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The Influence of Group Size on Learning and Problem-Solving in New Zealand Spotted Wrasse (*Notolabrus celidotus*)

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Abstract

Foraging dynamics are a fundamental ecological process influencing a variety of other important processes including population dynamics and reproduction. This study investigated the influence of group size on the foraging success of 40 New Zealand spotted wrasse (*Notolabrus celidotus*) using a problem-solving apparatus. A pilot study using four fish was initially carried out to test equipment and gain an understanding of the individual learning capacity of these fish. Following this pilot study, the full study was separated into four stages. Stage 1 involved observing individual fish attempting a problem-solving foraging task on their own. Stages 2 and 3 increased the group size of fish attempting this foraging task to two fish and four fish, respectively. Stage 4 involved individual fish attempting the task on their own, however, mirrors were fitted to the experimental tank to simulate an increase in group size. Results of this research showed that the presence/perceived presence of conspecifics resulted in increased success rates and reduced latency to solve the problem over time. These results suggest that group size is an important contributor to foraging efficiency in the New Zealand spotted wrasse, as larger groups outperformed smaller groups in most cases, and individual fish with simulated increases to group size outperformed individual fish without this effect. There are three potential explanations for these results. (1) The presence of conspecifics provides passive predator vigilance, enabling individual fish to put more time into solving the foraging task instead of scanning for predators. (2) As a function of increased competition for a limited resource, fish put more effort into solving the foraging task. (3) Social learning resulted in fish learning foraging strategies from conspecifics. It is likely that the effects of reduced predator vigilance and increased competition in larger group sizes influenced foraging success rates of the fish in this study concurrently. Additionally, the pair and group treatments displayed a reduced latency for fish to leave the starting arena and to orient toward the food reward than the other treatments. It is unlikely that

these results can be attributed to increased chance due to increased fish density, as fish from the pair and group treatments performed similarly in weeks one and three, despite the group treatment having twice as many fish per trial. This indicates the potential effect of a social learning mechanism, such as local enhancement, in the spotted wrasse in this study. Future studies could further assess the influence of social learning through use of reliable demonstrator fish in an observer-demonstrator experiment. Further study is required to conclusively suggest whether the effect of reduced predator vigilance, increased competition, or social learning has a greater influence on increased foraging success with increased group size in New Zealand spotted wrasse.

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Table of Contents

Abstract.....	i
Acknowledgements	iii
Table of Contents	iv
List of Figures.....	vi
List of Tables.....	vii
Chapter 1 Literature Review.....	1
1.1 Perception of Animal Intelligence.....	1
1.2 Measures of Intelligence	2
1.2.1 Behavioural Plasticity	2
1.2.2 Innovation	3
1.3 Problem-Solving.....	4
1.3.1 Associative Learning	5
1.3.2 Insightful Problem-Solving	6
1.3.3 Additional Examples of Problem-Solving.....	7
1.4 The Evolution of Social Groups.....	13
1.4.1 Predator Avoidance	13
1.4.2 Foraging Success	14
1.4.3 The Influence of Group Size on Problem-Solving Ability	15
1.5 Social Learning	16
1.5.1 Local and Stimulus Enhancement	16
1.5.2 Emulation and Imitation	17
1.5.3 Other Social Learning Mechanisms.....	18
1.6 Social Learning in Fish	19
1.7 The Spotted Wrasse (<i>Notolabrus celidotus</i>).....	21
1.8 Study Aims.....	23
Chapter 2 Methods	24
2.1 Subject Collection and Storage	24
2.2 Equipment	25
2.3 Pilot Study	29
2.4 Full Study	31
2.4.1 Stage 1: Solo Trials.....	31
2.4.2 Stage 2: Pair Trials.....	31
2.4.3 Stage 3: Group Trials.....	32
2.4.4 Stage 4: Solo Mirror Trials	32

2.4.5	Measurements	33
2.4.6	Data Analysis	34
Chapter 3 Results		36
3.1	Pilot Study	36
3.2	Full Study	37
3.2.1	Success Rate and Completion Time	37
3.2.2	Time to Exit the Starting Arena	42
3.2.3	Time to Orientate to Food Source	47
Chapter 4 Discussion		52
4.1	Key Findings and Interpretation	52
4.1.1	Predator Vigilance	53
4.1.2	Competition	54
4.1.3	Predator Vigilance vs. Competition	55
4.1.4	Social Learning	57
4.1.5	Individual Learning	58
4.2	Limitations and Future Studies	59
4.3	Conclusions	61
References		62

List of Figures

<i>Figure 1.</i> Housing tanks for fish storage during Stage 1 (one fish per tank segment), Stage 2 (two fish per tank segment), and Stage 4 (one fish per tank segment). Fish were separated with transparent perforated dividers which allowed water and oxygen flow from one side of the tank to the other.	26
<i>Figure 2.</i> Housing tanks for fish in Stage 3 (four fish in each half of the tank). Fish were separated with a transparent perforated divider which allowed water and oxygen flow from one side of the tank to the other.	27
<i>Figure 3.</i> This diagram shows the experimental set-up for the problem-solving foraging task apparatus in Stage 1, 2 and 3. The open ends of the acrylic tubes were covered with black insulation tape to make the opening of the tube more apparent to the fish.	28
<i>Figure 4.</i> This diagram shows the experimental set-up for the Stage 4. This is identical to the previous experimental tank aside from the addition two mirrors attached to the exterior walls facing inwards to simulate the presence of conspecifics. The open ends of the acrylic tubes were covered with black insulation tape to make the opening of the tube more apparent to the fish.	28
<i>Figure 5.</i> A survival analysis showing the success rate (%) and completion time (s) of the single fish in the pilot study over a four-week trial period.	36
<i>Figure 6.</i> A survival analysis showing the success rate (%) and completion time (s) of each treatment during week one (A.), week two (B.), and week three (C.). ...	37
<i>Figure 7.</i> A survival analysis showing the success rate (%) and completion time (s) of the single fish treatment (A.), mirror treatment (B.), pair treatment (C.), and group treatment (D.) over a three-week period.	41
<i>Figure 8.</i> A survival analysis showing the time for the first fish in a trial to leave the starting arena (s) in each treatment during week one (A.), week two (B.), and week three (C.).	43
<i>Figure 9.</i> A survival analysis showing the latency of fish to leave the starting arena (s) in the single fish treatment (A.), mirror treatment (B.), pair treatment (C.), and group treatment (D.) over a three-week period.	46
<i>Figure 10.</i> A survival analysis showing the time for the first fish in a trial to orientate to the food reward (s) in each treatment during week one (A.), week two (B.), and week three (C.).	48
<i>Figure 11.</i> A survival analysis showing the latency of fish to orientate to the food source (s) in the single fish treatment (A.), mirror treatment (B.), pair treatment (C.), and group treatment (D.) over a three-week period.	51

List of Tables

<i>Table 1.</i> An ethogram describing the fish behaviours measured during the problem-solving task.....	34
<i>Table 2.</i> Statistical comparisons pilot study trials to determine whether task solving improved over four successive weeks. “Undefined” means that a median value was not determined i.e., 50% of fish did not complete the task.	36
<i>Table 3.</i> Statistical comparisons between the problem-solving abilities of the different treatment groups in week one. 95% confidence intervals in parentheses. Bolded values indicate statistical significance. “Undefined” means that a median value was not determined, i.e., 50% of fish did not complete the task.	38
<i>Table 4.</i> Statistical comparisons between the problem-solving abilities of the different treatment groups in week two. 95% confidence intervals in parentheses. Bolded values indicate statistical significance. “Undefined” means that a median value was not determined, i.e., 50% of fish did not complete the task.	39
<i>Table 5.</i> Statistical comparisons between the problem-solving abilities of the different treatment groups in week three. 95% confidence intervals in parentheses. Bolded values indicate statistical significance.	40
<i>Table 6.</i> Statistical comparisons within each between treatment group to determine whether problem-solving ability improved over three successive weeks. 95% confidence intervals in parentheses. Bolded values indicate statistical significance. “Undefined” means that a median value was not determined, i.e., 50% of fish did not complete the task.	41
<i>Table 7.</i> Statistical comparisons between treatment groups in week one - time for first fish to exit the starting arena (s). 95% confidence intervals in parentheses. Bolded values indicate statistical significance.	44
<i>Table 8.</i> Statistical comparisons between treatment groups in week two - time for first fish to exit the starting arena (s). 95% confidence intervals in parentheses. Bolded values indicate statistical significance.	44
<i>Table 9.</i> Statistical comparisons between treatment groups in week three - time for first fish to exit the starting arena (s). 95% confidence intervals in parentheses. Bolded values indicate statistical significance.	45
<i>Table 10.</i> Statistical comparisons within each social group to determine whether time for first fish to exit the starting arena declined over three successive weeks. Bolded values indicate statistical significance.	46
<i>Table 11.</i> Statistical comparisons between treatment groups in week one - time for first fish to orientate to the food source (s). 95% confidence intervals in parentheses. Bolded values indicate statistical significance.....	49
<i>Table 12.</i> Statistical comparisons between treatment groups in week two - time for first fish to orientate to the food source (s). 95% confidence intervals in parentheses. Bolded values indicate statistical significance.....	49

<i>Table 13.</i> Statistical comparisons between treatment groups in week three - time for first fish to orientate to the food source (s). 95% confidence intervals in parentheses. Bolded values indicate statistical significance.....	50
<i>Table 14.</i> Statistical comparisons within each social group to determine whether time for first fish to orientate to the food source declined over three successive weeks. Bolded values indicate statistical significance.	51

Chapter 1

Literature Review

Animal cognition underpins many behaviours such as acquisition and retention of information, as well as enabling decision-making and problem-solving (Shettleworth, 2001). Due to the ecological value of problem-solving, studying this behaviour in a wide range of animals is beneficial in terms of understanding individual interactions between animals and their environments, as well as interactions between and within ecosystems on a larger scale. This thesis investigated the influence of group size upon the problem-solving ability of a native New Zealand estuarine fish, the spotted wrasse (*Notolabrus celidotus*), in relation to a foraging task. Before discussing the implications of problem-solving behaviour, it is useful to consider the concept of intelligence as it relates to animals, including fish.

1.1 Perception of Animal Intelligence

Fish, by number, are consumed by humans more than any other animal, are the second most occurring animal used in research after mice, and are also very common pet animals (Brown, 2015). Despite these important socio-economic connections with humans, and research indicating fish are intelligent, fish are still regarded as less-intelligent organisms by many, raising a need for further research (Brown, 2015). This is important to recognize, as a perception of low intelligence can result in reduced welfare and protection implications, with a less acceptable public attitude towards fish (Brown, 2015).

This mindset is well summarised by Howell et al. (2013), where it was found that the human perception of a dog's intelligence was dependent upon the owner's relationship with the dog, despite there being no real difference in intelligence between the dogs. This indicates a bias in general human perception of animal intelligence, as people would generally consider an animal as being more intelligent based on familiarity (Howell et al.,

2013). Thus, non-mammalian animals such as fish are likely perceived as less intelligent by the public due to being less familiar. Therefore, more research is needed to change this false perception that fish are non-intelligent organisms (Howell et al., 2013; Brown, 2015).

1.2 Measures of Intelligence

Defining animal intelligence is an ongoing issue due to the lack of a consistent definition (Roth & Dicke, 2005). Attempts to measure intelligence have been made, including examining an animal's behavioural flexibility/plasticity, their ability to innovate, as well as their ability to solve novel problems (Roth & Dicke, 2005; Seed & Call, 2010; Gamez, 2020).

1.2.1 Behavioural Plasticity

According to Roth and Dicke (2005) behavioural flexibility, often referred to as behavioural plasticity, is a good measure of intelligence as it enables animals to change or alter their behaviours to benefit themselves in novel situations. Behavioural plasticity refers to the degree to which an organism can alter its repertoire of behaviours to increase its survivability in a range of different environments and selection pressures (Snell-Rood, 2013). There are two types of behavioural plasticity: exogenous plasticity, which refers to how behaviour varies within an individual in response to external variables; and endogenous plasticity, which refers to how behaviour varies within an individual due to internal physiological or morphological mechanisms, not necessarily related to the external environment (Stamps, 2016). Endogenous plasticity is beyond the scope of this study, so iterations of "behavioural plasticity" in this thesis will be referring to exogenous behavioural plasticity. Within exogenous plasticity there exists contextual plasticity and developmental plasticity. Contextual plasticity refers to the extent of variation in an individual's immediate behaviour in response to an external stimulus; examples of this

include mate preference processes, and stimulus-response relationships (Stamps, 2016). Developmental plasticity refers to the extent to which the behaviour of an individual varies due to external factors that occurred in the past, including past learning (Stamps, 2016).

Behavioural plasticity can improve an animal's survivability in novel environments as it directly facilitates innovation, thus it is able to be used in general contexts as well as problem-solving contexts (Snell-Rood, 2013). This allows organisms with a high degree of behavioural plasticity to attempt a variety of potential solutions in a shorter length of time, which directly contributes to increased rates of success. In essence, the problem-solving performance of an animal is mediated by underlying cognitive mechanisms such as behavioural plasticity and innovation. These cognitive mechanisms are speculated to contribute to reduced extinction rates in a range of species, allowing them to acclimate and adapt to novel situations and environments in a rapidly changing world, driven by anthropogenic development (Ducatez et al., 2020).

1.2.2 Innovation

Innovation refers to the ability of animals to adopt new adaptive behaviours, or use previously learned behaviours in a novel situation, to overcome an obstacle (Brosnan & Hopper, 2014). An example of this outside the realm of problem-solving can be observed in Iberian waterfrog (*Pelophylax perezi*) tadpoles. When faced with a novel predator, the red swamp crayfish (*Procambarus clarkii*), these tadpoles became less active than usual to reduce chances of predation (Nunes et al., 2014). This example falls under the Brosnan and Hopper (2014) definition of innovation, as the tadpoles used a previously learned behaviour under novel circumstances to avoid an obstacle to survival, in this case predation.

While innovation and problem-solving are different mechanisms, innovation can directly influence an animal's ability to solve problems, enabling the animal to produce new behaviours to achieve a goal through indirect means; thus, innovation can be supplementary to problem-solving (Griffin & Guez, 2014). While the utilization of new and previously untested behaviours can hold risk-associated fitness costs, such as injury and wasted energy through failed foraging attempts, its prevalence within the animal kingdom is indicative of fitness benefits which outweigh these costs (Brosnan & Hopper, 2014). Innovation can be facilitated by other cognitive mechanisms such as behavioural plasticity (Snell-Rood, 2013).

1.3 Problem-Solving

In animal behaviour, problem-solving can be broadly defined as the ability of an animal to reach a goal when direct means of achieving said goal are unavailable (Seed & Call, 2010). Problem-solving has adaptive applications such as enabling an animal to overcome obstacles in order to obtain a desired state or commodity (e.g., food or territory), or to overcome obstacles to avoid or escape some adverse state (e.g., avoid predation) (Amram & Holekamp, 2012). For example, the outer shell of a food source such as a nut or shellfish, presents an obstacle to an animal attempting to access the food. To overcome this obstacle, the animal could employ problem-solving to break the shell, enabling access to the food source. Thus, in a foraging context, an animal that is more proficient at problem-solving is more likely to obtain more energy per unit effort, and thus gain more fitness benefits at a lower cost by decreasing handling time (Amram & Holekamp, 2012).

Some instances of an animal's problem-solving behaviour involve the use of tools. Tool-use is the ability of an organism to use an external object as a physical extension of the body (usually an extension of the hand/claw or mouth/beak) to reach an immediate goal or avoid an adverse state (Brown, 2011). Tools can allow a foraging organism to gain

access to previously unobtainable resources such as food. For example, the yellowhead wrasse (*Halichoeres garnoti*) is known to use jagged rocks as anvils to open scallops, enabling the yellowhead wrasse to take advantage of the high-energy food source inside the shell (Brown, 2011). The versatility of tool-using organisms enables them to access resources or avoid predation at reduced metabolic costs.

1.3.1 Associative Learning

In some cases, animals solve problems through trial and error, becoming more proficient at solving the problem over time through associative learning (Amram & Holekamp, 2012). Associative learning often involves an animal learning about the relationship between a specific action/event/behaviour and a stimulus/reward through reinforcement or punishment (Lukowiak et al., 1996). In this type of learning an animal can become more consistent at solving a problem due to associating certain behaviours with successful outcomes, rather than requiring a complex understanding of the problem itself.

This type of learning can be observed in spotted hyenas (*Crocuta crocuta*), whereby trial and error resulted in a refinement of foraging behaviours, eventually resulting in a completely different behaviour than what was originally attempted, allowing access to a food reward at a lower energetic cost (Amram & Holekamp, 2012). In this study, hyenas were presented with a large metal cage that contained a visible food reward, the cage could be opened by turning a latch on the door. Success likelihood was found to be related to the number of different behaviours employed by each hyena, with more explorative hyenas employing more behaviours and increasing the chance of opening the latch (Amram & Holekamp, 2012). It is therefore inferred that the first instance of success by the hyenas occurred by chance and was a product of both exploratory behavioural diversity and persistence, as less persistent individuals were less likely to solve the foraging task. Successful hyenas were found to solve the task quicker in subsequent trials, indicating that learning had occurred as success was not a one-time event, and successful

individuals became more proficient at solving the task with practice (Amram & Holekamp, 2012). Due to the low overall success rate within the sample population (14.5%), it is unlikely that the hyenas were using a complex problem-solving mechanism. The problem-solving behaviour of the hyenas was likely facilitated by a combination of innovation and associative learning in this study (Amram & Holekamp, 2012; Brosnan & Hopper, 2014).

1.3.2 Insightful Problem-Solving

Some species utilize more complex problem-solving mechanisms such as insightful problem-solving. Insightful problem-solving infers that an organism is able to suddenly produce an adaptive response in order to reach a goal, through a deeper understanding of the obstacles and potential solutions to a problem (Bird & Emery, 2009). This contrasts with trial-and-error based associative learning which operates solely through positive reinforcement of beneficial behaviours (Amram & Holekamp, 2012).

Insightful problem-solving has been observed in great apes such as orangutans (*Pongo abelii*) in their ability to solve complex foraging tasks, through implementing consistently successful strategies upon gaining an understanding of the obstacles present in the novel task (Mendes et al., 2007). In this study, orangutans were found to be able to manipulate the water level of a tube in order to gain access to floating peanuts. These tubes were transparent, so the orangutans were able to see the peanut inside, however the peanut was kept out of reach, preventing the orangutans from reaching into the tube and grabbing it. The tubes were in a fixed position, and not able to be manipulated (Mendes et al., 2007). Despite the difficulty of this task, all five orangutans were able to successfully access the peanut by filling their mouth with water and spitting it into the top end of the tube, causing the peanut to float up to the orangutan. The most informative result of this study was that all orangutans solved this novel task on the first trial and continued to solve the task in all subsequent trials. This is indicative of insightful problem-solving as success rate was not

influenced by trial and error, but rather by the orangutan's ability to understand the obstacles to the reward prior to implementing a solution. The evidence of insightful problem-solving is further supported by the fact that orangutans had to fill their mouths and return to the tube multiple times. Persisting at this behaviour until they were able to access the peanut, even if they were not immediately rewarded, indicates the use of a more complex learning mechanism such as insightful problem-solving, instead of learning solely via associative learning (Mendes et al., 2007).

1.3.3 Additional Examples of Problem-Solving

Due to the ecological significance of problem-solving and the fitness benefits associated with it, problem-solving exists in many species to varying degrees (Amram & Holekamp, 2012).

1.3.3.1 Non-Human Primates

Primates are often regarded as exceptional problem-solvers, thus are a good candidate to demonstrate some of the more complex applications of problem-solving in the animal kingdom (Mendes, Hanus, & Call, 2007). A good example of problem-solving in a natural setting can be observed in the tufted capuchin monkey (*Cebus apella*), which uses tools to access energy rich food such as nuts (Ottoni & Mannu, 2001). Nuts have a protective outer shell which makes them very difficult to break into directly via biting or scratching. Therefore, to reach the energy rich endosperm inside, capuchin monkeys employ problem-solving in the form of tool-use, by hitting the nuts against a solid surface. Capuchin monkeys developed an innovative solution by using two rocks: one larger rock was placed on the ground as an anvil, and another smaller rock was held in a monkey's hand and used as a hammer. The ability to problem-solve and synthesize these tools allowed the monkeys to crack open the nuts and access the energy rich food within (Ottoni & Mannu, 2001). This emphasizes the ecological value of problem-solving, as these

animals were able to obtain high energy food at reduced metabolic cost and reduced handling time.

1.3.3.2 Problem-Solving in Birds

Birds, ranging from common house sparrows (*Passer domesticus*) to parrots such as the kea (*Nestor notabilis*) have been documented as having problem-solving capabilities. A study on individual problem-solving in kea measured their ability to solve novel problems through use of a multi-access box (Auersperg et al., 2011). There were four pathways to access food rewards within this box; string manipulation, window manipulation, ball manipulation, and stick manipulation. Upon solving the problem, the bird would gain access to a food reward. Once the kea had become proficient at one pathway, that pathway would be blocked off and a new pathway would be presented. The ability of kea to change how they solve the problem was recorded and compared to the performance of the New Caledonian crow (*Corvus moneduloides*). The New Caledonian crow was chosen for comparison against the kea as it is well documented as being an innovative species (Mendes et al., 2007; Taylor et al., 2010). Results indicated that kea had a high degree of behaviour plasticity and innovation, finding more solutions to the problem than the New Caledonian crows (Auersperg et al., 2011). This study is a good example of the variation in problem-solving abilities that can be observed across different species.

A study by Papp et al. (2015) investigated the influence of urbanization on problem-solving in the house sparrow. The problem-solving ability of sparrows from rural areas was compared with that of urban sparrows, by testing their ability to gain access to a food reward through a series of four different problem-solving feeder boxes. Birds were separated by opaque plastic sheets during the experimental trials in order to avoid the potential of social learning through visual contact. Problem-solving performance of the birds was similar across three of the four tasks, but in one task, the urban birds were significantly more likely to solve it than the rural birds. This indicates that urban birds

may have had more behavioural plasticity relating to problem-solving tasks, likely due to rapid changes in their living environments caused by human influences (Snell-Rood, 2013; Papp et al., 2015). Additionally, it was found that the most accurate predictor of success rate in this study was the frequency of foraging attempts, indicating that success rate was dependent upon motivation and trial-and-error based learning (Papp et al., 2015).

1.3.3.3 Canids

Wolves (*Canis lupus*) have been found to outperform both domestic dogs and free-ranging dogs in a foraging-related problem-solving task (Brubaker et al., 2017). In this task, the animals were permitted to manipulate a puzzle box in order to gain access to a food reward within the box (Brubaker et al., 2017). Four groups of canines were tested in this experiment: human socialized wolves, free-ranging dogs, pet dogs in an indoor enclosure with a familiar human experimenter, and pet dogs in an outdoor enclosure with an unfamiliar human experimenter (Brubaker et al., 2017). Results showed that human socialized wolves performed significantly better in all comparisons with domestic dogs, regardless of whether the dogs were indoor, outdoor, or free-ranging (Brubaker et al., 2017). It was found that many dogs simply gave up before the trial had concluded, whilst the wolves would generally persevere until they had obtained the food, or the trial had ended. With these findings, it was concluded that persistence to solve the problem was the key factor influencing performance between the dogs and the wolves (Brubaker et al., 2017). This example demonstrates the importance of motivational state when attempting to solve a foraging task, indicating that not only intelligence and cognitive capacity, but also effort, is a significant factor in terms of an animal's ability to solve problems.

1.3.3.4 Dolphins

In a natural setting, bottlenose dolphins (*Tursiops* sp.) have been found to be able to utilize tools to assist them with foraging. A study by Patterson and Mann (2011) described the

ability of dolphins to protect their rostrum/beak from rocks and corals during foraging, by using sponges as a protective covering. This allows the dolphins to forage on harder substrates with reduced risk of injury, thus minimising costs associated with foraging (Patterson & Mann, 2011). This example shows that organisms can derive fitness benefits from problem-solving behaviour aside from just increasing foraging speed, reducing handling time, or avoiding predation.

1.3.3.5 Octopuses

In terms of invertebrates, the common octopus (*Octopus vulgaris*) is renowned as one of the most proficient problem-solving organisms. For example, it has been found that the common octopus can unscrew a transparent jar and obtain the visible prey (e.g., a crab) inside (Fiorito, Planta, & Scotto, 1990). This complex behaviour is possible due to various structural and physiological adaptations allowing the octopus to generate enough force to grip and twist the jar lid. However, this level of problem-solving ability would not be possible without complex cognitive capabilities as well.

The coconut octopus (*Amphioctopus marginatus*) presents a good example of how tool-use can complement anti-predator behaviours. This octopus has been documented using actively gathered materials, such as debris and coconut shells, to camouflage itself from potential predators (Finn, Tregenza, & Norman, 2009). This is consistent with Brown's definition of tool-use, as the octopus utilized an external object to avoid an adverse state (Brown, 2011).

1.3.3.6 Fish

Many instances of problem-solving in fish involve tool-use, this complex form of behaviour seeming particularly common in wrasse species. For example, the black-spot tusk fish (*Choerodon schoenleinii*) has been observed to solve foraging problems through tool-use, by using jagged rocks as anvils to open energy-rich shellfish (Brown, 2011).

The fish does this by gripping shellfish with its mouth and striking it against the rock to weaken the shell. Without the ability to problem-solve, the fish would be unable to use these well-armoured shellfish as a food source. Similar foraging methods are employed by other fish; for example, the broomtail wrasse (*Cheilinus lunulatus*) utilize corals as a tool to crush armoured sea urchins, enabling consumption of the flesh within (Brown, 2011). Similar behaviours have also been observed in captive fish. For example, in a study by Pasko (2010) it was found that the sixbar wrasse (*Thalassoma hardwicke*) were able to use a similar behaviour to the black-spot tusk fish, using a jagged rock placed within a fish tank to break up large food pellets into smaller, edible pieces. The ability of these fish to use problem-solving behaviours on various food sources, and in different environments, can likely be attributed to a degree of behavioural plasticity (Pasko, 2010; Snell-Rood, 2013).

The seven-spot archerfish (*Toxotes chatareus*) employs a different problem-solving strategy when foraging. These fish have been observed using water as a foraging solution, allowing them to capture out of reach prey such as insects resting on vegetation or flying above the water (Dill, 1977). These fish do this by forming a tube between their tongue and palate, enabling them to shoot pressurized streams of water at unsuspecting prey, causing them to fall into the water and making them accessible to the archerfish (Dill, 1977). Other species of archerfish, such as the banded archerfish (*Toxotes jaculatrix*) are also known to use this same behaviour to forage effectively (Brown, 2011).

Fish not only use problem-solving to assist foraging efforts, but also to increase the survivability of their offspring in some cases (Brown, 2011). For example, in various species of South American cichlid, parents have been found to use leaves and small rocks as tablets to move offspring out of dangerous situations, such as predation attempts (Brown, 2011). These fish also consider the size and density of the leaves and rocks on

which they place their eggs to ensure they are easy enough to move when necessary (Brown, 2011).

These above-described studies show examples of the ability of fish to use tools in order to reach a goal through indirect means; however, as previously discussed in animals such as primates and birds, there are different expressions of problem-solving behaviour such as insightful problem-solving and trial-and-error based learning. While fish have not been shown to be able to use the same problem-solving complexity as seen in organisms such as primates, they have been observed to learn how to solve simple problem-solving tasks outside the realm of tool-use based problem-solving. A good example of this is demonstrated by guppies (*Poecilia reticulata*) in a study by Laland and Reader (1999), where it was found that guppies were able to produce novel solutions through trial-and-error learning, to navigate a maze and reach a food reward. The experiment was conducted over three phases. Phase one tested the influence of sex and hunger level on success rate, while the second phase of the experiment tested the influence of body size on success rate. The third phase examined whether individual fish had a higher likelihood of succeeding compared to other fish, regardless of the previously mentioned factors to reduce the effect of potential confounds. It was found that smaller fish performed better than larger fish, food-deprived fish performed better than well-fed fish, and female fish performed better than male fish (Laland & Reader, 1999). These results were likely due to motivational state, indicating that because of hunger, these fish were able to solve the problem more consistently as a function of increased motivation for their foraging attempts (Laland & Reader, 1999).

In a study by Millot et al. (2014) Atlantic cod (*Gadus morhua*) were found to use associative learning in order to overcome a problem-solving task. In this study, Atlantic cod learned to use an externally attached dorsal tag to gain access to a feeder container, through purposefully tangling the tag around the pull-string of the feeder before pulling

the feeder open (Milot et al., 2014). Firstly, fish examined the pull-string of the self-feeder, using their mouths to bite and tug on the pull-string of the feeder, eventually freeing the food and reinforcing the behaviour. However, when a dorsal tag became entangled on the pull-string accidentally, fish initiated an escape response which resulted in the self-feeder being opened more easily (Milot et al., 2014). Over time, the fish began to purposefully entangle their external tags on the pull-string to open the feeder, indicating associative learning through positive reinforcement (Milot et al., 2014). This experiment took hundreds of trials, however, it provided evidence that fish are able to reduce foraging-related metabolic costs via associative learning.

Problem-solving ability and rate of learning can be improved by the presence of conspecifics through various types of social learning (Waal et al., 2015). Prior to discussing the implications of social learning, it is first important to understand the evolution of social groups, and the fitness benefits they provide to a population.

1.4 The Evolution of Social Groups

Sociality, or social grouping behaviour, refers to instances where multiple conspecifics live or interact with one another, resulting in the formation of complex relationships and social networks (Wey et al., 2008). Social groups can be observed in a wide range of organisms, including both predator and prey species. This grouping behaviour likely evolved due to selection pressures such as predator avoidance and foraging or hunting efficiency (Williams, Lutz, & Applegate, 2003).

1.4.1 Predator Avoidance

Being a member of a social group can be advantageous for multiple reasons. Firstly, in a group there are multiple individuals, increasing the chance that one or more may be able to detect the presence of threats such as predators (Roberts, 1996). This grants passive predator vigilance and reduces the predation risk of foraging individuals in the group.

This is known as the many eyes hypothesis (Roberts, 1996). Another benefit of living in a group is that an individual has a lower chance of being predated upon if they are in the presence of conspecifics. This is because a predator will have more available targets to attack, reducing the likelihood of an individual being targeted, this is known as the dilution effect (Roberts, 1996). Being in a group is also beneficial as the presence of multiple conspecifics can confuse a predator, causing it to make errors it would not necessarily have made if only chasing one target. This again reduces an individual's likelihood of mortality via predation when living in a group (Roberts, 1996). For these reasons, living in social group can reduce predator-associated mortality of prey individuals.

1.4.2 Foraging Success

Another factor that likely contributed to the evolutionary success of social groups is reduced foraging costs. The larger the group, the higher the likelihood that an individual will find a desired resource such as food by chance, thus allowing other individuals to access the resource. To avoid costs to the social group such as competition, and agonistic behaviour, optimal group sizes evolved. For example, in northern bobwhites (*Colinus virginianus*) a group size of approximately 11 birds appeared to be optimal, resulting in increased feeding efficiency and improved predator detection (Williams et al., 2003). Smaller groups had reduced survival rates due to reduced predator detection, while larger groups had reduced survival rates related to reduced body mass due to increased competition (Williams et al., 2003).

Predatory animals also utilize social grouping behaviour to effectively hunt prey, accessing food at reduced energetic cost. Social groups in predatory organisms can also reduce the chance of a failed hunt, saving energy and reducing the chance of injury (Amram et al., 2014).

1.4.3 The Influence of Group Size on Problem-Solving Ability

Studies show that group size can have an influence on the problem-solving efficacy of a social group of animals (Liker & Bokony, 2009). For example, in an experiment with house sparrows, seeds were placed in a well that could only be accessed through opening a lid. This novel behaviour had not previously been utilized by the sparrows, thus it had to be learned in order to retrieve the food within the well. By manipulating their group size, it was found that house sparrows in larger groups experienced greater success rates than those in smaller groups (Liker & Bokony, 2009). As explained previously, there is a possibility that this was due to larger groups having more passive vigilance, giving individuals more time to focus on foraging instead of looking out for predators. This could have directly influenced the amount of time an individual sparrow was willing to spend foraging, thus increasing the success rate of individuals in larger groups (Liker & Bokony, 2009). However, a more likely explanation behind these findings is that an increased group size contained more behavioural diversity, enabling individuals to learn certain behaviours from each other to apply to the problem-solving task. These useful behaviours were able to spread more quickly amongst the foraging group by way of observational social learning (Bokony et al., 2003; Liker & Bokony, 2009).

Like house sparrows, shoaling rainbowfish (*Melanotaenia duboulayi*) have been studied to observe whether group size influenced their efficacy for problem-solving (Brown & Warburton, 1999). The ability of the fish to escape trawl-nets after being trapped was found to increase significantly with group size, with fish in shoals of five escaping much faster than pairs. Over a series of five trials the escape frequency also increased in the shoal of five fish when compared to pairs (Brown & Warburton, 1999). These results indicate that larger groups of shoaling rainbowfish fare better than smaller groups in relation to this predator-avoidance scenario. This is likely due to fish following the movements of other fish in the shoal in order to escape the net (Brown & Warburton,

1999). This form of social learning enables a higher number of individuals to escape the net, an adaptive trait which could increase survivability of rainbowfish in the wild under similar circumstances.

1.5 Social Learning

In animal behaviour, social learning can be defined as the acquisition or modification of a behaviour, either partly or entirely, due to observing the behaviour of another organism (Biondi et al., 2010). This ability to learn behaviours from conspecifics is advantageous in some niches for situations such as predator avoidance or gaining access to a food source (Manassa, McCormick, & Chivers, 2013; Waal et al., 2015).

1.5.1 Local and Stimulus Enhancement

There are multiple types of social learning. Firstly, stimulus enhancement and local enhancement are more cognitively simple forms of social learning, in which an individual is able to learn from another individual via associative learning (Mersmann et al., 2011; Waal et al., 2015). Argued as the simplest form of social learning by Waal et al. (2015), local enhancement can be defined as a form of associative learning in which an individual is drawn to a location due to the presence of conspecifics which are interacting with the area (Weber & Chittka, 2014). For example, in a study conducted by Buckley (1996), North American black vultures (*Coragyps atratus*) were found to use local enhancement to forage more effectively and efficiently. In this study, black vultures more easily located animal carcasses due to the presence of conspecifics, increasing scavenging opportunities for foraging individuals. This social learning ability allowed black vultures to compete with turkey vultures (*Cathartes aura*) which, when solitary, find food faster than individual black vultures do, as a function of their acute scent detection (Buckley, 1996). This study highlights the significance of these simple yet powerful social learning abilities in a competitive foraging context.

Stimulus enhancement can be defined as a form of observational learning in which an individual learns the relationship between a stimulus and its result by observing a demonstrator individual, regardless of the location in which that stimulus is encountered (Weber & Chittka, 2014). An example of stimulus enhancement in a reproductive context can be shown in the mate selection behaviours of the guppy (*Poecilia reticulata*), whereby females will find male guppies more attractive if they are observed in the presence of another female guppy, as opposed to a solitary male (Zentall, 2010). The stimulus in this case is the presence of a competing female, with the result being a heightened attraction to the focal male. This is advantageous as mating is encouraged more frequently, potentially resulting in more offspring being produced.

Stimulus enhancement has also been observed in rhesus monkeys, resulting in anti-predator behaviour against snakes (Cook et al., 1985). After observing conspecifics employing avoidance behaviours in response to snakes, naïve monkeys will also develop a fear response to the snakes, producing similar predator-avoidance behaviours in the presence of snakes even if they have not witnessed a snake attack occur (Cook et al., 1985). This social transmission of information enables observer rhesus monkeys to reduce their own predation risk, as these individuals now react to potential predation attempts before an attack has occurred.

1.5.2 Emulation and Imitation

Imitation and goal-directed emulation are more complex forms of observational social learning, enabling an observer individual to access the desired commodity through observing an experienced/innovative demonstrator individual (Waal et al., 2015). Imitation refers to when an individual adopts the behaviour of a conspecific, whereas emulation is when an individual develops their own variation of a behaviour displayed by a conspecific (Waal et al., 2015). These social learning mechanisms have been observed in the vervet monkey (*Chlorocebus aethiops*) (Waal et al., 2015). In this study, vervet

monkeys observed competent demonstrator individuals open an artificial fruit to access food held within. This artificial fruit was a wooden box, with doors and sliders existing as the two main access points to the box. Observers were shown to copy the behaviours of demonstrators in some cases, suggesting imitation, and develop their own variations of behaviours displayed by the demonstrators in others, suggesting emulation. It is likely that goal-directed emulation was occurring alongside imitation in this example, as observers produced different solutions to what were employed by demonstrator individuals in multiple cases (Waal et al., 2015).

1.5.3 Other Social Learning Mechanisms

Vertical social learning is a learning process by which social information is transmitted from parent to offspring (Farine, Spencer, & Boogert, 2015). This is similar to oblique social learning, in which information is transmitted from an adult to an unrelated juvenile conspecific (Farine et al., 2015). Horizontal social learning describes the process of learning between unrelated conspecifics of the same age bracket (Garland et al., 2011).

Vertical social learning has been demonstrated in pigs (*Sus scrofa*). A study by Oostindjer et al. (2011) showed that piglets which had observed their mother eat had a higher incidence of eating similar foods, while piglets which could not observe the mother eat did not. This type of learning is beneficial as the young are able to learn and identify which foods are safe for consumption by observing what foods their mother chooses to eat.

Both oblique and vertical social learning have been observed in the zebra finch (*Taeniopygia guttata*). In an undisturbed environment, zebra finches display vertical social transmission of information, learning foraging behaviours from their parents (Farine et al., 2015). However, in a study conducted by Farine et al. (2015), juvenile zebra finches that had been stressed in early life displayed oblique social learning, exclusively

learning foraging behaviours from unrelated adults (Farine et al., 2015). It is suggested that the ecological function of this is altered behaviour is for the zebra finches to avoid repeating foraging mistakes that parent individuals had made (Farine et al., 2015). For example, in an ecological setting, poor parental foraging efficiency could lead to prolonged hunger in the chicks, resulting in a stress response. To avoid learning these inefficient foraging behaviours, the chicks focused their attention on unrelated adults (Farine et al., 2015).

Horizontal social learning has been demonstrated by male humpback whales (*Megaptera novaeangliae*) over a large geographical scale. A study by Garland et al. (2011) found that all males within a population would conform to the most current vocal sexual display to attract females, and that similarities in these vocal sexual displays could be adopted by males in entirely different populations within the same ocean basin.

1.6 Social Learning in Fish

Social learning is also exhibited in fish to varying degrees and has been studied more frequently in recent years due to ecological implications of this behaviour. Cartilaginous fish such as stingray and sharks, as well as multiple teleost fish such as rainbowfish and cleaner wrasse, have been investigated for their problem-solving and social learning abilities.

A study by Thonhauser et al. (2013) tested the social learning ability of the stingray (*Potamotrygon falkneri*) to solve a novel task in order to access a food reward. In this test, a demonstrator individual was given a problem to solve in which a food reward was placed within a pipe while an observer individual was permitted to watch. As the food was initially out of reach, the stingrays would commonly use their flat surfaced bodies to produce a pressure gradient to force the food out of the pipe for consumption (Thonhauser et al., 2013). Thirty minutes after the demonstrator had accessed the food, the observer

was given the opportunity to complete the task. The observer solved the problem quicker than the control, indicating that stingrays have an ability to learn socially through visual observation (Thonhauser et al., 2013).

In sharks, social learning can be beneficial in learning how to improve prey searching abilities, improve navigation and orientation abilities around the home range, increase success in finding a mate, and to distinguish between conspecifics and members of other species (Guttridge et al., 2009). A study by Guttridge et al. (2013) determined the social learning ability of lemon sharks (*Negaprion brevirostris*) by how quickly observer sharks were able to solve a novel foraging task when paired with an experienced demonstrator, compared to sharks paired with a non-experienced or “sham” demonstrator (Guttridge et al., 2013). The novel foraging task involved the sharks swimming in an open area and making contact with a target sensor, which upon contact, would release a food reward for the shark. After the naïve lemon sharks were given time to observe a demonstrator individual performing the task, they were isolated and given the opportunity to attempt to solve the task themselves. It was found that lemon sharks that had observed a demonstrator had a much greater success rate compared to sharks that had observed non-experienced “sham” demonstrators (Guttridge et al., 2013). This study, being one of the first to examine the social learning ability of elasmobranch fishes, indicated that juvenile lemon sharks display some capacity to learn socially from conspecifics. It is unclear to what extent this behaviour is being influenced by local enhancement or stimulus enhancement (Guttridge et al., 2013).

A study by Trapp and Bell (2017) found that three-spined sticklebacks (*Gasterosteus aculeatus*) benefitted somewhat from being able to observe demonstrators complete a problem-solving foraging task. The task involved the demonstrator fish entering a transparent tube that was open at one end and closed at the other. Food was placed in the closed end of the tube, so in order to access the food the fish had to take an indirect route,

gaining access from the open end of the tube on the far end of the tank. There was no significant difference in the success rate between sticklebacks that were permitted to observe a demonstrator, and those that were not permitted to observe a demonstrator, indicating that sticklebacks did not learn how to complete the task by observing the demonstrators. However, another key result was the latency of naïve sticklebacks to orient towards the food reward. On average, the naïve observers orientated to the food reward twice as fast as naïve sticklebacks that did not observe a demonstrator. Therefore, while this study did not show that stickleback problem-solving performance increased in the presence of a demonstrator, it did show that the presence of a demonstrator enabled sticklebacks to locate the food faster. This was likely a result of a simple social learning mechanisms such as local enhancement, which could have positive foraging implications in a natural setting (Trapp & Bell, 2017).

1.7 The Spotted Wrasse (*Notolabrus celidotus*)

The ecology of the current study species, the New Zealand spotted wrasse has been studied extensively in the past under a different name (*Pseudolabrus celidotus*). This species is found in high abundance in the coastal waters of north-eastern New Zealand and is an important benthic carnivore (Jones, 1984). Spotted wrasse subsist on gammarid amphipods and other small crustaceans while in the juvenile stage, moving to larger prey items as they grow in size (Jones, 1984).

The reproductive ecology of the spotted wrasse is mediated by their monandric biology, meaning that all individuals begin life as females, whilst a proportion of these juveniles (dictated by size) convert to males (Jones, 1980). This sex-change event occurs immediately prior to sexual maturity, enabling a male to mate with surrounding females upon reaching complete sexual maturity (Jones, 1980). The minimum size a fish must be before investment in reproduction is viable is between 10 and 11 cm standard length

(measured from the tip of the head to the caudal peduncle) (Jones, 1980). Another study by Jones and Thompson (1980) suggested that females can inhibit the maturation of one another in order to reduce reproductive competition, with smaller females showing slower rates of maturation when found in the presence of larger females.

A study by Jones (1984) investigated the influence of habitat and intraspecific behavioural interactions upon the local distribution of spotted wrasse in northern New Zealand. The key findings were that juveniles were found in aggregations/groups whilst adults were distributed more randomly, indicating that juveniles are more reliant upon the fitness benefits associated with being part of a social group, in this case predator avoidance (Jones, 1984). This is also supported by the habitat preference of juveniles, being more attracted to sheltered areas with high algal biomass, as opposed to adults whose distribution appears to be more limited by food availability rather than shelter from potential predators (Jones, 1984). This study notes that intraspecific aggression is infrequent at the juvenile level, facilitating the formation of schools due to reducing fitness costs associated with agonistic behaviour and aggression (Jones, 1984).

The schooling behaviour of juvenile spotted wrasse, their low incidence of aggressive behaviour, and their abundance in accessible New Zealand coastal environments makes them good candidates to study the influence of group size on a problem-solving foraging task. This presents an opportunity to gain more insight into the cognitive capabilities of fish, adding to our overall knowledge of the subject.

1.8 Study Aims

The aim of this study was to investigate whether group size influences the foraging success rate and completion time of spotted wrasse in a laboratory-based, problem-solving task. A secondary aim of this study was to identify which cognitive mechanisms are responsible for any influence of group size upon foraging success. It was hypothesized that an increase in group size would increase the performance of spotted wrasse in terms of success rate and completion time in a problem-solving task.

Chapter 2

Methods

The experimental design of this study was based on two similar studies conducted by Atton et al. (2014) and Trapp and Bell (2017), in which three-spined sticklebacks had to discover how to use a novel feeding apparatus in order to access a food reward using social information transmitted by conspecifics.

2.1 Subject Collection and Storage

Forty-seven spotted wrasse were caught by minnow traps and angling from Sulphur Point, Tauranga Harbour, Bay of Plenty. The fish were transported to the aquatic facility at the University of Waikato, Hamilton campus, where they were housed. Four fish were used for a pilot study, and 40 were used for the full study. The full study involved four treatments (stages): five fish were used for the initial single trials (Stage 1), 10 fish were used for the pair trials (Stage 2), 20 fish were used for the trials involving groups of four (Stage 3), and five fish were used for the mirror component (Stage 4). Three surplus fish were used to test potential methods for individual identification (details below).

The spotted wrasse were initially all contained within one holding tank (1.01 m x 0.48 m x 0.47 m) whilst the permanent housing tanks were being constructed. After two weeks, the fish were selected based on size so that the mean size of each group across each treatment was as consistent as possible. In the pilot study, as well as in Stages 1 and 4 of the full study, individual fish were kept in separate sections of a housing tank, whilst in Stages 2 and 3 of the full study the fish were separated into their trial groups (pairs for Stage 2 and groups of four for Stage 3) prior to the commencement of experimental trials. Keeping the average size of fish consistent across trial groups and treatments was done to ensure that the results were reflective of changing the fish group size only, ensuring that fish body size did not influence results.

Once fish were separated into their treatment groups, they were left to habituate for one week in their housing tanks, as well as being able to familiarise themselves with the experimental tank. During this week-long habituation period prior to behavioural trials, fish were fed frozen diced squid at 10 am each weekday. This consistent feeding time was to ensure that the fish were used to feeding at 10 am, which was also the planned start time of the behavioural trials.

Only juvenile female spotted wrasse were caught to reduce the chance of confounding factors related to sexual maturity. Most fish were between 5 and 10 cm long (standard length), however, out of the 40 fish, two were slightly larger than 10 cm. Due to their length, these two fish had the potential to convert from male to female (Jones, 1980). Fortunately, these fish remained female throughout the duration of the experiment, thus the size of these fish likely did not influence results. The mean length of fish across all treatments was 6.9 cm, with a standard deviation of 1.9 cm. A one-way ANOVA showed that the mean lengths of fish did not significantly differ between treatments or trial groups ($p = >0.05$). Animal ethics approval for this study was granted by the University of Waikato Animal Ethics Committee (protocol 1075).

2.2 Equipment

Two types of housing tanks were constructed in order to host different numbers of fish, each of these tanks were (1.01 m x 0.48 m x 0.47 m). The first tank was designed to house fish for the pilot study, as well as Stage 1, Stage 2, and Stage 4 (Figure 1), while the second tank was designed to hold the groups of four needed in Stage 3 (Figure 2). For individual identification and ease of capture/transfer, dividers were used to keep the fish separate within the housing tanks (Figure 1 and Figure 2). Each segment of the tank was numbered by using a whiteboard marker on the external walls of the tank, in order to keep track of which fish was which. For example, the segment that contained fish 1 in the solo

trials was labelled “1”, the segment that contained fish 2 was labelled “2”, and so on. The dividers reduced the time taken to catch the fish as they had less space to swim away from the net, likely reducing stress during the capture process. The dividers were transparent in order to allow visual contact between the fish, reducing stress in the holding tanks. Additionally, the fish were individually transferred between tank segments each day after trials to ensure that each fish got an equal opportunity to have visual contact with conspecifics. While the fish were being transferred, the numbers on each segment of the tank were swapped accordingly. To ensure that oxygen was able to flow throughout the tank, the pump-filtration system was set up so that the outflow was on the opposite side of the tank to the inflow, generating a weak current. Holes were drilled into the dividers to ensure water could flow from one side of the tank to the other, allowing the even distribution of oxygen. Small (8 cm x 7.5 cm) half plant pots and some synthetic plants were placed in each segment of the housing tanks to be used as habitat for the fish, and for environmental enrichment (Figure 1 and Figure 2).

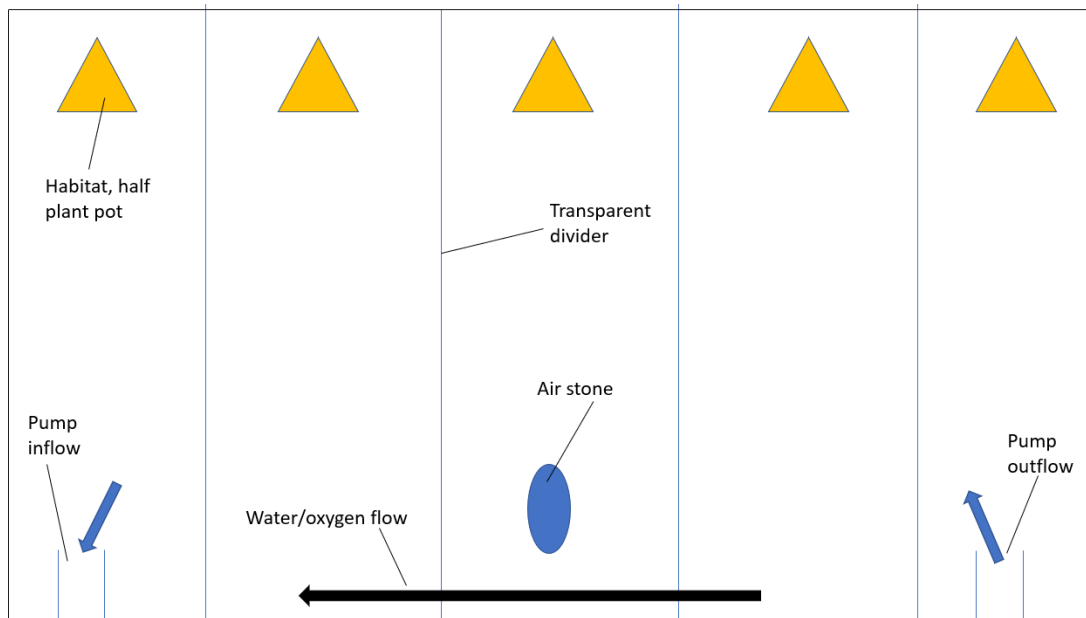


Figure 1. Housing tanks for fish storage during Stage 1 (one fish per tank segment), Stage 2 (two fish per tank segment), and Stage 4 (one fish per tank segment). Fish were separated with transparent perforated dividers which allowed water and oxygen flow from one side of the tank to the other.

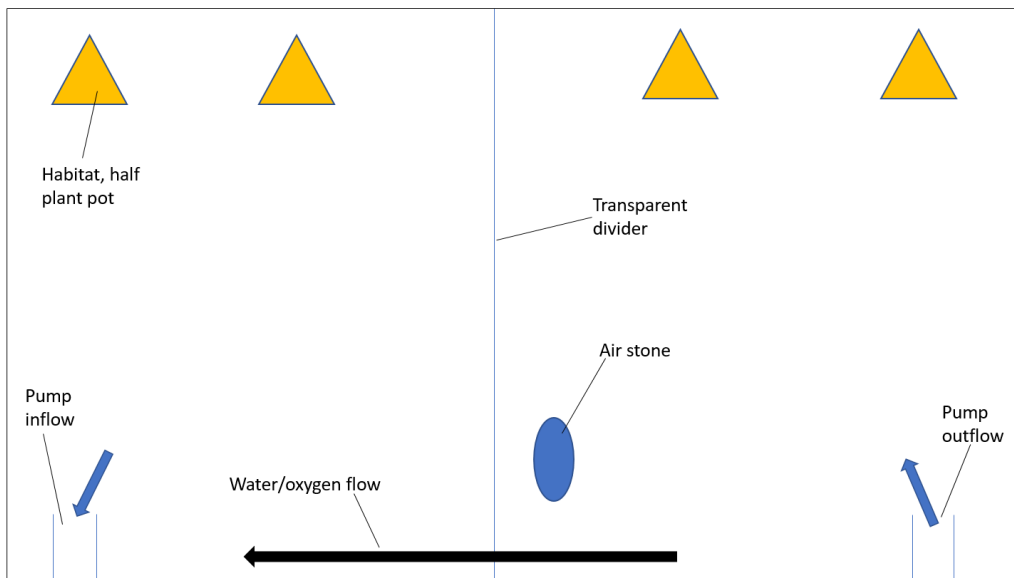


Figure 2. Housing tanks for fish in Stage 3 (four fish in each half of the tank). Fish were separated with a transparent perforated divider which allowed water and oxygen flow from one side of the tank to the other.

Each of the tanks were supplied with recirculated and filtered synthetic seawater. The water temperature was maintained at $17.5^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$ and was measured through use of a TidbiT data logger. One data logger was set up outside the fish tank, and one was set up inside the tank, to observe whether temperature fluctuations of the water were similar to that of the room temperature.

Two experimental tanks containing the problem-solving apparatus were constructed with the same dimensions as the holding tanks (1.01 m x 0.48 m x 0.47 m) (Figure 3 and Figure 4). The two experimental tanks were fitted with transparent, acrylic half-tubes (24 cm x 10 cm x 5 cm) which were used as the experimental problem-solving apparatus, similar to that used in Trapp & Bell (2017). Each tube had one closed end which was closest to the starting arena, and an open end which was furthest from the starting arena to make the path to the food less direct. The outer surface of the open ends of the acrylic tubes were covered with black insulation tape to make the opening of the tube more apparent to the fish. Width-wise slits were cut into the acrylic tubes to ensure that food scent was able to disperse throughout the tank, providing chemical cues for the fish to locate the

food. In order to solve the foraging task, fish needed to swim to the furthest end of the tank and enter the correct acrylic tube to gain access to the food reward.

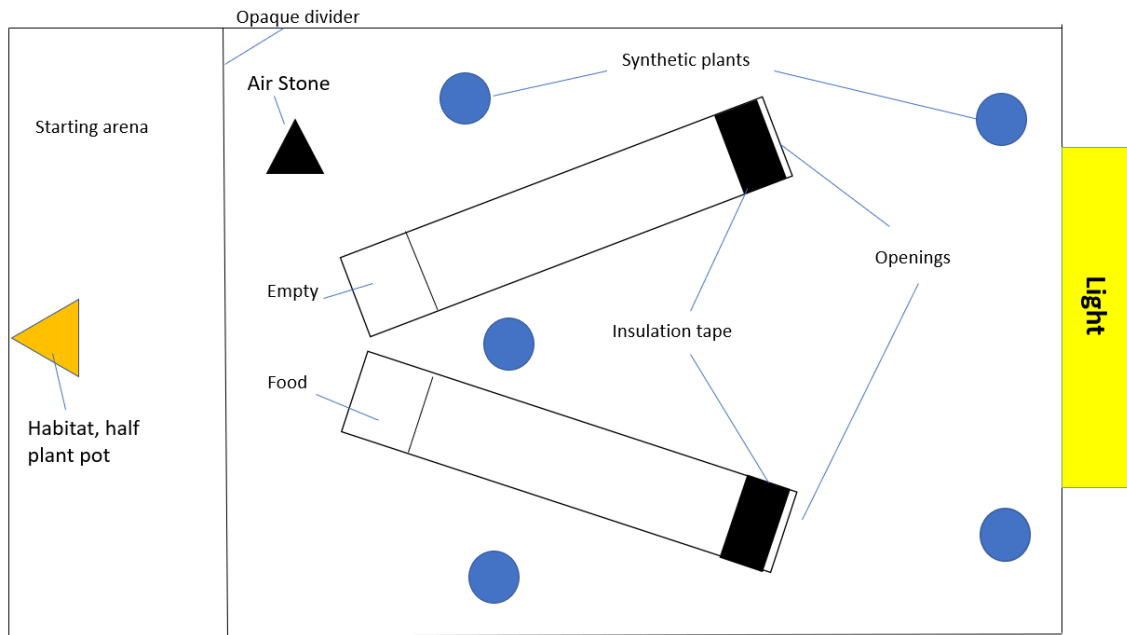


Figure 3. This diagram shows the experimental set-up for the problem-solving foraging task apparatus in Stage 1, 2 and 3. The open ends of the acrylic tubes were covered with black insulation tape to make the opening of the tube more apparent to the fish.

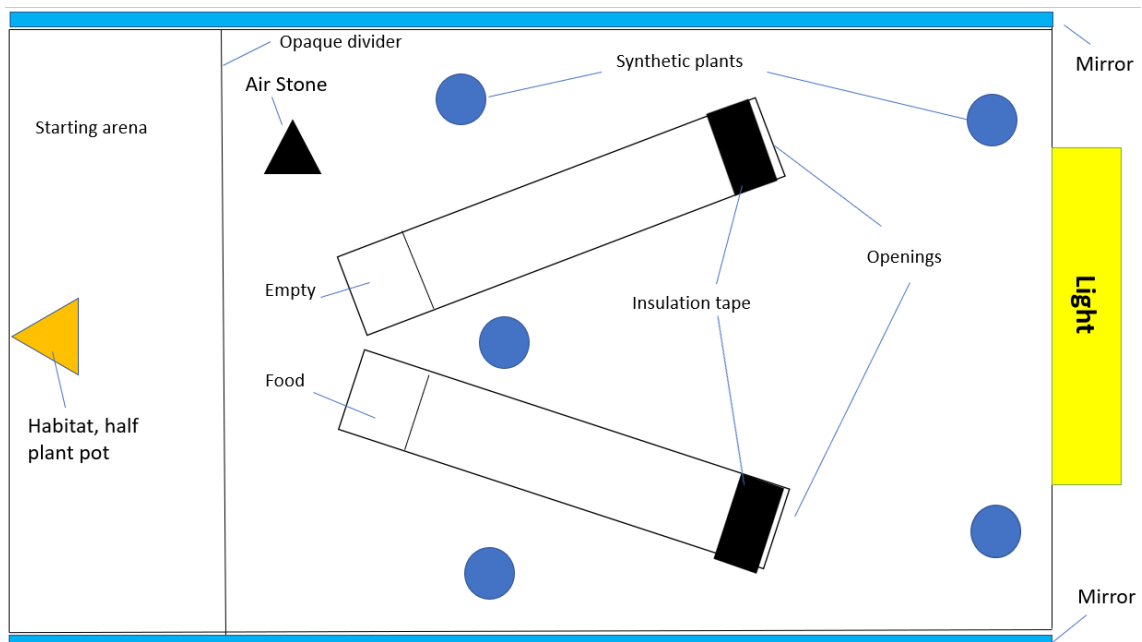


Figure 4. This diagram shows the experimental set-up for the Stage 4. This is identical to the previous experimental tank aside from the addition two mirrors attached to the exterior walls facing inwards to simulate the presence of conspecifics. The open ends of the acrylic tubes were covered with black insulation tape to make the opening of the tube more apparent to the fish.

GoPro Hero3+ video cameras were attached above the tanks and positioned to face straight down to allow observations of the fish throughout the whole tank. A grid made up of 7 cm x 7.6 cm rectangles was drawn on the polystyrene below the tank, which allowed for measurements such as fish body length to be taken from the footage.

These tanks also had two sections separated by a removable opaque divider: a starting arena where the fish would wait before and in between trials, and a foraging area where the fish would carry out problem-solving foraging trials. A half plant pot (13 cm x 11 cm) was installed in the starting arena of the experimental tanks, similar to how they were placed in the housing tanks, with the opening of the plant pot facing the foraging area. The exterior surfaces of both experimental tanks were covered with black polythene to prevent the fish seeing humans or fish from other tanks during the experiment. This covering made the tanks poorly lit, so a small fluorescent light was set up outside the tank facing inwards through a small slit cut into the polythene. The addition of the polythene occurred after the pilot study and was included to produce more consistent foraging conditions for fish in the full study. Five synthetic plants were added to each tank for habitat and environmental enrichment. These tanks also contained an air stone, which was left free flowing overnight and between trials to ensure that the water was well oxygenated prior to behavioural trials. The air stone was removed during the trials as the bubbles created surface disturbance and made the video footage difficult to see.

2.3 Pilot Study

A pilot study was conducted using four individuals, one of which died during the study. This pilot study was designed to develop equipment, ensure that all of the apparatus worked effectively, and to test if the fish could solve the problem within the time parameters, with the aim of using these fish as experienced demonstrators in an observer-demonstrator experiment.

The fish were given two opportunities to attempt the foraging task per day, both trials occurring one after the other, with a 5-minute break in between trials. Trials were conducted five days per week from Monday to Friday, so each fish attempted 10 trials per week over a four-week period. Prior to the first trial of each day, the opaque divider was removed, and each fish was allowed 10 minutes to habituate to the experimental tank. During this time period the experimental apparatus was present, however there was no food in either of the tubes. Once this 10-minute habituation period was complete, the opaque divider was returned, and the fish were transferred back into the starting arena using a small hand net. The fish were then left in the starting arena for 5 minutes whilst the food was placed into one of the tubes. After this 5-minute waiting period, the opaque divider was lifted, and the fish were given 15 minutes to forage and attempt to solve the task. A “success” was recorded if the fish managed to peck the food inside one of the transparent acrylic tubes within the allotted 15-minute trial period. The trials were left to run for the full 15 minutes regardless of whether the fish succeeded or not, as there was no human observer present during the trials to avoid inducing a potential stress response in the fish. Once the trial was complete the fish were returned to the starting arena via net, and the position of the acrylic tubes was swapped without the fish being able to see. The fish were left in the starting arena for 5 minutes before the second 15-minute trial commenced, with the food now in the opposite tube. Fish were fed a very small amount of food every day after trials, regardless of whether they solved the task or not, in order to preserve good health. Trials were to be continued until the fish were competent demonstrators, with a “competent demonstrator” being defined as the fish being able to complete 100% (10/10) of trials within a given week.

It was originally planned that these four fish were to be used as demonstrators in a social learning observer/demonstrator experiment, similar to the one conducted by Trapp & Bell (2017). However, the performance of these pilot study fish was too poor to justify using

them as demonstrators in the proposed next stage of experimentation (Figure 5 and Table 2). Therefore, a group-size experiment was favoured over an observer-demonstrator type experiment as the primary focus of this thesis.

2.4 Full Study

2.4.1 Stage 1: Solo Trials

The pilot study allowed for refinement of methods and equipment, and so the trials that were conducted in the pilot were repeated under optimized conditions in Stage 1 of the full study. The equipment used in the full study was the same as the equipment used in the pilot study, with minor adjustments including camera position, habitat enrichment, and the addition of black polythene strips to the tanks (described above).

The goal of Stage 1 was to see if the problem-solving success rate of individual fish increased over time, and whether their latency to succeed at the foraging task decreased over time. Five naïve fish were used in Stage 1. Trials were conducted twice daily on weekdays (Monday to Friday) for each fish, over three consecutive weeks, and thus each fish attempted 10 trials per week. A trial was considered a success when the fish had entered the acrylic half-tube and pecked at the food within.

2.4.2 Stage 2: Pair Trials

The purpose of Stage 2 was to test whether the presence of a single conspecific had any influence upon these fish in terms of foraging success and latency to succeed. Stage 2 used 10 naïve spotted wrasse which attempted the foraging task in familiarised pairs. The procedure of this experiment was similar to that of Stage 1, however, there were now two fish attempting to solve the foraging task concurrently. As in Stage 1, a trial was considered a success when at least one of the fish had successfully entered the acrylic tube and pecked at the food within.

Because fish from Stages 2 and 3 were housed and tested in their trial groups, it was proposed that each of these fish be dyed, which would allow individual identification in the footage to produce more informative data. At the beginning of the habituation period prior to testing, three surplus fish were daubed using a paste of Bismark Brown dye. This dye was selected as the best option according to Arnold (1966). One fish was dyed on the upper part of its head, one fish was dyed on the upper part of its tail, and one fish was dyed just above its left pectoral fin by daubing each of the body parts with the solution. The following day, the fish which had been daubed on the tail and pectoral fin no longer had visible stains, and the fish which was daubed on the head unfortunately experienced toxic effects and was euthanized. Alternative tagging methods were deemed unsuitable due to the small size of fish. For these reasons tagging was abandoned, and it was not possible to distinguish between different fish in the footage.

2.4.3 Stage 3: Group Trials

Stage 3 examined whether the presence of more conspecifics had an influence upon these fish in terms of foraging success. Twenty naïve spotted wrasse were used in Stage 3, with trial groups consisting of four fish that were familiar with each other. The procedure for this experiment was similar to that of Stage 1 and 2, however there were now four fish attempting to solve the foraging task simultaneously. A trial was considered a success when at least one of the fish had successfully entered the acrylic tube and pecked at the food within.

2.4.4 Stage 4: Solo Mirror Trials

Stage 4 tested the influence of a perceived increase in group size on the success rate and success latency of individual fish. Five naïve fish were used in Stage 4. These fish were put through trials individually in an experimental tank that had two large mirrors on the long outer walls of the tank facing inwards, thus providing reflected images of the focal

fish. A trial was considered a success when the fish had entered the acrylic half-tube and pecked at the food within.

The methodology for Stage 4 was identical to that of Stage 1, with the addition of mirrors to the outer walls of the tank. In order to prevent the fish from seeing additional food patch projections in the reflection, the synthetic plants were placed against the reflective surface near the food patch, making reflections of the food less obvious to the fish attempting the foraging task.

2.4.5 Measurements

Measured variables were selected based on those used in similar studies such as Atton et al. (2014), Trapp and Bell (2017), and Webster et al. (2017), and these measurements were the same across all stages. The latency of the first fish in a trial to leave the starting arena was recorded (Table 1). This was considered a suitable measure of foraging boldness or exploratory behaviour (Webster, Ward, & Hart, 2007). The latency of the first fish in a trial to first orient towards the food source was recorded as a measure of how quickly a fish could locate the food reward (Table 1). An orientation was recorded when a fish pecked the acrylic tube whilst facing the food reward (Table 1). A third measure taken was the time for the first fish in a trial to successfully complete the foraging task (Table 1). This was recorded to examine whether fish became faster at solving the task over time, and if group size or perceived group size influenced this latency to success. The success rate was also recorded and compared across each treatment over time.

Table 1. An ethogram describing the fish behaviours measured during the problem-solving task.

Behaviour	Description
Peck	The fish makes physical contact with the acrylic tube or food either from the inside or outside of the tube using the front-most portion of its mouth.
Orientation	The fish pecks at the acrylic tube while its head is pointed within a 30-degree angle of the food source.
Leave starting arena	More than 50% of the fish's body has crossed over the line separating the starting arena from the foraging area.
Success	Fish pecks at food within acrylic tube.

2.4.6 Data Analysis

Each trial was filmed, resulting in 108 15-minute fish foraging videos, totalling 27 hours of footage in the pilot study, while the full study resulted in 600 15-minute fish foraging videos being produced, totalling 150 hours of footage in the full study. These videos were stored on a 2-terabyte hard-drive supplied by the University of Waikato. Video footage was analysed through use of the animal behaviour coding software Solomon Coder (version: beta 19.08.02). Coded behaviours were: "Leaves starting arena," "Orientation," and "Success."

Intra-observer reliability checking was conducted after the initial video analysis was complete. This involved the researcher re-watching 15% of the footage, files were selected at random within each treatment for this reanalysis. The purpose of this was to ensure that the time values recorded on the second viewing matched the recorded time values from the initial viewing within a five-second margin. This ensured the reliability of the raw data prior to statistical analysis.

Due to the nature of this experiment dealing with success rate of a task within a pre-determined time slot, the data was right-censored. Relevant literature suggested the use of a survival analysis to analyse the type of right-censored data that these experiments had generated (Webster et al., 2017). A survival analysis is a statistical method used for analysing the amount of time before one or more expected events occur. This type of analysis has useful applications when analysing success rate and success latency data in animal behaviour trials, making it a suitable tool for the analysis of this time-based data. Also, because this data was right-censored, it was not normally distributed, thus nonparametric analyses were the most appropriate.

In order to compare the survival distributions of two treatments, a Mantel-Cox test was conducted. This test was used to explain the variation between measurements: time to leave the starting arena, the orientation latency, and the success latency. The Mantel-Cox test, otherwise known as the logrank test, gives equal weighting to successful trials at all time points, in contrast to the Gehan-Breslow-Wilcoxon test which gives more weight to successes at earlier time points. Gehan-Breslow-Wilcoxon test statistics were also provided for each measure for context.

To test for statistically significant differences across treatments a Mantel-Haenszel hazard ratio was calculated. This statistical test compares the probability of an event occurring, in this case a “success” in one group/treatment and compares it with the probability of the same event occurring in another group/treatment. A hazard ratio of 1 indicates a similar number of events are occurring between groups; therefore, the further this number is from 1, the more significant a difference is in a specific measure between two treatments. Using a hazard ratio was supplementary to the previous tests as they indicate the frequency of events occurring. All graphs and statistical analyses were conducted using GraphPad Prism 9.0.0 (GraphPad Software LLC, San Diego, USA).

Chapter 3

Results

3.1 Pilot Study

Fish from the pilot study showed no significant improvement in success rate or success latency over their four-week trial period ($p = >0.05$) (Figure 5 and Table 2).

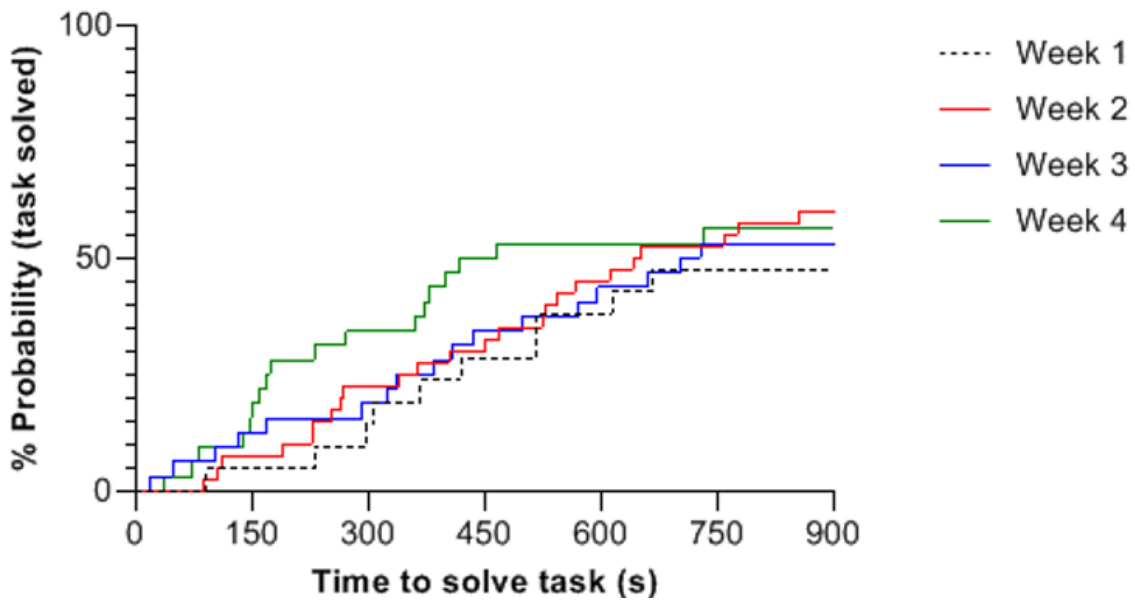


Figure 5. A survival analysis showing the success rate (%) and completion time (s) of the single fish in the pilot study over a four-week trial period.

Table 2. Statistical comparisons pilot study trials to determine whether task solving improved over four successive weeks. “Undefined” means that a median value was not determined i.e., 50% of fish did not complete the task.

Treatment Groups	Median time to success (s)	Mantel-Cox test	Logrank test for trend	Gehan-Breslow-Wilcoxon test
Singles	W1: Undefined W2: 646 W3: 714 W4: 442	$p = 0.768$	$p = 0.446$	$p = 0.585$

3.2 Full Study

3.2.1 Success Rate and Completion Time

Results show that, in general, increased group size corresponded to a higher success rates and faster completion times, with fish from the pair (Stage 2), group (Stage 3), and mirror (Stage 4) treatments outperforming fish from the singles (Stage 1) treatment across all three weeks.

3.2.1.1 Treatment Success Rates by Week

Single fish performed worse than fish from the other treatments over the study period, succeeding in 18% (9/50) of trials in week one, 30% (15/50) of trials in week two, and 60% (30/50) of trials in the third week (Figure 6). Fish from all other treatments succeeded in more than 50% (25/50) of trials in the first week and succeeded in at least 76% (38/50) and 84% (42/50) of trials in weeks two and three respectively (Figure 6).

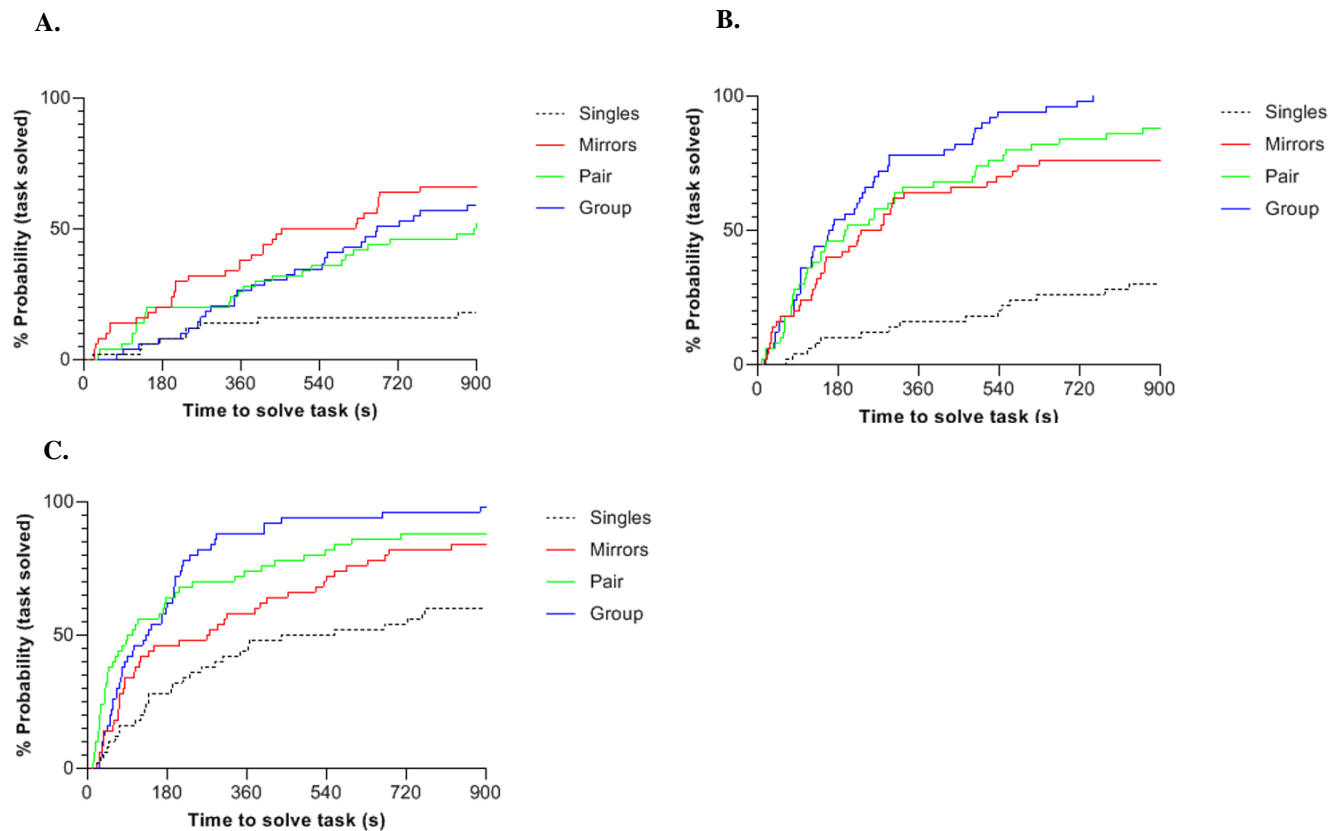


Figure 6. A survival analysis showing the success rate (%) and completion time (s) of each treatment during week one (A.), week two (B.), and week three (C.).

3.2.1.2 Success Frequency and Latency Statistics

Fish from the singles treatment performed significantly worse than all other treatment groups over each week in terms of success latency ($p = <0.05$) (Tables 3-5). Additionally, group treatment fish outperformed fish from the mirror and pair treatments in week two, and outperformed fish from the mirror treatment again in the final week ($p = <0.05$) (Tables 3-5).

When comparing fish from the singles treatment to fish of the mirror, pair, and group treatments, a hazard ratio score of 0.2 - 0.3 was produced (Table 3). This indicates that fish from the singles treatment had a 70 - 80% lower likelihood of success when compared to fish from other treatments in week one, with 95% confidence (Table 3).

Table 3. Statistical comparisons between the problem-solving abilities of the different treatment groups in week one. 95% confidence intervals in parentheses. Bolded values indicate statistical significance. “Undefined” means that a median value was not determined, i.e., 50% of fish did not complete the task.

Treatment Groups	Median time to success (s)	Mantel-Cox test	Gehan-Breslow-Wilcoxon test	Hazard ratio (Mantel-Haenszel)	Hazard ratio (logrank)
Singles vs Mirrors	undefined 538	$p = <0.0001$	$p = <0.0001$	0.224 (0.121 - 0.415)	0.202 (0.110 - 0.372)
Singles vs Pairs	undefined 896.5	$p = 0.0006$	$p = 0.0011$	0.311 (0.160 - 0.606)	0.289 (0.148 - 0.561)
Singles vs Groups	undefined 673	$p = <0.0001$	$p = 0.0004$	0.274 (0.144 - 0.521)	0.251 (0.132 - 0.475)
Mirrors vs Pairs	538 896.5	$p = 0.1288$	$p = 0.1331$	1.489 (0.891 to 2.487)	1.484 (0.889 - 2.476)
Mirrors vs Groups	538 673	$p = 0.2476$	$p = 0.1191$	1.343 (0.815 - 2.215)	1.340 (0.813 - 2.209)
Pairs vs Groups	896.5 673	$p = 0.6037$	$p = 0.8034$	0.869 (0.512 - 1.476)	0.869 (0.512 - 1.475)

Comparing the singles treatment to all other treatments in week two generated a hazard ratio score of 0.08 - 0.25, indicating that fish from the singles treatment had a 75 - 92% lower chance of succeeding in the foraging task compared to fish from the other treatments (Table 4). Comparing the group treatment to the mirror and pair treatments generated hazard ratio scores of 0.51 – 0.65, indicating that fish in the mirror and pair treatments were 35 - 49% less likely to succeed in the foraging task compared to fish from the group treatment. These observations were made with 95% confidence (Table 4).

Table 4. Statistical comparisons between the problem-solving abilities of the different treatment groups in week two. 95% confidence intervals in parentheses. Bolded values indicate statistical significance. “Undefined” means that a median value was not determined, i.e., 50% of fish did not complete the task.

Treatment Groups	Median time to success (s)	Mantel-Cox test	Gehan-Breslow-Wilcoxon test	Hazard ratio (Mantel-Haenszel)	Hazard ratio (logrank)
Singles vs Mirrors	undefined 253.5	$p = <0.0001$	$p = <0.0001$	0.229 (0.131 - 0.403)	0.242 (0.139 - 0.421)
Singles vs Pairs	undefined 198	$p = <0.0001$	$p = <0.0001$	0.161 (0.093 - 0.279)	0.184 (0.108 - 0.314)
Singles vs Groups	undefined 163.5	$p = <0.0001$	$p = <0.0001$	0.084 (0.048 - 0.148)	0.130 (0.077 - 0.221)
Mirrors vs Pairs	253.5 198	$p = 0.2580$	$p = 0.4310$	0.778 (0.504 - 1.202)	0.780 (0.505 - 1.203)
Mirrors vs Groups	253.5 163.5	$p = 0.0025$	$p = 0.0564$	0.511 (0.331 - 0.790)	0.535 (0.350 - 0.818)
Pairs vs Groups	198 163.5	$p = 0.0296$	$p = 0.2666$	0.627 (0.411 - 0.955)	0.649 (0.431 - 0.976)

A hazard ratio score of 0.26 – 0.54 was generated when comparing the singles treatment to each of the other treatments in the third week, indicating that fish from the singles treatment were 46 - 74% less likely to succeed in the foraging task when compared to fish from the other treatments (Table 5). The comparison between the group treatment and the mirror treatment resulted in a hazard ratio score of 0.49 – 0.54, indicating that mirror treatment fish had a 46 - 51% lower likelihood of succeeding in the foraging task than group treatment fish during week three. These observations were, again, made with 95% confidence. (Table 5).

Table 5. Statistical comparisons between the problem-solving abilities of the different treatment groups in week three. 95% confidence intervals in parentheses. Bolded values indicate statistical significance.

Treatment Groups	Median time to success (s)	Mantel-Cox test	Gehan-Breslow-Wilcoxon test	Hazard ratio (Mantel-Haenszel)	Hazard ratio (logrank)
Singles vs Mirrors	498 272.5	$p = 0.0084$	$p = 0.0178$	0.531 (0.332 - 0.850)	0.540 (0.339 - 0.861)
Singles vs Pairs	498 96.5	$p = <0.0001$	$p = <0.0001$	0.376 (0.234 - 0.607)	0.404 (0.252 - 0.647)
Singles vs Groups	498 136	$p = <0.0001$	$p = <0.0001$	0.261 (0.161 - 0.424)	0.319 (0.200 - 0.507)
Mirrors vs Pairs	272.5 96.5	$p = 0.1076$	$p = 0.0302$	0.703 (0.458 - 1.080)	0.709 (0.462 - 1.087)
Mirrors vs Groups	272.5 136	$p = 0.0016$	$p = 0.0216$	0.494 (0.319 - 0.766)	0.533 (0.349 - 0.813)
Pairs vs Groups	96.5 136	$p = 0.3578$	$p = 0.5407$	0.823 (0.543 - 1.247)	0.830 (0.553 - 1.247)

3.2.1.3 Weekly Success Rates by Treatment

Over a three-week period, an increase in success rate was observed in each treatment. The singles treatment recorded an 18% (9/50) success rate in week one, compared to a 60% (30/50) success rate by the end of the third week (Figure 7a). Fish of the mirrors treatment recorded a 66% (33/50) success rate in week one, while succeeding in 84% (42/50) of trials in week three (Figure 7b). Fish in the pair treatment showed a 54% (27/50) success rate in the first week, while achieving an 88% (44/50) success rate by the end of the third week (Figure 7c). Finally, fish in the group treatment recorded a 60% (30/50) success rate in week one and a 98% (49/50) success rate by the end of the third week (Figure 7d).

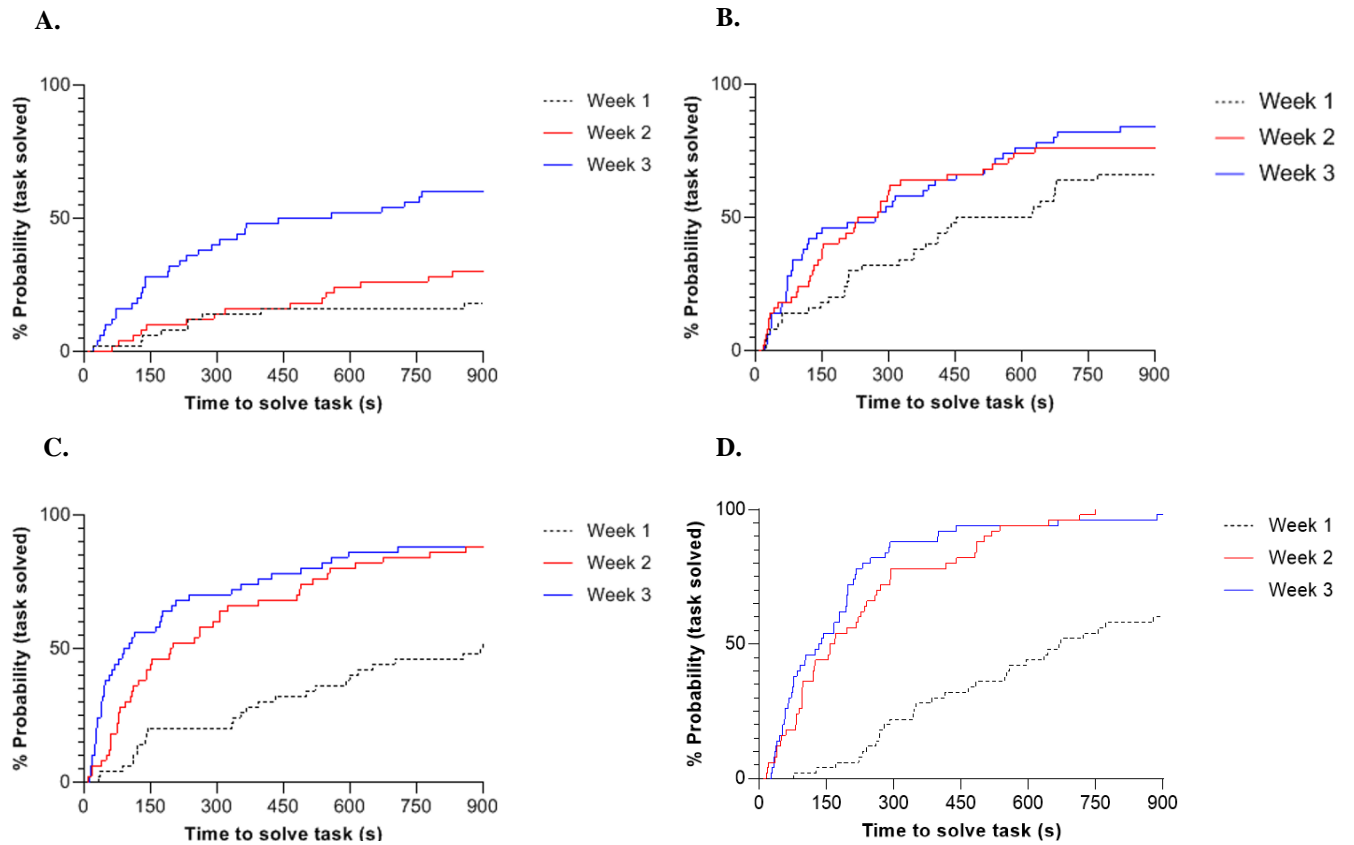


Figure 7. A survival analysis showing the success rate (%) and completion time (s) of the single fish treatment (A.), mirror treatment (B.), pair treatment (C.), and group treatment (D.) over a three-week period.

3.2.1.4 Success Latency Improvement Statistics

Fish from all treatments showed a statistically significant improvement ($p = <0.05$) when comparing success latency in week one to their success latency in week three (Table 6).

Table 6. Statistical comparisons within each between treatment group to determine whether problem-solving ability improved over three successive weeks. 95% confidence intervals in parentheses. Bolded values indicate statistical significance. “Undefined” means that a median value was not determined, i.e., 50% of fish did not complete the task.

Treatment Groups	Median time to success (s)	Mantel-Cox test	Logrank test for trend	Gehan-Breslow-Wilcoxon test
Singles	W1: Undefined W2: Undefined W3: 498	$p = <0.0001$	$p = <0.0001$	$p = <0.0001$
Mirrors	W1: 538 W2: 253.5 W3: 272.5	$p = 0.0387$	$p = 0.0128$	$p = 0.0269$
Pairs	W1: 896.5 W2: 198 W3: 96.5	$p = <0.0001$	$p = <0.0001$	$p = <0.0001$
Groups	W1: 671 W2: 163.5 W3: 136	$p = <0.0001$	$p = <0.0001$	$p = <0.0001$

3.2.2 Time to Exit the Starting Arena

Increased group size generally resulted in a higher frequency of fish to leave the starting arena, also resulting in the fish leaving the starting arena quicker in larger groups.

3.2.2.1 Treatment Exit Latency by Week

Fish of the singles treatment left the starting arena in 98% (49/50) of trials in the first week, 92% (46/50) of trials in the second week and left the starting arena in 100% (50/50) of trials in the final week (Figure 8). Fish in the mirror treatment left the starting arena in 98% (49/50) of trials in week one and two, leaving the starting arena in 100% (50/50) of trials in the third week (Figure 8). Fish from the pair and group treatments left the starting arena in 100% (50/50) of trials across all three weeks (Figure 8).

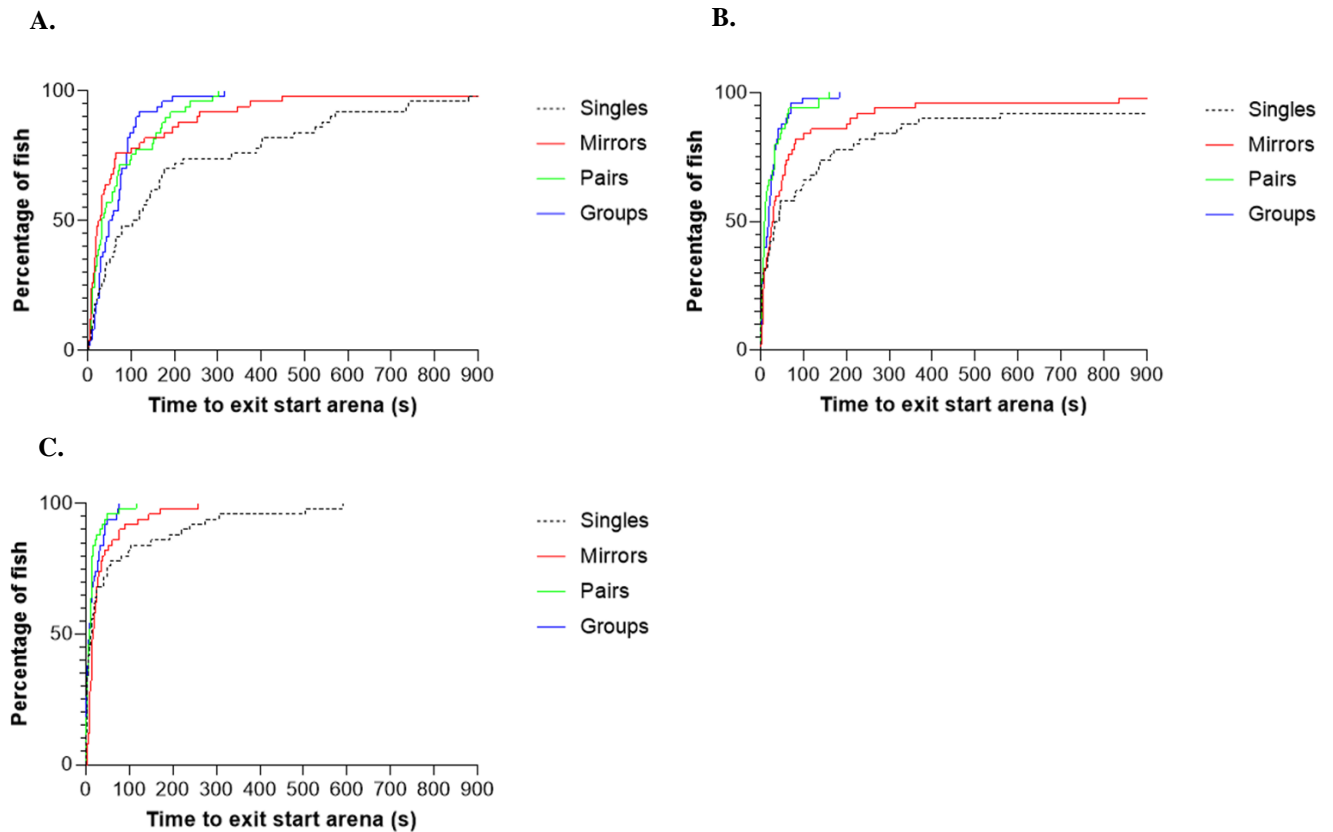


Figure 8. A survival analysis showing the time for the first fish in a trial to leave the starting arena (s) in each treatment during week one (A.), week two (B.), and week three (C.).

3.2.2.2 Exit Frequency and Latency Statistics

Fish in the singles treatment were significantly slower to exit the starting arena than fish from all other treatments in the first week, also leaving the starting arena slower than fish from the pair and group treatments in the second and third weeks ($p = <0.05$) (Tables 7-9). Fish from the mirror treatment were significantly slower to leave the starting arena than fish from the pair and group treatments in the second and third weeks of trials ($p = <0.05$) (Tables 7-9).

Hazard ratio scores comparing the singles treatment to all other treatments in week one generated values between 0.39 - 0.55, indicating that fish from the singles treatment were 45 - 61% less likely to leave the starting arena than fish from other treatments, with 95% confidence (Table 7).

Table 7. Statistical comparisons between treatment groups in week one - time for first fish to exit the starting arena (s). 95% confidence intervals in parentheses. Bolded values indicate statistical significance.

Treatment Groups	Median time to exit (s)	Mantel-Cox test	Gehan-Breslow-Wilcoxon test	Hazard ratio (Mantel-Haenszel)	Hazard ratio (logrank)
Singles vs Mirrors	110.5 26.0	$p = 0.0020$	$p = 0.0007$	0.512 (0.334 - 0.783)	0.550 (0.364 - 0.832)
Singles vs Pairs	110.5 33.0	$p = 0.0003$	$p = 0.0037$	0.444 (0.285 - 0.691)	0.510 (0.336 - 0.775)
Singles vs Groups	110.5 52.5	$p = <0.0001$	$p = 0.0111$	0.399 (0.253 - 0.629)	0.489 (0.322 - 0.743)
Mirrors vs Pairs	26.0 33.0	$p = 0.8496$	$p = 0.4032$	0.961 (0.639 to 1.447)	0.964 (0.649 - 1.432)
Mirrors vs Groups	26.0 52.5	$p = 0.9972$	$p = 0.0499$	1.001 (0.660 - 1.519)	1.001 (0.675 - 1.484)
Pairs vs Groups	33.0 52.5	$p = 0.9515$	$p = 0.3190$	0.988 (0.658 - 1.483)	0.988 (0.666 - 1.465)

A hazard ratio of 0.39 – 0.49 was generated when comparing the singles treatment to the group and pair treatments, indicating that single fish were 51 - 61% less likely to leave the starting arena than pair or group treatment fish, with 95% confidence (Table 8). Comparing the mirror treatment to the group and pair treatments produced a hazard ratio of 0.51 – 0.57, indicating a 43 - 49% lower likelihood of mirror treatment fish to leave the starting arena compared to fish from the pair or group treatments, with 95% confidence (Table 8).

Table 8. Statistical comparisons between treatment groups in week two - time for first fish to exit the starting arena (s). 95% confidence intervals in parentheses. Bolded values indicate statistical significance.

Treatment Groups	Median time to exit (s)	Mantel-Cox test	Gehan-Breslow-Wilcoxon test	Hazard ratio (Mantel-Haenszel)	Hazard ratio (logrank)
Singles vs Mirrors	38.0 28.5	$p = 0.1567$	$p = 0.6433$	0.741 (0.489 - 1.122)	0.754 (0.503 - 1.130)
Singles vs Pairs	38.0 9.5	$p = <0.0001$	$p = 0.0084$	0.395 (0.249 - 0.625)	0.485 (0.318 - 0.738)
Singles vs Groups	38.0 19.0	$p = <0.0001$	$p = 0.0175$	0.398 (0.251 - 0.630)	0.489 (0.321 - 0.744)
Mirrors vs Pairs	28.5 9.5	$p = 0.0025$	$p = 0.0060$	0.514 (0.334 to 0.791)	0.565 (0.376 - 0.851)
Mirrors vs Groups	28.5 19.0	$p = 0.0024$	$p = 0.0130$	0.511 (0.332 - 0.788)	0.566 (0.376 - 0.852)
Pairs vs Groups	9.5 19.0	$p = 0.7611$	$p = 0.5978$	1.065 (0.710 - 1.596)	1.061 (0.717 - 1.570)

Comparing the singles and mirror treatment to the pair and group treatments resulted in a hazard ratio of 0.51 – 0.63 and 0.44 - 0.6, respectively (Table 9). Singles treatment fish therefore had a 37 - 49% lower likelihood to leave the starting arena than pair or group treatment fish, while fish from the mirror treatment were 40 - 56% less likely to leave the starting arena than fish from the pair or group treatments. These observations were stated with 95% confidence (Table 9).

Table 9. Statistical comparisons between treatment groups in week three - time for first fish to exit the starting arena (s). 95% confidence intervals in parentheses. Bolded values indicate statistical significance.

Treatment Groups	Median time to exit (s)	Mantel-Cox test	Gehan-Breslow-Wilcoxon test	Hazard ratio (Mantel-Haenszel)	Hazard ratio (logrank)
Singles vs Mirrors	12.5 16.5	$p = 0.5760$	$p = 0.1659$	0.888 (0.584 - 1.348)	0.900 (0.608 - 1.333)
Singles vs Pairs	12.5 9.0	$p = 0.0034$	$p = 0.0763$	0.514 (0.329 - 0.803)	0.591 (0.394 - 0.887)
Singles vs Groups	12.5 8.5	$p = 0.0094$	$p = 0.0954$	0.556 (0.357 - 0.866)	0.626 (0.419 - 0.937)
Mirrors vs Pairs	16.5 9.0	$p = 0.0003$	$p = <0.0001$	0.441 (0.284 to 0.683)	0.507 (0.335 - 0.767)
Mirrors vs Groups	16.5 8.5	$p = 0.0052$	$p = 0.0010$	0.542 (0.353 - 0.833)	0.594 (0.396 - 0.890)
Pairs vs Groups	9.0 8.5	$p = 0.7359$	$p = 0.9200$	1.075 (0.705 - 1.639)	1.065 (0.719 - 1.576)

3.2.2.3 Weekly Exit Latency by Treatment

In week one, singles treatment fish left the starting arena in 98% (49/50) of trials, while in week three fish from the singles treatment left the starting arena in 100% (50/50) of trials. Fish from the mirror treatment left the starting arena in 98% (49/50) of trials in week one, while doing so in 100% (50/50) of trials during week three. Fish from the pair and group treatments left the starting arena in 100% (50/50) of trials over all three weeks. (Figure 9).

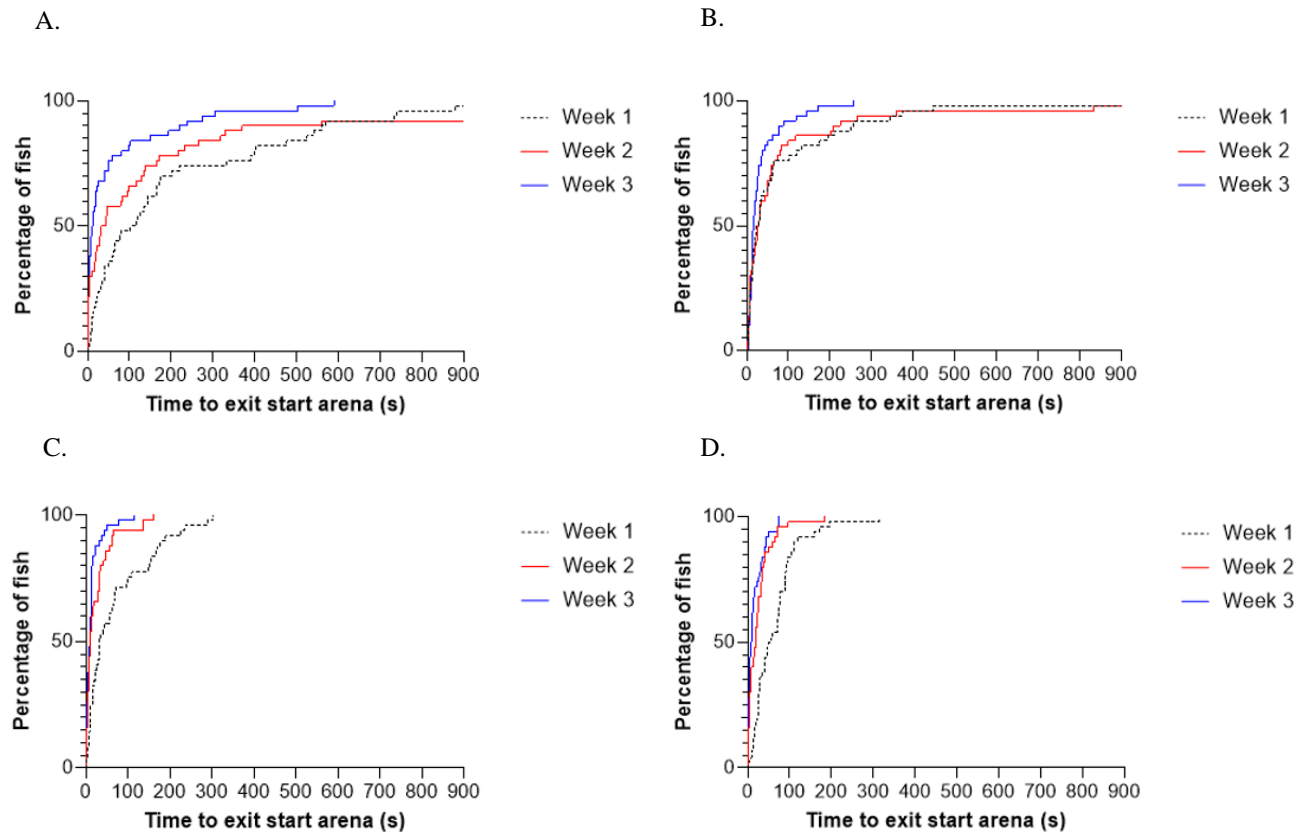


Figure 9. A survival analysis showing the latency of fish to leave the starting arena (s) in the single fish treatment (A.), mirror treatment (B.), pair treatment (C.), and group treatment (D.) over a three-week period.

Fish from all treatments became quicker to leave the starting arena over the three-week period ($p = <0.005$) (Table 10).

Table 10. Statistical comparisons within each social group to determine whether time for first fish to exit the starting arena declined over three successive weeks. Bolded values indicate statistical significance.

Treatment Groups	Median time to exit (s)	Mantel-Cox test	Logrank test for trend	Gehan-Breslow-Wilcoxon test
Singles	W1: 110.5	$p = 0.0003$	$p = 0.0002$	$p = <0.0001$
	W2: 38.0			
	W3: 12.5			
Mirrors	W1: 26.0	$p = 0.0459$	$p = 0.0303$	$p = 0.2773$
	W2: 28.5			
	W3: 16.5			
Pairs	W1: 33.0	$p = <0.0001$	$p = <0.0001$	$p = <0.0001$
	W2: 9.5			
	W3: 9.0			
Groups	W1: 52.5	$p = <0.0001$	$p = <0.0001$	$p = <0.0001$
	W2: 19.0			
	W3: 8.5			

3.2.3 Time to Orientate to Food Source

Increased group size correlated with more frequent, and faster orientation to the food source over all three weeks. In the final two weeks, fish from the pair and group treatments were the fastest to orientate to the food source, doing so more frequently than fish from other treatments.

3.2.3.1 Treatment Orientation Latency by Week

Fish from the singles treatment orientated to the food source in 78% (39/50) of trials in the first and third week, but only in 64% (32/50) of trials in the second week (Figure 10). Fish from the mirror treatment orientated to the food source in 92% (46/50) of trials in the first and third weeks, and in 90% (45/50) of trials in the second week (Figure 10). Fish from the pair and group treatments orientated to the food source in 96% (48/50) of trials in the first week, while doing so in 100% (50/50) of trials in the second and third week (Figure 10).

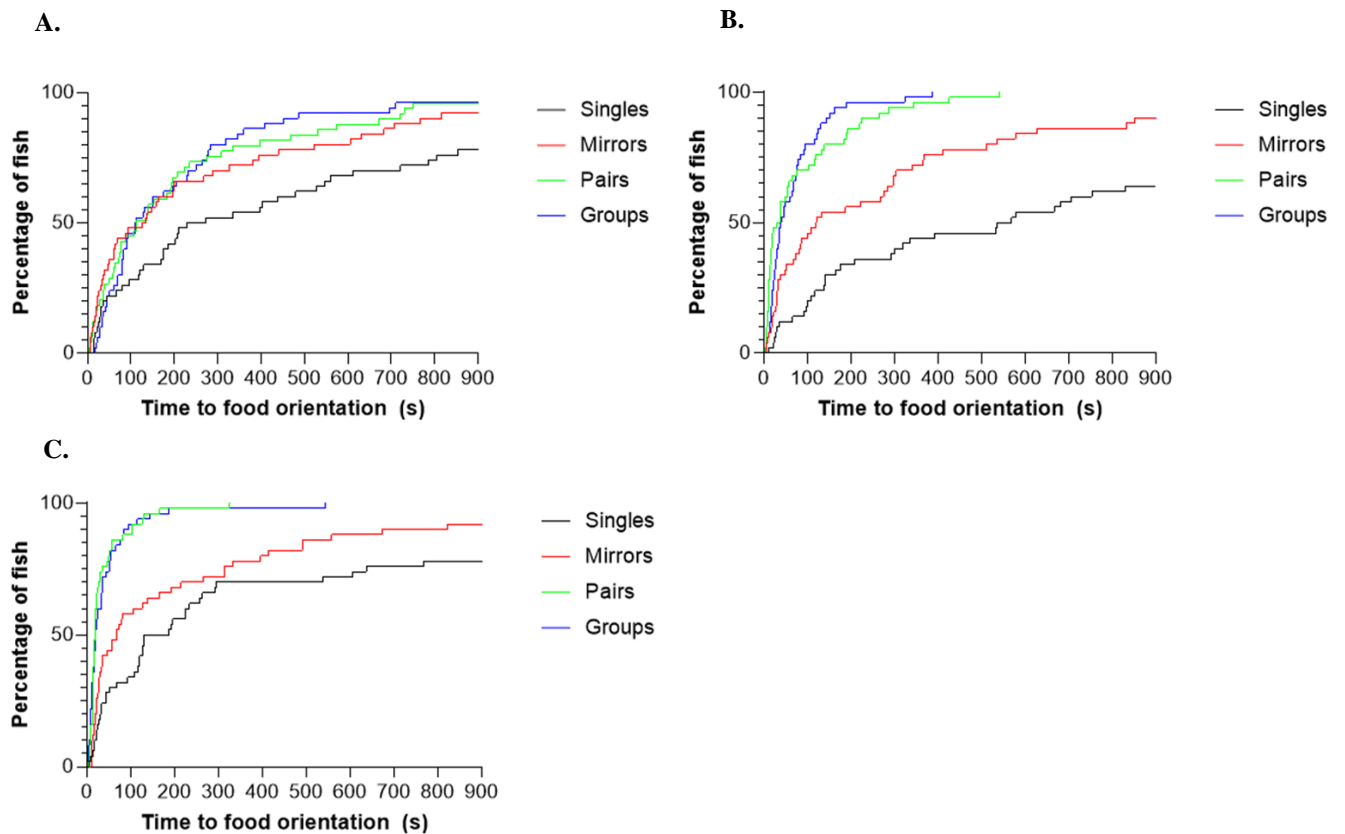


Figure 10. A survival analysis showing the time for the first fish in a trial to orientate to the food reward (s) in each treatment during week one (A.), week two (B.), and week three (C.).

3.2.3.2 Orientation Frequency and Latency Statistics

Fish from the singles treatment were the slowest to orientate to the food source in all three weeks when compared to all other treatments ($p = <0.05$) (Tables 11-13). Fish from the mirror treatment were significantly slower to orientate to the food reward than fish from the pair and group treatments in the second and third weeks ($p = <0.05$) (Tables 11-13). A hazard ratio score of 0.48 - 0.6 was generated when comparing singles to each other treatment, indicating a 40 - 52% lower likelihood of food orientations occurring in fish of the singles treatment compared to fish of other treatments. Observations were made with 95% confidence (Table 11).

Table 11. Statistical comparisons between treatment groups in week one - time for first fish to orientate to the food source (s). 95% confidence intervals in parentheses. Bolded values indicate statistical significance.

Treatment Groups	Median time to exit (s)	Mantel-Cox test	Gehan-Breslow-Wilcoxon test	Hazard ratio (Mantel-Haenszel)	Hazard ratio (logrank)
Singles vs Mirrors	251.5 130.0	$p = 0.0153$	$p = 0.0167$	0.583 (0.377 - 0.902)	0.596 (0.387 - 0.918)
Singles vs Pairs	251.5 113.0	$p = 0.0020$	$p = 0.0081$	0.498 (0.320 - 0.775)	0.524 (0.340 - 0.809)
Singles vs Groups	251.5 111.0	$p = 0.0013$	$p = 0.0177$	0.481 (0.308 - 0.751)	0.517 (0.336 - 0.796)
Mirrors vs Pairs	130.0 113.0	$p = 0.5484$	$p = 0.9249$	0.882 (0.586 to 1.329)	0.884 (0.588 - 1.328)
Mirrors vs Groups	130.0 111.0	$p = 0.5122$	$p = 0.6813$	0.871 (0.577 - 1.315)	0.876 (0.584 - 1.312)
Pairs vs Groups	113.0 111.0	$p = 0.8875$	$p = 0.6519$	0.971 (0.647 - 1.457)	0.972 (0.650 - 1.453)

Comparing singles to each other treatment produced a hazard ratio of 0.19 – 0.45, indicating that fish in the singles treatment were 55 - 81% less likely to orientate to the food reward than fish from the other treatments in the second week (Table 12). Additionally, a hazard ratio score of 0.34 – 0.44 was generated when comparing the mirror treatment to the pair and group treatments, suggesting that fish from the mirror treatment were 56 - 66% less likely to orientate to the food source than pair or group treatment fish. These observations were again made with 95% confidence (Table 12).

Table 12. Statistical comparisons between treatment groups in week two - time for first fish to orientate to the food source (s). 95% confidence intervals in parentheses. Bolded values indicate statistical significance.

Treatment Groups	Median time to exit (s)	Mantel-Cox test	Gehan-Breslow-Wilcoxon test	Hazard ratio (Mantel-Haenszel)	Hazard ratio (logrank)
Singles vs Mirrors	552 120	$p = 0.0003$	$p = 0.0004$	0.422 (0.265 - 0.672)	0.446 (0.282 - 0.706)
Singles vs Pairs	552 34.0	$p = <0.0001$	$p = <0.0001$	0.144 (0.086 - 0.242)	0.240 (0.147 - 0.390)
Singles vs Groups	552 38.5	$p = <0.0001$	$p = <0.0001$	0.119 (0.069 - 0.202)	0.226 (0.138 - 0.370)
Mirrors vs Pairs	120 34.0	$p = <0.0001$	$p = <0.0001$	0.377 (0.241 to 0.589)	0.442 (0.288 - 0.679)
Mirrors vs Groups	120 38.5	$p = <0.0001$	$p = 0.0003$	0.337 (0.213 - 0.535)	0.423 (0.275 - 0.651)
Pairs vs Groups	34 38.5	$p = 0.6259$	$p = 0.3399$	0.904 (0.601 - 1.358)	0.910 (0.615 - 1.348)

Week three comparisons between the singles treatment and all other treatments resulted in a hazard ratio of 0.18 – 0.64, indicating that singles treatment fish were 36 - 82% less likely to orientate to the food reward than fish of the other treatments, with 95% confidence (Table 13). A hazard ratio score of 0.29 – 0.42 was produced when comparing the mirror treatment to the pair and group treatments, indicating that fish from the mirror treatment had a 58 - 71% lower likelihood to orientate to the food source than fish from the pair or group treatments, with 95% confidence (Table 13).

Table 13. Statistical comparisons between treatment groups in week three - time for first fish to orientate to the food source (s). 95% confidence intervals in parentheses. Bolded values indicate statistical significance.

Treatment Groups	Median time to exit (s)	Mantel-Cox test	Gehan-Breslow-Wilcoxon test	Hazard ratio (Mantel-Haenszel)	Hazard ratio (logrank)
Singles vs Mirrors	131 67.5	$p = 0.0395$	$p = 0.0448$	0.635 (0.412 - 0.978)	0.643 (0.419 - 0.988)
Singles vs Pairs	131 18.0	$p = <0.0001$	$p = <0.0001$	0.635 (0.412 - 0.978)	0.643 (0.419 - 0.988)
Singles vs Groups	131 18.5	$p = <0.0001$	$p = <0.0001$	0.179 (0.108 - 0.297)	0.288 (0.180 - 0.460)
Mirrors vs Pairs	67.5 18.0	$p = <0.0001$	$p = <0.0001$	0.297 (0.186 to 0.475)	0.393 (0.254 - 0.608)
Mirrors vs Groups	67.5 18.5	$p = <0.0001$	$p = <0.0001$	0.337 (0.214 - 0.532)	0.416 (0.270 - 0.641)
Pairs vs Groups	18.0 18.5	$p = 0.7226$	$p = 0.8876$	1.076 (0.719 - 1.611)	1.071 (0.724 - 1.586)

3.2.3.3 Weekly Orientation Latency by Treatment

Fish from the singles treatment orientated to the food source in 78% (39/50) of trials in week one and week three. The fish of the mirror treatment orientated to food in 92% (46/50) of trials in weeks one and three. Pair and group treatment fish orientated to the food source in 96% (48/50) of trials in week one, and in 100% (50/50) in week three (Figure 11).

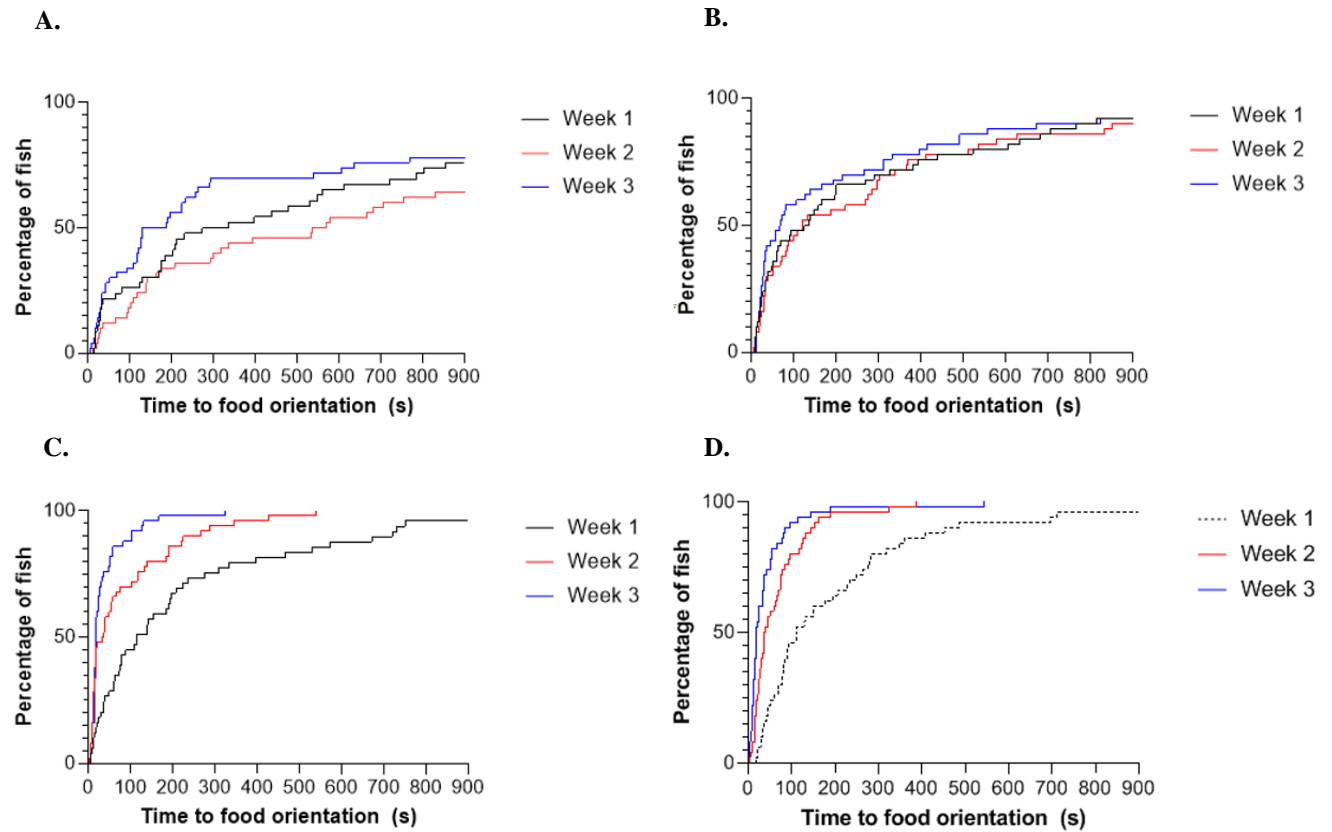


Figure 11. A survival analysis showing the latency of fish to orientate to the food source (s) in the single fish treatment (A.), mirror treatment (B.), pair treatment (C.), and group treatment (D.) over a three-week period.

Fish from the pair and group treatments showed a statistically significant decrease in orientation latency ($p = <0.005$) when comparing orientation latencies from week one to week three (Table 14).

Table 14. Statistical comparisons within each social group to determine whether time for first fish to orientate to the food source declined over three successive weeks. Bolded values indicate statistical significance.

Treatment Groups	Median time to exit (s)	Mantel-Cox test	Logrank test for trend	Gehan-Breslow-Wilcoxon test
Singles	W1: 251.5 W2: 552 W3: 131	$p = 0.0745$	$p = 0.5008$	$p = 0.0414$
Mirrors	W1: 130 W2: 120 W3: 67.5	$p = 0.5692$	$p = 0.4860$	$p = 0.3988$
Pairs	W1: 113 W2: 34 W3: 18	$p = <0.0001$	$p = <0.0001$	$p = <0.0001$
Groups	W1: 111 W2: 38.5 W3: 18.5	$p = <0.0001$	$p = <0.0001$	$p = <0.0001$

Chapter 4

Discussion

The aim of this study was to investigate the influence of group size on the ability of New Zealand spotted wrasse (*Notolabrus celidotus*) to solve a problem-solving foraging task. A secondary aim of this study was to investigate which mechanism played a greater role in influencing the likelihood of success, whether that be social learning, increased foraging time as a function of group vigilance, or increased foraging effort as a function competition for a limited resource. The key findings of this research support the hypothesis that group size has an influence upon the success rate and success latency of New Zealand spotted wrasse in relation to a foraging task.

4.1 Key Findings and Interpretation

The results of this study show that as group size increased, fish left the starting arena more rapidly and they orientated themselves to the food source more quickly. Larger groups were also more likely to succeed in solving the foraging task by accessing the food source, as well as being quicker to access the food source.

Perhaps the most important finding of this study was that across all three weeks, fish in the singles treatment (Stage 1) consistently performed the worst in terms of success rate and success latency compared to other treatments. These results are consistent with the poor performance of the single fish trialled in the pilot study. Additionally, single fish were significantly slower to orientate to the food source than all other treatments over the three-week period. These results are indicative of an improvement in foraging success and reduction in foraging time with increased presence/perceived presence of conspecifics, thus presenting evidence to support the primary hypothesis of this study.

These findings present three possible explanations as to why foraging performance improves with increased group size in the spotted wrasse. (1) The presence of conspecifics provides passive predator vigilance, enabling individual fish to put more time into solving the foraging task instead of scanning for predators. (2) As a function of increased competition for a limited resource, fish put more effort into solving the foraging task. (3) Social learning resulted in fish learning foraging strategies from conspecifics.

4.1.1 Predator Vigilance

The benefit of increased predator vigilance in grouping organisms is a well-documented phenomenon, with animals benefitting from the presence of conspecifics by way of the dilution effect and the many eyes hypothesis (Roberts, 1996). It has been speculated that living in groups enables individuals to increase foraging time, as risk-associated foraging costs such as predation are reduced (Beauchamp, 2003; Hintz & Lonzarich, 2018). A study by Sullivan (1984) found that individual downy woodpeckers (*Picoides pubescens*) foraged more efficiently when in the presence of conspecifics due to the effect of group predator vigilance. The predator vigilance behaviour of these birds was well-understood, thus was measurable by observing the head-cocking (head movement from left to right or vice versa) rates of the woodpeckers. A higher rate of head-cocking was attributed to a higher state of vigilance while a lower incidence of head-cocking behaviour was related to a reduced state of vigilance (Sullivan, 1984). It was found that solitary birds displayed high head-cocking rates and low rates of feeding, while individuals in the presence of three or more flock members displayed infrequent head-cocking and increased feeding rates (Sullivan, 1984). This example gives credence to the hypothesis that spotted wrasse forage more effectively in the presence/perceived presence of conspecifics as a result of group predator vigilance, enabling the fish to spend less time scanning for predators and more time attempting to solve the foraging task.

However, measuring the vigilance behaviours of fish is difficult, as fish generally do not display behaviours that can unequivocally be interpreted as predator vigilance behaviour (Magurran & Pitcher, 1983). Therefore, in order to quantify the vigilance level of fish such as the spotted wrasse, it would first be necessary to identify behaviours that are characteristic of predator vigilance, for example, the head-cocking behaviour displayed in downy woodpeckers (Sullivan, 1984). This would enable the influence of group size upon individual predator vigilance to be tested in spotted wrasse more conclusively, potentially enabling further extrapolation into the influence of group size on foraging success in these fish. A recent study by Hess, Fischer, and Taborsky (2016) quantified the vigilance level of a cichlid fish (*Neolamprologus pulcher*) by measuring the time it took for the fish to detect a predator model. To test the vigilance behaviour of the New Zealand spotted wrasse, a future study could take a similar measure of vigilance in response to a predator model. Reports of predation on spotted wrasse are sparse in literature, so it is unknown what the ideal predator model for this type of experiment would be. Perhaps a pelagic predator such as the barracouta (*Thyrsites atun*), which is known to consume fish of a similar size range to juvenile spotted wrasse, could potentially be a good candidate for this kind of experiment (O'Driscoll, 1998). Alternatively, a future study could focus on gaining a greater understanding of the food-web interactions of the spotted wrasse by observing these fish in a natural setting.

4.1.2 Competition

The effect of intraspecific competition is an equally plausible explanation for the improved foraging rate associated with increased group size found in the current study. Competition within conspecifics for a limited food source has been documented as a potential reason for increased foraging effort in various studies, whereby individuals may allocate more effort to foraging to increase their own energy intake when in the presence of conspecifics (Grand & Dill, 1999; Bednekoff & Lima, 2004). This potential

explanation is supported by a study on coho salmon (*Oncorhynchus kisutch*) by Grand and Dill (1999) in which an increase in foraging frequency with greater group size was attributed to an increase in competition for a scarce food resource. The authors tested the relative importance of risk-reduction (group vigilance) and increased competition by manipulating predation risk (predator model present vs. predator model absent), as well as group size (singles, pairs, groups of four). While fish from all treatments made fewer attempts to forage in the presence of the predator, individuals from larger groups still foraged more than those from smaller groups, whether they were in the presence of the predator model or not. This finding suggests that, while predation risk did play a factor in foraging frequency, it did not influence the trend of the relationship between group size and foraging or risk-taking behaviour. Therefore, it was suggested that increased foraging competition was the primary mechanism responsible for increased individual foraging rate in larger groups of coho salmon (Grand & Dill, 1999). This would support the hypothesis that spotted wrasse displayed greater foraging success rates and quicker completion times in larger groups, due to the presence/perceived presence of conspecifics competing for a limited food source.

4.1.3 Predator Vigilance vs. Competition

The predator vigilance and competition hypotheses often confound each other as they influence the findings of group size and foraging success research in similar ways (Elgar, 1989; Hintz & Lonzarich, 2018). Moreover, these variables not only have the potential to influence foraging success, but each other, making deductions based on these factors less conclusive (Hess et al., 2016). A study by Hess et al. (2016) found that the cichlid fish (*Neolamprologus pulcher*) were significantly less vigilant in the presence of a predator model due to the implications of competition for territory with conspecifics. This suggests that predator vigilance not only decreases due to the dilution effect and many eyes hypothesis, but also due to the implications of competition introduced by the presence of

conspecifics (Hess et al., 2016). This indicates the potential existence of a trade-off between competition with conspecifics and predator vigilance behaviour in relation to fitness benefits, making the relationship between these variables a more complex study objective.

Other studies have tested and manipulated these confounding variables to gain a greater understanding of the mechanisms responsible for increased foraging success in larger groups (Grand & Dill, 1999; Hintz & Lonzarich, 2018). A study by Hintz and Lonzarich (2018) examined the foraging success (number of feeding events per minute) of coho salmon in relation to group size. Measurements of predation risk (approximated by recording naturally occurring habitat features, preferred by predators of coho salmon such as herons and brown trout) and competition (measured by agonistic interactions) were also recorded. It was found that neither predation risk or competition were a strong contributor to foraging success in the coho salmon, contradicting the findings of Grand and Dill (1999). Hintz and Lonzarich (2018) suggested that the reason for the lack of a strong relationship between each variable was because both factors, predation risk and competition, likely contributed to foraging success in wild coho salmon populations concurrently. Therefore, it is likely that the increased performance of spotted wrasse in the presence/perceived presence of conspecifics can, in part, be attributed to decreased individual predator vigilance as well as increased competition for a scarce resource (Hintz and Lonzarich, 2018). To ascertain which mechanism(s) is responsible for increased foraging success in spotted wrasse within larger groups, further study would need to be conducted whereby both predation risk and group size are measured and/or manipulated, similarly to what was done in the studies by Grand and Dill (1999) and Hintz and Lonzarich (2018). This would present a greater understanding of the mechanisms responsible for the influence of group size on foraging success in the New Zealand spotted

wrasse, also serving as a valuable point of reference for future studies into the foraging ecology of fishes.

4.1.4 Social Learning

An alternative explanation to the predator vigilance and competition hypotheses, is that pairs and groups outperformed the singles treatment due to an effect of social learning, enabling individuals to learn how to solve the foraging task more quickly by observing conspecifics. Conspecifics learning how to solve problems through social learning is well-documented and has been observed in fish such as stingrays and sharks (Guttridge et al., 2013; Thonhauser et al., 2013). However, this explanation for increased performance in spotted wrasse is not supported by the results of the mirror treatment, as these fish performed significantly better than fish from the singles treatment, despite also having no access to information from conspecifics. Furthermore, fish from the mirror treatment also performed similarly to those from the pair treatment over all three weeks and performed similarly to fish from the group treatment in week one. These results indicate that the false perception of being in the presence conspecifics, offers similar foraging benefits to the actual presence of conspecifics, for fish in the foraging environment of this experiment.

However, results also show that fish from the pair and group treatments consistently displayed a lower latency to leave the starting arena and were quicker to orientate to the food source than other treatments. It is unlikely that this is due to a higher density of fish being present in the tank at one time, as fish from the pair and group treatments performed similarly across all measures, including success rate and completion time, despite the group treatment containing twice the density of fish. Therefore, the high performance of the pair and group treatments is likely not solely due to an effect of density-mediated encounter rate, but rather due to a social learning mechanism such as local enhancement. This is supported by a study on three-spined sticklebacks by Trapp and Bell (2017) where

it was concluded that reduced food-orientation latencies in the presence of conspecifics were likely due to an effect of social learning via local enhancement. It is probable that this effect of local enhancement occurs alongside the effects of reduced predator vigilance, and increased foraging competition, in larger groups of spotted wrasse (Brown & Laland, 2003; Hintz & Lonzarich, 2018).

4.1.5 Individual Learning

The results show that over the three weeks, improvement was observed in terms of fish latency to leave the starting arena and latency to succeed in the foraging task within each treatment. This improvement over time within each treatment indicates that regardless of the group size, the fish were able to become more proficient at the task, which is indicative of learning.

Results also show that the singles treatment was still recording relatively low success rates in the final week of trials, with fish from this treatment displaying a 60% likelihood to solve the foraging task, compared to an 84%, 88%, and 98% success rate in the mirrors, pairs, and group treatments, respectively. This result indicates that insightful problem-solving is likely not being utilized by the spotted wrasse, as organisms which use insightful problem-solving often show higher initial success rates and succeed in most future attempts at a problem they had previously solved (Mendes et al., 2007; Bird & Emery, 2009). Therefore, associative learning through positive reinforcement is likely the learning mechanism responsible for the increase in success rate, and decrease in success latency, across all treatments over the three-week period. This is similar to the learning displayed by hyenas whereby, through reinforcement of certain behaviours, the animals began to associate a specific behaviour with a reward, enabling them to solve a problem-solving foraging task (Amram & Holekamp, 2012). The spotted wrasse likely learned how to access the food source through trial and error, initially solving the foraging task by chance, but over time, learning to associate swimming into the correct tube with access

to the food source. This effect of positive reinforcement likely led to the increase in performance of fish from each treatment over time.

4.2 Limitations and Future Studies

This study faced multiple limitations which could be mitigated in future studies. One of the stand-out limitations of this study was the inability to distinguish one fish from another. Due to the habitat and environmental enrichment inserted into the tanks to reduce fish stress, fish were able to hide beneath objects, obstructing the view from the camera. Sometimes multiple similar sized fish would hide in the same place concurrently, making it impossible to tell one from the other in the footage. This made it difficult to speculate on factors such as social learning, as it was not possible to observe the likelihood of a second fish solving the task after another fish in the group had done so. Not being able to distinguish between individuals also made it more difficult to measure foraging effort per fish, as variables such as resting time, hiding time, and swimming time are only possible to measure if the focal fish is able to be tracked. Attempts to individually mark fish with a vital stain, recommended by Arnold (1966), were unsuccessful and other marking methods for small fish were deemed too invasive to produce marks that would be easily identifiable on video. Successfully marking individual fish could generate more informative results, presenting a more in-depth understanding of the behaviours of each individual. An animal-tracking software program called Toxtrac was also trialled to attempt to distinguish between individual fish in the footage, however, because the fish often hid under inserted habitat, it was not possible to track when multiple fish hid in the same location simultaneously. A future study could use different items for habitat and environmental enrichment, in order to ensure that fish are fully visible, or at least distinguishable, in the footage for the duration of the experimental trial. While using less habitat coverage would offer an unobstructed view for the camera, it could also increase individual stress levels as suggested by Näslund & Johnsson (2014). A future study on

juvenile spotted wrasse could spend more time habituating the fish to using less-covered pyramid-like structures such as those used in the study conducted by Atton et al. (2014). This could potentially increase the likelihood of foraging behaviour whilst also enabling each fish to be distinguishable in the footage.

Another potential limitation was the size range of fish within this study. A study by Laland and Reader (1999) suggests that, out of necessity, smaller female guppies were more outgoing and competitive foragers than larger conspecifics. Additionally, smaller poeciliid fish (*Brachyrhaphis episcopi*) have been documented to emerge from cover more quickly than larger fish, in order to resume feeding (Brown & Braithwaite, (2004). Therefore, it is possible that smaller spotted wrasse, may have invested more effort than larger spotted wrasse, as a result of increased motivation to gain the desired food source. This potential issue was managed by keeping the average size of fish within trial groups and between treatments as consistent as possible, with the average size of fish in each trial ranging from 6.2 to 7.2 cm standard length. Because the influence of fish size was not tested in this study, a future study may wish to investigate whether the size of a spotted wrasse has an influence upon motivation/effort to obtain the food reward in a similar foraging task. It is worth noting that the food particle size during trials was the same as what was used to feed the fish outside of experiment time (before the study had begun, and after trials each day during the study) to ensure that fish of all sizes were interested in the food source.

It would be interesting to successfully create an observer-demonstrator experiment, to see if the performance of individuals which had a demonstrator exceeds that of those without a demonstrator, which could indicate social learning more conclusively. Perhaps the “demonstrator” in a social learning study could instead be a group of four fish, a pair of fish, or an individual fish with mirrors, as the results of this study presented high success rates in each of these treatments. Thus, testing the foraging success of an individual with

no demonstrator and comparing that with a fish which had observed experienced conspecifics forage, may give some indication to the social learning abilities of the New Zealand spotted wrasse.

4.3 Conclusions

Results from this research support the hypothesis that group size has an influence upon the success rate and success latency of a problem-solving foraging task in juvenile New Zealand spotted wrasse. Due to the gradual improvement observed in the spotted wrasse, the learning mechanism responsible for individual learning during this study is likely associative learning through positive reinforcement, as opposed to insightful problem-solving which displays a more rapid rate of improvement.

The mechanism(s) responsible for the performance disparity between the single fish treatment and the other three treatments is likely a combination of: the effect of passive group vigilance, leading to increased foraging rate per individual; the effect of increased foraging competition, leading to increased foraging effort per individual; and the effect of simple social learning mechanism(s) such as local enhancement. Further study is required to conclusively suggest whether the effect of reduced predator vigilance, increased competition, or social learning, has a greater influence on increased foraging success with increased group size in New Zealand spotted wrasse.

Future studies could measure and/or manipulate variables such as predation risk, level of competition, and food availability, to gain a greater understanding of the mechanisms driving increased individual foraging success of spotted wrasse, when in the presence/perceived presence of conspecifics. Additionally, recreating an observer-demonstrator experiment, using experience demonstrator fish, could give further insight into the social learning behaviours of these fish.

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