

A Comparative Analysis of *Perca fluviatilis* Population Dynamics
from Two Lakes in New Zealand

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Abstract

This thesis comparatively examined the population dynamics of European *Perca fluviatilis* populations from Warkworth Quarry Lake and Lake Rototoa. A total of 206 fish samples from Warkworth Quarry Lake and 99 fish samples from Lake Rototoa were histologically analyzed and sagittal otoliths examined to obtain estimates of reproductive, age and growth parameters. Diet was analyzed through visual assessment of stomach contents while catch per unit effort provided an index of relative abundance of populations. Age and size structure analysis showed the dominance of females in the structure of both populations while the maximum age in Warkworth Quarry Lake and Lake Rototoa populations were 6+ and 7+ respectively. Growth rate was rapid in the first year in both populations while high growth rates were achieved in subsequent years in Lake Rototoa population. There were no significant differences ($p < 0.001$) in expected size-at-age between males and females of the two populations. There were differences in sex ratio between the populations and this was influenced by location, population growth rate and sampling gear. Sexual maturity was attained between year 1 and 2 and temperature was the main abiotic factor affecting the reproductive biology of *Perca fluviatilis*. This was reflected in the height of gonadosomatic index occurring during the winter months of New Zealand and an extended vitellogenic period of 9 months experienced by both populations. Additional reproductive anomalies present in both populations were the presence of atretic eggs, asynchronous egg cell development, lack of resorbing egg cells, scarce presence of post-ovulatory follicles and presence of individuals with gonadal stages associated with spawning outside the documented spring spawning season in New Zealand. Diets of fish 50 – 180 mm SL comprised of small aquatic invertebrates. Fish >180mm SL in Warkworth Quarry Lake were cannibalistic, whereas in Lake Rototoa they fed almost exclusively on *Paranephrops planifrons*. The results indicate the impact of *Perca fluviatilis* on native species and an adaptation to New Zealand waters through variation in growth patterns, feeding patterns and reproductive traits. Although this study provides tentative evidence of an extended spawning season, it is conclusive that *Perca fluviatilis* in New Zealand have life traits whose biological plasticity is attributed to latitudinal gradient.

Table of Contents

Abstract	iii
Table of Contents	iv
List of Figures	vi
List of Tables.....	vii
Attestation of Authorship.....	viii
Acknowledgements	ix
Chapter 1 General Introduction	1
1.1 Freshwater Ecosystems	1
1.2 Challenges in Management and Conservation of Freshwater Ecosystems	5
1.3 <i>Perca fluviatilis</i> (perch).....	9
Aims.....	14
Chapter 2 Age and Growth Structures of <i>Perca fluviatilis</i> in Two New Zealand Lakes.....	15
2.1 Introduction	15
2.2 Objectives.....	19
2.3 Material and Methods.....	19
2.3.1 Study Location.....	19
2.3.2 Sampling.....	23
2.3.3 Age and Growth Estimation	23
2.4 Results	27
2.4.1 Environmental variables	27
2.4.2 Age and Growth Estimation	27
2.5 Discussion	41
Chapter 3 The Reproductive Biology of <i>Perca Fluviatilis</i> from Two Lakes in New Zealand	44
3.1 Introduction	44
3.2 Objectives.....	49
3.3 Materials and Methods	49
3.3.1 Gonad development of <i>Perca fluviatilis</i>	49
3.4 Results	54
3.4.1 Warkworth Quarry Lake.....	54
3.4.2 Lake Rototoa.....	57

3.5 Discussion	63
Chapter 4 Diet and Relative Abundance of <i>Perca fluviatilis</i> from Two Lakes in New Zealand	68
4.1 Introduction	68
4.2 Objectives.....	70
4.3 Materials and Methods	71
4.3.1 Diet Analysis of <i>Perca fluviatilis</i>	71
4.3.2 Catch per Unit Effort (CPUE)	71
4.4 Results	71
4.4.1 Diet	71
4.4.2 CPUE	73
4.5 Discussion.....	75
Chapter 5 Key Findings, Significance and Future Direction	77
5.1 Introduction	77
5.2 General Discussion.....	77
References	83

List of Figures


Figure 1 <i>Perca fluviatilis</i>	10
Figure 2 Egg ribbons of <i>Perca fluviatilis</i>	12
Figure 3 Aerial Map View of Warkworth Quarry Lake	20
Figure 4 Photographic view of Warkworth Quarry Lake	21
Figure 5 Map of Lake Rototoa.....	22
Figure 6 Photographic view of Lake Rototoa	22
Figure 7 A pair of sagittal otoliths from <i>Perca fluviatilis</i> (left) and diamond disc cutter with grit 1200	24
Figure 8 A sectioned sagittal otolith from <i>Perca fluviatilis</i> showing 2 annual rings	25
Figure 9 Age distribution of female <i>Perca fluviatilis</i> in Warkworth Quarry Lake	28
Figure 10 Age distribution of male <i>Perca fluviatilis</i> in Warkworth Quarry Lake.....	29
Figure 11 Age distribution of female <i>Perca fluviatilis</i> in Lake Rototoa	30
Figure 12 Age distribution of male <i>Perca fluviatilis</i> in Lake Rototoa	31
Figure 13 Age distribution of <i>Perca fluviatilis</i> in Warkworth Quarry Lake and Lake Rototoa	31
Figure 14 Size distributions of <i>Perca fluviatilis</i> in Warkworth Quarry Lake and Lake Rototoa	32
Figure 15 Length-Weight Relationship of <i>Perca fluviatilis</i> in Warkworth Quarry Lake.....	33
Figure 16 Length-Weight Relationship of <i>Perca fluviatilis</i> in Lake Rototoa.....	33
Figure 17 Relationship between age and length of <i>Perca fluviatilis</i> in Warkworth Quarry Lake and Lake Rototoa	34
Figure 18 Mortality of <i>Perca fluviatilis</i> in Warkworth Quarry Lake	36
Figure 19 Mortality of <i>Perca fluviatilis</i> in Lake Rototoa	36
Figure 20 Photograph of an ovary extracted from <i>Perca fluviatilis</i>	52
Figure 21 Gonad development of female and male <i>Perca fluviatilis</i> in Warkworth Quarry Lake.....	55
Figure 22 GSI for female <i>Perca fluviatilis</i> in Warkworth Quarry Lake.....	56
Figure 23 GSI for male <i>Perca fluviatilis</i> in Warkworth Quarry Lake.....	56
Figure 24 Gonad development of female and male <i>Perca fluviatilis</i> in Lake Rototoa.....	58
Figure 25 GSI for female <i>Perca fluviatilis</i> in Lake Rototoa.....	58
Figure 26 GSI for male <i>Perca fluviatilis</i> in Lake Rototoa.....	59
Figure 27 Changes in proportion of <i>Perca fluviatilis</i> females with vitellogenic oocytes in Warkworth Quarry Lake and Lake Rototoa.....	59
Figure 28 Female stages of oocyte development in <i>Perca fluviatilis</i>	61
Figure 29 Stages of sperm development in <i>Perca fluviatilis</i>	62
Figure 30 <i>Paranephrops planifrons</i> (freshwater crayfish) removed from the stomachs of <i>P.fluviatilis</i> from Lake Rototoa.....	73
Figure 31 CPUE of <i>Perca fluviatilis</i> in Warkworth Quarry Lake.....	74
Figure 32 CPUE of <i>Perca fluviatilis</i> in Lake Rototoa.....	74

List of Tables

Table 1 The Age-Length Relationship of <i>P.fluviatilis</i> populations in New Zealand.....	37
Table 2 Likelihood Ratio Test of <i>P.fluviatilis</i> in Warkworth Quarry Lake and Lake	38
Table 3 Values of von Bertalanffy growth function parameters of different <i>Perca fluviatilis</i> populations and the corresponding ϕ^1 estimates	39
Table 4 Schedule of dehydration in tissue processor	50
Table 5 Haematoxylin and Eosin Staining Protocol for <i>Perca fluviatilis</i>	51
Table 6 Gonad Developmental Stages of <i>Perca fluviatilis</i>	53
Table 7 Proportion of maturational stages of <i>Perca fluviatilis</i> gonads in Warkworth Quarry Lake (n=206) and Lake Rototoa (n=99)	60
Table 8 Size of <i>Perca fluviatilis</i> at different ages in Warkworth Quarry Lake and Lake Rototoa.....	60
Table 9 Stomach Contents of <i>P.fluviatilis</i> from Warkworth Quarry Lake and Lake Rototoa as % Frequency of Occurrence.....	72

Attestation of Authorship

I hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published or written by another person (except where explicitly defined in the acknowledgements), nor material which to a substantial extent has been submitted for the award of any other degree or diploma of a university or other institution of higher learning.

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Chapter 1 General Introduction

1.1 Freshwater Ecosystems

Freshwater systems comprise approximately 2.5% of the total water resources on Earth (Rekacewicz, 2005). They are unique environments with a diverse global distribution and they have been instrumental in the foundation of civilizations throughout the history of mankind. Civilizations have been established based on proximity to fresh water since time immemorial. For example, primordial Mesopotamia thrived because of an abundant supply of water from the rivers Tigris and Euphrates; ancient Egypt flourished along the river Nile and the Roman Empire dedicated numerous resources in building complex systems of aqueducts to supply water to their cities. Despite the importance of the extractive uses of freshwater to human society, the remaining water in these systems have an equally important role to play in sustaining a healthy aquatic biome. The freshwater biome encompasses underground water, lakes, streams, rivers, and wetlands which contain functionally intact and biologically complex freshwater ecosystems.

Ecosystems can be defined as “thermodynamically open, hierarchically organized communities of producers, consumers, and decomposers together with the abiotic factors that influence species growth, reproduction, and dispersal” (Thorp & Covich, 2001). Freshwater ecosystems differ momentarily from one another according to type, climate and location. Although freshwater ecosystems occupy less than 2% of the total surface of the earth, they play a significant role in maintaining the integrity of the planet through their function and value. They provide goods such as food, freshwater to drink, transportation, agriculture, energy production, waste disposal and cultural considerations such as recreation. Ecological values include ecosystem regulation such as creation of rain and climate through the hydrological cycle as well as ecosystem support through nutrient recycling (Reid, Contreras & Csatadi, 2013). In order to maintain ecosystem resilience and a steady flow of goods and services, freshwater ecosystems require a supply of water within a certain range of quality and quantity (Dodds & Whiles, 2010). This causes a direct linkage with groundwater storage. It not only supplies water but it is also a freshwater ecosystem.

Groundwater ecosystems comprise an aquifer whose major feature is a continuum of permeability and average interstitial space. These govern the transfer of materials and limit the size of inhabitants. They are classified by their depth and degree of connectivity with terrestrial habitats and surface waters. Shallow groundwater ecosystems interact with lakes, streams and wetlands over the short term while deep groundwater ecosystems have considerable interaction with surface waters (Rekacewicz, 2005) for example in northern Wisconsin, the majority of lakes that occur in sandy glacial outwash are linked by deep groundwater ecosystems (Kratz, Webster, Bowser, Magnuson & Benson, 1997). Groundwater ecosystems are the only habitats that do not support primary production as they can only support bacterial 'producers' and primary consumers (Dodds & Whiles, 2010).

Ponds and lakes are diversified in both size and shape. Most freshwater lakes are located at high altitudes with nearly 50% of the world's lakes found in Canada alone (Baran, Jantunen & Chong, 2007). Many ponds are seasonal, for example sessile pools, while lakes can be established for several or more years at a time. The majority of lakes, especially those in arid regions, become salty through evaporation which results in a high concentration of inflowing salts. Examples of such lakes include The Caspian Sea, the Dead Sea, and the Great Salt Lake. Ponds and lakes are characterized by a narrow diversity of species as they are often isolated from one another and from other water sources like rivers and oceans (Culver, 1994). The food webs in these ecosystems are characterized by primary production; primary, secondary and tertiary consumers as well as detritivores. In shallow ponds and lakes, benthic primary production plays a significant role in which half or more of the production is attributed to littoral algae and macrophytes (Wetzel, 2001).

Streams and rivers, on the other hand, are freshwater ecosystems with flowing water moving in one direction (Moss, 1988). These ecosystems form a hydrologic mosaic with an estimated 263 international river basins covering 45.3% of the total global land surface, excluding Antarctica (Baines, Webster, Kratz, Carpenter & Magnuson, 2000). They originate at headwaters such as springs, snowmelt or even lakes, and the water flows to their mouths, usually another water channel, sea or ocean. This journey often results in a significant change in the characteristics of the stream or river due to differing conditions such as pH, dissolved oxygen, light intensity and salinity. The supported biota show corresponding differences from source to mouth, hence streams and rivers are highly diversified ecosystems. In comparison to streams, rivers have a higher level of primary production because they are wider with more

surface area exposed to sunlight. However; in large rivers, such as the Amazon River and Mississippi River, there is little primary production due to a high density of both organic and inorganic sediment which increases water turbidity. Collectors and predators are dominant organisms and fish species such as sturgeon and catfish are common as they feed on sediments.

Wetlands are areas of standing water that support aquatic plants and wetland ecosystems can be classified based on their association with rivers, estuaries or lakes. Some wetlands can have high hydrologic throughput due to the use of external nutrients for cycling, whereas others are fed mainly by precipitation and have low hydrologic throughput. Wetlands are important ecosystems as they have the greatest rates of primary productivity compared to other ecosystems (Williams, 1990). They are also important as they act as a natural filter for phosphates and pollutants from water found in freshwater ecosystems hence, they represent a hybrid between terrestrial systems and aquatic systems. Examples of natural wetlands are Laguna de Rocha in Argentina, the Pantanal in Brazil and Ratargul in Bangladesh.

Although freshwater ecosystems contain only 0.01% of the Earth's water and cover a small fraction of the planet's surface, rivers, lakes and wetlands contain a disproportionately high fraction of the Earth's biodiversity. Freshwater fish alone account for over one-fourth of all living vertebrate species (McAllister, Hamilton & Harvey, 1997). Freshwater biodiversity provides a broad variety of valuable goods and services and some of them are irreplaceable (Covich, Palmer & Crawl, 1999). The value of this biodiversity has several components: its direct contribution to economic productivity (e.g. fisheries); insurance value in light of unexpected events; value as a storehouse of genetic information; and value in supporting the provision of ecosystem services (e.g. nutrient cycling) (Pearce, 1998; Heal, 2000; Covich et al., 1999). This biodiversity is critical in maintaining ecosystem resilience and freshwater fish play a major role in this aspect.

Freshwater fish occupy a wide range of trophic levels in the food web due to differences in size, mobility, sensory capabilities and preferred habitat in the water column. Fish found in the littoral zone are usually small sized and are primary consumers that feed on plankton while those that dwell in the limnetic zone are both primary and secondary consumers. Carnivores include zooplanktivores, insectivores and piscivores and are found in both the littoral and benthic zone. Detritivorous fish are also in the benthic zone while omnivorous fish have the ability to consume floral, faunal and detrital material. Parasitic fish are found

on other fish or on large vertebrates within the water column. Most fish experience ontogenic diet shifts while some occupy different types of ecosystems throughout their life history. For example fish that reproduce in freshwater and spend most of their adult lives in the sea are called anadromous fish such as salmon, trout and three-spined stickleback. Catadromous fish are the opposite; they reproduce in salt water and spend their adult life in freshwater for example eels. All these factors enable freshwater fish to play numerous, important ecosystem functions.

Carnivorous fish regulate trophic structure which controls the stability and food web dynamics of freshwater ecosystems. The feeding pattern of fish influences temporal availability of nutrients and the potential for algal blooms in nutrient-rich ecosystems. In such ecosystems, fish are responsible for indirectly mediating the flux of carbon between the ecosystem and atmosphere. Bioturbation of fish results in the modification of the benthic zone for example, benthic algivorous fishes like *Campostoma anomalum* (central stoneroller), *C. oligolepus* (largescale stoneroller), and *Notropis nubilus* (ozark minnow) maintain a rapidly growing algal community and enhance food availability for collector-filterers by resuspending particulate organic matter. Migratory and prey fish serve as links of different ecosystems redistributing phosphorus, nitrogen and carbon.

Any changes that reduce the population sizes, community composition, or availability of fish will affect all facets of the ecology of these ecosystems (Covich et al., 1999). For these reasons, fish have been recognized as key indicators of biological and ecological integrity (Covich et al., 1999; McAllister et al., 1997). This is because they exhibit a wide variety of biotic responses such as changes in growth, distribution and abundance directly related to changes in habitat degradation, water pollution, eutrophication, introduced species and thermal changes. Fish, therefore, are vital elements of ecosystem monitoring programs.

1.2 Challenges in Management and Conservation of Freshwater Ecosystems

The increase in human water needs has significantly contributed to the global deterioration of freshwater ecosystems through a decline of freshwater species (Small & Cohen, 1999). These threats support the need for the long-term protection of these species. Although there is an awareness of conservation, several challenges are yet to be overcome in order to attain this goal and maintain provision of freshwater ecosystem goods and services.

Conservation efforts for freshwater biodiversity are constrained by the fact that most of the species in diverse communities are rare (Sheldon, 1988) and thus information on their natural histories is scarce. This negatively affects the ability to forecast the identities of taxa that are affected when notable reductions in overall species numbers take place. Furthermore, the unreliability of estimates of species richness in individual river basins, especially of the tropics, (e.g. the Mekong River) makes it virtually certain that museum collections, national inventories, and taxonomic knowledge in those regional parts are inadequate to document extinctions. Thus, widespread undetected extinctions of freshwater species have already taken place (Harrison & Stiassny, 1999; Stiassny, 2002). Coupled with this is the limited community awareness of the need to conserve freshwater biodiversity (Dudgeon, 2003). This knowledge impediment challenges both attempts to quantify the freshwater biodiversity crisis and the ability to alleviate it.

Another significant challenge to freshwater ecosystem conservation results from the saltwater and terrestrial barriers which separate one system from another creating restricted range for freshwater species. In the absence of human disturbance, this separation leads to inter drainage variation in biodiversity and high levels of endemism due to low gene flow and local radiation (Sheldon, 1988). This is particularly notable among assemblages that evolved in isolated lakes on islands or mountains and inland plateaux such as the Karstic regions of Burma and Southwest China (Kottelat & Whitten, 1996). These and similar tropical areas are poorly represented in existing protected-area networks (Rodrigues et al., 2004). Ancient lakes such as Lake Baikal in Siberia and those in the East African Rift Valley support well-known species of endemic crustaceans and fish however; there are important stocks of cichlids, cyprinids, catfishes and other fish elsewhere in Africa and the world. For example, there are endangered species among Cyprinidae in the Philippines, Telmatherinidae on Sulawesi Island in Indonesia, and Balitoridae in China (Kornfield & Carpenter, 1984;

Kottelat & Chu, 1988; Kottelat & Whitten, 1996). This results in the complexity that protection of one or a few water bodies cannot preserve all freshwater biodiversity within a region because species endemism hinders substitution of habitats.

Numerous conflicts arise from the multiple use of water constraining conservation and management efforts, especially in rivers. The elements of river biota range widely using different parts of the habitat at various times during their lives. Fish, crustaceans and river dolphins use different habitats at different times, and longitudinal migrations are an obligatory component of life histories for catadromous and anadromous species (Welcomme, 1979). These migrations particularly expose long-lived species to high risks of species decline and extinction from activities such as damming (Carolsfeld, Harvey, Carmen & Baer, 2004). Dams in tropical regions are generally constructed without appropriate fishways or fish passes, or based upon designs that are suitable only for salmonids, and thus they obstruct fish migrations (Roberts, 2001). Lateral migrations, between inundated floodplains or swamp forest and the main river channel, represent another axis of connectivity important for feeding and breeding in many fish and other organisms (Welcomme, 1979; Carolsfeld et al., 2004) that is dramatically altered by dams. Conservation goals in these instances do not converge with societal development.

An assessment of the extent of loss of benefit that accompanies degradation of freshwater ecosystems can be achieved through fish conservation, although this is not a sole appraisal index for the relative value of different catchment management strategies. For instance, income derived from the global sports fishing community provides an incentive to preserve the spawning habitat of *Salmo marmoratus* Cuvier (marble trout) in the Soca River, Slovenia (Sullivan, Jesensek, Jesenske & Zuza, 2003). Likewise, sport fishing in Lake Taupo, New Zealand, generates almost 10% of the activity in the local economy, which is based largely on tourism and forestry (Kirkwood, 2006). Unfortunately, widespread invasion and deliberate introduction of fish species for the purpose of sport fishing adds to the constraint of formulating sound conservation and management policies in freshwater ecosystems (Bunn & Arthington, 2002; Koehn & Mackenzie, 2004).

The number of species introduced worldwide has more than doubled (Gozlan, 2008) compared with estimates nearly three decades ago (Williamson & Fitter, 1996) due to a significant increase in global trade and human mobility (Sala et al., 2000; Gozlan, 2008).

Deliberate fish introductions in freshwater ecosystems for commercial, recreational fishing and biological control are widespread; for example approximately 80% of the alpine lakes in the western United States have been stocked with introduced fish (Bahls, 1992). In many areas, lakes and streams are continuously re-stocked to maintain populations for example *Limnothrissa miodon* (Kapenta) in Lake Kariba, Zimbabwe (Ndebele-Murisa et al., 2011).

Although these fisheries generate enormous income, fish introductions are always likely to present an ecological risk if the species integrate successfully into the ecosystem (Gozlan & Newton, 2009). This is achieved through fast dispersal mechanisms that create highly efficient competition for endemic species, predation or habitat alteration (Allan & Flecker, 1993; Schindler, 2001). Examples include the crayfish plague in Europe (Nelleman & Corcoran, 2010); salmonids in Southern Hemisphere lakes (Rahel, 2002) and the extinction of approximately 200 endemic cichlid species within a few decades in East Africa due to the introduction of the (*Lates niloticus*) (Nile perch) and several introduced Tilapia species (Ogutu-Ohwayo, 1990; Witte et al., 1992).

On the other hand, many species are introduced to and spread throughout freshwater ecosystems accidentally for example, through attachment to boats or transported in ballast or bilge water. *Dreissena polymorpha* (zebra mussel), which is native to Europe, was accidentally introduced to the Great Lakes in 1986 through ballast water (Welcomme, 1979). Aquaculture installations have led to diffusion along water courses and accidents from contaminants within batches of other fish that are being deliberately imported or released are common incidents for example, the cyprinid, *Pseudorasbora parva* (topmouth gudgeon), which was initially discovered in Europe in an aquaculture unit in Romania in 1961. It was introduced as a contaminant of a consignment of Chinese carps and is prominent throughout eastern, central, and western Europe (Holcik, 2003; Gozlan, Pinder & Shelly, 2002). The use of live finfish as bait has also led to accidental introductions for example the enrichment of Irish cyprinid fauna by anglers targeting *Esox lucius* L. (pike) (Caffrey et al., 2008) and *Gymnocephalus cernuus* (ruffe) in parts of northern England (Drake, 2005).

One way to improve conservation of freshwater biodiversity is to ensure that the risks of fish introductions on freshwater ecosystems and species are adequately and explicitly assessed prior to introduction (McDowall 1990; Pearsons & Hopley, 1999). Efforts towards this goal are evident in New Zealand. Fish introductions have taken place in New Zealand

since the 1860s, resulting in the establishment of 21 freshwater fish species (Dean, 2003). However, to manage these introductions as well as conserve freshwater ecosystems, any subsequent introduction of aquatic species to new habitats presently require the approval of the Minister of Conservation under the Conservation Act 1987 (Rowe & Graynoth, 2002). The introduction of fish and fish eggs to sports fish or game bird habitats requires the approval of the local fish and game council under the Freshwater Fisheries Regulations 1983 (Dean, 2003). The Biosecurity Act 1993 and Hazardous Substances and New Organisms Act 1996 contain additional tools to assist with the management of new incursions of introduced species (Dean, 2003).

In order to ascertain management direction of freshwater ecosystems in New Zealand, risk assessments have been carried out for some of the species prior to introductions, or upon detection of illegal releases. Some assessments have resulted in decisions not to liberate or retain some species in freshwater ecosystems for example *Ictalurus punctatus* (channel catfish), *Micropterus salmoides* (largemouth bass) and *Cherax tenuimanus* (marron crayfish). *Cyprinus carpio* (Koi carp), which were introduced as ornamental fish, are currently designated as pest fish (Freshwater Fisheries Act New Zealand, 1982) and unwanted (Biosecurity Act New Zealand, 1983) however; they were recently discovered in North Island ponds (Northland Regional Council, 2012). *Ctenopharyngodon idella* (grass carp), on the other hand, are increasingly requested for weed control in small ponds and lakes. *Gambusia affinis* (*Gambusia*) have recently been identified as a problem in New Zealand and declared ‘unwanted organisms’ under the Biosecurity Act 1983 but continue to be released into new waters for mosquito control (Rowe & Graynoth, 2002).

Introductions and transfers of native fish into lakes have also created problems for conservation and management. For example, smelt were introduced to many lakes to provide a forage fish for trout (salmonidae), but have reduced *Galaxias brevipinnis* (kaoro) stocks (Rowe, 1990). Elvers are being increasingly stocked into lakes and reservoirs to provide commercial fisheries, but may affect native fish such as *Gobiomorphus cortidianus* (common bullies) and *Galaxias gracilis* (dwarf inanga) (Rowe & Chisnall 1995; Rowe, 1994). The issue for lake users and managers alike is whether the potential benefits of such introductions and transfers outweigh the impacts.

Salmo trutta (brown trout), *Oncorhynchus mykiss* (rainbow trout), *Salvelinus fontinalis* (brook trout), *Salvelinus namaycush* (lake trout), *Salmo salar* (Atlantic salmon), *Oncorhynchus tshawytscha* (Chinook or quinnat salmon), and *Oncorhynchus nerka* (sockeye salmon) carry an important economic value in New Zealand however; they have been implicated in the decline of endemic fish through competition and predation. These impacts are thought to have resulted in the fragmentation of some native fish populations (McDowall, 2010; Townsend & Crowl 1991). These fish species together with *Perca fluviatilis* (perch), *Tinca tinca* (tench) and *Scardinius erythrophthalmus* (rudd) (in Auckland-Waikato only) are managed as sports fish (Rowe & Graynoth, 2002).

To date research on these introduced species in New Zealand in managed and natural ecosystems has focussed on improving appropriate techniques to conserve and restore endemic species (e.g. Allibone et al., 2010; McDowall, 2006; Dean, 2003). In spite of the measure of success brought about through research, there are gaps pertaining to the exact mechanisms in which introduced fish species employ to impact receiving ecosystems. This knowledge is relevant in order to develop controls that target specific stages in their life histories to enhance management within the ecosystem. This raises an awareness of the need for basic research, particularly population biology, as a foundation for the study of introduced species.

1.3 *Perca fluviatilis* (perch)

Perca fluviatilis, commonly known as perch, is a widespread species of predatory freshwater fish which has been introduced to a number of countries around the world as a sport fish (Global Invasive Species Database, 2012) (Figure 1). The natural range is throughout most of Europe and Asia with a reputation of having a distinct flavour in a market that prefers it over other carnivorous fish (Rougeot & Toner, 2008). *Perca fluviatilis* was introduced to New Zealand from an Australian Tasmanian stock in 1868 (McDowall, 2010). It belongs to the family Percidae, known for their aesthetic values, which consist of around 60 freshwater fish species that occur naturally in fresh and brackish temperate waters throughout the Northern Hemisphere (McDowall, 1990).

Research on this introduced species in New Zealand remains limited to a handful of studies on growth rates, feeding behaviour (Sabetian et al, 2014; Jellyman, 1980; Griffiths, 1976; Duncan 1967) and reproductive traits (Sabetian et al., 2014; Jellyman, 1980). In contrast, there is a substantial body of knowledge on *Perca fluviatilis* biology and ecology in Europe, with studies having been conducted into *Perca fluviatilis* diet (e.g. Craig, 1978; Mehner, Dörner & Schultz, 1998; Ceccuzzi, Terova, Brambilla, Antonini & Saroglia, 2011), habitat use (e.g. Rask, 1983; Bean & Winfield, 1995; Gillet & Dubois, 2007), predation effects (e.g. Tonn *et al.*, 1992; Heibo & Magnhagen, 2005) and competition (e.g. Persson & Greenberg 1990; Tolonen, Lappalainen & Pulliainen, 2003). Coupled with this are extensive research into *Perca fluviatilis* population size-structure, and population dynamics (e.g. Negri, 1999; Craig, 2000; Heibo & Vollestad, 2002). From this body of knowledge a general description of this species can be made.



Figure 1 *Perca fluviatilis*

The physical characteristics of *Perca fluviatilis* include a slightly deep body, rough edged scales and a defined dorsal hump to the rear of the head (Pagad, 2010). Its upper body ranges in colour from grey-green to green-yellow on the abdomen. There are dark vertical bands across the sides and a distinct blotch at the rear of the first dorsal fin. The anal, pectoral and pelvic fins are either orange-red or bright red or leading to the common name redfin perch. It varies in size among water bodies. In Europe, the maximum recorded length is 600mm (Kottelat, 1998); maximum recorded weight of 4,750g (Berg, 1965) and a maximum reported age of 22 years (Beverton & Holt, 1959). In comparison, New Zealand *Perca*

fluviatilis are much smaller with average size range of 200 – 350 mm (Froese & Pauly, 2014; McDowall, 1990), 1000 – 2000g weight and 8 years maximum recorded age (Jellyman, 1980).

Perca fluviatilis is a carnivorous fish that undergoes three major shifts in diet and habitat use during development (Heibo, Magnhagen & Vollestad, 2005; Persson, 1988). Larval perch (5–30 mm total length) are pelagic zooplankton feeders, then at intermediate sizes (30–80 mm total length) shift to feeding on benthic macro invertebrates (Persson, 1988; Heibo et al., 2005; Froese & Pauly, 2010). Individuals over 130mm total length are mainly piscivorous (Craig 1978; Le Cren 1987; Persson 1988). Diets of piscivorous *Perca fluviatilis* in New Zealand are predominantly native fish fauna (Duncan 1967; Griffiths 1976), although juvenile *Perca fluviatilis* encountered by the piscivorous adults are vulnerable to predation.

Cannibalistic adult *Perca fluviatilis* play an important role in structuring fish populations (Claessen, de Roos & Persson, 2000). When cannibalism occurs, juvenile recruitment is limited by a small number of adult fish resulting in a population dominated by large size classes (Treasurer, 1993). Although cannibalism largely affects the survival of *Perca fluviatilis* fry, there are implications that it is encountered at an early onset across all age groups (Thorpe, 1977). This indicates that this species is an opportunistic feeder that utilizes all available prey (Krol et al., 2013; Thorpe, 1977). Feeding behaviour is diurnal mainly at sunrise and sunset (Morgan et al., 2002; Jellyman, 1980).

Perca fluviatilis prefers slow-flowing sections of rivers that are characterized by an abundance of freshwater vegetation (Huet, 1954; Thorpe, 1977). In lakes, *Perca fluviatilis* prefers mesotrophic conditions up to 30m depth however; there is an abundance of this species in oligotrophic salmonid waters, dystrophic lakes (Rask, 1983) and in the optimal range of bream lakes (Bartley, 2006). Throughout all water systems, *Perca fluviatilis* occupies open waters in summer and ranges down to the thermocline but in winter this activity is minimal (Thorpe, 1977). It is agreed however, that behaviour in water systems is diversified depending on the characteristic of the habitat (Duncan, 1976; Jellyman, 1980; Negri, 1999).

While individuals on average reach maturity in 2–3 years, the onset of reproduction for males and females is often encountered at the end of the first and second years respectively (McDowall, 2000). The average length of perch at maturity can be environment-dependant, for example, in food deficient or densely populated environments length at first

maturity has been estimated at a total length of 120mm (Thorpe, 1977). Perch generally thrive in a temperature range of 4-31°C with an optimum of 22°C and a pH range of 7.0-7.5 (Froese & Pauly, 2014). Spawning occurs in spring after a period of conditioning through winter (Winfield, Fletcher & James, 2010). Externally fertilized eggs grouped in long white ribbons (Figure 2), containing approximately 200,000 eggs and up to 1m long, are laid over submerged aquatic debris with no subsequent parental care (Winfield et al, 2010). Hatching occurs after about a week and the young form shoals for a time, before becoming more solitary as they mature (McDowall, 2000).



Figure 2 Egg ribbons of *Perca fluviatilis*

(Source: Picture taken by Logan Sands (2012), Auckland University of Technology)

Perca fluviatilis has adapted well to New Zealand's freshwater environment, possessing high fecundity and flexibility in behaviour and habitat requirements (Hutchison & Armstrong, 1993). While its introduction to New Zealand was deliberate, local natural dispersion and illegal translocation have resulted in a sporadic, widespread distribution of this species. It is presently found throughout both the North and South Islands with centres of high abundance in Northland, Auckland, Hawke's Bay, Taranaki, Wellington, Hokitika, central Canterbury, Otago and Southland (McDowall, 2000). The freshwater fish fauna in

New Zealand is characterized by the absence of a principal piscivore (Jellyman, 1980; Sabetian et al., 2014). As a result, introduced piscivores such as *Perca fluviatilis* have the potential to significantly alter native freshwater communities in the absence of competition (Closs et al., 2003).

Although *Perca fluviatilis* is listed as a sport fish in the First Schedule of the Freshwater Fisheries Regulations 1983 in New Zealand, it has not been established as a popular game fish like trout or salmon (Sabetian et al., 2014). It is viewed diversely as a coarse fish, valuable food fish or a pest fish with little or no commercial value (Jellyman, 1980). As an introduced species, *Perca fluviatilis* is managed by regional councils, Department of Conservation and Fish & Game New Zealand with efforts on containment (Dean, 2003). Studies in other regions in the world where introduction has taken place have implicated *Perca fluviatilis* in the reduction and extinction of freshwater biodiversity. For example, predation of *Perca fluviatilis* on *Galexiella munda* (mud minnow) and *Cherax cainii* (smooth marron) has led to extinction and reduction in recruitment respectively in Western Australia (NSW DPI, 2012); extinction of endemic *Asipiorhynchus laticeps* in China (Bartley, 2006) and as a vector for Epizootic Haematopoietic Necrosis (NSW DP1, 2012). Although this virus has not been discovered in New Zealand, a study by Closs, Ludgate and Goldsmith (2003) emphasized the need to control *Perca fluviatilis* due to its potential to significantly alter endemic fish populations such as *Gobiomorphus cotidianus* (common bullies).

The feeding behaviour of *Perca fluviatilis* has also been implicated in New Zealand to a decline in water clarity and this was observed in lakes with a notable abundance of *Perca fluviatilis* (Rowe, 2007). Based on this, the Auckland Council (former Auckland Regional Council) are involved in the control and removal of *Perca fluviatilis* from selected water bodies and their catchments of high conservation value according to the Auckland Regional Pest Management Strategy 2007 (Sabetian et al., 2014). Only in the eleven selected water bodies is *Perca fluviatilis* considered a pest fish because its status as a sport fish remains throughout the rest of the Auckland region and require a sport license from Fish & Game New Zealand.

The present body of knowledge on *Perca fluviatilis* in New Zealand is not substantial to provide evidence of effects of this species on either freshwater ecosystems or endemic fish

species. Despite the steady increase of interest in coarse fishing in New Zealand, containment of *Perca fluviatilis* is imperative until more is known about its life history and biology in the different freshwater ecosystems of New Zealand (Rowe & Graynoth, 2002). A study conducted by Heibo, Magnhagen and Vøllestad in 2005 in Europe revealed that *Perca fluviatilis* show plastic life-history traits according to different spatial and latitudinal gradients. Given that the distribution of *Perca fluviatilis* in New Zealand is across different latitudinal gradients, the study by Jellyman (1980) on life history traits of *Perca fluviatilis* in Lake Pounui may not be applicable to other populations due to this plasticity. This creates the need to comparatively investigate demographic information of this species. Biological data on this species is important for management in order to evaluate if the potential environment risks presented by this species outweighs any benefits to give way to eradication for the conservation of endemic species. The goal of this study was to fill existing gaps by providing fundamental information on the mechanisms responsible for the success of *Perca fluviatilis* in New Zealand through comparison of different stocks.

Aims

The aim of this study was to enhance the understanding of *Perca fluviatilis* ecology and biology in New Zealand through application of more accurate methods of estimating age and analysis of reproductive parameters. The specific objectives were to conduct a long-term comparative analysis of *Perca fluviatilis* age and growth, reproductive biology, and abundance and diet between two lakes in Auckland New Zealand; Lake Rototoa (latitude 36°31'S and longitude 174°14'E) and Warkworth Quarry Lake (latitude 36°24'S and longitude 174°40'E).

The following chapters have been written in sequence in order to achieve the said objectives. In chapter two *Perca fluviatilis* age and growth are examined across 12 months from May 2013 to April 2014. Chapter three covers the reproductive parameters of *Perca fluviatilis* within these lakes while chapter four examines the diet and abundance of *Perca fluviatilis*. In Chapter Five the major findings from previous chapters are brought together to discuss the specific objectives of this study and its contribution to the understanding of perch population dynamics of *Perca fluviatilis* in New Zealand.

Chapter 2 Age and Growth Structures of *Perca fluviatilis* in Two New Zealand Lakes

2.1 Introduction

Information about fish age and growth is fundamental to understanding their biology and population dynamics (Jakubaviciute et al., 2011). Age structure of fish populations vary due to fluctuations in abundance of cohorts produced in individual years (Strickland, 1985). This abundance of annual fish cohorts is termed ‘year-class strength’ (Stauton-Smith et al., 2004). It was generally believed that year-class strength in fish depended mainly on the abundance of the adult spawning population (Beverton & Lee, 1965). However, later theories suggest that year-class strength could be controlled by survivorship at very early life stages, rather than by growth and survival patterns after maturity (Anderson & Akenhead, 1981). Thus, the strength of a year- class is established during the first few months of life but its effects persist throughout the life span of the cohort (Strickland, 1985).

Studies in Europe reveal that the year-class strength in *Perca fluviatilis* varies between stocks in different locations (e.g. LeCren, 1955; Polat, Bostanci & Yilmaz, 2000). McCormack (1965) added that along with variability between year-class strength, strong year classes become an exclusive year class as growth progresses. In England, on the other hand, year-class instability with poor age class representation was observed (Goldspink & Goodwin, 1979). While *P. fluviatilis* populations in some Norwegian lakes indicated intervals of several years between successful year classes (Heyardahl & Smith, 1971), other stocks from the same region showed neither strong nor weak year classes (Heibo, 2003). This leads to the conclusion that accurate determination of age composition in *P. fluviatilis* populations is complicated by variation in year-class strength which is an attribute of recruitment (Kipling, 1976; Koonce et al. 1977; Craig & Kipling 1983; LeCren 1987; Heibo, 2003). Furthermore, the occurrence of shoals of *P. fluviatilis* stratified by age and size creates a bias when sampling for age resulting in difficulties in determining accurate age composition (Thorpe, 1977).

The exact lifespan of *P. fluviatilis* is unknown due to a wide variation of observations on maximum age. North American populations, with the exception of Canada, have been considered relatively short lived with a lifespan between 5 and 7 years (Herman, 1964).

Canadian populations have a normal span of 9 – 12 years (Muncy, 1962; Scott & Crossman, 1973). European populations have a wider age range. For example, *P. fluviatilis* in Poland have a life span of 13 years (Backiel, 1971) and 18 years has been reported from Czech Republic (Vostradovsky, 1962) and Sweden (Neuman, 1974). The maximum reported age to date from Europe is 22 years in wild populations (Beverton & Holt, 1959) and 27 – 28 years from pond populations (Alm, 1952). Maximum age has also been reported to vary between dystrophic lakes (15+ years) and oligotrophic lakes (< 15+ years) in Europe (Alm, 1952; Thorpe, 1977). Maximum age in *P. fluviatilis* has been attributed to predation pressure, with long lifespan related to low predation pressure (Alm, 1959). Also, females have been observed to have a longer life span compared to males (e.g. Eschmeyer 1937, 1938; Hile & Jobes 1942; Carlander, 1950).

As with estimation of age composition of *P. fluviatilis*, size distribution is also strongly influenced by type of gear used in sampling, differential distribution of sexes within the population as well as the formation of stratified shoals (Thorpe, 1977). The maximum size of *P. fluviatilis* recorded in North America with respect to weight and standard length is 1,910 g (Scott & Grossman, 1973) and 530mm (McPhail & Lindsey, 1970), respectively. On the other hand, the maximum recorded weight of European *P. fluviatilis* ranges from 3,500g – 4,750g with standard length of 510mm (Berg, 1965; Kottelat & Freyhof, 2007). The maximum standard length recorded from Poland is a fish of 630mm with a weight of 2,410g (Leopold, 1973). Variation in size distribution indicates that factors affecting size are also important for growth in *P. fluviatilis* (Heibo & Magnhagen, 2005).

Growth is a measure of change in size of either the whole body or parts of the body while growth rate is a measure of size as a function of time (Coble, 1966). The growth of *P. fluviatilis* in Europe differs within populations and among populations (Heibo & Vøllestad, 2002). *P. fluviatilis* growth depends on several factors including water temperature (LeCren, 1958; Coble, 1966; Neuman, 1974; Sandstrom et al, 1995; Cecuzzi et al, 2011); population density (Alm, 1946; Le Cren, 1958; Mann, 1978; Rask, 1983; Cecuzzi et al, 2011); availability and quality of food (Craig, 1978; Mann, 1978; Rask, 1983; Persson & Greenberg, 1990; Cecuzzi et al, 2011) and photoperiod (Kelso, 1976). The relationship between length and weight has been reported in numerous studies throughout the natural range of *P. fluviatilis* (e.g. Carlander, 1950; Deelder, 1951; LeCren, 1958; Muncy, 1962; Berg, 1965; Honik, 1969; Thorpe, 1977). The general observation from these studies is that

there is no sex-specific difference in growth during the first 2 years of life but females subsequently grow faster than males afterwards to achieve larger ultimate size.

With the exception of a few populations (e.g. Lake Windermere population in England (Thorpe, 1977)) the growth pattern of *P. fluviatilis* can be described by the von Bertalanffy Growth formula (VBGF) which indicates a decline in growth as a fish attains maximum age (Ceccuzzi et al., 2011). The VBGF parameters include t_0 (hypothetical age at length zero), K (curvature coefficient), and L_∞ (mean asymptotic size). These will be explained in detail later. The growth of *P. fluviatilis* can be classified according to L_∞ of the VBGF as: a) very good: fish greater than 20 cm (L_∞) at 2 years old; (b) good: fish greater than 20 cm (L_∞) at 3 years old; (c) moderate: fish greater than 16 cm (L_∞) at 3 years old; (d) poor: fish less than 16 cm (L_∞) at 3 years old; and (e) very poor: all fish less than 16 cm (L_∞) (Tesch, 1955; Ceccuzzi et al., 2011). According to the VBGF parameters reported in the literature for other *P. fluviatilis* populations, the growth performance tends to increase from northern to southern localities in Europe (Craig, 1974; Lorenzoni et al., 1993; Heibo & Magnhagen, 2005; Ceccuzzi, 2007). This has been linked to a longer annual period with temperature suitable for growth at lower latitudes (Linl kken, 1988).

The age structure, size distribution and growth of *P. fluviatilis* populations in the southern hemisphere, where they are introduced, are slightly different from the above description of *P. fluviatilis* populations in the northern hemisphere. Heibo et al (2005) proved that all life history traits in *P. fluviatilis* with the exception of L_∞ are correlated with latitude due to phenotypic plasticity. Hence New Zealand *P. fluviatilis* populations, for example, should be expected to have a decreased lifespan corresponding to smaller maximum age compared to European *P. fluviatilis* populations. However, there is paucity of data on the longevity of *P. fluviatilis* populations in New Zealand, with Jellyman (1980) being the only significant study on *P. fluviatilis* to date to report a maximum age of 12 years. The same study revealed a lack of evidence of strong year classes (Jellyman, 1980) although, similar to European populations, females tend to dominate all age classes (Jellyman, 1980; Sabetian et al., 2014).

Latitudinal variation in life history traits of *P. fluviatilis* is accountable for dissimilarity in maximum size of New Zealand populations relative to European populations. As mentioned earlier, the maximum recorded size of *P. fluviatilis* in New Zealand is 3,000g

and 350mm respectively (McDowall, 1990) and these populations appear to have growth rates that are comparatively greater than European populations at equivalent age (e.g. Le Cren, 1987; Sandstrom et al. 1995; Linlökken & Holst, 1996; Heibo & Vøllestad 2002; Ceccuzzi et al. 2011). This phenomenon is a common factor for reported *P. fluviatilis* populations in the southern hemisphere and one possible reason for this is the higher water temperature regimes in this region (Duncan, 1967; Jellyman, 1980; Morgan et al., 2002; Sabetian et al., 2014). For example, *P. fluviatilis* in Lake Wainamu (New Zealand) have a higher growth rate in the first year compared to all European counterparts (Sabetian et al., 2014).

Studies on growth pattern in New Zealand have revealed that *P. fluviatilis* growth increments conform well to the VBGF model (Jellyman, 1980; Sabetian et al., 2014) against the background that growth in European populations does not always follow this model due to changes in diet with size (Le Cren, 1958; Williams, 1967; Shafi & Maitland 1971). It has been reported that L_{∞} of the VBGF model is not suited well to latitude however; the growth coefficient (k), which describes how fast a fish approaches L_{∞} , increases with decreasing latitude (Heibo et al., 2005). This has been observed in New Zealand *P. fluviatilis* (Jellyman, 1980; Sabetian et al., 2014). This information is also important in establishing the growth season for this species. European studies show that *P. fluviatilis* populations in the north grow for only 3-4 months while those in the south grow for 8 months (Petrovski, 1960; Weatherly, 1967; Lind et al, 1973; Thorpe, 1977). This seasonal growth was observed in Australian populations (Morgan et al., 2002) and is yet to be verified in New Zealand.

The above information reveals a knowledge gap in the age structure and growth patterns of *P. fluviatilis* in New Zealand. Given the plasticity of these traits with latitudinal gradient, it is imperative to compare *P. fluviatilis* populations in different locations in order to understand factors responsible for fluctuations in these traits. Furthermore, reported studies of *P. fluviatilis* populations in the southern hemisphere have relied on ageing techniques that have been demonstrated to underestimate the age of older individuals (e.g. Jellyman, 1980; Morgan et al., 2002); specifically the use of opercular bone and whole otoliths, respectively. These techniques have an impact on the resulting estimates of age structure, lifespan and growth rates (Campana, 2001). Also, growth rates of fish are directly affected by water temperature (Le Cren, 1958; Coble 1966; Neumann, 1976; Sandstrom et al, 1995; Alessio et al, 1991; Cecuzzi et al, 2011) and this currently varies over the geographical range of *P. fluviatilis* in New Zealand. Thus, the patterns reported so far by Duncan (1967), Jellyman

(1980) and Sabetian et al (2014) may not be universal for all populations in New Zealand. Consequently, a detailed synopsis of age structure and growth patterns at multiple locations is essential to enhance the current body of knowledge of this introduced species. This information is necessary before detailed studies on life history strategies and ecology of *P. fluviatilis* in New Zealand can be carried out.

2.2 Objectives

Estimates of age and growth are vital biological parameters for accurate stock assessment aimed to ensure fishery development, effective management and ecosystem conservation (Meriem, Al-Marzouqi, Al-Mamry & Al-Mazroui, 2011). Age-based estimates of growth and longevity are also fundamental for the decision making process on introduced fish (Dudgeon, 2003), for example when setting harvest levels for recreational fisheries or eradication programmes. In this study, *P. fluviatilis* were aged using sectioned otoliths as it is a precise method, particularly for older fish (Secor *et al.* 1995). The specific objectives of this chapter were to (1) establish the age and size structure of *P. fluviatilis* population from two lakes in Auckland, New Zealand and (2) ascertain the growth and longevity of the studied populations by using the obtained age and length-at-age data of individual fish and applying the Francis' reparameterized von Bertalanffy Growth Function (rVBGF) and the von Bertalanffy Growth Function (VBGF). The information generated can then be compared to reported studies as an initial step in understanding the population dynamics of *P. fluviatilis* in New Zealand.

2.3 Material and Methods

2.3.1 Study Location

This study focussed on two lakes that are part of Auckland Council's eradication programme; namely Lake Rototoa and Warkworth Quarry Lake. The choice of lakes was primarily due to their location and accessibility. Both lakes are found in the same latitude with Warkworth Quarry Lake on the North East (Figure 3 & 4) while Lake Rototoa located on the North West of Auckland (Figure 5 & 6). This study investigates the difference in life history traits between populations found in these lakes and those already documented by Jellyman (1980) and Sabetian et al (2014), while at the same time investigating inter-

population differences not attributed to latitudinal gradient. Both lakes have similar climate which is classified as Cfb according to Köppen-Geiger climate map (Rubel & Kottek, 2010). The Köppen-Geiger climate map classifies climate based on annual and monthly averages of temperature and precipitation with each letter representing a class within the system. In this instance C represents a moist mid-latitude climate with mild temperature, f distinguishes the precipitation pattern and b describes the monthly temperature characteristics. Hence, Lake Rototoa and Warkworth Quarry Lake have a warm and temperate climate with average annual temperature of 15.2°C and average annual precipitation of 1422mm.

Warkworth Lake is located in Warkworth, New Zealand as part of old cement works quarry that closed down in 1928 and was subsequently flooded (The Fishing Website, 2011). The total length of the lake is 0.73 kilometres. Although exact depth is unknown, information provided by divers reveal that it descends in shelves with the first shelf at 3m, second at 6m and third at 9m. The furthest exact depth reached to date is 25m (The Fishing Website, 2011). The fish fauna of the lake is largely exotic such as *Cyprinus carpio* (carp), *Scardinius erythrophthalmus* (rudd), *Tinca tinca* (tench) and *Perca fluviatilis* (perch) however; *Anguilla dieffenbachia* (eels) are a common occurrence as a top predator in the lake. Communities in this lake are disconnected to other water bodies due to lack of stream inflows and outflows. The surrounding dense vegetation in the shallow banks is a significant contributor of nutrients in the lake.



Figure 3 Aerial Map View of Warkworth Quarry Lake

(Source: www.flickr.com/photos/mikeymack/9872677054/)



Figure 4 Photographic view of Warkworth Quarry Lake

Lake Rototoa is an elongated dune lake which is more sizeable than Warkworth Quarry Lake. It has a large surface area of 1.6 km² and 29m depth. The lake has a catchment area of about 5.1 km² almost equally divided between native forest/scrub, exotic pine forest and pasture (Barnes & Burns 2005). It is situated between steep pastured hills on the eastern side and pine tree plantations on the sand dunes on the western side, with the native forest and scrub covering the steep western shores and the stream channel at the northern end of the lake. The lake has one small stream inflow (about 15 Ls⁻¹) plus several ephemeral streams but there are no surface outlets. Although there is no data on groundwater, it is likely that there are areas of groundwater inflow through the sand into the lake and possibly a groundwater discharge from the lake (Gibbs, 2006). Like Warkworth Quarry Lake, it has similar exotic fish species however; it differs in the large presence of *Oncorhynchus mykiss* (trout) introduced for angling purposes.

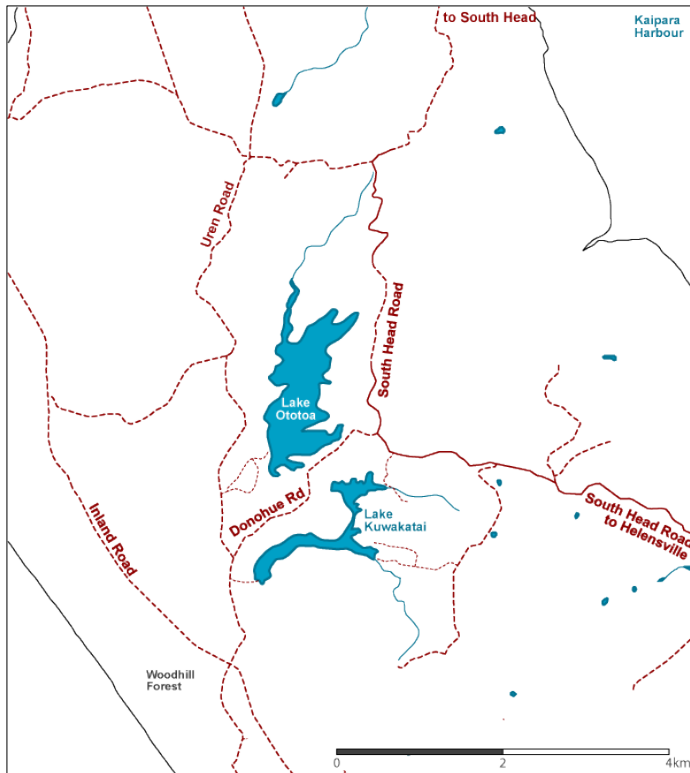


Figure 5 Map of Lake Rototoa

(Source: www.nzfishing.com/FishingWaters/AucklandWaikato/AWMaps/OtotoaMap.htm)



Figure 6 Photographic view of Lake Rototoa

2.3.2 Sampling

The two locations were sampled monthly from May 2013 to April 2014 using gill nets positioned perpendicular to the shoreline in the littoral margins. In an endeavour to prevent this method from being selective regarding fish size, three different mesh sizes were used (14, 25, 43mm). This activity took place in two consecutive days in which the nets were laid out in the late afternoon of the first day. These were left overnight and collected the next day before midday. This strategy took advantage of the feeding times of adult perch, which have been observed to be between afternoon and dusk. As soon as the fish were recovered from the net they were placed on ice and taken to the laboratory for same day processing to prevent decomposition of samples.

Measurement of water quality characteristics was not carried out directly. Due to the collaborative nature of this study, data on pH, dissolved oxygen and water temperature were obtained from the Auckland Council which regularly monitors the condition of the lakes.

2.3.3 Age and Growth Estimation

Otoliths were used for age analysis. Otoliths are calcium carbonate nodules found in the posterior and ventral regions of the cranial cavity surrounded by the otic bones that form the otic capsule. Every fish possesses three pairs of otoliths whose function include auditory reception and vestibular regulation. As a fish grows, these otoliths form periodic translucent and opaque growth rings due to the accumulation of calcium carbonate and the protein otolin. The decision to use sagittal otoliths for ageing in this study was based on their size, being the largest of the three pairs, and because they have the best defined annual rings.

To remove the sagittal otoliths, a cut was made with a knife horizontally across the top of the eye. This exposed the brain as it sliced through the braincase. After removal of the brain, the sagittal otoliths (Figure 7) were extracted from the otic capsules using diamond tweezers. They were then cleaned using distilled water and dried. Only one sagittal otolith from each pair was processed and the other kept as a backup. The otolith was then mounted on the edge of a microscope slide to reveal half the centrum using a mounting media called Crystalbond™. This is a type of glue that carries the advantage of being re-mountable. Using

a diamond disc cutter with grit 1200 (Figure 7), the otolith was ground down to the slide edge. For smaller otoliths, the grit size was 3000.

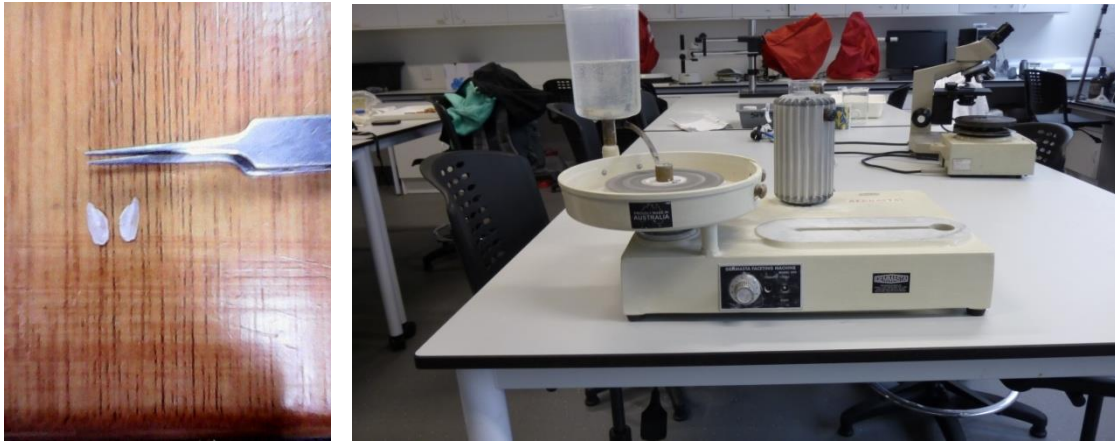


Figure 7 A pair of sagittal otoliths from *Perca fluviatilis* (left) and diamond disc cutter with grit 1200

The otolith was then removed from the glue by re-heating the slide to melt it. The cut edge of the otolith was then placed facing down on a new, labelled slide. The other end of the otolith was ground while the slide was held horizontally. During this step, the otolith was checked for readability by viewing through a transmitted white light microscope. The opaque growth rings can be counted with this microscope as they will appear dark under transmitted light (e.g. Figure 8). After grinding sufficiently, the slide was covered with the mounting glue to protect the otolith, fill in any scratches caused by the grinding and increase the optical quality of each sample. The birth date of all *P.fluviatilis* samples was set as 1 September based on the current spawning season of *P.fluviatilis* in New Zealand (Jellyman, 1980; Sabetian et al., 2014).

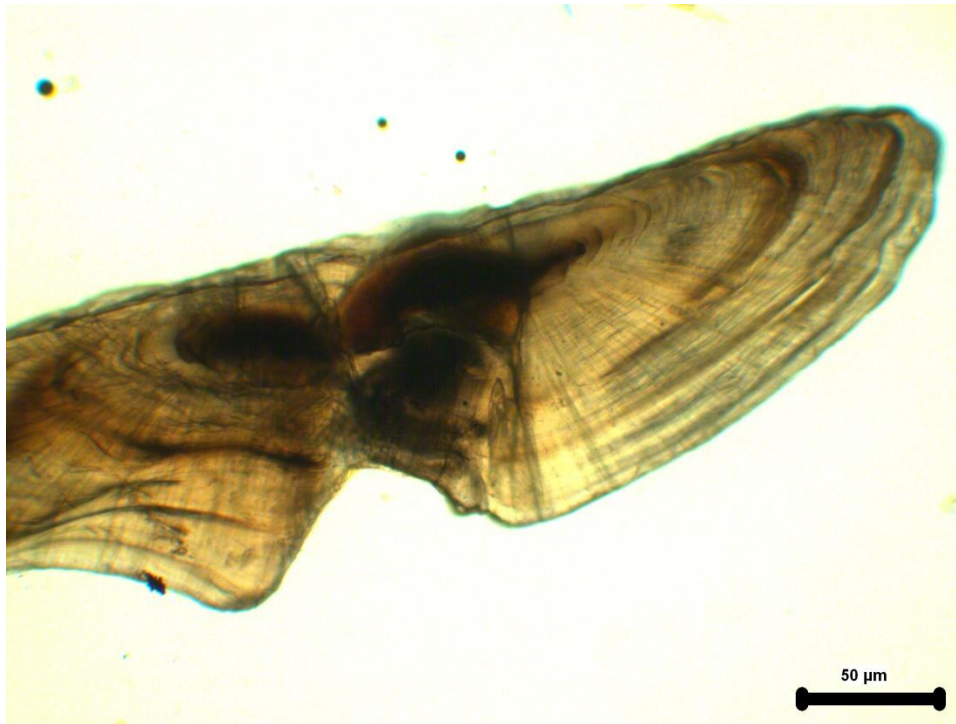


Figure 8 A sectioned sagittal otolith from *Perca fluviatilis* showing 2 annual rings

Before any extraction (otolith and gonads), individual fish were placed on a dissecting board and three straight length measurements taken with the aid of a tape measure graduated in millimetres. The three length measurements were:

- a) Total length (TL) which is the greatest length of the fish from the anterior-most extremity to the end of the tail fin.
- b) Standard length (SL) which is the measured from the anterior-most extremity of the fish to the posterior end of the last vertebra that excludes the entire caudal fin.
- c) Fork length (FL) which is measured from the anterior-most extremity of the fish to the tip of the median rays of the caudal fin.

Several of the fish caught were noted to have frayed or shortened tail fins as a result of abrasion with the netting. Consequently, SL was used in all of the analysis. Each fish was weighed using a digital scale for total weight and gutted weight. Periodically, fish were weighed twice to check for accuracy. Weights were recorded in grams.

Growth curves were then plotted from the information derived from the processes mentioned above to determine the relationship between size and age. This study utilized both

the von Bertalanffy Growth Function (VBGF) and the Francis' reparameterized von Bertalanffy Growth Function (rVBGF). The von Bertalanffy growth equation is $L_t = L_\infty (1 - e^{-K(t-t_0)})$, where L_t is the length at age t (years), L_∞ is the asymptotic length, K is the growth coefficient and t_0 is the hypothetical age at which members of the population would have the length zero (Kimura, 1980). VBGF was used for size-at-age data to compare differences in growth with other reported populations of perch.

rVBGF was used to provide parameter estimates for expected average body size at three ages of tau, omega, and nu. This is an improvement over the standard VBGF in that the results are effectively applicable for comparison between two populations or sexes which is relevant for this study. Tau and nu are randomly selected ages from the sample with omega being the mean of tau and nu (Francis, 1988). Tau, omega and nu used in this study were 1, 3 and 5 years, similar to Sabetian et al (2014) with the aim of comparing the two studies.

To avoid errors resulting from growth model parameter estimates, the growth functions used in this study were fitted by constraining size-at-age zero to mean size-at-hatching. According to Sabetian et al (2014) mean size-at-hatching was 6.8 mm (± 0.2 S.E.) in total length for *P. fluviatilis*. This was calculated from 20 newly hatched individuals in captivity.

A likelihood ratio tests (LRT) was used to compare growth between sampled perch from the two lakes, and between males and females in both lakes (Kimura, 1980; Cerrato, 1990; Sabetian et al., 2014). The null hypothesis for this is that there is no difference in growth between populations and was rejected at $\alpha = 0.05$, with degrees of freedom defined as the number of parameters being constrained.

2.4 Results

2.4.1 Environmental variables

New Zealand is known to have temperate climate, but due to being a cluster of Islands is heavily influenced by variable oceanic weather. The summer months in New Zealand are December to February; autumn from March to May; winter occurs from June to August while spring is from September to November.

In 2013/2014 there was significant rainfall in Warkworth Quarry Lake with an average annual temperature of 15.3°C and average annual rainfall of 1517mm. The driest month was November with an average of 100mm precipitation and most precipitation occurred in June with an average of 180mm. The warmest month was February with a mean temperature of 19.8°C while the coldest month on record was July with an average temperature of 10.9°C. The average variance in temperature was 8.9°C throughout the year.

Lake Rototoa experienced similar weather patterns with an average annual temperature of 15.2°C and average annual rainfall of 1298mm. The driest month was February with an average precipitation of 78mm while the month with highest recorded precipitation was June with an average of 148mm. February was also the warmest month with mean temperature of 19.8°C. The lowest average temperature was recorded in July at 10.7°C and temperature variation throughout the year was 9.1°C.

2.4.2 Age and Growth Estimation

In Warkworth Quarry Lake, a total of 243 specimens were caught over 12 months, however only 206 were used for analysis as the 37 of them were too damaged in the gillnets. Fewer fish were obtained from Lake Rototoa, with a total of 112 specimens and 99 used for analysis.

General population structure and life span

The population sample from Warkworth Quarry Lake contained 94 males and 112 females. Age, determined from sectioned sagittal otoliths (e.g. Figure 8), was distributed among 7 age classes with a positive skew (Figure 9). The rate at which increments were

formed in the otoliths of *P. fluviatilis* was previously assessed through an analysis of marginal increments (Morgan et al., 2002) however in this study, this was further validated through analysis of otolith weight and age of fish. There was a strong relationship between otolith weight and age for the 206 samples with an R^2 value of 0.75 (Table 2.1) confirming the validity of the assumption that otolith growth is related to age of *P. fluviatilis*. Based on the approximate birth date of New Zealand *P. fluviatilis* set at 1 September (Jellyman, 1980; Sabetian et al., 2014), all ages in this study were expressed as 0+, 1+, 2+ etc.

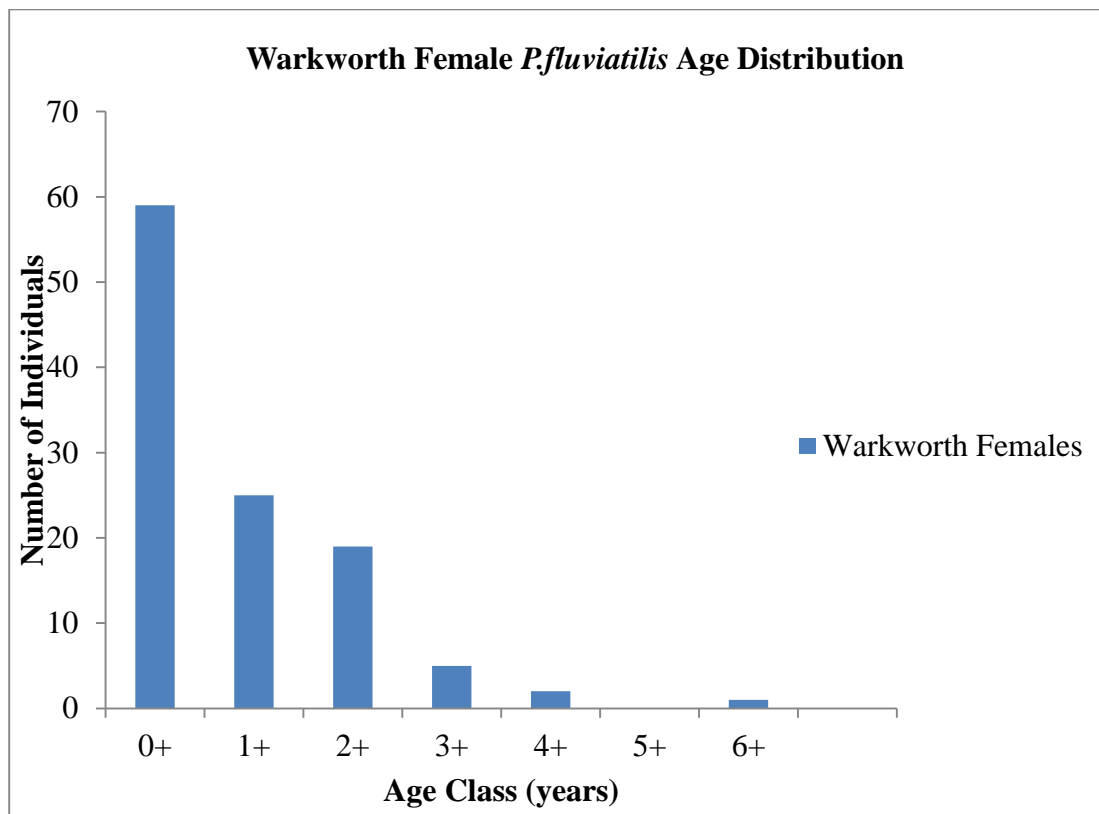


Figure 9 Age distribution of female *Perca fluviatilis* in Warkworth Quarry Lake

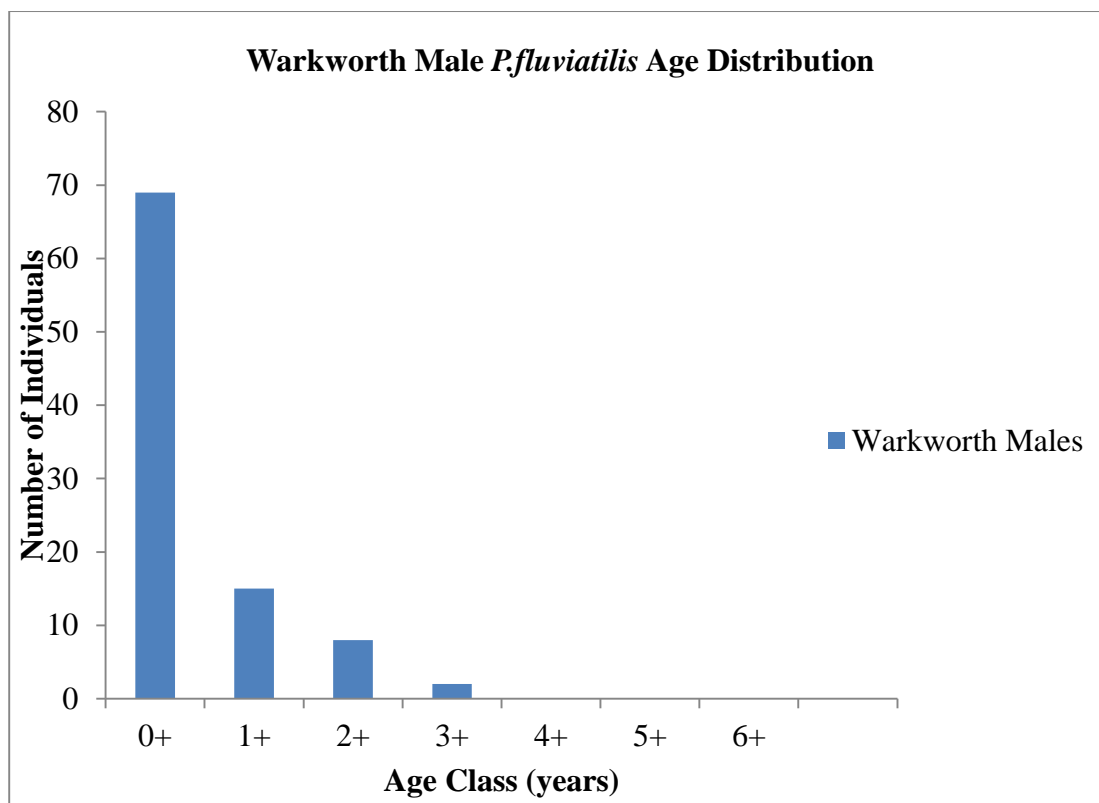


Figure 10 Age distribution of male *Perca fluviatilis* in Warkworth Quarry Lake

As shown in Figure 8 and Figure 9 age distribution analysis shows most of the specimens to be in the 0+ and 1+ age class and the amount of fish caught decreased progressively over the older age classes. The maximum observed age was 6+ (Figure 13). Smaller otoliths analyzed for daily growth rings showed that the expected spring period of spawning (Jellyman, 1980) to be true. A sample processed and analyzed for daily growth rings from a sagittal otolith had 87 rings, placing the birth date of this 0+ fish at 10 September, 2013. The standard length (SL) of *P.fluviatilis* ranged from 90mm to 239mm with an average of 132.6mm SL for all individuals; 90mm – 239mm SL (average 139.5mm SL) for females and 97mm - 221mm SL (average 123.9mm SL) for males (Figure 14). Mean total body weight was 36.9g for all individuals caught in this lake; 43.2g and 29.3g for females and males, respectively.

In Lake Rototoa, a total of 22 males and 77 females were distributed among 8 age classes (Figure 13) with a positive skew. The 99 samples from this population also showed a strong relationship between otolith weight and age with an R^2 value of 0.79 (Table 1). Most of the specimens were in the 1+ and 2+ age classes (Figure 11 & Figure 12) and the amount

of fish caught also decreased over older age classes as in Warkworth Quarry Lake. However, there were notable gaps in ages 5+ and 6+. The maximum observed age was 7+ (Figure 13). A sample analyzed for daily growth rings from a sagittal otolith revealed 184 rings and the birth date of this specimen was recorded as 29 November, 2012. The total length of *P. fluviatilis* ranged from 99mm - 381mm SL with an average of 191.1mm for all individuals; 102mm – 381mm SL (average 199.1mm SL) for females and 99mm - 218mm SL (average 159.5 mm SL) for males (Figure 14). Mean total body weight was 152.1g for all individuals caught in this lake; 170.7g and 80.3g for females and males, respectively.

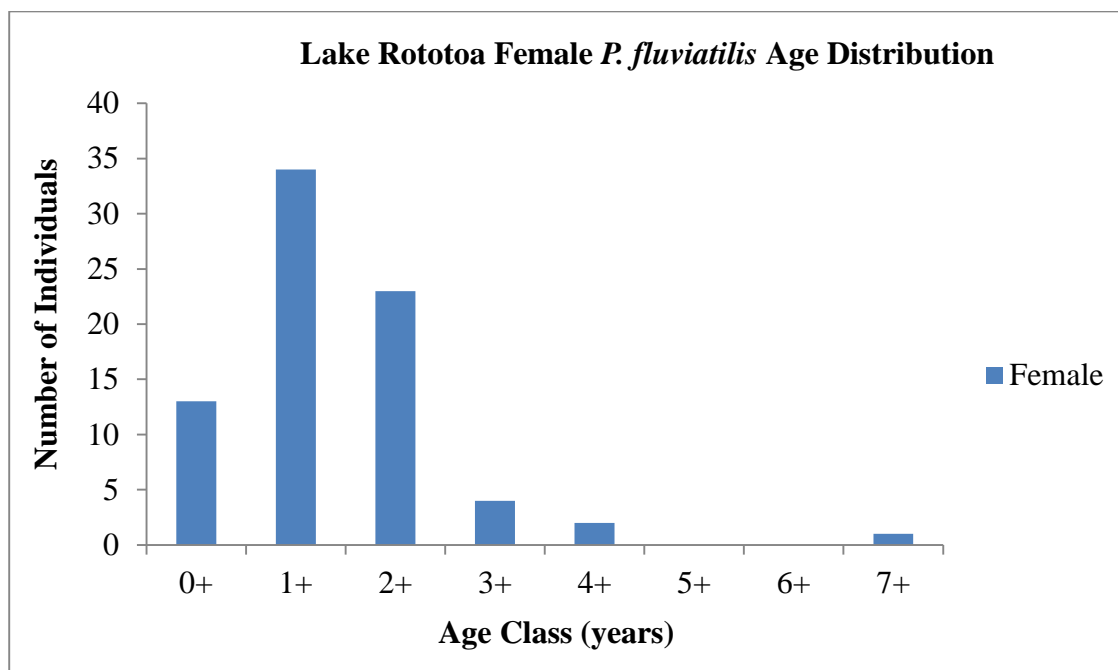


Figure 11 Age distribution of female *Perca fluviatilis* in Lake Rototoa

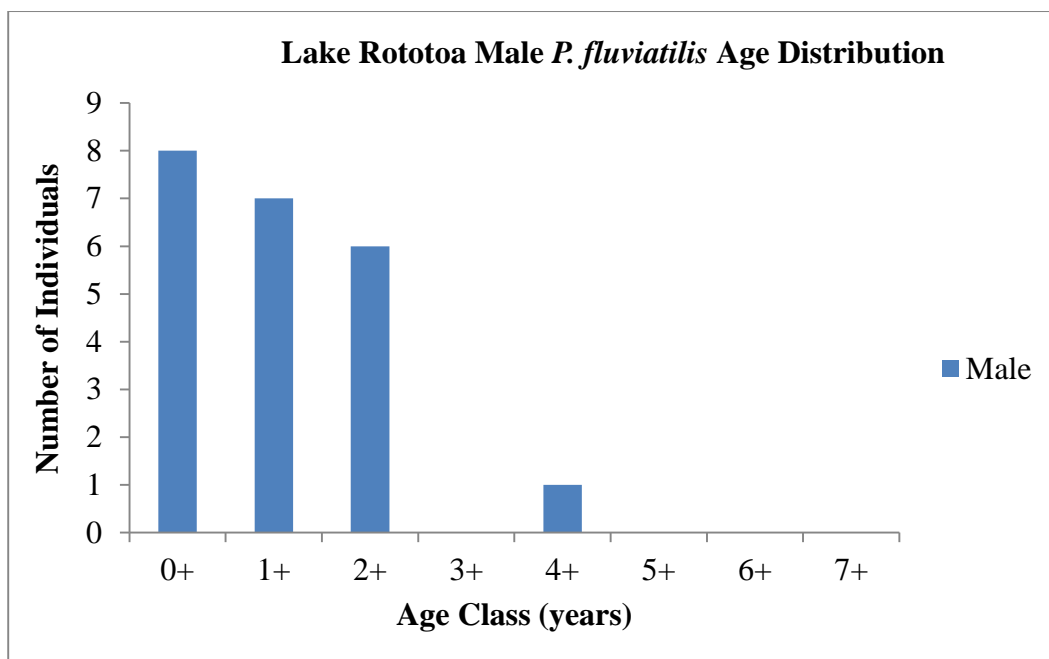


Figure 12 Age distribution of male *Perca fluviatilis* in Lake Rototoa

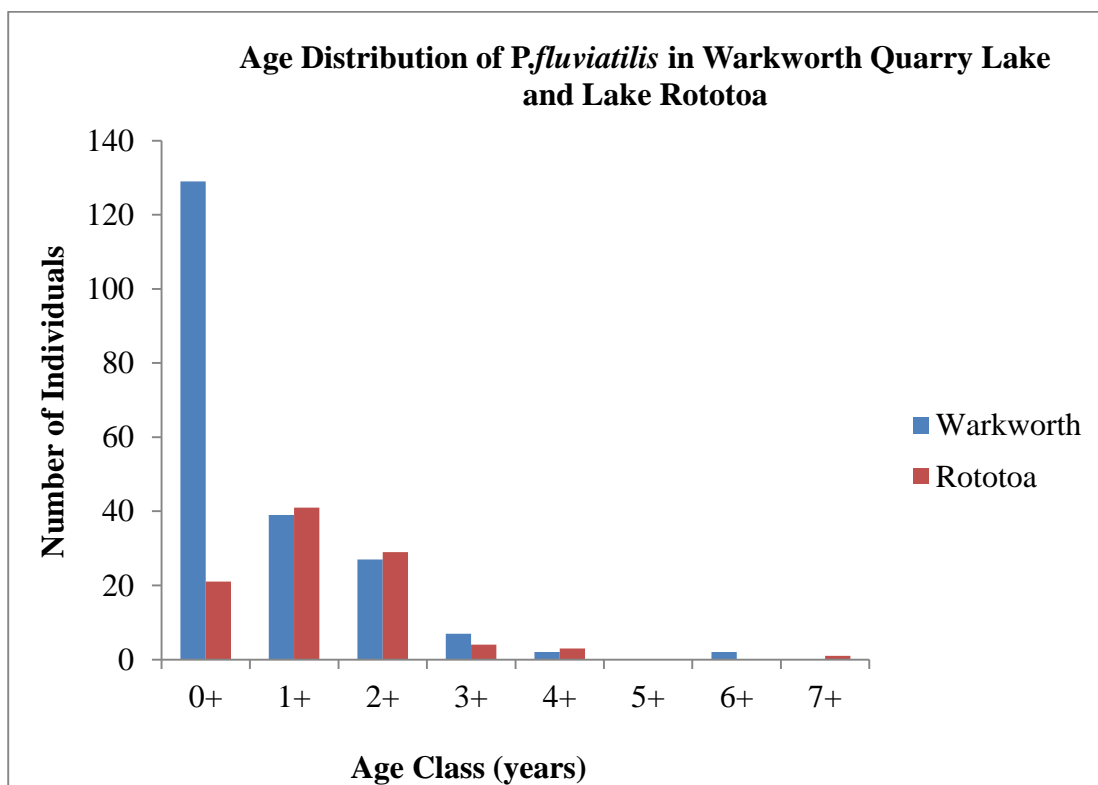


Figure 13 Age distribution of *Perca fluviatilis* in Warkworth Quarry Lake and Lake Rototoa

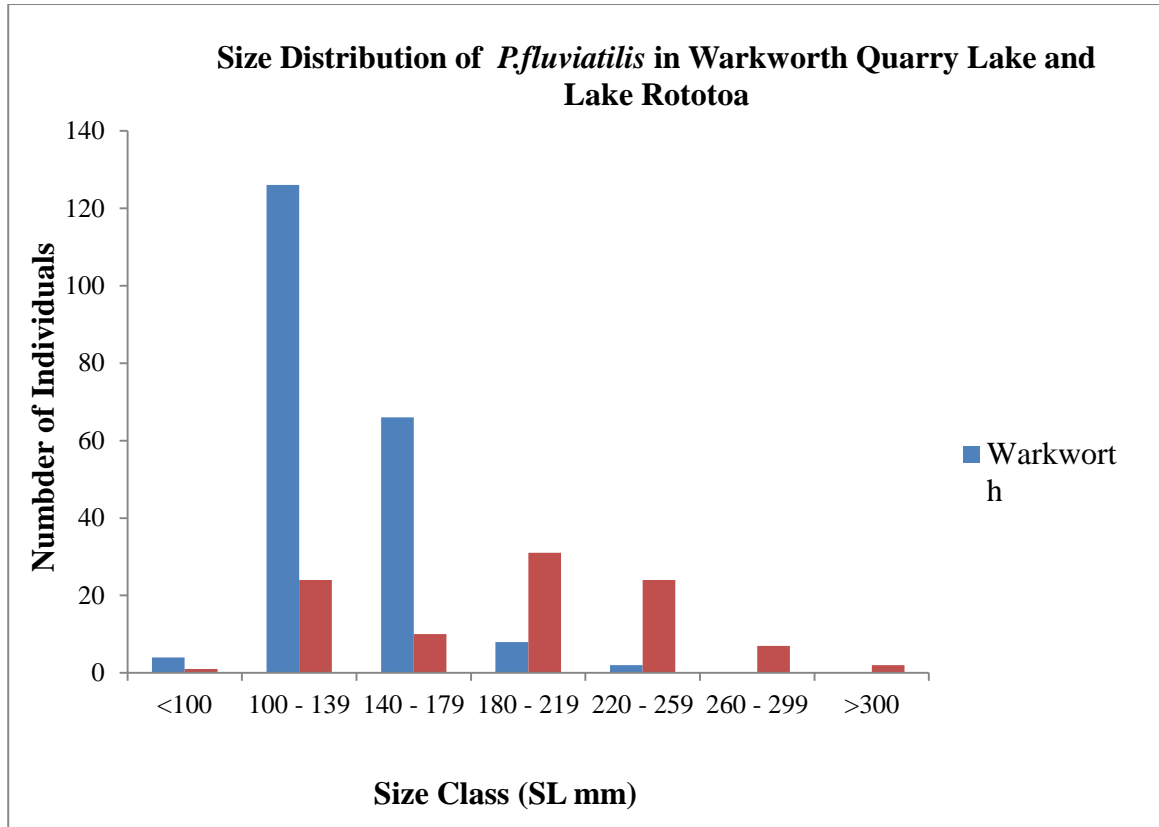


Figure 14 Size distributions of *Perca fluviatilis* in Warkworth Quarry Lake and Lake Rototoa

The length-to-weight relationships in Warkworth Quarry Lake were $W = 0.93 \times L^{0.0224}$ for the population ($r^2 = 0.89$); $W = 1.42 \times L^{0.0236}$ for males ($r^2 = 0.80$) and $W = 1.87 \times L^{0.0211}$ ($r^2 = 0.92$) for females (Figure 2.10). The b value (2.8214) for this population showed an isometric length-weight growth (Table 2.1). On the other hand, the length-to-weight relationships in Lake Rototoa were $W = 3.26 \times L^{0.018}$ for the population ($r^2 = 0.936$); $W = 3.23 \times L^{0.0181}$ for males ($r^2 = 0.83$) and $W = 3.07 \times L^{0.0179}$ ($r^2 = 0.95$) for females (Figure 16). The b value (3.3548) for this population showed a positive allometric length-weight growth (Table 1). This b value highlights that *P. fluviatilis* individuals in Lake Rototoa were heavier compared to Warkworth individuals at equivalent lengths.

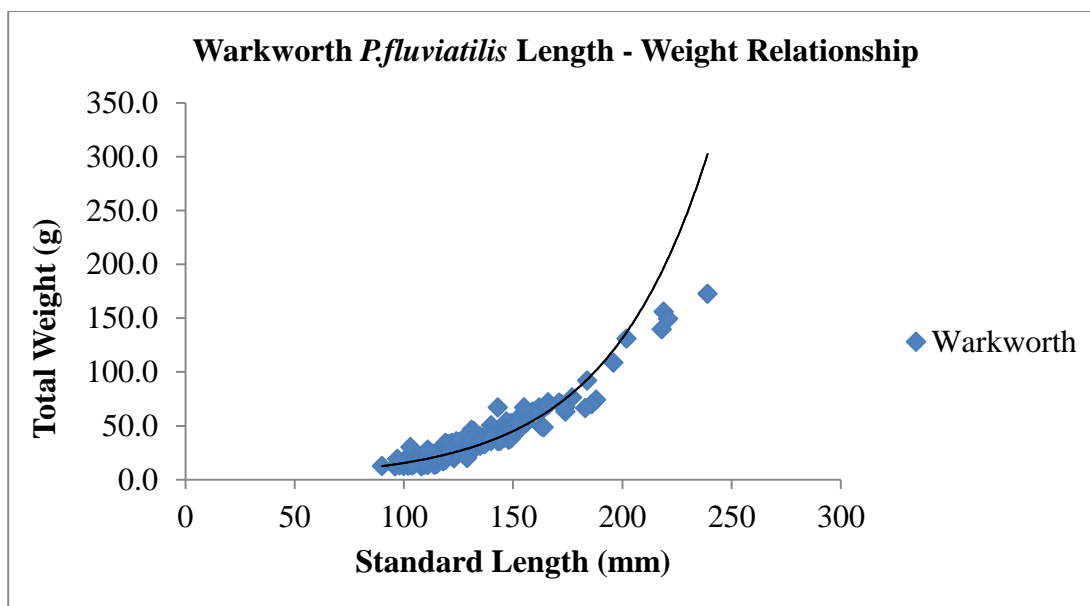


Figure 15 Length-Weight Relationship of *Perca fluviatilis* in Warkworth Quarry Lake

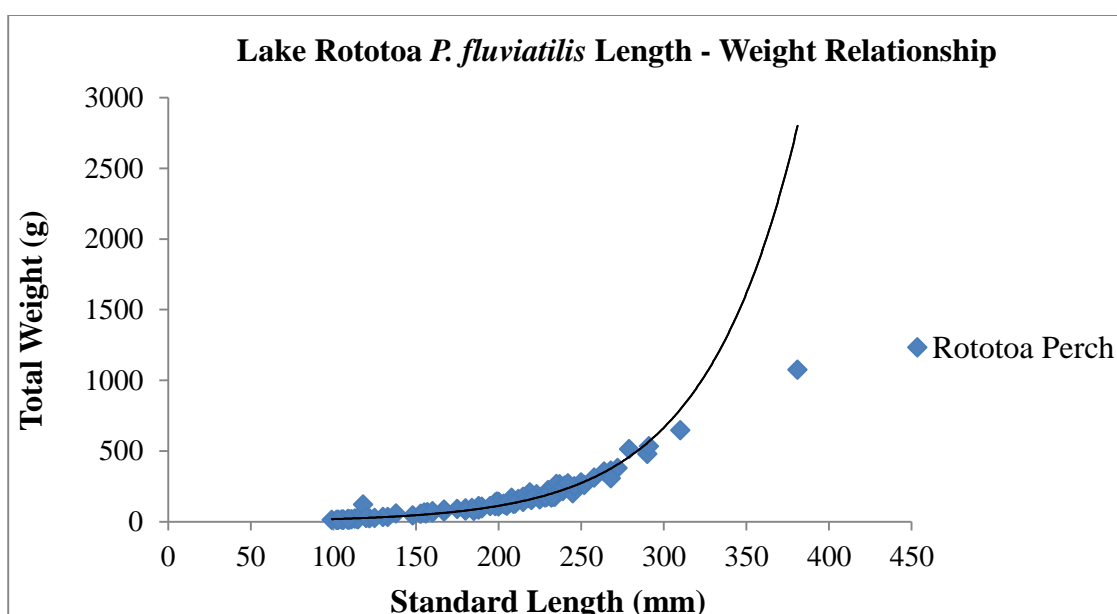


Figure 16 Length-Weight Relationship of *Perca fluviatilis* in Lake Rototoa

Growth

The age-length structure of the *P. fluviatilis* population in Warkworth Quarry Lake is presented in Table 1. Analysis of length-at-age using the Von Bertalanffy Growth Function (VBGF) showed asymptotic length (L_{∞}) of *P. fluviatilis* to be 251.2mm (SL) with growth curvature (K) = 0.24. Thus, the VBGF was $L_t = 251.2 (1 - e^{-0.24(t+2.24)})$. The growth performance index ϕ' was estimated to be 2.18 using the formula $\phi' = \text{Log}(K) + 2\text{Log}(L_{\infty})$. The reparameterized Von Bertalanffy Growth Function (rVBGF) indicated mean sizes of 154.8mm, 167.8mm and 167.9mm at ages 1, 3 and 5 respectively using standard length. The likelihood ratio test (LRT) (Table 2) revealed no differences in growth trajectories in expected mean size-at-ages 1, 3 and 5 between males and females of this population however; males achieved larger observed sizes than females at ages 1, 3 and 5.

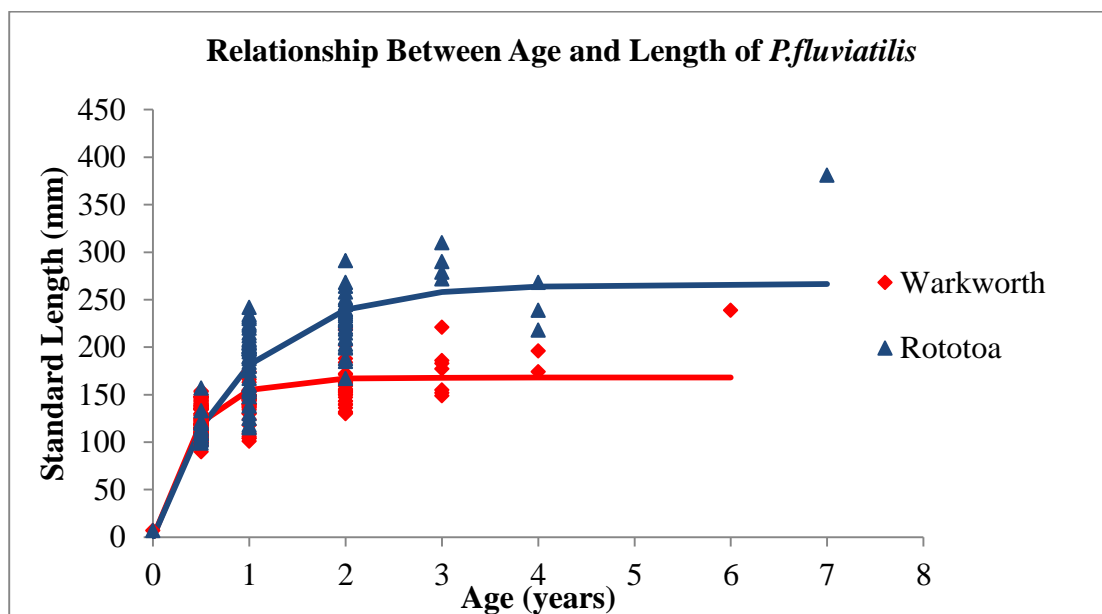


Figure 17 Relationship between age and length of *Perca fluviatilis* in Warkworth Quarry Lake and Lake Rototoa

The growth pattern of *P. fluviatilis* population of Lake Rototoa is also presented in Table 1. An analysis of the age-length structure showed L_{∞} of 274.5mm (SL), $K = 0.98$ and the VBGF was $L_t = 274.5 (1 - e^{-0.98(t+0.082)})$. The growth performance index ϕ' was calculated as 2.86. The expected mean standard length at ages 1, 3 and 5 were 181.4mm, 257.9mm and 265.7mm respectively. The LRT (Table 2) also showed no significant differences in growth

trajectories between males and females. Females in this population attained larger observed sizes at ages 3 and 5.

A comparison between *P.fluviatilis* in Warkworth Quarry Lake and Lake Rototoa shows differences in growth trajectories between the two populations (Figure 17). The length and age class mode of *P. fluviatilis* from Warkworth Quarry Lake was 100 – 139 mm and 0.6 year, and 180 – 219 mm and 1.6 years in Lake Rototoa (Figure 17). Lake Rototoa population contains individuals in the larger size groups of 260 – 299 mm and > 300mm which are absent in the Warkworth Quarry Lake population. The rVBGF parameters suggest differences in expected mean size-at-ages 1, 3 and 5 years between the two lakes (Table 1). Individuals sampled in Lake Rototoa achieved significantly larger mean size at ages 1, 3 and 5 years and standard VBGF parameters indicate a higher asymptotic size compared to Warkworth Quarry Lake population.

Mortality

Mortality rate for Warkworth Quarry Lake and Lake Rototoa was calculated from frequency of age within each population. The log of frequencies was plotted against age (Figures 18 & 19) and calculation of the exponential of the slope *100 were presented as survivorship. Accordingly, 44% of the Warkworth Quarry Lake *P.fluviatilis* population was surviving from year to year while 55% survived in Lake Rototoa.

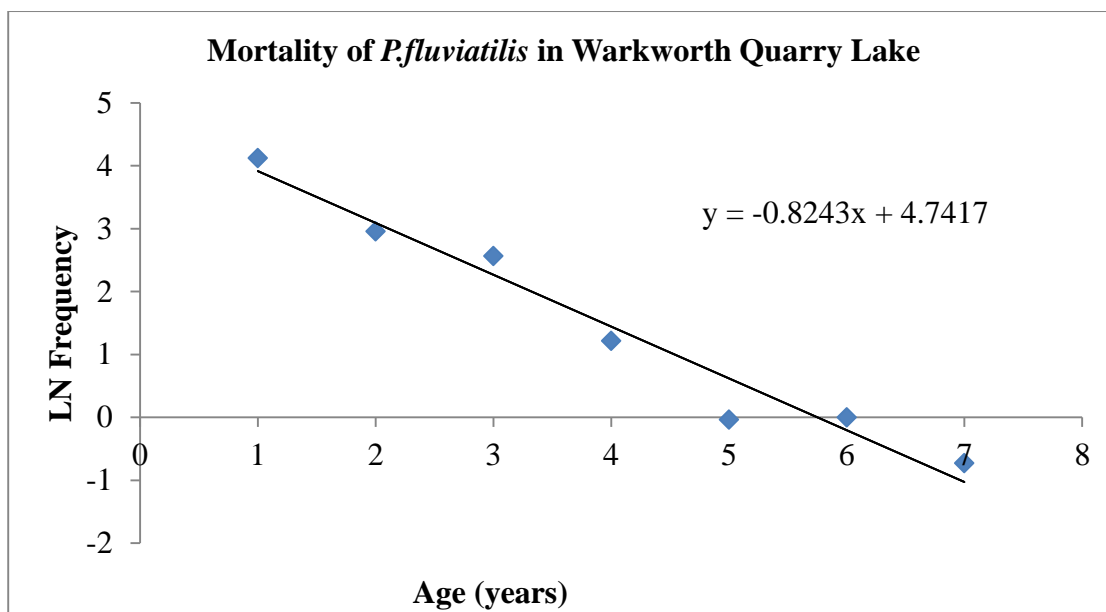


Figure 18 Mortality of *Perca fluviatilis* in Warkworth Quarry Lake

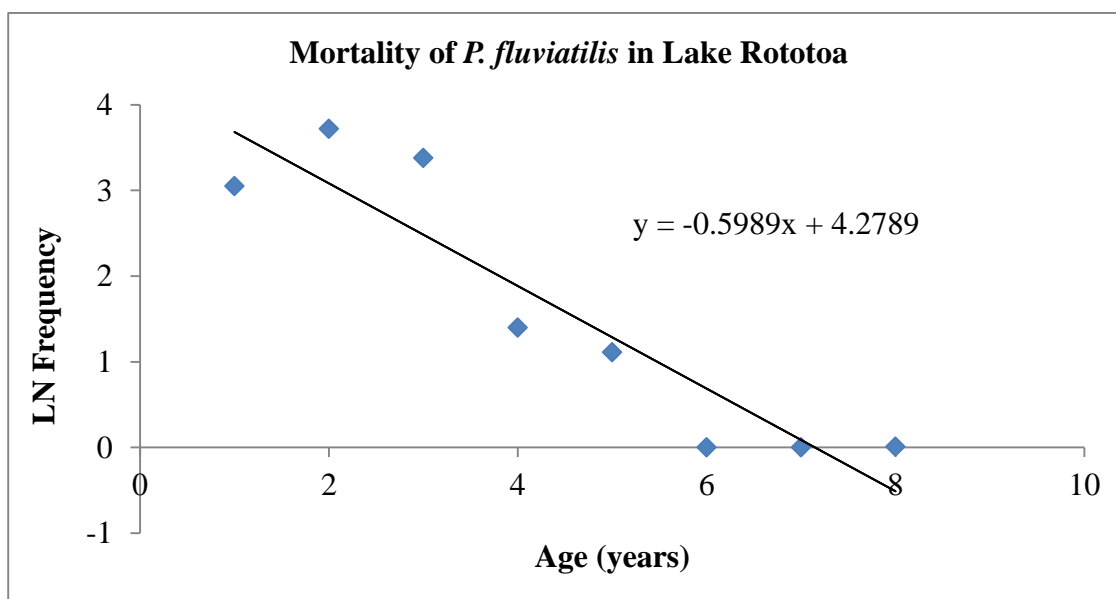


Figure 19 Mortality of *Perca fluviatilis* in Lake Rototoa

Table 1 The Age-Length Relationship of *P.fluviatilis* populations in New Zealand

Function	Parameters	Warkworth Q. Lake	Lake Rototoa	Lake Wainamu (2012)*	Lake Wainamu (2013)*
<i>rVBGF</i>	<i>L1</i>	154.8 (mm)	181.4 (mm)	141.0 (mm)	151.3 (mm)
	<i>L3</i>	167.8 (mm)	257.9 (mm)	177.0 (mm)	230.5 (mm)
	<i>L5</i>	167.9 (mm)	265.7 (mm)	178.7 (mm)	242.7 (mm)
<i>rVBGF (male)</i>	<i>L1</i>	158.7 (mm)	169.4 (mm)	135.4 (mm)	150.0 (mm)
	<i>L3</i>	172.5 (mm)	212.2 (mm)	158.0 (mm)	200.5 (mm)
	<i>L5</i>	172.6 (mm)	214.0 (mm)	158.5 (mm)	204.4 (mm)
<i>rVBGF (female)</i>	<i>L1</i>	151.1 (mm)	184.9 (mm)	142.9 (mm)	153.1 (mm)
	<i>L3</i>	163.8 (mm)	268.2 (mm)	184.3 (mm)	239.9 (mm)
	<i>L5</i>	163.9 (mm)	277.7 (mm)	186.7 (mm)	255.1 (mm)
<i>VBGF</i>	<i>L_∞</i>	251.2 (mm)	274.5 (mm)	178.8 (mm)	245.0 (mm)
	<i>K</i>	0.24	0.98	1.51	0.93
	<i>t₀</i>	-2.24	-0.08	-0.02	-0.03
<i>VBGF (male)</i>	<i>L_∞</i>	219.3 (mm)	211.5 (mm)	159.0 (mm)	202.8 (mm)
	<i>K</i>	0.18	1.75	1.88	1.36
	<i>t₀</i>	-0.05	0.06	-0.02	-0.0004
<i>VBGF (female)</i>	<i>L_∞</i>	213.4 (mm)	293.7 (mm)	186.0 (mm)	256.7 (mm)
	<i>K</i>	0.45	0.84	1.48	0.91
	<i>t₀</i>	-1.41	-0.15	-0.00	-0.0004
<i>Length-weight relationship</i>	<i>n</i>	206	99	110	145
	<i>b</i>	2.8214	3.3548	2.9987	3.2915
	<i>R²</i>	0.89	0.936	0.98	0.99
<i>Otolith weight-age relationship</i>	<i>R²</i>	0.7479	0.7906	0.7663	0.8125
<i>Sex ratio</i>	(<i>F: M</i>)	0.84:1	0.29:1	1.75:1	1.4:1

*Data from Sabetian et al (2014)

Table 2 Likelihood Ratio Test of *P.fluviatilis* in Warkworth Quarry Lake and Lake Rototoa

(a) Warkworth vs. Rototoa (N = 305):

	Base Case	Coincident curves	=L1	=L3	=L5
RSS _ω	416092.4	168405.9	155405.9	158405.7	188405.2
χ^2	-	17.55	27.69	27.69	17.02
d.f.	-	3	1	1	1
<i>P</i>	-	<0.001	<0.001	<0.001	<0.001

(b) Warkworth Males vs. females (N = 206) Rototoa Males vs. females (N=99)

	Base Case	Coincident curves	Base Case	Coincident Curves
RSS _ω	82908.3	82815.8	79925.2	80025.2
χ^2	-	0.23		0.13
d.f.	-	3		1
<i>P</i>	-	0.97262		0.72231

Table 3 Values of von Bertalanffy growth function parameters of different *Perca fluviatilis* populations and the corresponding ϕ^1 estimates

Site	All Sexes			Females			Males			References
	L_{∞} (cm)	K	ϕ^1	L_{∞} (cm)	K	ϕ^1	L_{∞} (cm)	K	ϕ^1	
Slapton Ley, England				25.0			22.0			Craig (1974)
Lake Pounui, New Zealand				34.8	0.20	2.39	24.8	0.25	2.18	Jellyman (1980)
River Po basin, Italy	18.76	0.41	2.15							Alessio et al., (1991)
Lake Trasimeno, Italy	26.67	0.40	2.46							Lorenzoni et al., (1993)
Lake Ijssel, Netherlands	29.40	0.93	1.43							Machiels & Wijsman (1996)
Lake Como, Italy				24.6	0.42	2.40	19.0	0.61	2.34	Negri (1999)
Lake Lugano, Italy	48.23									Puzzi et al., (2001)
Lake Langtjern, Norway	19.52	0.33	2.10							Heibo & Vøllestad (2002)
Lake Ainijarvi, Finland	31.06	0.03	1.43							Tolonen et al., (2003)
Lake Angersjon, Sweden				35.3	0.19	2.37	27.6	0.24	2.27	Heibo & Magnhagen (2005)
Lake Stocksjon, Sweden				32.4	0.16	2.23	23.4	0.27	2.17	Heibo & Magnhagen (2005)
Lake Trehorningen, Sweden				28.1	0.18	2.15	20.7	0.27	2.07	Heibo & Magnhagen (2005)
Lake Piediluco, Italy	49.09	0.13	2.49							Pedicillo et al., (2008)

Lake Varese	33.17	0.22	2.39	35.5	0.19	2.37	32.9	0.20	2.34	Cecuzzi et al., (2011)
Big Brook Dam, Australia				45.2	0.18		302. 1	0.00 2		Morgan et al., (2002)
Lake Wainamu (2012), New Zealand	17.9	1.51		15.9	1.88		18.6	1.48		Sabetian et al., (2014)
Lake Wainamu (2013), New Zealand	24.5	0.93		20.3	1.36		25.7	0.91		Sabetian et al., (2014)
Warkworth Quarry Lake, New Zealand	25.1	0.24	2.18	21.9	0.18	1.94	21.3	0.45	2.31	*
Lake Rototoa, New Zealand	27.5	0.98	2.86	21.2	1.75	2.89	29.4	0.84	2.86	*

*Current study

2.5 Discussion

The total number of specimen ($n = 305$) used for age and growth analysis proved to be adequate for the scope of this study. However, the oldest age classes were under represented in both lakes (particularly in Warkworth Quarry Lake), possibly reflecting the smaller mesh sizes which favoured smaller fish. The results indicate an almost equal proportion of males and females in age class 0+ in both Warkworth Quarry Lake and Lake Rototoa populations. These results are similar to those reported from Lake Pounui (Jellyman, 1980), strongly suggesting that both sexes are represented at hatching.

The age distribution in Warkworth Quarry Lake (Figures 8 & 9) shows the greatest number of individuals in age class 0+ and 1+. McCormack (1965) and LeCren et al (1977) reported that successful age classes can dominate a population. This is evident in this population because both male and females are well represented in the age distributions of these classes. Thereafter, females dominate subsequent age classes. Females dominate early in Lake Rototoa at age 1+. Jellyman (1980) and Alm (1959) attributed the overall dominance of females to high mortality of males due to selective predation on males by older fish as well as other predatory fish such as Rainbow trout *Oncorhynchus mykiss*. This top predator is absent in Warkworth Quarry Lake but prevalent in Lake Rototoa. This could account for the presence of a high proportion of males in young age classes in Warkworth Quarry Lake. A decrease in proportion of individuals between 1+ and subsequent age classes may indicate the role of cannibalism as a determinant of age distribution in both lakes. A high mortality rate between younger and older age classes is expected when juvenile fish are vulnerable to cannibalistic adult fish. The survivorship of both populations fall in the range regarded as the natural annual mortality rate in *P. fluviatilis* of between 43-70% due to cannibalism (Thorpe, 1977).

One of the advantages of using sagittal otoliths in age determination of fish is that they provide a record that is often the clearest and of highest potential temporal resolution (Chambers & Miller, 1995). Otoliths enable extracting the most information from data collected given the frequent difficulty in obtaining reliable and representative observations on growth (Miller et al., 1988). This study demonstrated this in two ways. First, the data from Warkworth Quarry Lake and Lake Rototoa showed a strong relationship between otolith

weight and age which is critical in estimating the size of fish at a previous age, contributing to its history. Second, the regularity of the daily deposition of otolith increments (Panella, 1971) not only provided a means of ageing the fish but enhances an understanding of major life events such as hatching date. The hatching dates obtained in this study have significant relevance in the reproductive biology of *P. fluviatilis* and this will be discussed in detail in the following chapter.

P. fluviatilis in Warkworth Quarry Lake and Lake Rototoa follow a similar growth pattern to Lake Wainamu population (Sabetian et al., 2014) with rapid growth in the first year. Although this indicates the importance of fast early growth in *P. fluviatilis*, possibly due to the impact of cannibalism in age structure determination (Sabetian et al., 2014), analysis of growth patterns particularly in Lake Rototoa indicate continued high growth trajectory in subsequent years. According to the growth performance index ϕ' (Table 3), growth rates for both Warkworth Quarry Lake and Lake Rototoa can be classed as 'very good' and 'moderate' respectively according to Tesch (1955). These rates compare favourably with studies in the Northern hemisphere (Alessio et al., 1991; Lorenzoni et al., 1993; Machiels & Wijsman, 1996; Heibo & Vøllestad, 2002; Tolonen et al., 2003; Pedicillo et al., 2008; Cecuzzi et al., 2011). According to literature *P. fluviatilis* populations in southern hemisphere localities have rapid growth rates in early life but attain smaller maximum sizes as adults resulting in stunted populations (Alm, 1946; Rask, 1983; Morgan et al., 2002). Sabetian et al (2014) found a similar pattern in Lake Wainamu in which *P. fluviatilis* attained a larger size by age one but smaller sizes in subsequent years in comparison to European *P. fluviatilis*. This does not seem to be the case for *P. fluviatilis* in Lake Rototoa which has the highest growth performance index presented in Table 3. Morgan et al (2002) also found higher growth rates of *P. fluviatilis* compared to European populations. Thus, this shows that some *P. fluviatilis* in this region are also capable of achieving high growth rates and do not necessarily conform to the generic classification of being stunted (Jellyman, 1980; Morgan, 2001).

Further comparisons with New Zealand *P. fluviatilis* studies indicate that expected sizes at age one are higher in both sexes for Lake Rototoa compared to Lake Wainamu (Table 1) and Lake Pounui (Jellyman, 1980). Of particular interest are the observations that Lake Rototoa *P. fluviatilis* maintain high growth trajectories throughout the age distribution; they show positive allometric growth compared to Warkworth population and that there are no differences in expected growth between males and females of the population. Lake Rototoa

is a bigger lake in comparison to Warkworth Quarry Lake and this has a significant impact in the marked difference in overall growth between the two *P. fluviatilis* populations. It is expected that growth is stunted in Warkworth Quarry Lake due to the increase in competition for resources, such as food. This factor alongside the interaction of a warm climatic regime (Morgan et al., 2002; Sabetian et al., 2014) and abundance of food supply are presumably responsible for the high growth rates in Lake Rototoa.

Lake Rototoa is known for its high biodiversity with fish species such as *Gorbiomorphus cotidianus* (common bully), *Galaxias species* (galaxiids) and *Paranephrops planifrons* (Cray fish) (Auckland Regional Council, 2008). This abundance of food provides high quality prey for *P. fluviatilis* and will be further explored in chapter four. Also, a warmer climatic regime has been associated with higher number of young-of-the-year cohort that becomes prey for different-sized cannibalistic *P. fluviatilis* (Le Cren 1992; Persson et al., 2000; Sabetian et al., 2014). This could also attribute to the high growth rate in Lake Rototoa. Sabetian et al (2014) highlighted that this hypothesis of ‘increased food consumption’ may be supported by a positive allometric growth of *P. fluviatilis* that shows more girth per unit size. A similar assumption may be made for this study as Lake Rototoa *P. fluviatilis* also exhibit a positive allometric growth.

While it is generally accepted that female *P. fluviatilis* grow faster than males (e.g. Craig, 1974; Thorpe, 1977; Jellyman, 1980; Cecuzzi et al., 2011; Sabetian et al., 2014) this is not the case in both Lake Rototoa and Warkworth Quarry Lake which showed no significant difference in expected size-at-age throughout the populations. In fact, males in Warkworth Quarry Lake had higher observed size-at-age than females. This change in growth pattern is of interest while the higher growth rate of males over females can be attributed to the utilization of food resources solely for somatic growth with less energy for reproduction compared to females (Steimle, n.d.). The geographic origin may also influence the growth patterns of *P. fluviatilis* in this population (Mandiki et al., 2004). However; this observation warrants further investigation for an adequate explanation.

Chapter 3 The Reproductive Biology of *Perca fluviatilis* from Two Lakes in New Zealand

3.1 Introduction

Reproduction is the process by which species propagate. The reproductive strategy, as reflected in anatomical, behavioural, physiological, and energetic adaptations, is an essential commitment to future generations. Temporal variation in this reproductive strategy may be the result of biotic and abiotic conditions (Pankhurst, Purser, Van Der Kraak, Thomas & Forteath, 1997). For example the timing of reproduction can depend on a range of environmental variables including water temperature, photoperiod, and diet (Glasser et al., 2004). In some fish species gonad investment changes seasonally while the initiation and duration of the spawning period may vary with geographic distribution among the populations (Brown-Peterson et al., 2001). This suggests that reproductive success in fish is dependent on adaptability to fluctuating environmental conditions (Moyle & Czech, Jr., 2000).

In order for reproductive success in fish to take place there is need to take into account reproductive parameters. Reproductive parameters provide important information about the propagating and regenerative capacity of the fish species. These include sex ratio, size and age at sexual maturity, gonadal development, and spawning periodicity. Sex ratio, for example, is an important parameter in the reproductive biology of fishes. Not only does it provide information on the representation of male and female fish present in a population, it also constitutes important information essential for assessing reproductive potential and stock size estimation (Vicentini & Araujo, 2003). The sex ratio of European *Perca fluviatilis* populations has been demonstrated to be extensively divergent between different locations (Thorpe, 1977). It is predominantly skewed towards females, particularly in older age classes (Beckman, 1949; Krizenecky & Pulankova, 1953) but has also been found at a ratio of 1:1 in small pond and lake populations because of high population density (Alm, 1959; Thorpe, 1974). Sex ratios of *P. fluviatilis* also differ between populations with divergent growth rate; for example a higher proportion of males are found in slow-growing stocks compared to fast-growing stocks (Dryagin, 1948; Konovalova, 1955).

Perca fluviatilis on average reach maturity in 2–3 years. However, the onset of reproduction for males and females is often encountered at the end of the first and second years, respectively (Tesch, 1955; Thorpe, 1977; McDowall, 2000). In some populations, particularly stunted ones, females reach sexual maturity at age 1 (Healy, 1954; Shilenkova, 1959; Lake, 1959). Size at first maturity, on the other hand, varies between populations. Among males the size ranges from 50 – 120 total length (TL) mm (Thorpe, 1977) to 160mm (TL) (Laskar, 1943) and in females the ranges are 120 – 180mm (TL) (Thorpe, 1977) and 240mm (TL) (Thorpe, 1974). Weight at first maturity has also been reported; 10 – 60g in males and 20 – 240g in females (Thorpe, 1977). The size and age at first maturity can be influenced by a number of factors, including growth rate within a year class and genetic factors between year classes and populations (Alm, 1954, 1959), and also a size threshold and environmental conditions such as temperature and eutrophication (Hartman, 1974; Thorpe, 1977). These factors also influence gonad development.

Gonadal tissue development in *P.fluviatilis* follows a seasonal pattern and differs between males and females (Le Cren, 1951, Lind et al, 1973; Hutchinson, 1974). The gonad somatic index (GSI) in males increases up to 7% GSI between September and October and this proportion is maintained until spawning (Lind et al., 1973). On the other hand, the ovaries of immature females maintain a constant value of about 0.5% of total body weight while mature females experience a steady increase of up to 23% of body weight from July to April (LeCren, 1951; Lind et al., 1973). The lower maximum sizes for gonads in both sexes varies from population to population depending on the resting period. The resting period refers to the time when growth of gonads ceases in favour of conditioning prior to spawning (Hutchinson, 1974). Resting period is initiated by cold water temperatures during winter and disrupted by warmer periods during spring.

The resting period is also dependant on local climatic and seasonal conditions. For example, Finnish *P.fluviatilis* have gonad resting period of 1 and 2 months for males and females, respectively, while English *P.fluviatilis* go through 3 and 4 months of resting, respectively (Lind et al., 1973). The gonad development cycle directly affects the body condition of *P.fluviatilis* (LeCren, 1951). The maximum body condition in immature fish is realized in mid-summer and their minimum in mid-winter whereas in adult fish this cycle is interrupted by gonad development and liberation of contents at spawning (Lind et al., 1973, Mann, 1978).

In their natural Northern hemisphere range, *P.fluviatilis* spawn once in spring between February and July after the conditioning period in winter (Winfield, 2010; Cecuzzi et al., 2011). The timing of spawning differs between localities due to variances in photoperiod, which affects maturation, and temperature (Thorpe, 1977). This timing is also dependant on latitude with females spawning at an earlier date in populations in lower latitudes (Thorpe, 1977; Heibo et al., 2005). However, in higher latitudes females spawn at a lower temperature in comparison to populations in lower latitudes (Thorpe, 1977). Temperature and photoperiod vary from year to year and this also causes the date of first spawning to vary between years in a single population of *P.fluviatilis*. Other local factors such as spring floods (Balon, 1963; Popova, 1965), first rains after periods of drought (Lake, 1967) and food resources (Thorpe, 1977) affect time of spawning in conjunction with temperature. Spawning has been reported to initiate in temperatures as low as 4°C (Filatov & Duplakov, 1926) however; the optimal temperature is generally around 14°C (Echo, 1955).

The spawning period of *P.fluviatilis* varies between populations. For example, duration of 3 days was recorded for *P.fluviatilis* population in the River Volga in Russia (Dryagin & Muratova, 1948); 16 days for Loch Leven stocks in Scotland (Thorpe, 1977) and not more than 2 weeks for Rybinsk Reservoir population in Russia (Zakharova, 1955). The principal spawning areas are among aquatic vegetation and males have been observed to arrive on spawning grounds days or weeks in advance of females and remaining behind afterwards (Herman, 1964; Tsai & Gibson, 1971; Kukko & Lind, 1972).

There are also records of *P.fluviatilis* populations indicating lack of and delayed spawning in some years (e.g. Thorpe, 1977; Lukseine & Sandstrom, 1994; Sandstrom et al., 1995). Lack of spawning has been attributed to absence of food resources (Pivnicka & Svatora, 1977). Sandstrom and colleagues (1995), however, attributed lack of spawning to extremely low temperatures which reduced the body condition of individuals to a critical level during spawning in the first year leading to high mortality rate. The surviving fish, in turn, postponed spawning by several years. Spawning in *P.fluviatilis* can also be delayed with increasing latitude (Thorpe, 1977) and egg resorption when gonad development does not take place or is disrupted (Lukseine & Sandstrom, 1994). The exact mechanisms governing these occurrences are presently unavailable in the literature.

Some characteristics of the reproductive biology of *P. fluviatilis* populations in the southern hemisphere, where they are introduced species, have been described in a few studies (Jellyman, 1980; Morgan et al., 2002; Sabetian et al., 2014). The sex ratio values range from 1.4:1 (F: M) in New Zealand populations (Jellyman, 1980; Sabetian et al., 2014) to 1.7:1 (F: M) in a West Australian population (Morgan et al., 2002). Although the sex ratio in the West Australian population of Morgan et al., (2002) is slightly higher, it is of interest to note that Sabetian et al., (2014) reported F: M ratio of 1.75:1 in the first year of their study in Lake Wainamu, New Zealand. However, we have to be mindful that other factors such as sample size, gear selectivity and differential distribution of the sexes can influence reported sex ratio (Hartman, 1974; Thorpe, 1974; Thorpe, 1977). What these studies do confirm is the fact that the sex ratio of *P. fluviatilis* is females dominated in both the Southern and Northern Hemispheres. A homogeneous proportion of males and females are found in Age 0+ in *P. fluviatilis* populations, however, 0+ males are either more active than females in their search for food or lose body condition to meet the high energy costs associated with gonadal development (Alm, 1959; Jellyman, 1980; Morgan et al., 2002). Furthermore, they are more vulnerable to predation and / cannibalism by faster growing older piscivorous females resulting in female dominance in older classes (Morgan et al., 2002).

The size and age at first maturity also varies with growth rates in Southern hemisphere *P. fluviatilis* populations. Although Jellyman (1980) and Morgan et al (2002) agree that *P. fluviatilis* populations in this region are fast growing, the age at maturity has been reported as age 1 in males and age 2 in females. This is similar to some populations in the Northern hemisphere, which have been classified as stunted (Healy, 1954; Shilenkova, 1959; Lake 1959). Detailed information on the size at first maturity for the Southern Hemisphere is scarce.

A seasonal pattern of gonad tissue growth has also been described for *P. fluviatilis* populations in the Southern hemisphere. Gonad development initiates in late summer and females attain maturity from June to August in Big Brook Dam, Western Australia (Morgan et al., 2002). The temperature regime for spawning is between 8°C - 14°C resulting in a spawning season of August to September (Morgan et al., 2002) while *P. fluviatilis* in Lake Pounui, New Zealand, have been reported to spawn between September and November (Jellyman, 1980). A high proportion of males congregate on spawning grounds during the few days of spawning in Lake Pounui and disperse immediately after spawning contrary to

the behaviour in the Northern hemisphere *P.fluviatilis* (Jellyman, 1980). Failure to spawn has been observed in a population in Hamilton Lake in New Zealand due to adverse conditions (Jellyman, 1980); however this is less common than reported for European *P.fluviatilis*.

From these description there are evident information gaps regarding the gonad development of males and females; gonad resting period and its relation to body condition; environmental effects on spawning and spawning periodicity of *P.fluviatilis* populations in the Southern hemisphere, particularly in New Zealand. Given the plasticity in reproductive characteristics of *P.fluviatilis* with latitude and geographical region (Heibo & Magnhagen, 2005; Komsari et al., 2104) a spatial specific focus does provide a comparative reference. For example, the slight difference in spawning season between Australian (Morgan et al., 2002) and New Zealand (Jellyman, 1980) *P.fluviatilis* populations does provide a point of discussion around the influence of environmental factors. Accordingly, investigation of reproductive parameters in several populations of *P.fluviatilis* in New Zealand is essential for comparative purposes in order to understand the variations that have enabled *P.fluviatilis* to adapt to New Zealand environment as well as further indicate the plasticity of their reproductive traits (Komsari et al., 2014).

Much of the reproductive information of *P.fluviatilis* in New Zealand is based solely on Jellyman (1980). However, the information provided by Jellyman is limited due to the methodology he employed. There are various methods to study the gonad development of fishes; macroscopic staging of whole oocytes, use of gonad indices, assessment of ovarian maturation based on oocyte measurements and oocyte size frequency distributions, and histological techniques (West, 1990). Jellyman's (1980) study used the macroscopically staged method by Laevastu (1965). Although this method is simple and rapid, it has the disadvantages of being subjective, having an uncertain accuracy and requiring histological validation. Histology, to date, is a more accurate method despite its time consuming and expensive nature (West, 1990). It offers detailed information on gonad development with the ability to identify transitional stages of development, atresia and presence of post-ovulatory follicles in ovaries (West, 1990). Histological techniques were employed for this study in order to provide a detailed description of the reproductive characteristics of *P.fluviatilis* populations in Northern New Zealand.

3.2 Objectives

The purpose of this study was to establish life history parameters of *P.fluviatilis* populations from Warkworth Quarry Lake and Lake Rototoa. The specific objectives were to ascertain sex ratio, age and size at sexual maturity and seasonal pattern of gonad development, while also describing the life history stages associated with gonadal development within these two populations.

3.3 Materials and Methods

Study sites and sampling procedures are previously described in Chapter Two.

3.3.1 Gonad development of *Perca fluviatilis*

Gonads from each fish (Figure 20) were weighed on a digital scale and placed in a formaldehyde based fixative in preparation for histological analysis. After 7 days a thin cross section was taken from the mid part of each of the gonad. The gonad cross sections were then placed in histology cassettes and dehydrated in a tissue processor. The aim of this process is to remove water from the tissues and replace this with a medium which solidifies so that thin cross sections can be taken while maintaining the integrity of cell structure. The medium chosen for this study was paraffin wax. Dehydration was achieved by transferring the samples through progressively higher concentrations of ethanol. This was then washed out by xylol and finally infiltrated in paraffin wax in preparation for embedding according to the schedule in Table 4.

Table 4 Schedule of dehydration in tissue processor

Reagent	Duration (hours)
70% Alcohol	2
75% Alcohol	2
90% Alcohol	1 ½ hours
95 % Alcohol	1 ½ hours
100% Alcohol	1 ½ hours
100% Alcohol	1 ½ hours
100% Alcohol	2 hours
100% Xylol	2 hours
100% Xylol	2 hours
100% Xylol	2 hours
Paraffin Wax	2 hours
Paraffin Wax	2 hours

After a 21.5 hour cycle of preservation the samples were placed in embedding trays, covered with paraffin wax to cover the entire sample and cooled to harden the mould. The samples were then sectioned. Four micrometer (μm) thick tissue sections were cut perpendicular to the surface of the tissue using a microtome. Three good sections were selected from each sample and placed in a 43°C water bath to allow the tissue to expand and then mounted on microscope slides. They were set aside overnight to dry and then stained.

Mayer's Haematoxylin and Young's Eosin-Erythrosine were used for staining. Haematoxylin stains nucleic acids into a deep blue-purple colour while Eosin stains proteins none specifically in varying degrees of pink. The regressive method of staining was used in this study, meaning that the samples were over stained deliberately then differentiated to reach an endpoint. Scott's tap water was used to blue the haematoxylin and has the advantage that it minimizes loss of tissue sections and cells from the glass slides compared to other blueing solutions (Table 5).

Table 5 Haematoxylin and Eosin Staining Protocol for *Perca fluviatilis*

Staining Compound	Time Spent in Compound
Xylol	5 minutes
Xylol	5 minutes
100% Alcohol	1 minute
95% Alcohol	1 minute
95% Alcohol	1 minute
70% Alcohol	1 minute
Tap water	20 seconds
Haematoxylin	8 minutes
Tap Water	20 seconds
Scott's Tap Water Substitute	1 minute
Tap water	2 minutes
Eosin	5 minutes
Tap water	Rinse well to remove excess stain
70% Alcohol	8 dips
95% Alcohol	8 dips
95% Alcohol	8 dips
100% Alcohol	8 dips
Xylol	1 minute
Xylol	1 minute

After exposure to xylol a cover slip was placed over each slide using DPX mounting glue. Viewing of slides was done under a transmitted white light microscope. The developmental stages of the gonads were evaluated from the latest stage of sperm growth or non-atretic oocyte present (Grier, 1981; West, 1990; Sabetian et al, 2014). Reproductive activity was assessed according to criteria presented by Sabetian et al (2014) in Table 3.3.

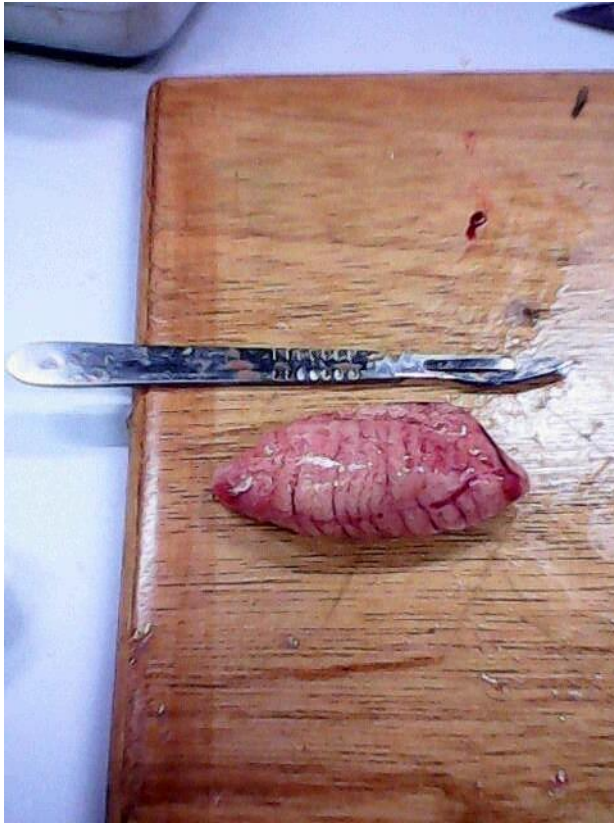


Figure 20 Photograph of an ovary extracted from *Perca fluviatilis*

Gonadosomatic Index

The gonadosomatic index (GSI) was calculated for all sexually identified specimens using the formula:

$$GSI = 100W_g/W_t$$

W_g is gonad mass in grams and W_t is total body mass in grams. The purpose of this index is to provide an insight into the changes in ovary size (West, 1990).

Table 6 Gonad Developmental Stages of *Perca fluviatilis*

Sexual Identity	Latest most abundant stage present	Reproductive activity	Gonad Developmental stage	Reproductive stage
Female	Peri-nucleolar oocytes	Inactive	Inactive (immature or resting)	1 – 2
	Cortical alveoli oocytes	Active	Mature developing	3
	Vitellogenic oocytes	Active	Mature developing	4
	Hydrated oocytes	Active	Mature spawning	5
	Peri-nucleolar and cortical alveoli oocytes, and degenerating vitellogenic or hydrated oocytes present in the lumen	Active	Spent	6
	Atretic oocytes with no post-ovulatory follicles and hydrated oocytes	Active	Atretic	Atretic
Male	Spermatogonia, or both spermatogonia and spermatocytes present	Inactive	Inactive (immature or resting)	1
	Spermatids	Active	Mature developing	2
	Spermatozoa	Active	Mature spawning	3

3.4 Results

3.4.1 Warkworth Quarry Lake

The sex ratio of *Perca fluviatilis* in Warkworth Quarry Lake (n = 206) was 1:1.17 (F:M). Age and size of first sexual maturity was assessed for both females and males. At age 0+ of average size 118.9 mm SL, 11.16% of the males had developed testes, whereas 6.79% of the females in the same age group had developed ovaries, at average size of 122.2 mm SL. At age 1+ and average size of 144.1 mm SL, 7.76 % of the females were mature while only 6.79% of the males with an average size 132.7 mm SL had mature testes. Table 7 gives a summary of the proportion of the maturation stages of gonads while Table 8 shows the average size at maturity in Warkworth Quarry Lake. Male and female *P.fluviatilis* in Warkworth Quarry Lake are sexually mature between their first and second year of life when they spawn for the first time.

Histological analysis of gonads showed that 50% of individuals had gonads in maturation while 50% had immature gonads or were collected after the spawning or spent stage. Males had 50% inactive, 33% developing, 1% spawning and 16% resting out of the 94 specimens analysed in this study (Figure 21). Of the 112 total females, on the other hand, 47% were inactive, 29% were developing, 2.7% were spawning, 2.7 % were spent, 14.3% were resting and 0.9% had signs of atresia. Asynchronous development was present in 0.9% of the females. Vitellogenesis occurred in female oocytes throughout the months of February to October and was absent in November to January (Figure 27).

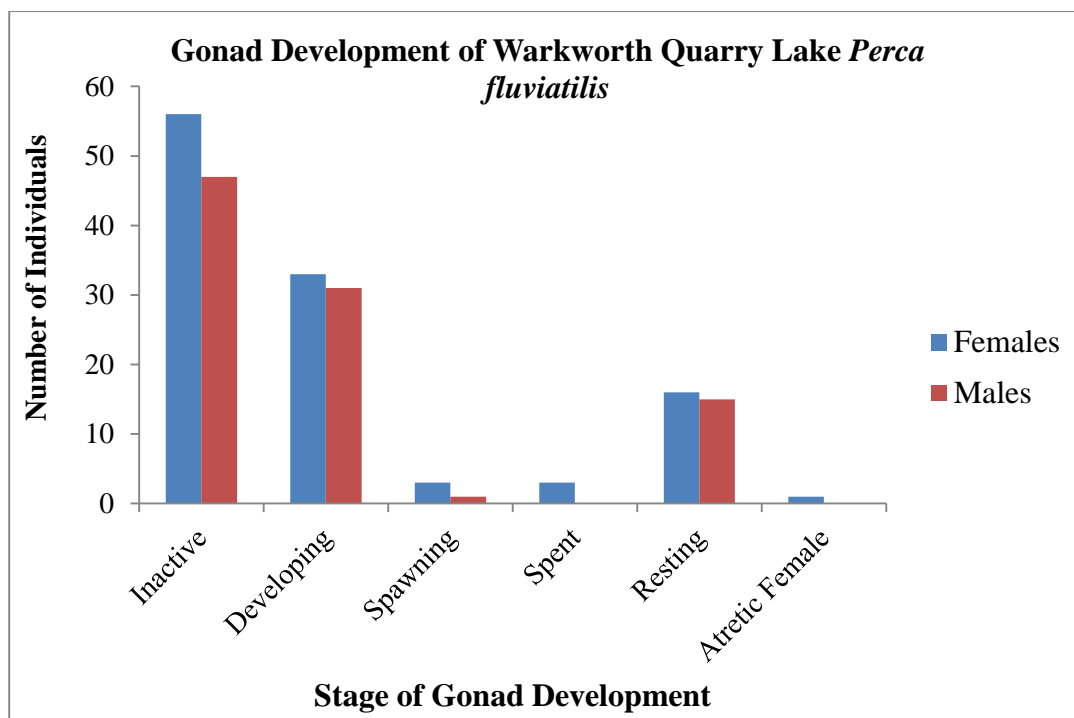


Figure 21 Gonad development of female and male *Perca fluviatilis* in Warkworth Quarry Lake

The annual trend in GSI for Warkworth Quarry Lake was similar for both sexes reaching a maximum in July (Figure 22 & Figure 23) with a sharp decrease in August for females and a gradual decrease between August and October for males. The decrease in GSI continued for both sexes till February and thereafter a gradual increase up to the maximum in July.

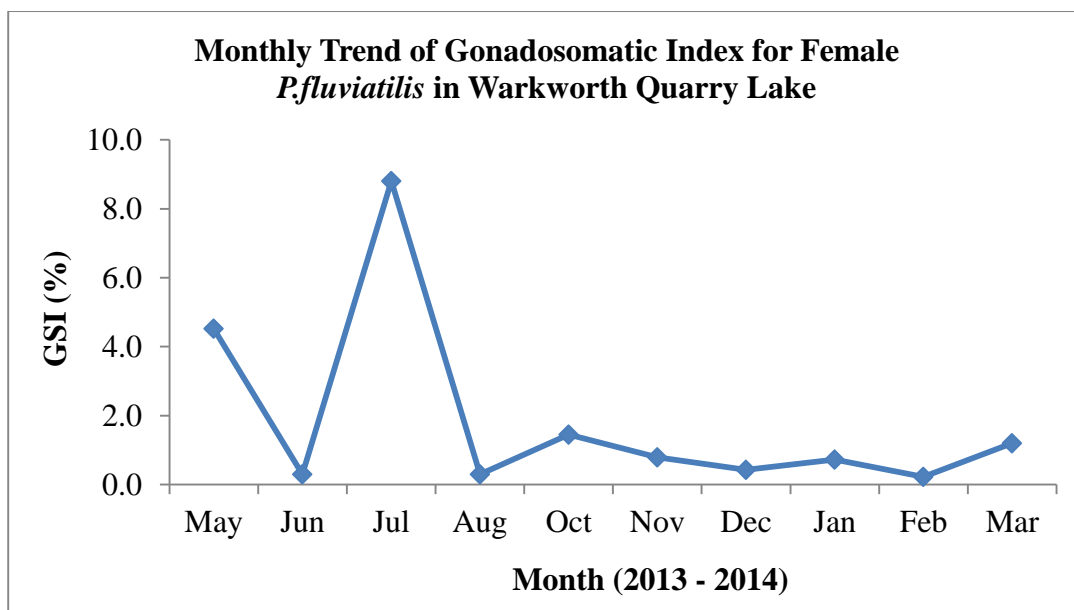


Figure 22 GSI for female *Perca fluviatilis* in Warkworth Quarry Lake

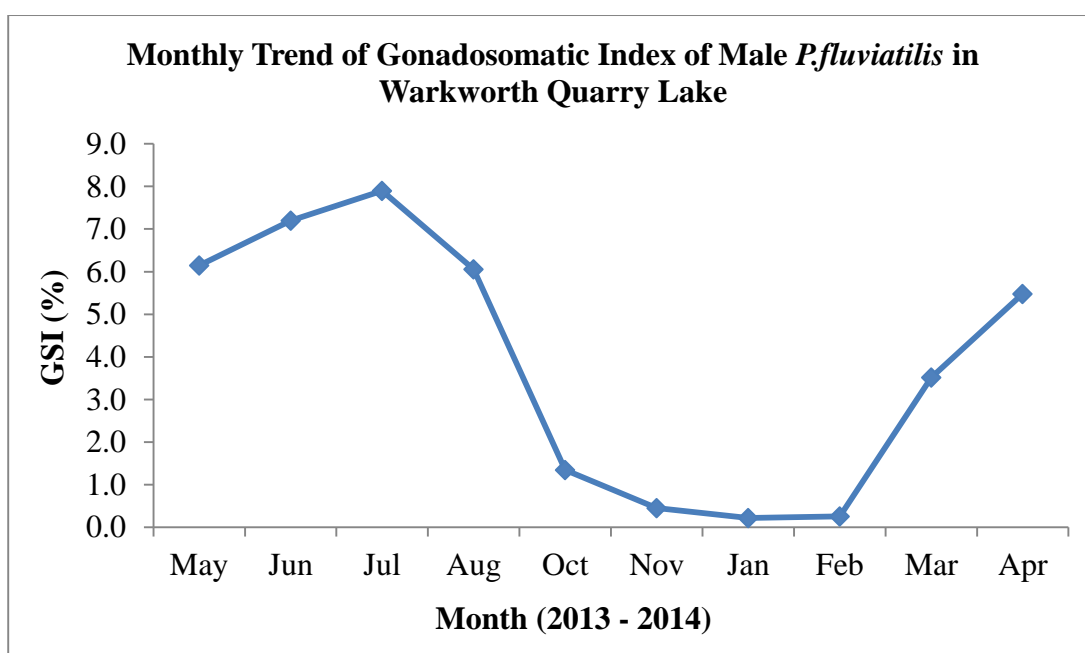


Figure 23 GSI for male *Perca fluviatilis* in Warkworth Quarry Lake

3.4.2 Lake Rototoa

Lake Rototoa *P. fluviatilis* (n=99) on the other hand showed a highly females skewed sex ratio of 1:3.5 (F: M). As shown in Table 7 and Table 8, 8.1% of males at age 0+ and at average size of 113.5 mm SL had developed testes, whereas 2.02% of females in the same age group and with an average size of 113.8 mm SL had developed ovaries. At age 1+ and average size 191.2 mm SL, 26.26 % of females were mature while only 7.07% of males with an average size 166.1 mm SL had developed testes. Lake Rototoa *P. fluviatilis* males and females are also sexually mature between their first and second year similar to Warkworth *P. fluviatilis*.

Histological analysis of gonads showed that 77.8% of the specimens in this lake were mature while 22.2% were immature or were collected after the spawning or spent stage. There were no males that were inactive out of the 22 males used in this study from this lake. However; 90.9% of males were developing and 9.1% showed signs of resting (Figure 24). Of the 77 females analysed from Lake Rototoa; 28.6 were inactive, 66.2% were developing, 1.3% were spawning, 1.3 % were spent, 1.3% were resting and 1.3% were atretic. 5.2% of females showed asynchronous development (Figure 24). Vitellogenesis occurred in female oocytes throughout the months of December to August and was absent in September to November (Figure 27).

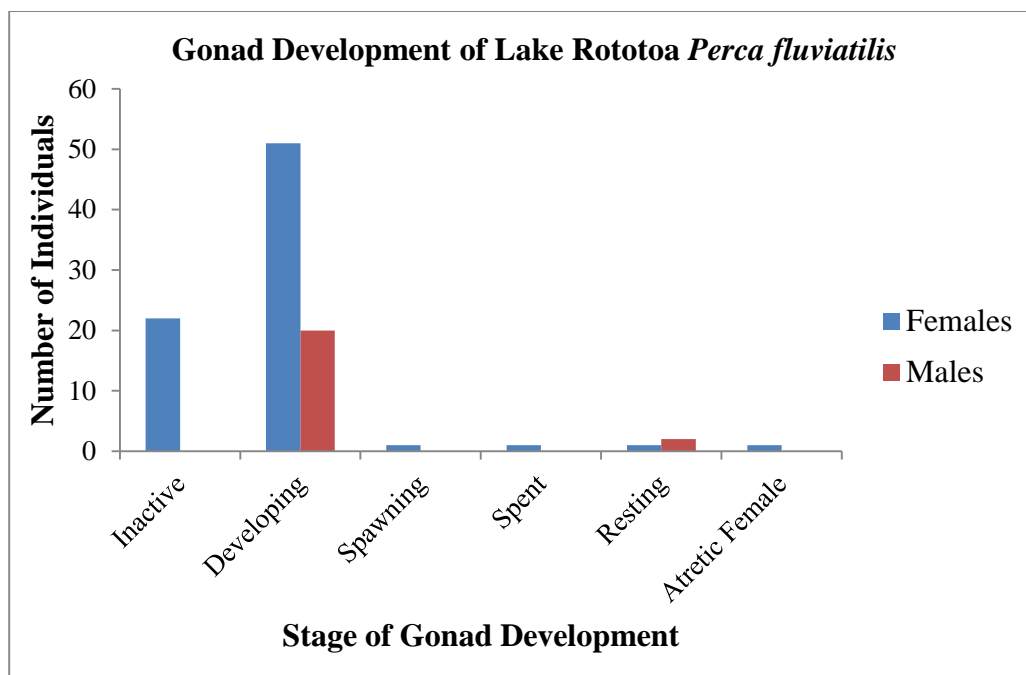


Figure 24 Gonad development of female and male *Perca fluviatilis* in Lake Rototoa

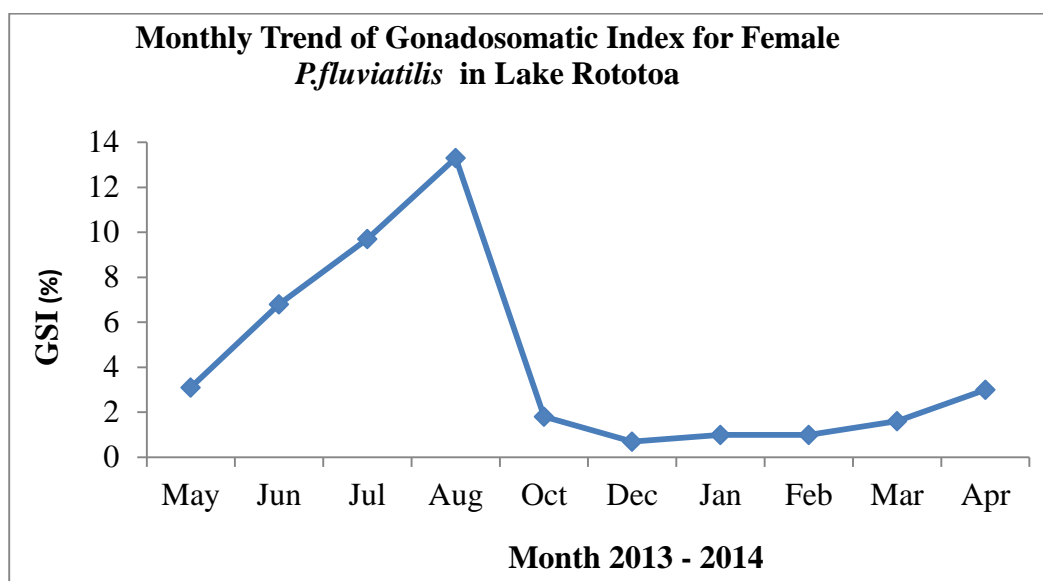


Figure 25 GSI for female *Perca fluviatilis* in Lake Rototoa

The annual trend in GSI was similar for both sexes reaching a maximum in August (Figure 25 & Figure 26) with a sharp decrease in October for females compared to a gradual decrease in males. The decrease in GSI continued for both sexes till February and thereafter a gradual increase up to the maximum in August.

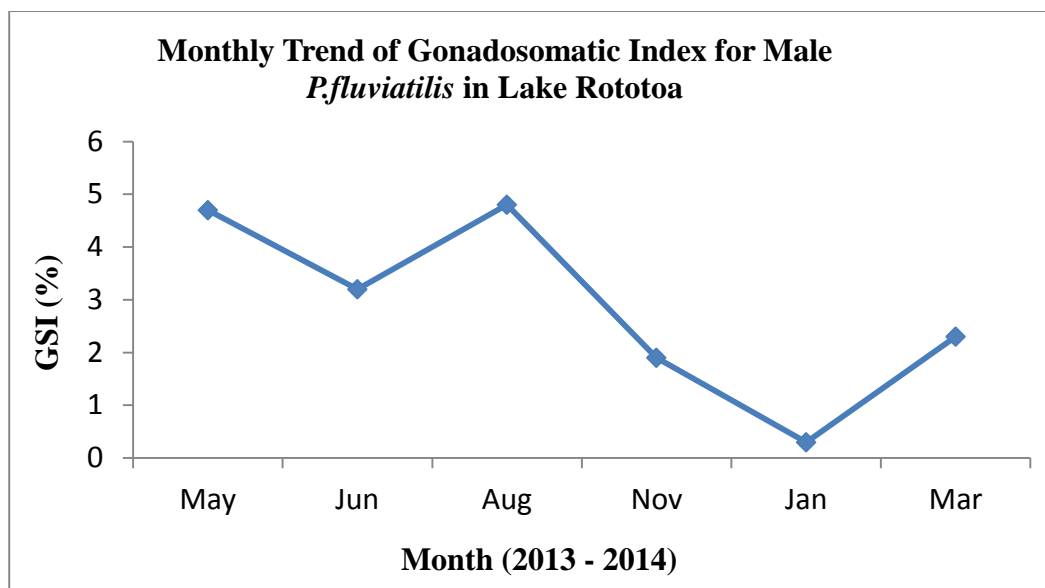


Figure 26 GSI for male *Perca fluviatilis* in Lake Rototoa

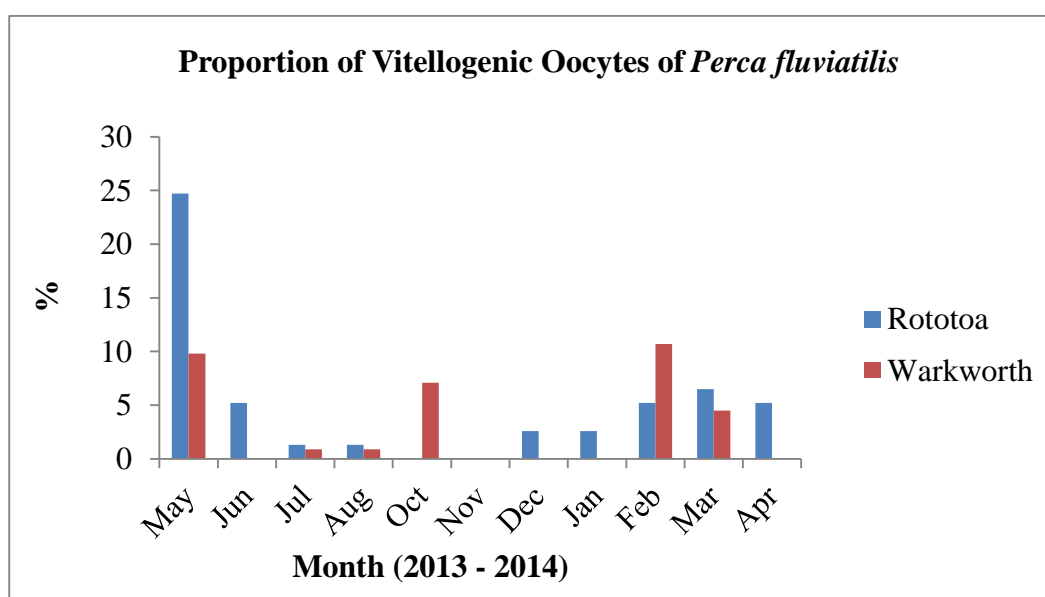


Figure 27 Changes in proportion of *Perca fluviatilis* females with vitellogenic oocytes in Warkworth Quarry Lake and Lake Rototoa

A comparison of the males and females between the two lakes showed that there were no inactive males in Lake Rototoa while Warkworth Quarry Lake had 22.8% of the total male population showing the inactive gonad stage (Table 7). There were also no males showing signs of spawning while this was observed in 0.5% of males in Warkworth Quarry Lake. In females, Lake Rototoa has a slightly higher percentage of atretic oocytes than Warkworth Quarry Lake and had the highest observations of vitellogenic oocytes at 51.5%. On the other

hand, 10.8% of the population in Warkworth Quarry Lake either showed spawning, spent or resting phases, which was higher than Lake Rototoa (Table 7).

Table 7 Proportion of maturational stages of *Perca fluviatilis* gonads in Warkworth Quarry Lake (n=206) and Lake Rototoa (n=99)

Gonad Developmental Activity	Warkworth			Rototoa		
	Males (%)	Females (%)	Total (%)	Males (%)	Females (%)	Total (%)
Inactive	22.8	27.2	50.0	-*	22.2	22.2
Mature developing	15.0	16.0	31.1	20.2	51.5	71.7
Mature spawning	0.5	1.5	1.9	-*	1.01	1.01
Mature spent	-*	1.5	1.5	-*	1.01	1.01
Mature resting	7.3	7.8	15.1	2.02	1.01	3.03
Atretic female	-*	0.5	0.5	-*	1.01	1.01

*No sample showing this developmental stage

Table 8 Size of *Perca fluviatilis* at different ages in Warkworth Quarry Lake and Lake Rototoa

Age (years)	Warkworth (SL mm)		Rototoa (SL mm)	
	Males	Females	Males	Females
0+	118.9	122.2	113.8	113.5
1+	132.7	144.1	166.1	191.2
2+	137.3	169.1	202.8	234.7
3+	185.0	170.6	-*	287.8
4+	-*	185.0	218.0	253.5
5+	-*	-*	-*	-*
6+	-*	239.0	-*	-*
7+	-*	-*	-*	381.0

*No fish catch in this age group

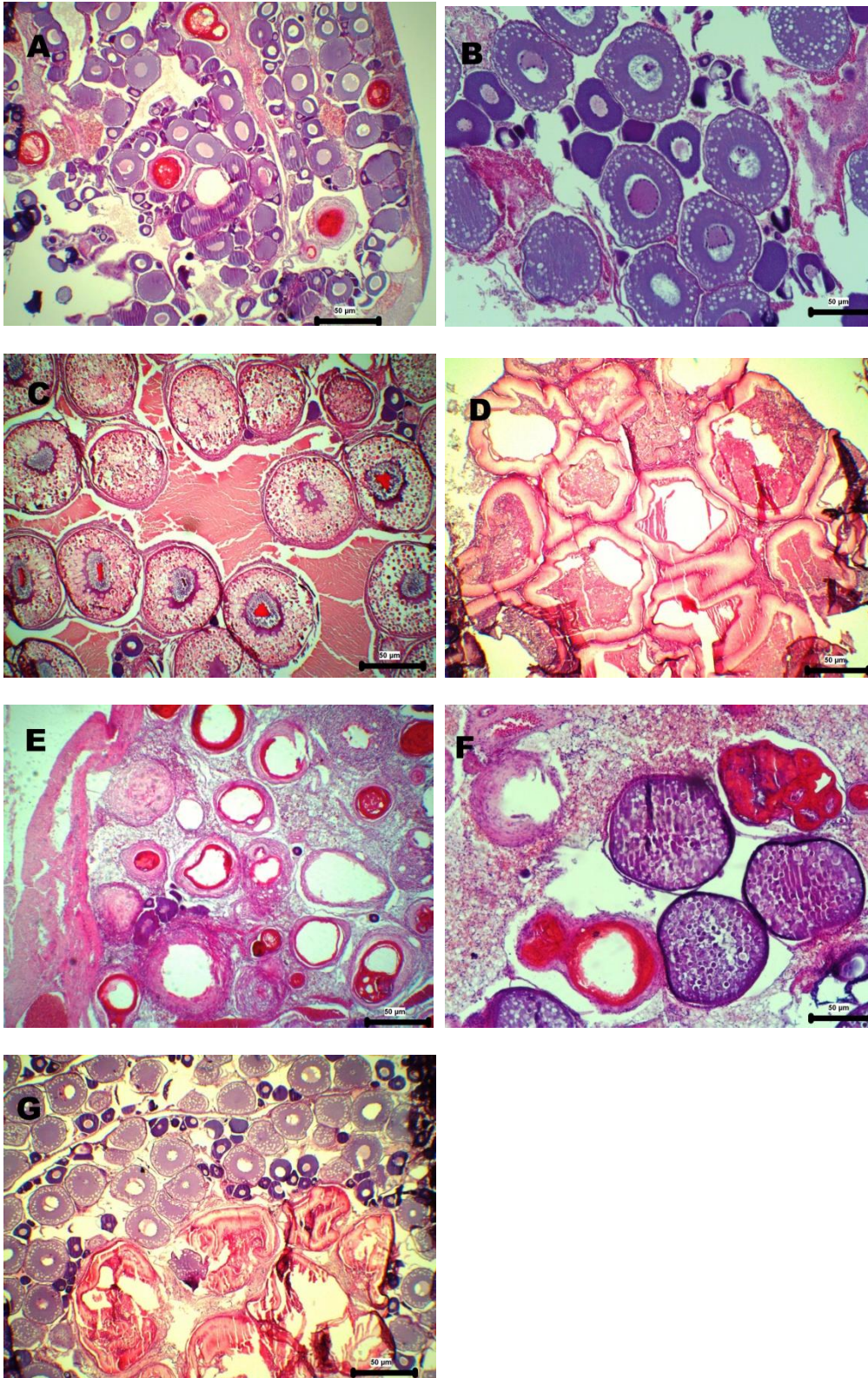


Figure 28 Female stages of oocyte development in *Perca fluviatilis*

A) Peri-nucleolar oocytes of resting female. B) Cortical alveoli oocytes. C) Vitellogenic oocytes. D) Hydrated oocytes. E) Atretic oocytes. F) Vitellogenic and atretic oocytes. G) Asynchronous cortical alveoli, vitellogenic and hydrating oocytes. All images had a scale of 50µm.

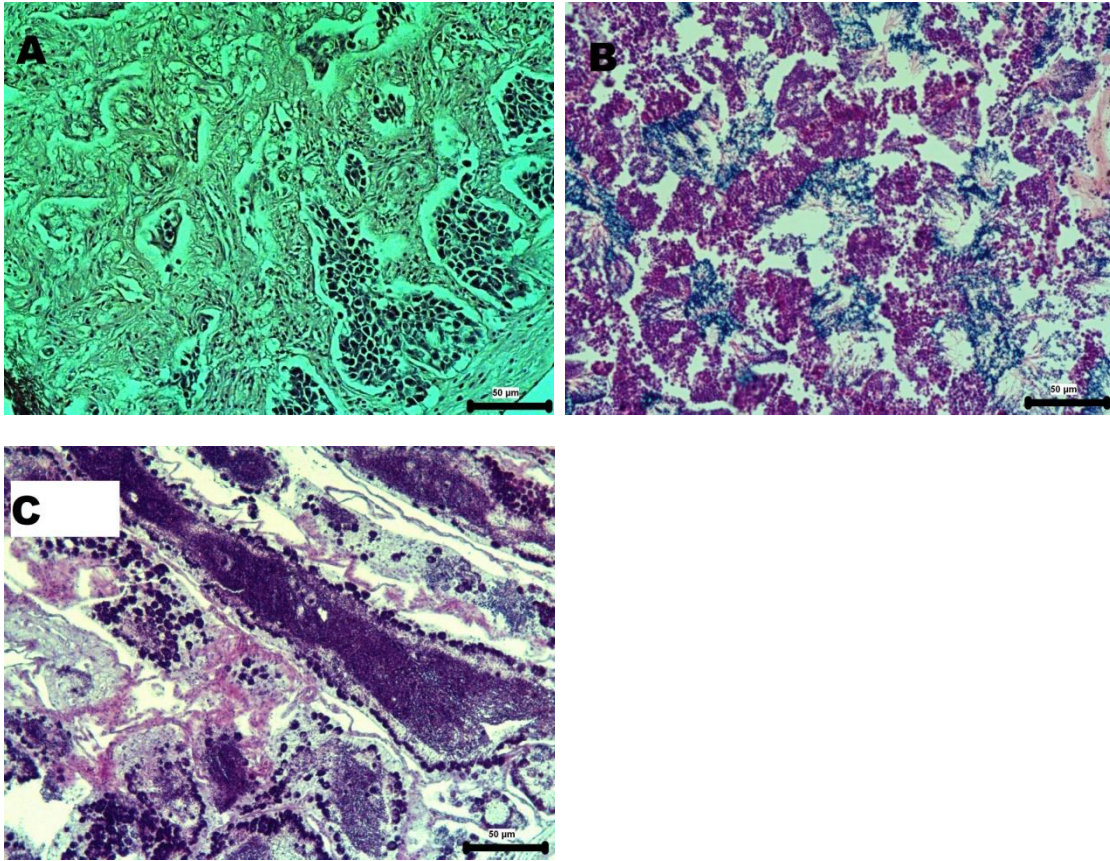


Figure 29 Stages of sperm development in *Perca fluviatilis*

A) Inactive male with spermatogonia. B) Inactive male with spermatocytes. C) Mature developing male with spermatids. All images had a scale of 50µm.

3.5 Discussion

Sex ratios of *P.fluviatilis* populations are generally reported to be female dominated (Hartman, 1974; Thorpe, 1977). In this study the sex ratio of *P.fluviatilis* from Warkworth Quarry Lake was 1:1.7 while that of Lake Rototoa was 1: 3.5. This difference could be explained in part by the type of gear used for sampling and the sample size. Most gear are selective, for example traps in some instances can favour males over females (Thorpe, 1974), gillnets target a specific size of fish (Emmanuel & Chukwu, 2010) and seine nets are non-selective (Hartmann, 1974). It is possible that in this study the impact of gillnet selectivity translated into small sample size, particularly in Lake Rototoa. Small sample sizes result in sharp fluctuations in population sex ratios (Scott & Duncan, 2008) hence the fluctuation between Lake Rototoa and Warkworth Quarry Lake.

The extreme dominance of females over males in Lake Rototoa may be because the population structure of *P.fluviatilis* in this lake is more affected by piscivory, which has been noted in literature (e.g. Thorpe, 1977; Jellyman, 1980). In particular, the fish assemblage in Lake Rototoa is more diverse compared to Warkworth Quarry Lake with top predators such as *Onchorynchus mykiss* (rainbow trout) (released regularly by Fish & Game New Zealand) competing with older *P.fluviatilis* for piscivory. This aspect combined with the higher activity of males compared to females may result in a small proportion of males to females within this population. It has also been suggested that sex ratio is influenced by growth rate of *P.fluviatilis* populations where fast growing populations have a smaller proportion of males compared to slow growing populations (Dryagin, 1948; Konovalova, 1958). This is because in favourable ecological conditions, females thrive better than males (Konovalova, 1958). Although this seems plausible in this study due to the stunted nature of Warkworth *P.fluviatilis*, it is not conclusive.

The size and age at maturity differs slightly between the two populations. *P. fluviatilis* males and females attain sexual maturity in the first year of life in Warkworth Quarry Lake. Males mature at an average size of 118.9mm SL while females have an average size of 122.2mm SL. On the other hand, Lake Rototoa *P.fluviatilis* males attain sexual maturity in their first year with an average size of 113.5mm SL while females attain sexual maturity in their second year at an average size of 191.2mm SL. The age at first maturity in Lake Rototoa is consistent with Lake Pounui *P.fluviatilis* population (Jellyman, 1980). Early

sexual maturation for both *P.fluviatilis* sexes has been reported by several authors (Holcik, 1969; Craig, 1974; Mann, 1978, Jellyman, 1980) and, as in the present study, females are invariably larger than males at first spawning.

Early maturation for males in both Warkworth Quarry Lake and Lake Rototoa populations can be accounted for by growth rates. Sexual maturation has been shown to vary with growth rates and fast-growing *P.fluviatilis* populations are characterized by early age at first maturation (Tesch, 1955; Petrovski, 1960; Thorpe, 1977; Jellyman, 1980; Treasurer, 1981; Morgan et al, 2002). Morgan et al (2002) suggests that early age at first maturity in male *P.fluviatilis* accounts for sex ratio particularly in older classes because of the high energy demands required for gonadal development. To meet this demand males either have to be more active or lose body condition, which in turn makes them more vulnerable to predation compared to females.

Temperature is the main abiotic factor determining gonad development in *P.fluviatilis* (Cecuzzi et al, 2011). Morgan et al (2002) noted that gonadal development initiates in late summer with the majority of females attaining gonadal maturation in winter. Observation of GSI revealed a similar pattern in this study. GSI is a measure of gonadal development (Yoneda et al, 2013) and in Warkworth Quarry Lake the GSI of both *P.fluviatilis* sexes increased from March to July and decreased from August to February the following year. On the other hand, the GSI of both *P.fluviatilis* sexes in Lake Rototoa increased from March to August and decreased from September to February. Gonad development initiated late summer in both lakes. The highest value of GSI coincided with the lowest recorded temperature of the year for both Warkworth Quarry Lake and Lake Rototoa (Metservice New Zealand, 2014). The height of GSI in both *P.fluviatilis* populations is variable because both gonad and somatic masses, on which GSI is calculated, vary in relation to individual condition, the maturational status of the gonads and environmental factors (Yoneda et al., 2013).

In lakes, *P.fluviatilis* hibernate in deep waters during winter and the low temperatures impede their swimming ability (Bergman, 1987; Morgan et al, 2002). This is specifically why it was difficult to capture fish during this period, especially in the significantly bigger Lake Rototoa. It can be inferred that GSI peaks in winter as a result of increased energy utilization for gonad growth due to minimal somatic growth. According to literature, the height of GSI

is the height of spawning and gonad growth precedes conditioning (Adebiye, 2013). In this study gonad growth seems to precede conditioning however the height of GSI does not coincide with height of spawning.

Spawning in *P.fluviatilis* requires an optimal water temperature range of 8°C – 14° C (Lake, 1967; Thorpe, 1977; Gillet & Dubois, 2007) and the height of GSI occurs below this temperature range. This height of GSI in both lakes is an indication of possible earlier spawning activity. In addition, the pattern of increase in GSI for Warkworth Quarry Lake females and Lake Rototoa males show a decrease in GSI in winter accompanied by an increase until the height is reached (Figure 22 & Figure 26). These outliers were identified through histology and observed with gonadal stages associated with spawning activity. This evidence suggests slightly earlier spawning activity than the documented spawning season for New Zealand *P.fluviatilis*. This could be a result of the warmer climate and shorter cold winters experienced in New Zealand.

Duration of gonad development of *P.fluviatilis* in Warkworth Quarry Lake and Lake Rototoa was protracted over 9 months from February to October and December to August respectively (Figure 27). The vitellogenic stage was observed throughout these months. Vitellogenesis usually takes place over 4 months in most European *P. fluviatilis* populations and accumulation of vitellogenin during this process leads to an increase in oocyte size (Komsari et al., 2013). This increases the GSI accordingly. In contrast, the effect of vitellogenesis on oocyte size was not observed in both populations of *P. fluviatilis* in this study. Also, the initiation of vitellogenesis is independent of low temperature in both lakes. European studies reveal that exposure of *P.fluviatilis* to cold temperatures not only synchronizes vitellogenesis but also induces ovary development (Komsari et al., 2013). The exact reason for the variation in observation between European studies and the present study are yet to be determined in a controlled aquaculture setting in New Zealand although, latitude and warmer temperature regimes could account for this. For example, Treasurer and Holliday (1981) reported 7 months of gonadal development while 5 months was recorded for Anzali wetland (Komsari et al., 2013) due to differences in latitude, temperature and day length.

It was also concluded that ovulation and spawning of European *P.fluviatilis* occurred earlier in lower latitudes compared to higher latitude regions (Thorpe, 1977; Gillet & Dubois, 1995; Komsari et al, 2013). A similar observation was made in this study. Histological

analysis of gonad stages suggested that spawning took place over 3 months from September to November in Warkworth Quarry Lake. This is consistent with the population in Lake Pounui (Jellyman, 1980). On the other hand, there was substantial histological evidence of spawning in Lake Rototoa over the 4 months of October to January. Importantly, there were also outliers in both populations with individuals showing signs of spawning outside these mentioned periods. In Warkworth Quarry Lake, 3 females were recorded as spawning in January while 2 males showed signs of spawning in April and 1 female in May in Lake Rototoa. This is a significant finding, which in conjunction with the early peak GSI months in both populations, may indicate an extended spawning season for *P.fluviatilis* in northern New Zealand.

A similar observation was made by Sabetian et al. (2014) with regard to specimens showing signs of possible spawning outside (March) the period reported by Jellyman (1980). However, Sabetian et al. (2014) decided against concluding that those individuals were showing definite signs of spawning due to the snap shot nature of their study. This study however, with the aid of a 12-month analysis, does provide tentative evidence that the spawning season of *P.fluviatilis* may be extended in northern New Zealand. Difference in temperature regimes may account for this as spawning in *P.fluviatilis* has been noted to vary over years in relation to temperature and annual climate (Thorpe, 1977; Cecuzzi et al., 2011).

The summer of 2013-2014 was the third warmest on record according to the country climate report (NIWA, 2014). Warm temperatures have been associated with disrupted and extended spawning season, oocyte atresia during vitellogenesis and asynchronous egg cell development in freshwater fish, including *P.fluviatilis* (Luksiene et al., 2000). Luksiene et al., (2000) reported these observations from nuclear power plants releasing water in to adjacent basins, which is anthropogenic in nature. However, trends such as oocyte atresia and asynchronicity have also been shown in natural environments in New Zealand (e.g. Sabetian et al., 2014). In this study the presence of atretic eggs (Figure 28E) and asynchronous egg cell development (Figure 28G) was recorded during gonadal development of both Warkworth Quarry Lake and Lake Rototoa. The occurrence of this anomaly in both populations coupled with vitellogenic oocytes in the majority of the year, lack of resorbing egg cells and scarce presence of post-ovulatory follicles support the impact of warmer temperature over the reproductive biology of *P. fluviatilis* in New Zealand.

It is extremely difficult to capture large samples of spawning *P.fluviatilis* because of their spawning behaviour, which is iteroparous and spans a short duration of time (Thorpe, 1977). It is therefore not surprising that a small sample of spawning individuals were identified in this study. However, this is an impediment into sequentially following their reproductive strategy from month to month, and a much larger sample from the wild maybe needed to conclusively ascertain if the life history of *P.fluviatilis* has adapted to local conditions 145 years after being introduced.

Chapter 4 Diet and Relative Abundance of *Perca fluviatilis* from Two Lakes in New Zealand

4.1 Introduction

One of the keys to understanding the role of fish in freshwater ecosystems and fish ecological requirements is knowledge of their diet and feeding behaviour (Ramírez-Luna, Navia & Rubio 2008). While these roles indicate relationships based on feeding resources, they also reveal competition and predation effects on community structure (Krebs, 1999). Knowledge of feeding ecology is also fundamental in understanding the processes that function at the individual and population levels because the factors that influence diet can have major impacts on the condition, growth, survival and recruitment of fish. For example, the knowledge on how food is shared among different age classes of the same population is essential in understanding its functioning. Hence, conclusions of field studies on feeding patterns and diet are essential in studying the biology of a fish species. This chapter will briefly discuss the diet of *Perca fluviatilis*, which is an example of a predatory freshwater fish species. *P. fluviatilis* is a Percid and these often play a major part in food web dynamics (Craig, 2008).

Thorpe (1977) presented a detailed account of the feeding behaviour of *P. fluviatilis* in European populations. *P. fluviatilis* are adapted physiologically to daylight feeding (Lagler, Bardach & Miller, 1962) and literature reports that the principal feeding periods are morning and evening (Scott & Crossman, 1973). This feeding rhythm seems to be dependent on availability of food (Ward & Robinson, 1974; Thorpe, 1977) as well as seasonal changes in food availability (Thorpe, 1977; Craig, 1978). The general area of feeding is determined by limnodromous movement. European *P. fluviatilis* swim offshore during the day which leads to open water feeding particularly in the sub-littoral regions (Thorpe, 1977). In the open waters, juvenile *P. fluviatilis* feed in both the pelagic and benthic zones of lakes while adults feed heavily in shallow littoral zones (Klemetsen, 1973). Eutrophication affects the feeding behaviour of adult *P. fluviatilis* which results in sub-littoral and pelagic zone feeding (Thorpe, 1977).

The diet spectrum of European *P.fluviatilis* has been presented in several studies (e.g. McCormack, 1965; Craig, 1978; Rask, 1983; Persson, 1987; Persson & Greenberg, 1990; Heibo, 2005). These studies agree that *P.fluviatilis* have 3 ontogenic niche shifts. The diet of juvenile *P.fluviatilis* shifts from plankton to benthic invertebrates while the diet of adults is primarily comprised of fish. The shift from invertebrates to fish takes place when *P.fluviatilis* have a total length (TL) of 18cm (Allen, 1935; Persson et al, 1991). Most adults are cannibalistic, preying on juvenile *P.fluviatilis* within the population.

Cannibalism is an important factor in *P.fluviatilis* populations because it affects recruitment however; it is regulated by the availability of food (Rask, 1983). Adult *P.fluviatilis* will consume whatever prey is most available hence; they are opportunistic feeders (Herman et al. 1964). In the absence of other prey fish cannibalism dominates in piscivorous *P.fluviatilis* (Mehner et al., 1996). Rask (1983) reported little cannibalism while Mann (1978) reported no cannibalism in piscivorous *P. fluviatilis* due to presence of suitable alternative prey such as *Bythotrephes longimanus* (spiny water flea) as well as spatial separation of juveniles from piscivorous *P.fluviatilis*.

Another important aspect of the diet of *P.fluviatilis* is the effect of temperature on the feeding behaviour. Temperature changes are associated with seasonal changes and Hartman (1974) recorded a change from plankton feeding in summer to benthos feeding in winter in the Bodensee by juvenile *P.fluviatilis*. On the other hand, piscivorous *P.fluviatilis* tend to occur in deep waters in winter where food turnover is not high (Hartman, 1974; Craig, 1978) leading to low level of feeding on benthic prey. Higher temperatures in summer have been reported to trigger piscivory (Mehner et al, 1996) with observations of a wider range of organisms consumed by piscivorous *P.fluviatilis* in the summer (McCormack, 1965; Craig, 1978). A similar observation was made in *P.fluviatilis* populations in Australia in which low temperatures in winter led to a reduction in feeding while a preference of decapods over fish was made by piscivorous *P.fluviatilis* in the summer (Morgan et al., 2002).

Piscivorous *P.fluviatilis* in Western Australia were reported as opportunistic feeders that fed exclusively on *Cherux tenuimanus* (marron) (Morgan et al., 2002). A similar conclusion was given by Duncan (1967) and Griffiths (1976) on the diet of New Zealand *P.fluviatilis*. Piscivorous *P.fluviatilis* predominantly fed on the most abundant size class of bully (*Gobiomorphus cotidianus*) in the Selwyn River, Canterbury and invertebrates were not

exclusive to benthivores but were also significant in piscivores (Griffiths, 1976). Observations on the feeding patterns of New Zealand *P.fluviatilis* indicate a lack of variation with season as observed in European and Western Australian *P.fluviatilis* populations (Griffiths, 1976). These observations, coupled with a clear lack of detailed knowledge of the diet of New Zealand *P.fluviatilis* warrant further investigation.

Although it is known that New Zealand *P.fluviatilis* pose a great threat to native fish species as they prey upon them (e.g. Duncan, 1967; Griffiths, 1976), a better understanding on diet can be achieved through comparative analysis of different populations. Physiologically perch are adapted to a diet of small prey, such as small fish, because anatomically they possess backward-slanting teeth that line their jaws and comb-like rakers that line the inner edges of the gills (Thorpe, 1977). In spite of this adaptation, localized studies on *P. fluviatilis* populations have revealed an important deviation from this. Numerous appendages of large *Cherax tenuimanus* were found in the stomach contents of *P.fluviatilis* which implies that *P.fluviatilis* have also adapted the ability to amputate legs and claws of prey of similar size or greater (Morgan et al, 2002). Such differences are important in the study of the diet of *P.fluviatilis* in order to fully describe the biology of *P.fluviatilis* in New Zealand.

Information on diet of *P.fluviatilis* populations in New Zealand is important in explaining the relative abundance of the species within the ecosystem. This is because the availability and type of food resource depends on the characteristic of the environment (Persson & Greenberg, 1990) and this differs between freshwater systems for *P.fluviatilis* populations. Catch per unit effort (CPUE) is an index which is fundamental in assessing the abundance of stock present in an area (Gulland, 1969). A comparison of CPUE between locations reveals which locality is more favourable. At present there is no information regarding the CPUE of *P.fluviatilis* in New Zealand. Knowledge of CPUE can be useful in formulating effective management practices for this species in New Zealand.

4.2 Objectives

In this study, the stomach contents of *P.fluviatilis* were analyzed and the CPUE calculated to determine catch effort. The specific objectives of this chapter were to (1) describe the diet of *P.fluviatilis* and determine if there are any differences between

populations from two lakes in New Zealand and (2) compare the relative abundance of *P.fluviatilis* among populations from two lakes in New Zealand using CPUE as an index.

4.3 Materials and Methods

Study sites and sampling procedures are previously described in Chapter Two.

4.3.1 Diet Analysis of *Perca fluviatilis*

Stomach contents of 90 *P.fluviatilis* samples from Warkworth Quarry Lake and 75 *P.fluviatilis* samples from Lake Rototoa were visually identified and allocated to 3 categories namely 'empty', 'invertebrates' and 'fish'. Intact invertebrates and fish were specified by scientific name and the frequency of each category from each lake was recorded for each month.

4.3.2 Catch per Unit Effort (CPUE)

CPUE was calculated with the primary assumption that the number of *P.fluviatilis* captured in Warkworth Quarry Lake and Lake Rototoa was proportional to the amount of effort expended (Hubert et al., 2012). Other assumptions made for CPUE were that both populations were in equilibrium; the units of effort operated independently from one another; catchability was constant throughout the entire sampling period and that every individual in the populations had the same probability of capture (Seber, 1982). The time of sampling and the total number of fish caught from both lakes were recorded. The total sampling time was converted into hours and the result used to divide the total number of *P.fluviatilis* caught. The resulting output of this calculation will provided a CPUE estimate in the form of number of fish/net/hour.

4.4 Results

4.4.1 Diet

The composition of diet of *P.fluviatilis* in Warkworth Quarry Lake fell into two prominent categories of invertebrates and fish. Although the invertebrates were not identified they were the most frequent component (82.3%) followed by fish (3.3%), identified as *P.*

fluviatilis, as shown in Table 4.1 Empty stomachs had a % frequency occurrence of 9.9. Invertebrates had the highest % frequency of occurrence in November (23.3%) and the lowest in December (1.1%). *P.fluviatilis* as a prey was found only in fish greater than 180 mm standard length (SL) whereas individuals measuring (50 – 180) mm SL preyed on small invertebrates or had empty stomachs.

Table 9 Stomach Contents of *P.fluviatilis* from Warkworth Quarry Lake and Lake Rototoa as % Frequency of Occurrence

Month	Empty (%)		Invertebrates (%)		Fish (%)	
	Warkworth	Rototoa	Warkworth	Rototoa	Warkworth	Rototoa
May	2.2	18.7	18.9	33.3	-	-
June	-	2.7	6.7	8.0	-	-
July	-	-	-	-	-	-
August	2.2	-	16.7	2.7	-	-
October	2.2	1.3	10.0	-	-	-
November	2.2	2.7	23.3	2.7	1.1	-
December	-	1.3	1.1	6.7	-	-
January	1.1	1.3	5.6	9.3	1.1	1.3
February	-	-	-	4.0	-	1.3
March	-	-	-	5.3	1.1	-
Totals	9.9	28.0	82.3	72.0	3.3	2.6

Similarly, the diet composition of *P.fluviatilis* in Lake Rototoa fell into two prominent categories of invertebrates and fish. The invertebrates were identified as *Paranephrops planifrons* (freshwater crayfish) (Figure 30) and were the most frequent component (72.0%) followed by empty stomachs (28.0%) and *P.fluviatilis* (2.6%) as shown in Table 4.1. *Paranephrops planifrons* had the highest % frequency of occurrence in May (33.3%) and the lowest in August and November (2.7%). Differences in diet were observed between length classes of the specimens caught. *Paranephrops planifrons* and *P.fluviatilis* were only found exclusively in fish samples over 150mm SL. Fish samples measuring (50 – 150) mm SL either contained empty stomachs or consumed small invertebrates.



Figure 30 *Paranephrops planifrons* (freshwater crayfish) removed from the stomachs of *P. fluviatilis* from Lake Rototoa

4.4.2 CPUE

The CPUE of *P. fluviatilis* for both populations in Warkworth Quarry Lake and Lake Rototoa was highest in the month of May with values 0.3 fish/net/hr and 0.6 fish/net/hr respectively. It decreased in both lakes with shared minimum value of 0.006 fish/net/hr (Figure 31 & Figure 32).

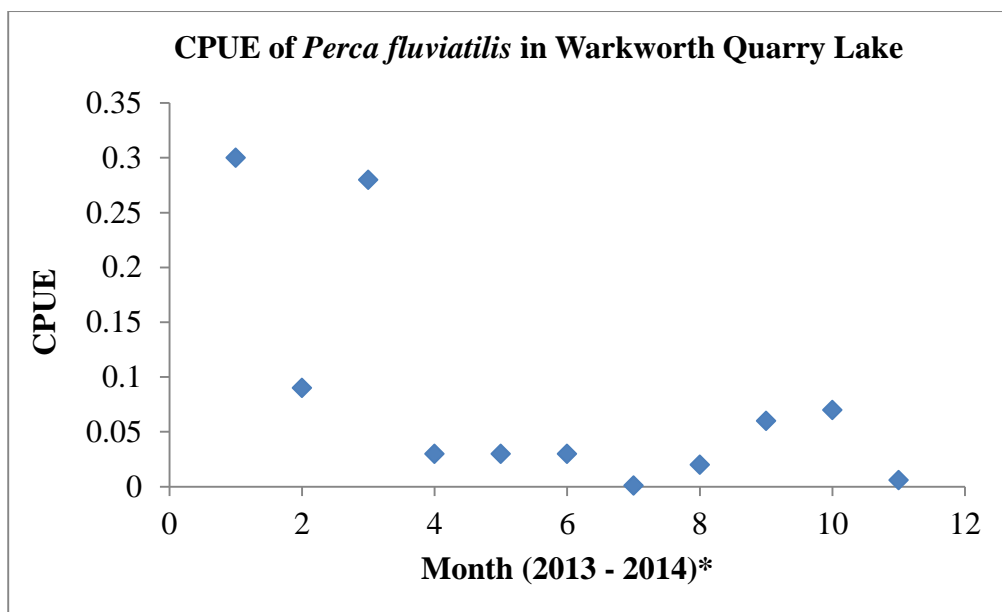


Figure 31 CPUE of *Perca fluviatilis* in Warkworth Quarry Lake.

(*Numbers of axis represent a month where 1= May, 2 = June, 3 = July etc)

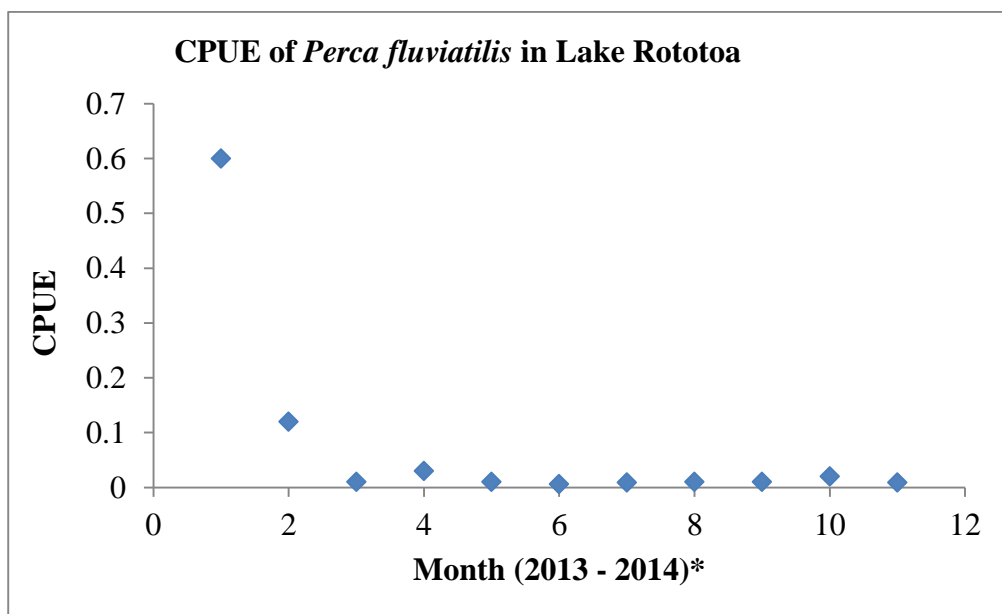


Figure 32 CPUE of *Perca fluviatilis* in Lake Rototoa

(*Numbers of axis represent a month where 1= May, 2 = June, 3 = July etc)

4.5 Discussion

Small invertebrates play a major role in the diet of *P.fluviatilis* populations in both Warkworth Quarry Lake and Lake Rototoa. Similar observations have been recorded in literature (e.g. Persson, 1988; Heibo et al., 2005; Froese & Pauly, 2014) in which invertebrates are important to *P.fluviatilis* juveniles of length > 80 mm TL (Craig, 1978; Persson, 1988). In this study, the dietary shift from invertebrates to piscivory occurred at > 180mm SL in Warkworth Quarry Lake and >150mm SL in Lake Rototoa. Although SL was recorded in this study, this observation falls within the range of > (130 – 180) mm TL recorded in European studies (Craig, 1978; Persson, 1988; Persson et al., 1991). Hence; *P.fluviatilis* in these populations are similar to European *P.fluviatilis* and can be described as maintaining 3 ontogenic diet shifts and habitat use during development.

The presence of *P.fluviatilis* in the diet of piscivorous adults in both populations from Warkworth Quarry Lake and Lake Rototoa indicates the importance of cannibalism. Cannibalism in both lakes was encountered in older size classes which indicate that cannibalistic adult *P. fluviatilis* play a role in structuring these fish populations (Goldspink & Goodwin, 1979). This occurs because it limits juvenile recruitment leading to a population dominated by large size classes (Treasurer, 1993). It explains the population structure of *P.fluviatilis* in Lake Rototoa however; cannibalism is more prominent in Warkworth Quarry Lake. This could be due to the habitat nature of the lake whereby competition of resources, primarily food sources, has limited piscivory adults to cannibalism. Despite this observation, *P.fluviatilis* are opportunistic feeders.

In Lake Rototoa piscivory *P.fluviatilis* predate heavily on native *Paranephrops planifrons* (freshwater crayfish). This is attributed by the occupation of *Paranephrops planifrons* in the littoral zone of the lake (Imbrock, Appenzeller & Eckmann, 1996) during dusk at homogeneous times when *P.fluviatilis* are actively feeding (Craig, 1978; Morgan et al., 2002). Morgan et al. (2002) recorded similar observations with piscivory *P.fluviatilis* preying on *Cherux tenuimanus*. This predation substantiates the claims on the negative impact of *P.fluviatilis* on native species in New Zealand (Duncan, 1967; Griffiths, 1976). *Paranephrops planifrons* is a threatened species whose populations are in gradual decline (Whitmore, Huryn, Arbuckle & Jansma, 2000) however; its predation by *P.fluviatilis* makes it a vulnerable species. Its predation also highlights the possible adaptation of *P.fluviatilis* to

consuming prey larger to their body size. Not only were appendages of large *Paranephrops planifrons* found in the majority of stomachs analyzed but also intact samples of large individual prey. A similar conclusion to the observation made by Morgan et al. (2002) can be constructed with regards to *P.fluviatilis* in Lake Rototoa. This population has enhanced its capability as an opportunistic feeder by developing an ability to consume whole or amputate prey larger than body size.

Griffiths (1976) highlighted that *P.fluviatilis* in New Zealand showed no variation of feeding patterns with season. In this study, *P.fluviatilis* populations in both lakes showed seasonal variation in feeding pattern. A higher incidence of samples with no stomach contents were encountered during the winter months between June and August. The highest temperatures were experienced from December to February and coincided with an increased frequency of food occurrence in the stomachs. This can be credited to the effect of temperature on feeding behaviour of *P. fluviatilis*. In winter when temperatures are cold *P.fluviatilis* occur in deep waters and with nominal feeding on benthic prey (Craig, 1978; Golspink & Goodwin, 1996; Morgan et al., 2002) while in summer the level of feeding increases due to warmer temperatures and increased availability of food (Craig, 1978).

It is often reported that using catch per unit effort (CPUE) as a measure of fish abundance will show a proportional relationship whereby CPUE will increase due to an increase in total population size (Ross, 2014). In this study the primary assumption for using CPUE as an index of relative abundance was satisfied. The number of *P. fluviatilis* captured at each sampling period in Warkworth Quarry Lake and Lake Rototoa were proportional to the amount of effort expended (Hubert et al. 2012). In spite of this, it is difficult to further outline the relative abundance of *P.fluviatilis* within both populations because CPUE decreases over the sampling months in both lakes despite an increase in total population size due to reproduction. Also, the behaviour of *P.fluviatilis* in both lakes over the winter period does not conform to the assumption that catchability is constant throughout the entire sampling period. This cannot be disregarded as it is an important factor in the biology and population dynamics of *P.fluviatilis*. In view of this, further investigations are required so that an outline of the CPUE of *P.fluviatilis* in Warkworth Quarry Lake and Lake Rototoa can be conferred.

Chapter 5 Key Findings, Significance and Future Direction

5.1 Introduction

This study focused on enhancing the understanding of the biology and population dynamics of *Perca fluviatilis* in New Zealand through the use of more accurate methods of age estimation and analysis of reproductive parameters. This was examined comparatively between two lakes in North Island of New Zealand namely Warkworth Quarry Lake and Lake Rototoa. These are located at latitude 36°24'S, longitude 174°40'E and latitude 36°31'S, longitude 174°14'E respectively. They were sampled for *P.fluviatilis* once a month over a duration of 12 months. The estimation of age was based on otolith increment analysis in Chapter 2. A combination of body measurements and age estimates was used to evaluate the growth patterns. The results also provided information on differences in size and age based population characteristics compared across latitudinal gradients.

Chapter 3 focused on establishing reproductive parameters including sex ratio, size and age at sexual maturity through gonad histology. Further information on life history stages associated with gonadal development was generated. An attempt at generating catch per unit effort as an index for relative abundance was made in Chapter 4 as well as comparative analysis of diet between the two populations. This was essential in determining the role and impact of *P.fluviatilis* on the freshwater ecosystems within the area of study. The aim of this chapter is to highlight the key findings of this study, discuss their significance and identify priority areas for further research if required.

5.2 General Discussion

Comparative analysis of age and size structure of *P.fluviatilis* revealed the presence of an almost equal proportion of males and females in the youngest age class present (age class 0+) in both Warkworth Quarry Lake and Lake Rototoa populations. Similar results were obtained in Lake Pounui *P.fluviatilis* population (Jellyman, 1980) and a conclusion can be reached that both sexes are equally represented at hatching in New Zealand populations. Successful age classes (0+ and 1+) subsequently dominate the population in Warkworth Quarry Lake compared to Lake Rototoa population. Females dominate both populations in

general and this dominance can be attributed to high mortality of males due to selective predation on males by older fish or other predatory fish (Thorpe, 1977; Jellyman, 1980).

Data on growth patterns of *P. fluviatilis* in Warkworth Quarry Lake and Lake Rototoa follow a similar growth pattern to Lake Wainamu population (Sabetian et al., 2014) with rapid growth in the first year. This displays the importance of fast early growth in *P. fluviatilis*. According to the growth performance index ϕ' of European *P. fluviatilis* provided by Tesch (1955), growth rates for both Warkworth Quarry Lake and Lake Rototoa can be classed as 'very good' and 'moderate' respectively. Warkworth Quarry Lake population was similar to other *P. fluviatilis* populations in the southern hemisphere (e.g. Morgan, et al., 2002; Sabetian et al., 2014) with regards to having rapid growth rates in early life but attaining smaller maximum sizes as adults. This subsequently leads to a stunted population (Alm, 1946; Rask, 1983; Morgan et al., 2002). On the other hand, *P. fluviatilis* in Lake Rototoa had higher growth rates compared to European populations. This indicates that populations in New Zealand cannot be wholly described as stunted because high growth rates can be achieved under favourable conditions such as abundance of food and warmer climate regime.

Another key finding in Chapter 3 was expected size-at-age. While it is generally accepted that female *P. fluviatilis* grow faster than males (e.g. Craig, 1974; Thorpe, 1977; Jellyman, 1980; Cecuzzi et al., 2011; Sabetian et al., 2014) this was not the case in both Warkworth Quarry Lake and Lake Rototoa *P. fluviatilis* populations. There were no significant differences in expected size-at-age between males and females of both populations. This change in growth pattern is of significant interest as it could be an adaptation trait.

Use of otolith increment analysis in age determination proved advantageous in this study. Validation of both daily and annual growth increments was provided through the presence of a strong relationship between otolith weight and age and the regularity of daily deposition of otolith increments (Panella, 1971). Annual increment analysis showed a maximum age of 6+ and 7+ in Warkworth Quarry Lake and Lake Rototoa respectively. Although this does not describe the lifespan of *P. fluviatilis*, it offers a fundamental aspect regarding this life trait. Observations on maximum age have been varied (e.g. Muncy, 1962; Scott & Crossman, 1973; Thorpe, 1977) however; it can be inferred that *P. fluviatilis* populations in the two lakes are relatively short lived with a lifespan between 5 and 8 years.

Prior to this study, the birth date of *P.fluviatilis* samples was set as 1 September based on the current spawning season of *P.fluviatilis* in New Zealand (Jellyman, 1980; Sabetian et al., 2014). Random sampling from individuals used in this study showed that the hatching date of *P.fluviatilis* in Warkworth Quarry Lake was 10 September and 29 November in Lake Rototoa. An understanding of this major life event was provided through analysis of daily otolith increments. These hatching dates have significant relevance in the reproductive biology of *P. fluviatilis*.

The reproductive biology of *P.fluviatilis* in Warkworth Quarry Lake and Lake Rototoa was presented in Chapter 3. The sex ratios of the two *P.fluviatilis* populations were different. This finding is similar to European *P.fluviatilis* in which the sex ratio differs with location, growth rate and sampling gear (Thorpe, 1977). Based on growth and location, the proportion of females in Lake Rototoa *P.fluviatilis* was higher in comparison to Warkworth Quarry Lake *P.fluviatilis*. The use of gillnets in this study resulted in small sample size for both lakes and this lead to sharp fluctuations in population sex ratios (Scott & Duncan, 2008). The influence of sampling gear in sex ratio of *P.fluviatilis* contributes significantly to the management of this species in New Zealand. Accordingly, the most appropriate sampling gear can be selected to fulfil the management objectives set for *P.fluviatilis* in a particular ecosystem.

An analysis of size and age at maturity established early sexual maturity for *P.fluviatilis* in Warkworth Quarry Lake and Lake Rototoa. Both sexes in Warkworth Quarry Lake reached maturity in their first year while male matured in their first year and females in their second in Lake Rototoa. The results in Lake Rototoa were similar to those observed in Lake Pounui (Jellyman, 1980). Females in all *P.fluviatilis* populations studied in New Zealand are invariably larger than males at first spawning. This finding is significant in understanding the biology of *P.fluviatilis* in New Zealand. Sexual maturation has been shown to vary with growth rates and fast-growing *P.fluviatilis* populations are characterized by early age at first maturation (Tesch, 1955; Petrovski, 1960; Thorpe, 1977; Jellyman, 1980; Treasurer, 1981; Morgan et al, 2002). In this study it can be concluded that the two populations have a high growth rate in younger year classes which results in early sexual maturation within the population.

Temperature was the main abiotic factor determining gonad development in *P. fluviatilis* in Warkworth Quarry Lake and Lake Rototoa. This was evident in gonadosomatic index (GSI) which initiated an increase in February. Morgan et al (2002) observed a similar trend in which gonadal development began in late summer and the majority of females attained maturation in winter. Gonad growth preceded conditioning in both lakes however; the height of GSI does not coincide with height of spawning. The presence of individuals from both lakes with gonadal stages associated with spawning as well as the height of GSI in the winter months strongly suggest slightly earlier spawning than the documented spring spawning for *P. fluviatilis* in New Zealand. This adaptation could be attributed by the warmer climate and shorter cold winters experienced in New Zealand compared to conditions in Europe.

Vitellogenesis usually takes place over 4 months in most European *P. fluviatilis* populations and cold temperatures synchronize vitellogenesis and induce ovary development (Heidinger & Kayes, 1986; Komsari et al., 2013). The evidence in this study shows that vitellogenesis takes place over 9 months in Warkworth Quarry Lake and Lake Rototoa *P. fluviatilis* populations. In addition, initiation of vitellogenesis was independent of low temperature and asynchronous development was recorded in some individuals. With the exclusion of outliers, spawning took place over 3 months from September to November in Warkworth Quarry Lake and over 4 months from October to January in Lake Rototoa. Although spawning in Warkworth Quarry Lake was consistent with Lake Pounui (Jellyman, 1980), the difference observed in Lake Rototoa indicates the effect of latitude, temperature and day length on reproduction. The significance of this finding is that it substantiates the claim that latitudinal gradient accounts for differences in reproductive traits between different *P. fluviatilis* populations and provides tentative evidence of an extended spawning season for this species in northern New Zealand. This has major impacts on effective management practices for this species.

The impact of temperature on reproduction was demonstrated through the presence of atretic eggs and asynchronous egg cell development which was recorded during gonadal development of both Warkworth Quarry Lake and Lake Rototoa *P. fluviatilis* populations. Warm temperatures have been associated with disrupted and extended spawning season, oocyte atresia during vitellogenesis and asynchronous egg cell development in freshwater fish, including *P. fluviatilis* (Luksiene et al., 2000, Sabetian et al., 2014). *P. fluviatilis*

populations in this study revealed the lack of resorbing egg cells and scarce presence of post-ovulatory follicles in addition to the presence of vitellogenic oocytes throughout most of the year, atresia and asynchronous development. The summation of these characteristics supports the influence of warmer temperature over the reproductive biology of *P. fluviatilis* in New Zealand.

Chapter 4 analysed the diet of *P. fluviatilis* populations in Warkworth Quarry Lake and Lake Rototoa. *P. fluviatilis* in these lakes experience 3 ontogenic diet shifts similar to European *P. fluviatilis* and habitat use during development. Cannibalism encountered in both populations. This characteristic coupled with observations on age structure and male mortality presented in Chapter 2 provides adequate evidence of the important role of cannibalism as a determinant of age structure in the population of *P. fluviatilis*. There was an outstanding decrease in proportion of individuals between age 1+ and subsequent age classes in both lakes due to the vulnerability of juvenile fish to cannibalistic adult fish. The significance of this finding contributes to the knowledge of the biology of *P. fluviatilis* in New Zealand as it explains the mortality rate. The survivorship of *P. fluviatilis* in Warkworth Quarry Lake and Lake Rototoa populations fall in the range regarded as the natural annual mortality rate in *P. fluviatilis* of between 43-70% due to cannibalism (Thorpe, 1977).

The difference in diet preference of adult *P. fluviatilis* in Warkworth Quarry Lake and Lake Rototoa is an important finding. Adults in Warkworth Quarry Lake were exclusively cannibalistic while those in Lake Rototoa primarily fed on *Paranephrops planifrons* (freshwater crayfish). This leads to the conclusion that piscivorous *P. fluviatilis* in New Zealand are opportunistic feeders similar to other populations (e.g. Duncan, 1967; Griffiths, 1976; Morgan et al., 2002). The evidence presented in Chapter 4 strongly suggests that *P. fluviatilis* have developed an ability to consume prey larger than their body size. A similar suggestion was made by Morgan et al. (2002). This is a vital aspect with regards to the negative impact of *P. fluviatilis* on native species in New Zealand. Predation of *Paranephrops planifrons* by *P. fluviatilis* in Lake Rototoa substantiates the claims that this species threatens biodiversity (Duncan, 1967; Griffiths, 1976; Closs et al., 2002).

There is seasonal variation in the feeding patterns of *P. fluviatilis* in this study. This is contrary to the findings presented by Griffiths (1976) who highlighted a lack of variation of

feeding patterns with season. Temperature affects feeding patterns because the level of feeding increases with an increase in temperature (Craig, 1978).

An attempt to determine relative abundance from catch per unit effort (CPUE) was impeded by the observation of a decrease in CPUE with increase in total population size. This finding is significant for further studies as it provides a reference point for improvement in sampling methods.

While the aims and objectives of this study were addressed, there remain a few gaps in relation to the population dynamics of *P.fluviatilis* populations in Warkworth Quarry Lake and Lake Rototoa. Firstly, a further exploration of the reasons why a lack of difference in expected size-at-age for males and females in the two *P.fluviatilis* populations is required. The general notion is that female *P. fluviatilis* grow faster than males (e.g. Craig, 1974; Thorpe, 1977; Jellyman, 1980; Cecuzzi et al., 2011; Sabetian et al., 2014). This finding is essential as it suggests an adaptation of *P. fluviatilis* to New Zealand freshwater ecosystems and warrants further investigation.

There is strong evidence of a possible extended spawning season of *P.fluviatilis* in this study however; several questions need to be answered before this finding is conclusive. Much can be gained from larger samples captured over a longer period of time. In this study, a small sample of spawning individuals was identified due to the difficulties experienced in capturing spawning *P.fluviatilis*. The spawning behaviour of *P.fluviatilis* is iteroparous and spans over a short duration therefore a longer period of sampling increases the chances of capturing a larger volume of spawning individuals. In addition, the observations on GSI and extended duration of vitellogenesis in these populations can be better understood in a controlled aquaculture setting. This would be an effective way to conclusively ascertain the mechanisms behind the successful adaptation of *P.fluviatilis* to local conditions in New Zealand.

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