impoverished life-history skills and may take longer to train than those separated by fewer generations.

RECENT DEVELOPMENTS IN FISH SOCIAL LEARNING

Suboski & Templeton (1989) postulated that social learning methods could be used to improve the post-release survival of hatchery-reared fishes. In the years since their paper, studies in animal behaviour have shown the learning ability of many fish to be far greater than previously conceived (e.g. Croy & Hughes, 1991; Hughes *et al*., 1992; Kieffer & Colgan, 1992; Csanyi & Doka, 1993; Dittman *et al*., 1996; Laland & Williams, 1997; Girvan & Braithwaite, 1998; Lopez *et al*., 1999). A quick search of the literature reveals that from 1990 to the present over 250 papers have been published on various aspects of learning in fishes, and much of this literature could be applied to fisheries biology. The literature reveals that fish are capable of learning not only by trial and error and associative processes but also through social learning, that is, learning by observing or interacting with others (Suboski & Templeton, 1989; Ryer & Olla, 1991; Laland & Williams, 1997; Reader & Laland, 2000). For example, members of fish shoals are able to make decisions by observing changes in the behaviour of their fellow shoal mates (Magurran & Higham, 1988). Many fish species are highly social and form shoals for most or some part of their life and are therefore excellent candidates for studying social learning.

Growth in the field of social learning over the last decade, including the development of new protocols such as transmission chains (see below), has provided the key to the development of effective means to train hatchery-reared fish *en masse*. Recent models examining how novel behaviours spread through populations (Reader & Laland, 2000 and references therein) have further aided our understanding of the underlying social mechanisms at play. These factors combined with our increasing understanding of the components of shoal formation (Hagar & Helfman, 1991; Krause *et al*., 1998), shoal-mate selection (Pitcher & Parish, 1993; Barber *et al*., 1998) and the importance of familiarity and kin recognition (Giffiths & Magurran, 1997; Hojesjo *et al*., 1998; Arnold, 2000), have enabled us to predict the likely success of social learning protocols and develop them further.

It is well established that social interactions play a major role in the acquisition and development of learned behaviours in many animals (Galef, 1988; Lefebvre & Palameta, 1988). Ethologists and behavioural ecologists have been increasingly interested in social learning because it appears to enable animals to learn about their environments rapidly and efficiently, without having to engage in potentially hazardous or energetically costly learning trials, or explore the features of their environment for themselves. Animals can acquire useful skills more rapidly, simply by copying the behaviour of others. Over the past decade studies into social learning have proliferated and social learning is now a major topic of research in ethology, behavioural ecology, primatology and comparative psychology (Heyes & Galef, 1996; Box & Gibson, 1999). Moreover, it is now recognized that social learning is not restricted to large-brained or ' clever ' species, but is widespread among vertebrates, and occurs in many invertebrates.

Most cases of social learning in animals appear to result from very simple processes. For example, social learning through local enhancement occurs when the behaviour of one individual draws the attention of a second naive animal to a particular locality in the environment, about which it subsequently learns something. Stimulus enhancement is a similar phenomenon, occurring when attention is directed to a particular object, rather than a location. Social facilitation occurs when the behaviour of one animal evokes the same behaviour in a second individual, and the expression of this behaviour may result in learning. Observational conditioning refers to situations in which animals respond emotionally (e.g. fearfully) to stimuli emitted by another emotionally aroused individual (e.g. a predator), and eventually learn to respond directly to the stimulus. A characteristic feature of all these forms of learning is that the information transferred between individuals is little more than a tip off, but nonetheless this can frequently result in learning in the observer and the diffusion of the behaviour through the group (Galef, 1988).

A variety of fish species have been found to exhibit these forms of learning. For instance, fish have been found to acquire foraging patch information from others, to recognize predators by responding to the fright response of conspecifics, to identify suitable prey items and microhabitats habitats, learn migration routes and even identify suitable mates (Laland & Williams, 1997 and references therein). The rate of spread of a novel behaviour through a fish population is frequently determined by the number of individuals displaying the behaviour (Sugita, 1980; Lachlan *et al*., 1998). This can result in a conformity effect, with individuals doing what the majority do much of the time (Lachlan *et al*., 1998). Three areas where social learning may play a vital role in the development of fish behaviour are predator avoidance, foraging and migration. We address the role of social learning in each of these areas in turn, but pay particular attention to anti-predator behaviours.

PREDATION

Predation is the principal cause of mortality among released hatchery fish (Howell, 1994) and as such is the primary area on which to concentrate if we are to improve post-release survival. Naive fish often do not recognize predators or respond inappropriately when exposed to them. For example, naive fish can be attracted to movements made by predators and the entire shoal often approaches out of curiosity, a response that is frequently fatal (Brown & Warburton, 1999*a*). Predator-wary fish, on the other hand, rarely approach predators. When they do approach they do so cautiously, remain a relatively safe distance away and show attack cone avoidance (Magurran & Seghers, 1990). It has been hypothesized that the higher mortality rates experienced by hatchery-reared fish may be due to the fact that they have had no prior experience of predation and are subsequently easy prey for predators. Indeed there is evidence that predators switch their prey preferences from wild to hatchery-reared smolt as soon as the hatchery fish are released (Thompson & Tufts, 1967). However, there is ample evidence demonstrating that repeated exposure to predators improves anti-predator responses in fish (Kanayama & Tuge, 1968; Fraser, 1974; Olla & Davis, 1989; Csanyi & Doka, 1993; Jarvi & Uglem, 1993; Berejikian, 1995; Brown & Smith, 1996; Mirza & Chivers, 2000). Furthermore, if a naive fish is given the opportunity to observe another fish fleeing or being attacked by a predator it often invokes an escape response in the naive individual (Magurran & Higham, 1988). Fish often then retain the escape response and it may be invoked when it later comes into direct contact with the predator itself. This social transmission of predator recognition has been reported in a number of fish species, including European minnows (*Phoxinus phoxinus,* L.), fathead minnows *(Pimephales promelas*, Rafinesque), zebra danios (*Brachydanio rerio*, Hamilton), guppies (*Poecilia reticulata*, Peters), chinook salmon (*Oncorhynchus tshawytsha,* Walbaum), rainbow trout (*Oncorhynkis mykiss*) and three-spined sticklebacks (*Gasterosteus aculeatus,* L.), and is probably commonplace in shoaling species (Pitcher, 1986; Magurran & Higham, 1988; Suboski *et al*., 1990; Ryer & Olla, 1991; Mathis *et al*., 1996). This process also occurs in mixed-species shoals, and can result in the transmission of information between species (Krause, 1993). Controlled laboratory experiments have also demonstrated the social learning of escape responses to an artificial predator (Brown & Warburton, 1999*a*; C. Brown & K. Laland, unpubl. obs.). For example Sugita (1980) found that fish learn to avoid an electric shock by following trained demonstrator fish to a safe compartment in a shuttle box.

PAIRING PREDATOR ODOUR WITH ALARM SUBSTANCES

In 1938 von Frisch discovered that mechanical damage to the skin of European minnows results in the release of a chemical alarm substance or ‘schreckstoff’ that, at very low concentrations, causes fright responses in receiver fish. Recently, Hall & Suboski (1995) found that control of the alarm reaction could be transferred to previously neutral stimuli via paired conditioning and could provide a mechanism whereby naive animals learn to recognize predators without ever coming into direct contact with them. Following work by Suboski and his colleagues, Chivers & Smith (1995) demonstrated that minnows were also capable of associating conspecific alarm substances with chemical cues emanating from both predators and risky habitats and subsequently learned to avoid both the predator and locations where predators had recently been. When naive fish were placed in a tank with experienced ones the naive fish exhibited alarm reactions to chemical cues emitted by predators through some form of social enhancement. Later, when tested alone, the naive fish maintained the alarm reaction in the presence of risky habitat cues, indicating that learning had taken place. Experiments by Mathis *et al.* (1996) showed that this fright response to chemical cues emitted from predators could also be transmitted to brook sticklebacks (*Culaea inconstans*, Kirtland), which often occur in mixed species shoals with fathead minnows. It was previously thought that the use of chemical cues (such as Schreckstoff) in the social transmission of predator recognition was restricted to members of the super-order Ostereophyses, but it is becoming increasingly clear that it is much more widespread. A number of other species, including rainbow trout and chinook salmon, also learn to recognize the chemical cues emanating from a predator via social mechanisms (Magurran, 1989; Chivers & Smith, 1995; Mathis *et al*., 1996; Brown & Smith, 1998; Berejikian *et al*., 1999). In the case of chinook salmon, pre-exposure to such chemical cues has been shown to increase the survival of hatchery reared smolts post-release (Berejikian *et al*., 1999). Chinook salmon where conditioned after just one exposure to the pairing of skin extract of a conspecific and the predator odour. The response was lost by day 10 post-conditioning, but Brown & Smith (1998) demonstrated that rainbow trout retained predator recognition for at least 21 days post-exposure. The strength of the response to the predator odour, decays with time (Brown & Smith, 1998), but it seems likely that the retention period would not have to be very long for smolt to make use of their newly acquired knowledge. It is likely that if the smolt can retain conditioned recognition for just a few days to a week then it's survival chances following release will be greatly improved. This factor coupled with the knowledge that fish can learn to avoid predators after observing attacks on conspecifics (reviewed below) suggests that reinforcement post-release is likely to further aid the development of anti-predator behaviours in hatchery reared individuals.

EXPOSURE TO PREDATION AND OBSERVING CONSPECIFICS

Several attempts have been made to condition hatchery-reared salmonids to recognize predators using a number of different approaches. One approach was to pair negative stimuli (e.g. electric currents) with the appearance of a model predator (Thompson, 1966). In a second, fry were placed in an aquarium with a live predator (Kanid'hev *et al*., 1970; Jarvi & Uglem, 1993). A third method allowed fry to observe a predator from behind a clear partition (Jarvi & Uglem, 1993; Berijikian, 1995). These methods provided mixed results, but they do provide a promising platform from which to launch new approaches.

Members of shoals often monitor the behaviour of their fellows in an attempt to gain information about the location of foraging sites or approaching predators. This behaviour is common to virtually all vertebrates that form social groups (for a review see Elgar, 1989). Utilizing information gained from observing conspecifics is especially advantageous as it allows the adoption of appropriate behaviours without the need to independently verify the approach of a predator. Both the Trafalgar effect (Webb, 1980) and chorus line effect (Potts, 1984) occur when individuals respond to the flight response of neighbours rather than directly to the advancing predator itself, resulting in apparently synchronous behaviours of individuals in shoals of fish or flocks of birds. In both cases the rate of information transfer through the group far exceeds the speed of the approaching danger and consequently results in the phenomenon of collective detection. Collective detection assumes that all members of a group are rapidly alerted to the presence of a predator once a single group member has detected it (Lima, 1995). Brown & Warburton (1999*b*) attributed improved escape responses in larger groups of fish to behavioural monitoring, whereby individuals received a cue as to the whereabouts of an escape route from fish that escaped successfully. Magurran & Higham (1988) clearly showed that minnows showed a significant increase in the frequency of flight responses after observing the flight response of minnows in a neighbouring tank that had been threatened by a predator. Similar observations where made by Pitcher *et al*. (1986) in their

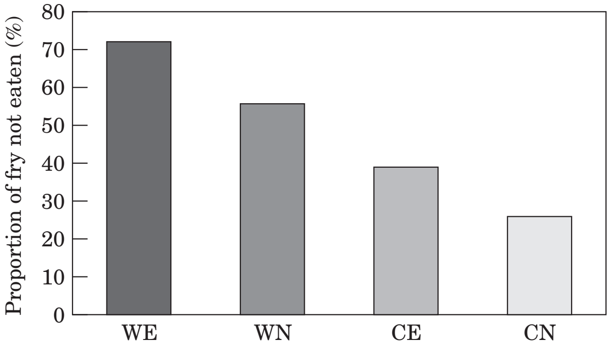

FIG. 1. The proportion of steelhead fry not eaten when placed in an experimental tank with a predator. W, Wild stock; C, captive/hatchery stock; E, predator experienced; N, predator naive, based on Berejikian (1995). There was a significant difference between the four treatment groups ($\chi^2=13{\cdot}07$, d.f.$=3$, $P<0{\cdot}005$).

analysis of the change of the behaviour of shoal mates following the return of an individual from a predator inspection visit. It is likely that shoal mates gauge the behaviour of the inspector and alter their behaviour to match the perceived level of threat.

Berejikan (1995) reared two populations of steelhead trout (*Oncorhynchus mykiss*, Walbaum) in the laboratory (one bred from wild fish and the other from hatchery fish). The hatchery stock had been bred from fish derived from the same wild population but had been kept under hatchery conditions for some 20 years before the experiment took place. Half of the juveniles from each population observed a predator chasing and eating sacrificial conspecifics behind a clear perspex barrier. After 24 h all fish were allowed to interact with the predator and the number of surviving fry recorded. A higher proportion of hatchery-reared fish were eaten compared to wild fish, but training improved the survivorship of both populations (Fig. 1).

Conditioning fish individually is unlikely to be cost effective, and simple exposure to a predator is often not sufficient to condition naive animals. However, visual and olfactory exposure to a predator in the presence of a limited number of pre-trained (or wild), predator wary conspecifics as well as the introduction of skin extract from conspecifics is likely to be a highly effective means of mass conditioning predator recognition in hatchery-reared fishes.

FORAGING

As with predator avoidance, the foraging behaviour of hatchery reared fish may also show deficiencies caused by the rearing environment (Sosiak *et al.*, 1979; Johnsen & Ugedal, 1989). Laboratory experiments indicate that salmonids such as pink salmon (*Oncorhynchus gorbuscha*, Walbaum), rainbow and brown trout all improve feeding behaviour with learning. For example, Stradmeyer & Thorpe (1987) showed that hatchery Atlantic salmon changed from pellet foods to wild prey over 16 trials in just one and a half hours. Similar results have been obtained for coho salmon but not all fish make the transition successfully (Paszkowski & Olla, 1985). Atlantic salmon are able to alter their prey choice with experience to a pattern which closely matches that of wild fish (Reiriz *et al.*, 1998). While an improvement occurs in recognition, most of the improvement is probably made in prey handling and selection. Learning in this regard is especially important in the wild as it can improve foraging efficiency by adjusting foraging behaviour to match changing circumstances (Hughes *et al*., 1992).

In the wild, prey abundance and trophic value can alter considerably and learning is the process through which individuals adjust their behaviour to match the costs and benefits associated with feeding upon certain prey types. Accurate recognition and efficient prey handling are, therefore, critical to achieve optimal diets under a wide variety of circumstances (Reiriz *et al*., 1998). When hatchery salmonids are released, however, they consume less food, fewer prey types and are slow to switch between prey types in comparison to their wild counterparts (Sosiak *et al*., 1979; Ersbak & Haase, 1983). Consequently they often show poor growth rates and have lower survival. This inferior foraging behaviour may be the manifestation of a number of other confounding factors. For example, fish often cease feeding when introduced to a novel environment and it may take a number of days before feeding begins again (Paszkowski & Olla, 1985). Furthermore, hatchery fish often choose inappropriate microhabitats. For example hatchery-reared fish may take up positions in mid-stream in order to gain access to prey items but they are also exposed to consistently high water velocities. Wild fish by contrast take up positions in eddies and dart out into the current to grab prey items as they drift past. Hatchery fish may also be found higher in the water column where they are not only exposed to avian predators but also decrease their contact with benthic prey items and are also exposed to stronger current velocities (cf. those found at a stream bed). Finally, hatchery fish frequently fail to disperse and are therefore often found in higher densities than wild fish, resulting in increased competition for limited food resources (Olla *et al*., 1998). Fish weakened by hunger are more likely to fall victim to predators, and thus inappropriate foraging behaviour may indirectly contribute to the higher predator related mortality observed in hatchery-reared fish.

Despite the complexity of the deficiency in foraging behaviour in hatchery reared fish, there is little doubt that exposure to live food increases foraging efficiency and attraction to novel food items may be enhanced in a social context (Morgan & Colgan, 1987; Morgan, 1988; Ryer & Olla, 1991, 1992; Sundstrom & Johnsson, 2001). It is well established that foraging efficiency increases with group size when food is patchily distributed (Pitcher *et al*., 1982; Pitcher & House, 1987). Social learning may be partly responsible for this improvement when fish require up-to-date foraging information by observing the behaviour of their shoal mates (Pitcher & House, 1987; Laland & Williams, 1997). Fish may also learn the location of food resources by shoaling with knowledgeable conspecifics (Laland & Williams, 1997).

The term forage area copying is a well-known example of social learning. In forage area copying (Barnard & Sibly, 1981) the behaviour of successful foragers is recognized by conspecifics and draws them towards the foraging patch where they subsequently encounter food and forage themselves. In doing so they also promulgate a successful foraging cue, which in turn attracts further animals to the patch. Watching others consuming particular prey items may directly influence the diet preferences of an individual. Templeton (1987), for example, found that juvenile rock bass (*Ambloplites rupestris*, Rafinesque) when given visual access to experienced conspecifics consuming a novel food later consumed the novel prey item more readily than naive control fish. Although there is now ample evidence for learning and social learning in the development of foraging skills in fish, the potential to train hatchery-reared fish *en masse* using social learning protocols remains largely untested (but see Sundstrom & Johnsson, 2001).

MIGRATION AND ORIENTATION

Laboratory work by Laland & Williams (1997, 1998) suggests that fish can learn the location of foraging patches through social learning. ' Demonstrator ' guppies were trained to take one of two alternative routes to feed, and then naive subjects were allowed to swim these routes with their demonstrators. Laland & Williams found that when subsequently tested alone, guppies tended to take the same route to feed as their demonstrators had, and the more demonstrators they had swam with, the stronger the effect. Thus simply by shoaling with knowledgeable conspecifics, fish can learn the route to a food source. Laland & Williams found that this process is sufficient to maintain arbitrary and even maladaptive traditions for exploiting particular routes to feed, while Reader & Laland (2000) have found that similar foraging skills can diffuse through populations of guppies. A similar process may underlie the traditional mating site preference, daytime schooling sites and twilight migration routes of coral reef fish (Helfman & Schultz, 1984; Warner, 1988) and the migration between spawning sites and feeding sites in walleye fish *Stizostedion vitreum*, Mitchill (Olson *et al*., 1978).

Helfman *et al.* (1982) showed that specific resting sites in coral reefs contained groups of sub-adults and juveniles that were repeatedly comprised of the same individuals. These groups were often joined by newly recruiting individuals. Later, Helfman & Shultz (1984) showed that these newly recruited individuals learned the migration path from the overnight resting place to the day time feeding grounds by following the more experienced group members. This provided the first real evidence of social learning of migration routes in the wild. Helfman & Shultz (1984) transplanted juveniles between resting locations and allowed to migrate with the residence for 2 days prior to testing in the absence of the residents. In the control group the residence were removed prior to transplanting and testing. The results clearly showed that control fish continued to migrate along the same compass bearing as if they were still at their home site. Fish that had had just 2 days of migrating with residents, on the other hand, migrating along similar paths to the residents.

Similar socially transmitted traditions have been observed in the mating sites of the bluehead wrasse *Thalassoma bifasciatum* Bloch (Warner, 1988). The mating locations of bluehead wrasse remain constant over many generations and it was thought that this might simply be a result of individual assessment of prevailing resource quality. When Warner (1988) removed entire populations of bluehead wrasse and replaced them with transplanted individuals, not only did the transplanted individuals establish new mating sites, but these new locations continued to be used long after the initial manipulation. This evidence, combined with the fact that in the 12 years of studying 22 patches on the reef not once was a new mating site established or lost despite fluctuations in the wrasse population size, provides compelling evidence for the maintenance of mating sites by social learning.

Further evidence of the role of social learning in migration is provided by Grunbaum (1998). Grunbaum (1998) suggested that schooling enables fish to rapidly home in on natal streams as they work together to orientate towards their goal in response to odours at a very low concentration. As with foraging and anti-predator behaviours, no one has yet attempted to utilize social learning to train hatchery-reared fish to forage in particular locations.

FUTURE DIRECTIONS AND IMPEDIMENTS

To date few fisheries managers have made use of the information available on learning and social learning in fishes and applied it to hatchery release programs. A few papers have recently recognized the importance of learning and pre-release training and have made some recommendations towards improving pre-release experience (Howell, 1994; Olla *et al*., 1994; Brown & Smith, 1998). However, only a few trials of pre-release training have occurred (Thompson, 1966; Kanayama, 1968; Jarvi & Uglem, 1993; Berejikian *et al*., 1999). The outcome of the pre-release training in all of the above cases was promising and succeeded in reducing mortally to some extent. As far as we are aware, with the exception of a single laboratory experiment (Sundstrom & Johnsson, 2001), no trials of social learning of survival skills have occurred in hatchery-reared fish prior to release. This is surprising considering that these methods have long been employed in conservation based reintroduction programs, which essentially face the same problems and target the same outcomes as fisheries restocking (Olney *et al*., 1994; Sutherland, 1998; see Griffin *et al*., 2000 for a review), and may in part reflect the pervasive view that underestimates the learning abilities of fish. However, it is important to acknowledge the gulf between the experimental demonstration of social learning in non-commercial species in academic laboratories and the widespread application of social learning protocols to train large numbers of commercial fish in hatcheries. In order to facilitate the implementation of social learning methods to hatchery fish, in this section we outline a practical guide into the research necessary to address this problem and highlight some of the impediments to further research.

In order to initiate pre-release training protocols using social learning paradigms, there appear to be three practical steps required before these protocols could be utilized at the hatchery level. In the first instance it is important to establish to what degree the species involved relies on social learning and to what extent it is able to utilize public information. Our lack of knowledge regarding the relative importance of social learning in the acquisition of novel behaviours in commercial species remains the single greatest obstacle in the development of this field. Nevertheless, experimental procedures involving foraging tasks as outlined by Laland & Williams (1997) and anti-predator tasks along the lines of Magurran & Higham (1988) and Berejikian *et al*. (1999) could be implemented with relative ease. A number of simple trials will be necessary to establish if the candidate species in capable of social learning either by visual or olfactory means. Some procedures (e.g. Laland & Williams, 1997) require the training of demonstrator fish, which may require weeks of conditioning. Alternatively wild fish could be used as demonstrators, however, these fish may take some time to habituate to captivity, a problem that may negate the benefits of using them at all. While highly solitary, aggressive or territorial species are probably less likely to be suitable candidates, research into animal social learning has not demonstrated that such species are less able social learners. However, many species of fish form social groups at some stage in their life cycle, or at least are capable of social learning even though they may not commonly form social aggregations. A judicious choice of age, sex or life-history stage may facilitate the opportunity for a successful demonstration of social learning in commercial species. Future investigations into the effects of these demographic factors on social learning are required for the development of species-specific training programs.

Having established that the species is capable of simple forms of social learning, population-level analyses of social learning would be the next step. Appropriate methods include the use of transmission chain experiments (Curio *et al*., 1978; Laland & Plotkin, 1993; Galef & Allen, 1995; Laland & Williams, 1998, see further explanation below). The goal of such studies would be to establish whether relevant learned survival skills could be socially transmitted through a population of the fish species in question. Social learning studies have established that the demonstration that an animal is capable of social learning is insufficient to guarantee that a particular behaviour will spread through populations of such animals (Laland *et al*., 1993). Moreover, as it is difficult to establish whether an animal is capable of social learning within the framework of a population-level analysis, both the basic social learning experiments and the population-level studies are necessary steps to the instigation of a training regime.

Experimental studies of social learning have recently commonly adopted a transmission-chain design in which untrained animals learn skills from trained demonstrators, and then are made the demonstrators to the next set of animals in the chain, with the process repeated (Galef & Allen, 1995; Laland & Williams, 1997, 1998). Such studies typically begin with founder populations trained to perform a target behaviour. Subsequently the composition of the population is gradually changed by replacing trained individuals with naive individuals. Therefore, not all fish in a group need to undergo direct training (*sensu* Olla *et al*., 1994). If the target behaviour remains present in the population when all the founders have been removed, a behavioural tradition has been established. It would be possible to utilize this design effectively among hatchery fish, in the same manner that Laland & Williams did with guppies. For instance, a founder population of wild fish that respond appropriately to a predator could gradually be replaced with hatchery fish, and if they acquire the relevant behaviour the transmission chain could be continued with further naive hatchery fish replacing the experienced hatchery fish. The introduction of a predator, either behind a clear partition or directly into the holding tanks, in addition to appropriate chemical stimuli and prior training of a small proportion of individuals should be enough to invoke appropriate anti-predator responses. Precise protocols could be developed with lower stocking densities in combination with habitat-enriched tanks (e.g. Berejikian *et al*., 2000). It is likely that responses such as fleeing and finding cover and context dependent foraging tasks will be biologically more meaningful under these circumstances.

If successful, transmission chain protocols could enable the rapid conditioning of all fish within a hatchery with either no pre-training of founders required at all, or intensive pre-training only required for only a small number of individuals to begin with. Wild individuals from the system into which the hatchery fish are to be released could be brought in to start the chain off, thus insuring that naive fish obtain behaviour that is locally adaptive. In all cases the food items, foraging locations and predators used during training should be selected to represent the type of experiences to which wild fish are likely to be exposed. This stage would also allow researchers to determine the optimal ratio of experienced to naive fish for effective transmission. Once again, further research will be required in this area for each target species.

The final stage in the implementation of a training protocol is testing its effectiveness in trials. Ironically, Berejikian *et al.* (2000) suggest that perhaps one of the problems of previous attempts to assess the effects of training fingerlings before release is that both trained and untrained fish have been released together. This enables the control fish to rapidly acquire anti-predator behaviour from the trained fish through social learning processes, but the improved survivorship of the control fish offsets the apparent affect of the training procedure by reducing differences in mortality between test and control fish. It has also been noted that the survivorship of hatchery reared fingerlings increases if they are released amongst shoals of wild conspecifics (Hvidsten & Johnsen, 1993). Patten (1977) demonstrated that naive coho salmon fry placed with predator-experienced fry were better able to avoid predation. Such observations reflect the need for properly controlled trials in which trained and untrained fish are released independently. The best trial would involve a tag-recapture experiment using both trained and untrained fish. The fish should be released in small batches at various locations, times of day, etc. Most importantly, the trained and untrained fish should not be introduced simultaneously in the same location.

SUMMARY

It is becoming increasingly evident that the aquaculture hatchery environment causes large deficiencies in the behaviour of the captive-reared stock. Some of these deficiencies are currently being addressed, but in many cases the solutions appear to be incompatible with the production of large numbers of fish for release. Perhaps it is time to shift the emphasis from quantity to quality in an attempt to improve hatchery efficiency where it counts most; the improvement of post-release survivorship. Large-scale training of foraging skills and anti-predator behaviour is feasible, relatively simple and inexpensive to initiate. Recent advances in social learning and in particular the use of transmission chain protocols provide a significant opportunity for advancement and implementation of large scale training programs. It is envisaged that a pre-release survival training programs with emphases on foraging and anti-predator behaviours could be implemented in an intensive hatchery system a few days to a week before the release of juveniles into the wild. The exact pattern of training required is likely to be species or even population specific. Most salmoniids appear to respond favourably to training and early attempts at applying these protocols should initially concentrate on these fisheries. Conservation based captive breeding programs for endangered or threatened fish would also benefit greatly from post-release training regimes (Andrews & Kaufman, 1994). The benefits associated with improving the post-release survivorship of hatchery-reared animals are too great to ignore. It is time that large-scale training protocols were developed and taken on board as an intrinsic part of hatchery production.

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