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In addition to the above conditions, authors give their consent for the digital copy of their work to be used subject to the conditions specified on the Library Thesis Consent Form and Deposit Licence.
Early life history of snapper
(*Chrysophrys auratus*) in northern New Zealand.

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A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy in Marine Sciences, University of Auckland, 2013.
Figure 1. *Chrysophrys auratus* larvae (scale bar = 1 mm)
Abstract

Snapper (*Chrysophrys auratus*) is a commercially-important fish in New Zealand and Australia. Variability in interannual recruitment is high in this species, which affects subsequent adult abundances, and therefore, an understanding of the factors that affect recruitment is critical to the successful management of fished populations. Research presented in this thesis investigates some aspects of the early life history of *C. auratus* in four harbours (Kaipara, Manukau, Mahurangi and Huruhi) in northern New Zealand.

Histological gonad analyses showed that recruitment to the Kaipara Harbour must originate from spawning activity outside the harbour. Adult fish captured within the harbour had underdeveloped gonads and reabsorbed their oocytes prior to spawning. Analyses of daily otolith increments showed that larvae spent 17–33 days in the plankton before settling in shallow waters of all four harbours. The successful spawning period that produced settled juveniles was only 29–109 days, despite a spawning season of ≤4 months, indicating that recruitment to some harbours may be limited by environmental conditions that affect larval survival or transport to settlement habitats. Daily settlement was significantly positively correlated with temperature, tidal range and on-shore winds (of the previous day) in some harbours, suggesting that these variables facilitate the on-shore transport of larvae. High temperatures are likely to be important for larval survival, with average water temperatures during the pelagic larval duration (PLD) >18 °C for 91% of fish captured.

Recruitment may also be affected by growth rate and resource-allocation strategies. Growth rates varied significantly among sites, with fish from the Kaipara and Huruhi Harbour sites having the fastest growth. Faster-growing larvae spent less time in the plankton and continued to grow faster as juveniles, which is likely to decrease their mortality rate. Resource-allocation in 0+ year fish was found to change from maximising growth in summer to maximising lipid accumulation in mid-autumn. Lipid concentrations in fish during summer and early autumn were very low, making them very vulnerable to starvation mortality. Overall, these results provide us with a better understanding on the ecological processes that affect the recruitment of *C. auratus*, which can be used to more effectively manage populations of this important species.
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Chapter 1

General Introduction

1.1 Factors affecting larval abundance and recruitment of fishes

The vast majority of marine teleost fishes have a pelagic larval phase that is a critical period in the life history of fishes (Houde 2008, 2009). Interannual variability in recruitment (defined in this study as the abundance of recently-settled 0+ year fish) is often extremely high, and this can have major impacts on the subsequent abundance of juvenile and adult fishes (e.g., Bradford 1992; Leggett and DeBlois 1994; Hamer and Jenkins 2007; Hamer et al. 2010). Hjort (1914) first proposed that variations in larval abundance could determine the size of adult fish populations with his critical period hypothesis. This hypothesis proposed that larvae must commence feeding before a certain critical period that occurred shortly after yolk-sac absorption, otherwise the larvae would pass a point-of-no-return and die. Hjort concluded that mass mortality of larvae was likely to occur when feeding conditions were not suitable, which in turn, would regulate adult population size. This hypothesis led to a suite of related hypotheses that proposed that prey abundance is the critical factor in determining larval survival, the most well-known being Cushing’s match/mismatch hypothesis (Cushing 1969; Cushing 1990), Lasker’s stable ocean hypothesis (Lasker 1978), and Cury and Roy’s optimal environmental window hypothesis (Cury and Roy 1989).

Cushing’s match/mismatch hypothesis proposed that high recruitment success will occur when peak abundance of fish larvae and their prey occurs simultaneously (Cushing 1969; Cushing 1990). He hypothesised that a relatively fixed time of spawning coupled with a variable time of plankton blooms produced variability in interannual recruitment. Cushing’s match/mismatch hypothesis has received considerable support, particularly for annual-spawning fish species found in high latitudes (e.g., Ellertsen et al. 1989; Fortier et al. 1995; Kristiansen et al. 2011).
Lasker’s stable ocean hypothesis proposed that in periods of calm weather temporary vertical stratification will occur in upwelling systems that will produce high concentrations of fish larvae and prey at the strata interfaces, resulting in high feeding rates and good survival for fish larvae (Lasker 1978). There is some evidence supporting Lasker’s hypothesis, particularly for clupeiform larvae (Peterman and Bradford 1987; Somarakis et al. 1997; McClatchie et al. 2007). The optimum environmental window hypothesis proposed that moderate wind stress produces the highest recruitment levels in wind-driven upwelling systems by increasing the supply of nutrients, and hence, the primary productivity, to an area (Cury and Roy 1989).

The critical period hypothesis and related prey-driven recruitment hypotheses were the focus of fisheries recruitment research for much of the 20th century (Houde 2008), however, reviews on recruitment variability for larval fish have shown that often the relationship between food abundance and recruitment is poor (Anderson 1988; Leggett and DeBlois 1994; Cowan and Shaw 2002). Later studies have shown that predation (Bailey and Houde 1989) and environmental conditions (Werner et al. 1997; Myers 1998) are also critical influences on recruitment. After nearly 100 years of research on recruitment variability it is now generally accepted that no single mechanism or process is responsible for recruitment variability in fish populations, but numerous abiotic and biotic factors interact over the entire larval duration, influencing the growth and survival of larvae, and ultimately, their abundance (Leggett and DeBlois 1994; Cowan and Shaw 2002; Houde 2008, 2009). In a recent review of larval fish recruitment processes, Houde (2008) concluded that five dominant mechanisms generally regulate recruitment variability; 1) water temperature, 2) physical processes, 3) food availability, 4) predation and 5) growth and size. In addition, the influence of growth and survival processes on fish larvae is highly species specific because it is affected by the life history and behaviour of the species.

1.1.1 Spawning stock size and spawning behaviour

The supply of new recruits to a particular settlement location is initially dependent on the supply of eggs and larvae to the region. Production of eggs and larvae is influenced by the size of the spawning population, fecundity, fertilization success and egg quality (Hilborn and
Walters 1992; Myers and Barrowman 1996; Trippel 1999; Marteinsdottir and Begg 2002). Often, older, larger fish produce bigger, better quality eggs, which, in turn, produce bigger larvae that have a higher recruitment success (Trippel 1998; Higashitani et al. 2007; Sogard et al. 2008).

Spawning behaviour also affects recruitment variability, and fish can maximize their reproductive success by forming spawning aggregations (Rowe and Hutchings 2003), spawning in regions or periods of high plankton productivity (Zeldis et al. 2005; Kristiansen et al. 2011), or by selecting spawning areas that favour larval retention or transport to settlement habitats (Iles and Sinclair 1982; Hutchings et al. 2002; Sponaugle et al. 2002).

1.1.2 Transport of larvae to settlement habitats

Physical processes, such as currents, fronts, upwellings and wind stresses, act to transport and/or retain fish larvae. For demersal species that settle in particular habitats after a pelagic larval duration, recruitment success is not only dependent on abiotic and biotic factors that promote good larval survival, but is also governed by physical processes that facilitate the transport of larvae to settlement habitats (Jenkins et al. 1997). Prior to the development of swimming ability, early-stage larvae may be transported large distances by prevailing currents or winds as relatively passive particles (Jenkins et al. 1997; Jenkins et al. 1999). Older fish larvae of most perciform species have well-developed swimming abilities and many are capable of sustaining swimming speeds that are faster than mean ambient current speeds for long periods of time (Leis 2006). Furthermore, the late-stage larvae of many species are capable of directional travel towards settlement cues e.g., odours or sound (Leis 2006). Late-stage fish larvae are often found to utilise physical processes to their advantage, e.g., by facilitating their entry into estuaries by selective tidal stream transport (Rijnsdorp et al. 1985; Rowe and Epifanio 1994), by utilizing tidal fronts and tidal streams (Kingsford et al. 1991; Kingsford and Suthers 1996; Churchill et al. 1999; Forward Jr et al. 1999), or by using boundary layers to ensure their retention in settlement habitats that have high current flows (Breitburg et al. 1995). Several studies have demonstrated significant correlations between the settlement of fish larvae and environmental parameters such as lunar cycle and tidal amplitude (Findlay and Allen 2002; D’Alessandro et al. 2007; Vallès et
al. 2009), winds (Jenkins et al. 1997; Findlay and Allen 2002; Raventos and MacPherson 2005) and solar radiation (Bergenius et al. 2005). Complex coupled biophysical models that link physical hydrodynamic processes with biological processes and larval behaviour have been developed that explain a significant proportion of the recruitment variability in some fish populations (Miller 2007).

1.1.3 Growth and survival

Numerous studies have shown that faster-growing larvae generally experience higher survivorship in the plankton (e.g., Meekan and Fortier 1996; Hare and Cowen 1997; Takasuka et al. 2003; Shahidul Islam et al. 2010). Anderson (1988) expanded on the concept that larval recruitment was controlled by both predation and starvation with his growth-mortality hypothesis. This hypothesis combines three earlier theories; 1) larger fish larvae are less susceptible to predation, 2) faster-growing fish larvae are less vulnerable to predation because they spend less time as small larvae, and 3) faster-growing fish larvae reach metamorphosis faster reducing their overall larval mortality rate. Much evidence exists that supports this hypothesis (e.g., Plaza and Ishida 2008; Shahidul Islam et al. 2010; Takahashi et al. 2012). Faster-growing fish larvae are also usually in better condition at the time of settlement, which leads to their further success as juveniles (Searcy and Sponaugle 2001; Shima and Findlay 2002; Sponaugle and Grorud-Colvert 2006).

Growth of fish larvae is mainly determined by water temperature and food availability (Houde 2009). Water temperature often explains a substantial amount of the interannual recruitment variability in many marine fish species (e.g., Francis 1993; Jacobson and MacCall 1995; Jenkins and King 2006), particularly for high latitude populations at the limit of their geographical range (Myers 1998). Temperature affects fish recruitment by both direct and indirect processes. Metabolic activity, food consumption, rate of development and growth of larval fishes all increase with increasing water temperature, up to a thermal maximum (Blaxter 1992). Water temperature also affects food availability (quantity and timing), as well as the growth and survival of predators and competitors (Houde 2009).

Starvation is generally accepted to be one of the major factors that influences the abundance of larval fish (Hjort 1914; Cushing 1990; Leggett and DeBlois 1994), although
relationships between prey abundance and recruitment are often weak (Leggett and DeBlois 1994; Cowan and Shaw 2002). Larvae need to consume approximately 50–150% of their body weight per day to maintain observed growth rates (Houde and Schekter 1989; Frommel and Clemmesen 2009). Initially, it was thought that prey levels in most marine environments were too low to support the growth of fish larvae, and the majority of larvae died of starvation (Lasker 1975; Hunter 1981). Subsequent research indicates that microturbulence and prey patchiness can increase the prey encounter rates for fish larvae considerably (Rothschild and Osborn 1988; MacKenzie et al. 1994). As a consequence, fish larvae are capable of high consumption rates, even at low prey concentrations (Munk 1995). However, it is still probable that during unfavourable environmental conditions a substantial proportion of fish larvae will be in poor nutritional condition (e.g., Clemmesen 1996; Buckley et al. 2006), which is likely to lead to lower growth rates, starvation and/or increased mortality via predation (Vigliola and Meekan 2002; Takasuka et al. 2003; Houde 2008).

For many species, variability in the abundance of late-stage fish larvae can have major impacts on the subsequent abundance of juvenile fish (e.g., Bradford 1992; Mertz and Myers 1995), often producing 10 to 100 fold interannual differences in recruitment (Pope and Macer 1996; Houde 2009). The ability to predict recruitment and year-class strength for any given year would greatly assist fisheries management, however, the relationship between recruitment and its governing factors is complex, and for most fish species there is still much to learn before we can accurately predict recruitment levels.
1.2 Taxonomy, general biology and early life history of *Chrysophrys auratus*

![Figure 1.1. A newly-recruited *Chrysophrys auratus* hovering above the seafloor](Photo: Crispin Middleton, NIWA)

*Chrysophrys auratus* (Forster in Bloch & Schneider 1801) is commonly known as snapper in New Zealand and is widely distributed throughout the warm temperate waters of Australia and New Zealand. It is a member of the family Sparidae (Order Perciformes) that contains 33 genera and over 110 species, which are distributed throughout the tropical and temperate waters of the Atlantic, Indian and Pacific Oceans (Froese and Pauly 2010). The taxonomic status of *C. auratus* is complex and is currently unresolved. Historically, more than 20 scientific names have been used to describe the species (Paulin 1990). Prior to 1990, *C. auratus* was the name used in New Zealand, while *Chrysophrys unicolor* Quoy & Gaimard 1824, *Chrysophrys guttulatus* (Valenciennes 1830) or *C. auratus* were used in Australia. Paulin (1990) found no differences in the morphometric measurements of *C. auratus*, *C. unicolor*, *C. guttulatus* and the closely related Japanese species, *Pagrus major*. On this basis,
Paulin synonymised all four species into a single species, namely *Pagrus auratus*. However, recent mitochondrial DNA (mtDNA) analyses of *P. major* and *P. auratus* showed that while they are closely related, there are sufficient genetic differences between the two to separate them into two species (Tabata and Taniguchi 2000; Chiba *et al.* 2009). Furthermore, mtDNA analyses showed that the genus *Pagrus* is not monophyletic; *P. major* and *P. auratus* were found to share a different ancestor from the other three species of *Pagrus* tested (*P. pagrus, P. auriga, and P. caeruleostictus*) (Orrell and Carpenter 2004; Chiba *et al.* 2009). Based on the mtDNA data, Gomon (2008) recommended that the genus *Chrysophrys* should be reinstated for New Zealand and Australian snapper, and accordingly, the name *C. auratus* is used in this thesis. However, the assignment of *C. auratus* to the genus *Chrysophrys* has been questioned by some researchers (M. Gomon, pers. comm.) and many researchers continue to use *P. auratus*.

*Chrysophrys auratus* is distributed throughout Australia south of 18 °S, and in New Zealand north of 42 °S (MacDonald 1982; Paulin 1990; Fowler *et al.* 2005; Ministry of Fisheries 2010). It is the only representative of the Sparidae present in New Zealand and is a highly-prized fish that supports significant commercial, recreational and customary (indigenous) fisheries. At least three genetically distinct stocks of *C. auratus* occur in northern New Zealand; an east coast stock that is distributed from the Bay of Islands to East Cape, a west coast stock that is distributed from Ninety Mile Beach down the west coast of the North Island, and a southern stock that is distributed around the northern part of the South Island (Smith *et al.* 1978; Bernal-Ramirez *et al.* 2003). *Chrysophrys auratus* is a predatory, demersal fish that is found from shallow waters of estuaries and bays to beyond the edge of the continental shelf in waters up to 200 m deep (MacDonald 1982). It inhabits a wide variety of habitats from sandy or muddy substrata to rocky reefs, but is most commonly found over mud or sand at depths of less than 50 m (Crossland 1981; Francis 1993). *Chrysophrys auratus* is an opportunistic feeder consuming a wide variety of prey. Copepods, mysid shrimps and caridean shrimps are the primary prey for small fish (<100 mm fork length, FL) (Usmar

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1 mtDNA results show that *P. major* and *C. auratus* are sister species (Chiba *et al.* 2009), and thus, they should be in the same genus. However, the taxonomy of the two species is currently unresolved leaving the two species in different genera.
2012), whereas larger fish (>100 mm FL) primarily consume crustaceans, molluscs, echinoderms, polychaetes and fish (Colman 1972; Crossland 1981; Kingett and Choat 1981; Usmar 2012).

The reproductive biology of *C. auratus* varies greatly across its geographic distribution, which may be a reflection of the adaptability of this species to local environmental conditions. *Chrysophrys auratus* is a serial broadcast spawner with separate sexes (Crossland 1977a). Age and size of sexual maturity varies considerably with geographic location from 2–7 years and 220–515 mm FL, respectively (Crossland 1977a; Coutin et al. 2003; Wakefield 2006; Jackson et al. 2010). In New Zealand, onset of sexual maturity occurs at 230 mm FL when the fish are 3–5 years old. The majority of *C. auratus* are sexually mature by 250 mm FL and all *C. auratus* are sexually mature by 300 mm FL (Crossland 1977a, 1981).

*Chrysophrys auratus* are daily spawners and in New Zealand spawning occurs between October and March, with peak spawning occurring in November–December (Scott and Pankhurst 1992; Francis 1994b). Often spawning fish will migrate to form transient spawning aggregations that can occur inside bays and gulfs (Fowler et al. 2007; Hamer et al. 2011), outside harbours, estuaries and bays (Crossland 1977a; Paul and Sullivan 1988; Scott et al. 1993; Jackson 2007; Wakefield et al. 2011), and in open, coastal waters ≤100 m deep (Moran et al. 2003). Pelagic larvae spend 18–32 days in the plankton (Francis 1994b; Fowler and Jennings 2003) before settling in the shallow waters of harbours and estuaries at lengths of 9–14 mm SL (Miskiewicz 1986; Trnski 2002; Hamer and Jenkins 2004). It is thought that entry into estuaries generally occurs late in the larval period, because *C. auratus* are mainly caught entering estuaries as late-stage larvae during flood tides (Miskiewicz 1986; Neira and Potter 1992; Trnski 2002). However, in some locations such as Port Philip Bay in Victoria, Australia, larvae are thought to spend their entire larval duration within the harbour (Hamer et al. 2010).

Very little is known about the ecological processes that affect larval recruitment and settlement behaviour of *C. auratus* in New Zealand. To date, knowledge on *C. auratus* larvae in New Zealand is restricted to information on larval development in artificial rearing trials (Cassie 1956; Atkinson 1987; Pankhurst et al. 1991), larval abundance in the Hauraki Gulf
(Kingsford 1986; Zeldis et al. 2005), and some limited information on the diet of larval snapper (Atkinson 1987). Research from Australia indicates that interannual recruitment variability of *C. auratus* is driven by larval recruitment processes, because the abundance of larvae was found to be strongly correlated with the subsequent abundance of 0+ year fish (Hamer et al. 2010). Previous research indicates that water temperature (Francis 1993; Francis et al. 1997) and prey availability (Zeldis et al. 2005; Murphy et al. 2012) can be important influences on interannual variability in the abundance of *C. auratus* larvae and new recruits, though these relationships are not consistent among populations and/or years.

Growth of *C. auratus* is relatively slow, with fish reaching approximately 110–140 mm FL after one year, 160–200 mm FL after two years, and 230–340 mm FL after four years (Longhurst 1958; Paul 1976; Horn 1986; McKenzie et al. 1992; Walsh et al. 2006). After the first five years, growth becomes much slower and varies greatly between individuals (Walsh et al. 2006). Growth rates vary considerably between different *C. auratus* stocks, with fish from the western coast of the North Island (SNA8 stock) growing faster than fish from northeastern New Zealand (SNA1 stock) (Longhurst 1958; Davies et al. 2003). *Chrysophrys auratus* can live up to 55–60 years of age and reach 1.3 m in length and 20 kg in weight (Francis et al. 1992b; Grant 2002; Gomon et al. 2008).

Juvenile *C. auratus* typically spend the first 1–3 years in shallow harbours and bays before migrating out to coastal waters (Fowler et al. 2005). Migration rates can be high in juvenile and sub-adult *C. auratus*, and fish have been recorded to travel ≤300 km from their settlement estuary (Fowler et al. 2005; Hamer et al. 2005; Hamer and Jenkins 2007). Adult *C. auratus* display polymorphic behaviour; a proportion of the population are primarily resident with typical home ranges of 0–20 km (Willis et al. 2001; Hartill et al. 2003; Moran et al. 2003; Parsons et al. 2003; Sumpton et al. 2003; Parsons et al. 2011), while the remainder of the population are migratory, moving to shallow inshore waters in summer and moving to deeper offshore waters in winter (Paul 1976; MacDonald 1982; Willis et al. 2003; Parsons et al. 2011). These seasonal migrations are thought to be associated with spawning activity (Crossland 1982; MacDonald 1982; Fowler et al. 2007).
1.3 Study sites
This study was primarily conducted in the Kaipara Harbour, which is an important nursery area for *C. auratus* on the west coast of the North Island (Morrison 2008). Sampling was also conducted at three other comparison sites; the Manukau Harbour, the Mahurangi Harbour and Huruhi Harbour in Great Mercury Island (Fig. 1.2).

![Figure 1.2](image_url)

**Figure 1.2.** Map of the North Island of New Zealand showing the location of the Kaipara, Manukau, Mahurangi and Huruhi Harbours. Inset maps show the sampling locations for larval (stars) and juvenile (triangles) *C. auratus* within each harbour.
1.3.1 The Kaipara Harbour

The Kaipara Harbour is the largest harbour in the Southern Hemisphere, encompassing an area of approximately 947 km$^2$ and 900 km of coastline (Heath 1975; Fahy et al. 1990). The natural harbour is an extensive, shallow estuary system surrounded by rural areas, and does not contain any large port. A sand bar exists at the mouth of the harbour, which extends approximately seven kilometres out to sea. The majority of the harbour is shallow and flat bottomed, although parts of the entrance channel are more than 50 m deep (Haggit et al. 2008). The harbour is exposed to the prevailing south-westerly winds and currents in the harbour are strongly wind and tidal-driven, with current speeds reaching 2 m s$^{-1}$ at the harbour entrance (Haggit et al. 2008). The harbour is well-flushed each tide with a maximum tidal range of 4.2 m and a tidal prism of approximately 1990 million m$^3$ during a spring tide (Haggit et al. 2008). Water in the harbour is frequently turbid, which is probably the result of re-suspension of seabed sediments, as well as terrigenous sediment and nutrient input (Hewitt and Funnell 2005; Haggit et al. 2008).

The Kaipara Harbour contains one of the few extensive areas of subtidal seagrass ($Zostera muellneri$) meadows left in New Zealand. Large mosaic patches of $Z. muellneri$ cover approximately 15 km$^2$ of the intertidal and subtidal sandflats in centre of the harbour adjacent to Kakaraia Flats (Morrison et al. 2009). These seagrass meadows support high abundances of juvenile fishes, particularly $C. auratus$, triplefins ($Forsterygion$ spp.), trevally ($Pseudocaranx$ georgianus) and pipefish ($Stigmatopora$ spp.) (Morrison et al. 2007). Sampling for 0+ year $C. auratus$ for this study was conducted within these subtidal seagrass meadows in the centre of the harbour and at a second, inner harbour site over bare mud (Fig. 1.2).

Recent research on otolith microchemistry of $C. auratus$ indicates that the Kaipara Harbour is a critical nursery area for juvenile $C. auratus$ with up to 98% of all west coast North Island $C. auratus$ (SNA8 stock) originating from the Kaipara Harbour (Morrison 2008). These results indicate that the Kaipara Harbour is critical to the recruitment of the entire SNA8 stock and that careful management of the harbour is needed to ensure that the SNA8 $C. auratus$ fishery is protected. However, very little is known about the ecology of larval and juvenile $C. auratus$, particularly for the west coast of the North Island.
1.3.2 The Manukau Harbour

The Manukau Harbour is the second largest harbour in New Zealand, encompassing an area of 340 km$^2$ and 386 km of shoreline (Heath et al. 1977). The harbour has a narrow entrance (2.2 km wide) and currents in the harbour are strongly tidal-driven, with current speeds of $\leq 2.25$ m s$^{-1}$ at the harbour entrance (Heath et al. 1977). The harbour is situated on the west coast of the North Island adjacent to Auckland City, and high concentrations of nitrogen and phosphorus ($\leq 0.3$ mg L$^{-1}$) are a problem at several locations within the central and upper harbour (Scarsbrook 2008). Sampling for *C. auratus* was conducted in the shallow subtidal waters of Clarks Beach, which is located at the southern end of the harbour and is mainly surrounded by rural land (Fig. 1.2).

1.3.3 The Mahurangi Harbour

The Mahurangi Harbour is a narrow, sheltered estuary on the northeast coast of the North Island. The shallow estuary has an area of 24.5 km$^2$ and water depths of less than 20 m (Harrison and Grierson and Partners 1974). The surrounding catchment area is mainly pasture or forest, with only 3% of the catchment area zoned urban/residential (Feeney 1984). Sampling for newly-recruited *C. auratus* was conducted in the central harbour, near Grant Island (Fig. 1.2) in water depths of approximately 3 m.

1.3.4 The Huruhi Harbour

Great Mercury Island lies about 6 km offshore of the eastern Coromandel Peninsula on the northeast coast of the North Island. The island is 18 km$^2$ in area and encloses Huruhi Harbour, which is a small, sheltered bay at the northern end of the island (Wright 1976). The harbour has an area of approximately 0.5 km$^2$ and a substrate of muddy sand (Grace and Grace 1976). The inner harbour has fringing intertidal and shallow subtidal seagrass beds, whereas the outer regions of the harbour has mainly muddy sand seafloor interspersed with stands of macroalgae. Sampling for newly recruited *C. auratus* was conducted throughout the shallow harbour (Fig. 1.2).
1.4 General aims of this thesis

The overall aim of the research presented in this thesis is to provide information on the early life history of *C. auratus*, particularly within the Kaipara Harbour. An understanding of the processes that affect larval abundance and recruitment is critical to the successful management and protection of *C. auratus* populations, because variation in larval abundance appears to determine the subsequent abundance of 0+ year *C. auratus* (Hamer et al. 2010), which in turn, governs the population dynamics in adult stocks (Hamer and Jenkins 2007). Large variations in interannual recruitment of 0+ year fish is a common feature of *C. auratus* populations, both in New Zealand and overseas (Hamer et al. 1998; Zeldis and Francis 1998; Fowler and Jennings 2003), which leads to large variations in the strength of year-classes (Fowler et al. 2005). The west coast North Island *C. auratus* stock is particularly vulnerable to overfishing and losses through environmental degradation because up to 98% of west coast stock is thought to originate from the Kaipara Harbour (Morrison 2008). Furthermore, adult snapper form large spawning aggregations outside the Kaipara Harbour, which are heavily targeted by commercial fishers. Therefore, careful management of the *C. auratus* population and the habitat of this fish within and around the Kaipara Harbour is required to ensure that the fishery is protected.

This thesis contains four experimental chapters, each written as separate manuscripts, which individually address separate research aims as follows:

Chapter 2 compares the reproductive condition of adult *C. auratus* sampled from inside and outside the Kaipara Harbour using gonad histology. Spawning aggregations of *C. auratus* are known to occur outside the Kaipara Harbour during late spring and early summer (Smith et al. 1978) but, according to Māori kaumatua (tribal elders) and recreational charter boat operators working in the Kaipara Harbour, *C. auratus* does not appear to spawn within the harbour, despite the presence of an extensive resident population of adult fish. Knowledge of the relative contribution of resident and migratory fish to local recruitment is important for fisheries management to assess the impact that fishing of spawning aggregations will have on future population levels. The aims of this chapter were to test the hypotheses that; 1) *C. auratus* do not spawn in the Kaipara Harbour, and 2) the population of *C. auratus* in Kaipara Harbour has a lower mean age than the population of *C. auratus* from the surrounding coastal waters.
Chapter 3 describes the patterns of larval abundance, pelagic larval duration and daily settlement of *C. auratus* in northern New Zealand using otolith microstructure and fish abundance data, and investigates whether these patterns were related to local environmental conditions. Abundances of *C. auratus* larvae were measured over a series of night flood tides in the Kaipara and Huruhi Harbours to determine the temporal abundance of larvae. Recently-settled *C. auratus* were also caught from the Kaipara, Manukau, Mahurangi and Huruhi Harbours. Age of fish, pelagic larval duration, and spawn and settlement dates were determined from daily otolith increments. Pelagic larval duration and settlement dates were compared with daily wind, rain, sea surface temperature, solar radiation and tide data, to determine whether pelagic larval duration or daily settlement were correlated with any of these environmental variables.

Chapter 4 models the growth rate of larval and early juvenile *C. auratus* from the four harbour sites using back-calculated length-at-age data obtained from daily otolith increments, and tests the hypothesis that fish with a short pelagic larval duration (≤20 days) grew faster than did fish with a long pelagic larval duration (>24 days) during both the larval and juvenile periods. Differences in larval and juvenile growth rates among *C. auratus* from different locations may affect their contribution of recruits to adult populations, because it has been demonstrated that faster growth rates in the larval and early juvenile period are correlated with higher survival rates in adult fish (Moss *et al.* 2005; Robert *et al.* 2007; Duffy and Beauchamp 2011).

Chapter 5 investigates the relationship between growth and energy reserves in 0+ year *C. auratus*. Larval and early juvenile temperate fishes face competing demands for consumed energy during their first summer/autumn if food is limited. It is advantageous for small fish to maximise their growth in order to out-grow predators, but they also need to ensure that they have sufficient energy reserves to sustain them through the winter. Thus, to maximise their chances of survival, juvenile fish must balance the amount of available energy that they allocate to growth versus the accumulation of energy reserves (Post and Parkinson 2001; Díaz *et al.* 2009). The objectives of this chapter were to determine whether; 1) the resource allocation in *C. auratus* changed from maximising growth to maximising energy storage over the course of their first growing season (summer–autumn), and 2) if recent
growth rates in 0+ year fish, determined by peripheral otolith increments, were correlated with protein, lipid or carbohydrate reserves.

Chapter 6 concludes this thesis with a general discussion on the research presented in the preceding chapters. Information generated by this study provides us with a better understanding of the ecological processes that affect larval recruitment of *C. auratus*, which in turn, influences the population dynamics of adult *C. auratus*. This information can be used to more effectively manage fished *C. auratus* populations, commercial and recreational harvesting, and to provide appropriate protection for critical nursery habitats, such as the seagrass nursery habitats in the Kaipara Harbour, against environmental degradation.
Chapter 2

Localised spawning omission in snapper, *Chrysophrys auratus* (Sparidae)

This chapter has been published as:

2.1 Abstract

Failure to spawn in a significant proportion of adult fish may greatly decrease the reproductive output of a population and lead to overestimates of recruitment to the fish stock. Reproductive output of the commercially important sparid, *Chrysophrys auratus*, around the Kaipara Harbour, New Zealand, is particularly important as this harbour is the primary source for the *C. auratus* population along the west coast of the North Island of New Zealand. We tested the hypothesis that *C. auratus* do not spawn inside the Kaipara Harbour by comparing monthly gonad and otolith samples from fish caught within the harbour with those of fish from surrounding coastal waters. Fish from coastal waters showed normal gonad development with peak spawning in spring. By comparison, almost all adult fish from the harbour had underdeveloped gonads, with mean gonadosomatic indices $\leq 1$. Histological gonad analyses of *C. auratus* caught in the harbour showed vitellogenic oocytes were reabsorbed before spawning. Therefore, recruitment to the harbour must originate from spawning that occurs outside the harbour. This first record of spawning omission in *C. auratus* has important implications for fisheries management, as it may lead to overestimation of the spawning stock and increase the risk of broad-scale population depletion, through the targeted fishing of spawning aggregations.
2.2 Introduction

Knowledge of the reproductive biology of an exploited fish species is essential to the effective management of the fish stock. Estimates of the reproductive output of fish populations predicted by stock-recruitment models typically assume that iteroparous fish spawn annually once they reach sexual maturity. However, there are a number of examples of iteroparous fish exhibiting spawning omission (i.e., the failure of annual spawning fish to spawn in a particular year; see Rideout et al. 2005 for review). Spawning omission can be caused by a number of factors including poor nutrition (e.g. Burton and Idler 1987; Rijnsdorp 1990; Skjæraasen et al. 2009), low temperatures (e.g. Pawson et al. 2000; Pörtner et al. 2001), shortage of mates (Trippel and Harvey 1990), and exposure to pollutants (McFarlane and Franzin 1978). Failure of a significant proportion of the sexually mature population to spawn during certain years will result in a reproductive output that is markedly lower than model predictions if they are based on the assumption that all sexually mature fish will spawn annually.

There are three types of spawning omission: resting, reabsorbing, and retaining. Resting omission is the failure to start vitellogenesis (yolk accumulation), reabsorbing omission is the breakdown and reabsorption (via follicular atresia) of all oocytes that enter vitellogenesis, and retaining omission is the failure of fish to shed fully mature eggs (Rideout et al. 2005). Both resting and reabsorbing omission are caused by factors experienced prior to the spawning season, primarily poor nutrition and/or unsuitable temperatures (Rideout et al. 2005). Retaining omission is caused by factors experienced during the spawning season e.g., shortage of mates, lack of spawning sites or pollution (Rideout et al. 2005). Retained eggs are eventually reabsorbed by the fish (Trippel and Harvey 1990).

*Chrysophrys auratus* (formerly *Pagrus auratus*) (Sparidae: Perciformes), commonly known as snapper, is widely distributed throughout the warm temperate waters of New Zealand and Australia (Gomon et al. 2008; Ministry of Fisheries 2010). It is a highly prized fish that supports significant commercial, recreational and customary (indigenous) fisheries in New Zealand and Australia. In 2009–2010, the total allowable commercial catch (TACC) for *C. auratus* in New Zealand was 6357 tonnes (t), generating NZ$36 million in export earnings.
Spawning omission in Chrysophrys auratus


The reproductive biology of C. auratus has been well studied for populations in north-eastern New Zealand (Crossland 1977a, b; Scott and Pankhurst 1992; Scott et al. 1993) and Australia (Jackson et al. 2010; Stewart et al. 2010; Wakefield 2010), and spawning habitats and minimum size at sexual maturity have been found to be highly variable between locations. None of these studies reported the occurrence of spawning omission, although the identification of sexually mature but non-reproductive individuals can be difficult as it requires the confirmation that post-ovulatory follicles (POF) are absent in the gonads during the spawning season (Rideout et al. 2005). The preparation of histological samples of the gonads is required for the identification of non-spawning fish, which is a time-consuming and labour-intensive process. Spawning omission is not unprecedented in the Sparidae, with spawning omission recorded for yellowfin bream, Acanthopagrus australis from Queensland, Australia (Pollock 1984).

Chrysophrys auratus is a serial broadcast spawner with asynchronous ovaries (i.e., ovaries that contain oocytes at various stages of development). Fish spawn daily during the spawning season, which occurs from late spring to early autumn (October–March) in New Zealand, with peak spawning occurring in November–December (Crossland 1977a; Scott et al. 1993). Little is known about the reproductive biology of C. auratus from north-west New Zealand. Chrysophrys auratus from the west coast of New Zealand are genetically distinct from the stocks on the east coast (Smith et al. 1978), and thus, their reproductive biology may differ. Spawning aggregations of C. auratus are known to occur outside the Kaipara and Manukau Harbours on the west coast of the North Island during late spring and early summer (Smith et al. 1978) and these have been targeted by commercial trawlers for over 50 years (Paul and Sullivan 1988). However, according to Māori kaumatua (tribal elders) and recreational charter boat operators working in the Kaipara Harbour, C. auratus does not appear to spawn within the harbour, despite the presence of an extensive population of adult fish.
The Kaipara Harbour is the largest estuary in the Southern Hemisphere encompassing an area of approximately 947 km$^2$ and 900 km of coastline (Heath 1975; Fahy et al. 1990). The natural harbour is an extensive, shallow estuary system surrounded by rural areas, and does not contain any large ports. The harbour contains one of the few remaining extensive subtidal seagrass (*Zostera muelleri*) meadows in New Zealand, which supports a high abundance of juvenile fishes (Morrison et al. 2007). Otolith microchemistry research indicates that the Kaipara Harbour is a critical nursery area for juvenile *C. auratus*, with up to 98% of the population of this fish on the west coast of the North Island originating from the Kaipara Harbour (Morrison 2008). These results highlight the need for careful management of the Kaipara Harbour to ensure the protection of the west coast North Island *C. auratus* stock, which comprises 20% of the total New Zealand TACC for this species (Ministry of Fisheries 2011).

There is evidence that as snapper grow there is a gradual outwards movement from harbours and shallow coastal waters to deeper, offshore waters, as indicated by differences in the spatial abundance of juvenile and adult snapper around New Zealand (Paul 1976; Morrison 2008; Compton et al. 2012). Thus, the adult snapper population in the Kaipara Harbour may be younger and have a lower reproductive output (Crossland 1977b) than snapper from deeper coastal waters.

Lack of knowledge on the reproductive strategy and spawning locations of *C. auratus* creates uncertainty over the relative importance of resident populations versus migratory spawning aggregations as sources of larvae that may underpin localised recruitment processes (Hamer et al. 2011), such as occurs in the Kaipara Harbour. Knowledge of the relative contribution of resident and migratory fish to local recruitment is important for fisheries management to assess the impact that fishing of spawning aggregations will have on future population levels. In this study, we tested the hypotheses that; 1) *C. auratus* do not spawn in the Kaipara Harbour, and 2) the population of *C. auratus* in Kaipara Harbour has a lower mean age than the population of *C. auratus* from the surrounding coastal waters.
2.3 Materials and methods

2.3.1 Field sampling

Gonad samples were removed from legal-sized adult *C. auratus* (>270 mm FL) caught inside the Kaipara Harbour approximately monthly from February 2010 to March 2011. Fish were caught by recreational fishers from a charter boat using a rod and line, with the majority of fish caught from the northern side of the harbour mouth, known locally as ‘The Graveyard’. Where possible, 30–40 fish were sampled per trip. However, it is uncommon to catch *C. auratus* in the Kaipara Harbour during the winter months and insufficient fish were caught during July and August 2010 to provide gonad samples. During the spawning season (October–March), *C. auratus* that aggregate in the coastal waters outside the harbour entrance were also sampled each month if the weather and swell conditions permitted the charter vessel to cross the harbour bar (Fig. 2.1). In total, 435 *C. auratus* were sampled; 251 fish from the Kaipara Harbour and 184 fish from coastal waters.

Fish were measured to the nearest 5 mm (fork length, FL) and weighed to the nearest 10 g. Both sagittal otoliths were removed from the fish, rinsed in fresh water to remove any attached flesh, and stored in paper envelopes. Gonads were removed from the fish and immediately stored in ice slurry until they could be processed back at the laboratory.
Figure 2.1. Location of the Kaipara Harbour, New Zealand. Inset map shows the location of sampling locations. The dark grey area shows the area from which the harbour samples were taken and the light grey area shows the area from which the coastal samples were taken.
2.3.2 Gonad staging

Histological preparations of all gonad samples collected were made to assess the reproductive development of *C. auratus*, and to determine whether mature, non-reproductive individuals were present in the samples. Gonads were weighed to the nearest 0.1 g and sexed. A 2–4-mm cross-sectional sub-sample was taken from the mid-region of one gonad from each fish for histological examination. The sub-sample was fixed in Bouin’s fluid for 48 h and then transferred to 70% ethanol for storage prior to sectioning. Samples were embedded in paraffin wax, sectioned at 8 µm with a microtome, and stained with Gill’s haematoxylin and eosin stain. The sections were examined using a compound microscope and microscopically-staged based on the highest gamete developmental stage present following the criteria of Mackie *et al.* (2009) and Rideout *et al.* (2005) (Tables 2.1 and 2.2). Terminology used to describe the development of oocytes follows that of West (1990).

Non-spawning females, which we labelled stage 7, were identified by the presence of a large number of atretic vitellogenic oocytes together with the lack of post-ovulatory follicles (POF). In addition, these samples lacked hydrated oocytes and empty spaces in the ovaries that are left by spawned eggs. Differentiation of these mature, non-spawning individuals from spent fish can be difficult, as the primary difference between the two stages is the lack of POF in reabsorbing gonads. However, POF deteriorate with time and thus, may not be present in spent fish (Rideout *et al.* 2005). To avoid confusion between reabsorbing fish and spent fish, Rideout *et al.* (2005) recommended that sampling should not be conducted late in the spawning season when spent fish that have already degenerated their POF are likely to occur.

Mean monthly gonadosomatic indices (GSI) were calculated for males and females as:

\[
GSI = \left( \frac{W_g}{WW - W_g} \right) \times 100
\]

where \( W_g \) = gonad weight and \( WW \) = total wet weight of fish.
Table 2.1. Histological staging of the reproductive condition of female *Chrysophrys auratus* (Criteria amended from Mackie *et al.* (2009) and Rideout *et al.* (2005)). PN = perionucleolus, CN = chromatin nucleolus, CA = cortical alveoli, YG = yolk globule, MN = migration nucleus, POF = post-ovulatory follicles.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Histological characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Immature</td>
<td>Ovary compact, lamellae ordered, gonad wall thick and tight, few or no yellow-brown bodies. PN and CN stages present. No evidence of previous reproductive activity.</td>
</tr>
<tr>
<td>2. Resting</td>
<td>PN and CN stages present. Atretic vitellogenic oocytes may also be present. Shortly after spawning the ovary has empty lamellae, much vascular tissue, yellow-brown bodies, and gonad wall is loose and thin. This evidence of prior spawning gradually diminishes until ovary is similar in appearance to late stage 1.</td>
</tr>
<tr>
<td>3. Developing</td>
<td>Gonad wall is usually quite thick and contracted, lamellae are packed with PN and CN oocytes. CA oocytes are also present indicating onset of reproductive activity.</td>
</tr>
<tr>
<td>4. Developed</td>
<td>Gonad wall expanded, thin. Ovary enlarged and lumen reduced. Lamellae contain YG stage oocytes.</td>
</tr>
<tr>
<td>5a. Pre-spawning</td>
<td>Brief stage just prior to ovulation. Ovary at maximum size. MN stage or hydrated oocytes present within the lamellae.</td>
</tr>
<tr>
<td>5b. Spawning</td>
<td>Brief stage when fish are ‘running ripe’ and ovulated oocytes are present within the lumen ready to be spawned. New POF are present on the periphery of the lamellae.</td>
</tr>
<tr>
<td>5c. Post-spawning</td>
<td>Brief stage when new and old POF are present within the ovary. No MNS or hydrated oocytes.</td>
</tr>
<tr>
<td>6. Spent</td>
<td>Gonad wall loose, thin. Lamellae disorganised, few oocytes. Much vascular tissue, empty space, and yellow-brown bodies. More than 50% of vitellogenic oocytes are atretic.</td>
</tr>
<tr>
<td>7. Reabsorbing</td>
<td>Oocytes fail to develop completely. Majority of vitellogenic oocytes are atretic. No POF. No hydrated oocytes. Oocytes are closely packed together and there is little vascular tissue.</td>
</tr>
</tbody>
</table>
Spawning omission in *Chrysophrys auratus*

Table 2.2. Histological staging of the reproductive condition of male *Chrysophrys auratus* (Criteria amended from Mackie *et al.* (2009)). SG = spermatogonia, SC = spermatocytes, ST = spermatids, SZ = spermatozoa, RSS = radial sperm sinuses, CSS = central sperm sinus.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Histological characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Immature</td>
<td>Testes very small and mainly composed of connective tissue. SG and SC dominate, ST may be present in small quantities. CSS is present but this contains little sperm. RSS poorly developed.</td>
</tr>
<tr>
<td>2. Resting</td>
<td>At the end of the spawning season the testes are small and contain little germ tissue (mainly SG and SC). CSS is large. Closer to the spawning season ST become more common and the RSS are more prominent (but contain few SZ).</td>
</tr>
<tr>
<td>3. Developed</td>
<td>SC and ST dominate. Many crypts of ST have broken down, mixing their contents. Many SZ are found within the RSS. Spermiogenesis still underway.</td>
</tr>
<tr>
<td>4a. Early spawning</td>
<td>Testes large and running ripe. CSS and RSS enlarged and filled with sperm. ST and SZ dominate.</td>
</tr>
<tr>
<td>4b. Late spawning</td>
<td>Testes greatly reduced in size and crypts are smaller. ST and SZ dominate, CSS filled with sperm. Very little SG and SC.</td>
</tr>
</tbody>
</table>

2.3.3 Otolith aging

The formation of annual otolith rings has been validated for *C. auratus* (Francis *et al.* 1992b). The age of sampled fish was determined from their sagittal otoliths to test the hypothesis that *C. auratus* from inside the Kaipara Harbour were younger than fish from the surrounding coastal waters. Otoliths were prepared for reading following the methods of Davies and Walsh (1995). One randomly selected otolith from each fish was sectioned transversely with a fine hacksaw just to one side of the otolith core. The otolith half containing the core was ground by hand with P600 grit wet aluminium oxide sandpaper and then polished with P1200 grit wet aluminium oxide sandpaper. The sectioned surface was wiped clean before burning on the flame of an alcohol burner. Otoliths were held approximately 2 mm away from the blue part of the flame until the surface of the otolith changed to a uniform, caramel brown colour. Under a dissecting microscope, a series of
alternating dark and light rings that radiated out from the core were discernible on the
burnt surface. Immersion oil (Oodina oil 68, Shell Company of Australia Ltd, Melbourne,
Victoria) was used to enhance the resolution of the rings.

In 0+ and 1+ year *C. auratus*, dark (opaque) rings indicate periods of slow growth and are
laid down in winter whereas light rings indicate periods of fast growth and are laid down in
summer (Ferrell et al. 1992). However, in adult *C. auratus* the outmost dark ring is often not
clearly visible until early summer (Francis et al. 1992b). The dark rings on the otolith were
counted by two readers who were “blind” to the size of the fish. Otoliths were also classified
as line, narrow or wide, depending on the proximity of the outermost dark ring to the edge
of the otolith. In line otoliths, the outermost ring is at the edge of the otolith, in narrow
otoliths there is a narrow light band at the edge of the otolith, and in wide otoliths there is a
wide light band at the edge of the otolith. A theoretical birth date of 1 January was assumed
for *C. auratus*. Fish that were caught from late summer to winter would either have a line or
narrow otolith, and therefore their estimated age is equal to the number of dark rings. Fish
that were caught in spring and early summer would have a wide otolith, and thus, their age
was assumed to be the age of the number of dark rings plus one (e.g., a fish with a 5-wide
count would be classified as being 6-years-old).

If the ring counts of the two readers were different, then the otolith in question was re-read
and discussed to reach a consensus on the age of the fish. If no consensus could be reached,
the otolith was discarded from the analysis.

2.3.4 Statistical analyses

The length and age data for the fish were natural log-transformed to meet the assumptions
of equal variance and normality. The mean length of female and male fish, mean age of fish
from the harbour and coast, and mean length of fish from the harbour and coast were
compared with separate Welch two-sample t-tests using R software (version 2.13.0, R
Foundation for Statistical Computing, Vienna, Austria). Reported means and 95% confidence
intervals were back-calculated from the log-transformed values (Sokal and Rohlf 1995).
2.4 Results

2.4.1 Age and length of fish

The size and age of *C. auratus* caught in the harbour ranged from 275–650 mm FL and 2–12 years, respectively, while the size and age of *C. auratus* caught in coastal waters ranged from 290–615 mm FL and 2–16 years, respectively (Fig. 2.2). There were significant differences in the mean age and length of fish from the harbour and coast. Fish caught in the harbour were, on average (mean=363 mm FL), significantly smaller than fish from the coast (mean = 386 mm FL) ($t_{377} = -3.80, P<0.001, 95\%$ c.i. = 0.91–0.97). Fish caught in the harbour were also significantly younger (mean = 3.8 years) than fish from the coast (mean = 5.4 years) ($t_{360} = -9.17, P<0.0001, 95\%$ c.i. = 0.67–0.76). Both sites were dominated by fish that were under six years-of-age. Inside the harbour, 91\% of fish were less than six-years-old and only one fish was older than ten years. On the coast, there was a greater proportion of older fish, with 67\% under six-years-old and 9\% over 10 years-of-age (Fig. 2.3).

![Figure 2.2](image)

**Figure 2.2.** Estimated age and length (FL) of *C. auratus* caught in the Kaipara Harbour and from the surrounding coastal waters.
2.4.2 Gonad development

All female *C. auratus* sampled were sexually mature, but four male *C. auratus* were still immature and were between 275–330 mm FL and 2–4 years-of-age. Regardless of sampling location, female fish had a significantly higher mean length (380 mm FL) than male fish (365 mm FL) (*t*<sub>433</sub> = 2.48, *P* = 0.01, 95% c.i. = 1.01–1.07).

There were marked differences in the mean GSI of *C. auratus* from the harbour and coast during the spawning season (October to March) (Fig. 2.4). Fish caught within the harbour maintained a low mean GSI of ≤1 for the entire sampling duration, showing little change in GSI during the spawning season. In comparison, the GSI of fish caught in coastal waters showed a pronounced increase over the spawning season, rising from <1 in late April 2010 to >4 by the end of October, and to a maximum of 6 in November. Between December and March GSI decreased rapidly to a minimum of <0.5 in late March 2011.

Histological analyses of the gonads of female *C. auratus* from the harbour and coast matched the general trends observed in the GSI (Fig. 2.5). Female fish caught in coastal waters showed extensive gonad development during spring, and the majority (67–100%) of females caught during October–December were in spawning condition with hydrated oocytes. During October, the majority of females from coastal waters did not show any sign
of previous spawning activity, with no POF present in the gonad sections, whereas by November POF were present in most of the gonad sections indicating that spawning had commenced. By January, the female *C. auratus* from coastal waters were at a variety of stages; some fish were still spawning (25%), some were spent (33%), some were resting (25%), and some were still developing (17%). Spawning had ceased by March and the gonads of all female fish were at the resting stage.

**Figure 2.4.** Average gonadosomatic indices (GSI) (± S.E.) of male and female *C. auratus* from the Kaipara Harbour and the surrounding coastal waters between February 2010 and March 2011, and in relation to water temperature. Water temperature data was collected by the Research, Investigations and Monitoring Unit of the Auckland Council.
Figure 2.5. Proportion of female *C. auratus* at each gonad maturity stage from the Kaipara Harbour and the surrounding coastal waters from February 2010 to March 2011. All fish sampled were above the minimum legal size of 270 mm FL. Black bars indicate fish in spawning condition and striped bars indicate mature non-spawning fish.
Figure 2.6. Proportion of male *C. auratus* at each gonad maturity stage from the Kaipara Harbour and the surrounding coastal waters from February 2010 to March 2011. All fish sampled were above the minimum legal size of 270 mm FL. Black bars indicate fish in spawning condition.
Figure 2.7. Histological section of a stage 7 (reabsorbing) *C. auratus* ovary containing numerous atretic (A) oocytes sampled from a fish caught in the Kaipara Harbour in November 2010. Scale bar = 100 µm.

By comparison, most of the female *C. auratus* from the harbour failed to produce fully developed eggs during the spawning season from October to March, reflected in their low mean GSI (≤1) over this period (Fig. 2.4). Oocytes began to mature over winter with 76% of females at stage 3 in September. However, ovarian maturation failed to continue for the majority of fish, and by November only 17% of fish were at stage 4, and only 8% were in spawning condition with hydrated oocytes. Instead, a number of fish (13%) had begun to reabsorb their vitellogenic oocytes prior to spawning (stage 7), as indicated by the high number of atretic oocytes together with a lack of POF (Fig. 2.7). By December, the percentage of females at stage 7 from the harbour had risen to 38% and almost all other females were at resting stage. Non-spawning females that possessed atretic oocytes were between 335 and 430 mm FL and between 4 and 5 years of age.
Gonad development and estimated time of spawning in male *C. auratus* from coastal waters match the development and spawning times of female *C. auratus* from coastal waters. The majority (83%) of male *C. auratus* captured in coastal waters during October were in spawning condition. Over the next two months, the percentage of spawning males decreased to 17% and the male population was dominated by males with developing gonads (58–83%). By March, spawning had ceased and all males from coastal waters were at resting stage (Fig. 2.6).

Gonad development of male *C. auratus* from the harbour showed little monthly progression with gonads remaining small in the vast majority of males, as indicated by the very low GSI (≤1). However, fish with mature sperm were present in seven of the eight sampling occasions, and during November and December 100% of males captured in the harbour were at spawning stage despite the small size of their gonads.

### 2.5 Discussion

#### 2.5.1 Reproductive development and spawning omission in female *C. auratus* from the Kaipara Harbour

Our results support the two hypotheses; 1) *C. auratus* do not spawn in the Kaipara Harbour, and 2) the population of *C. auratus* in Kaipara Harbour has a lower mean age than the population of *C. auratus* from the surrounding coastal waters. Despite the large population of adult *C. auratus* that reside within the Kaipara Harbour, very little reproductive development occurred in these fish and the mean GSI of *C. auratus* remained ≤1 throughout the year. Female *C. auratus* with vitellogenic or hydrated oocytes were rarely caught within the harbour. Instead, a notable proportion (17–38%) of the female *C. auratus* caught within the harbour during November and December had begun to reabsorb their vitellogenic oocytes prior to spawning. While fish from the harbour were significantly smaller and younger than fish from the coast, all female fish sampled were sexually mature and even large fish (>400 mm FL) caught in the harbour had poorly developed gonads.
In contrast to the lack of reproductive development in *C. auratus* captured in the Kaipara Harbour, reproductive development of *C. auratus* from surrounding coastal waters corroborated earlier reproductive studies from north-eastern New Zealand (Crossland 1977a; Scott and Pankhurst 1992). Adult *C. auratus* from the coast were found to have extensive gonad development during spring with the majority of fish ready to spawn by October. Peak spawning occurred during November and December, thereafter, mean GSIs declined rapidly to <2, and by March all spawning had ceased. No reabsorbing fish were captured from coastal waters where the fish were spawning. Instead, only spent fish were captured there late in the spawning season (January).

Spawning omission may be a regular phenomenon in some fish species, with a significant proportion of the sexually mature population skipping spawning in any particular year. It is estimated that approximately 30–33% of mature female *Gadus morhua* (Rideout et al. 2000; Jørgensen et al. 2006), 34–35% of mature female *Macrouronus novaezelandiae* (Livingston et al. 1997), and 43% of mature female *Perca fluviatilis* (Holmgren 2003) do not spawn each year. The most common reason for spawning omission in fish is poor nutritional condition of spawners (e.g. Burton and Idler 1987; Rijnsdorp 1990; Skjæraasen et al. 2009). Alternatively, fish may opt to channel their energy into growth and survival instead of reproduction to increase their future reproductive success (Jørgensen et al. 2006). For example, Holmgren (2003) demonstrated that sexually mature *P. fluviatilis* that were non-reproductive grew significantly faster in the preceding year than fish that were in reproductive condition.

### 2.5.2 Spawning migrations in *C. auratus*

It is possible that the resident population of *C. auratus* in the Kaipara Harbour segregates during the spawning season, with spawning individuals migrating out to the coast in early spring to join spawning aggregations, and non-spawning individuals remaining inside the harbour. Lack of participation in spawning migrations by mature, non-reproductive individuals has been shown for several other fish species, such as *Hoplostethus atlanticus* (Bell et al. 1992), *Lates calcarifer* (Moore and Reynolds 1982), and another sparid *A. australis* (Pollock 1984). *Acanthopagrus australis* is an estuarine species that has similar life
Spawning omission in Chrysophrys auratus. Pollock (1984) found that a large proportion of the adult population of A. australis in Moreton Bay, Australia, did not participate in the annual spawning migrations but remained inside the estuary during the spawning season. Non-migratory female A. australis developed vitellogenic oocytes, but failed to develop any hyaline-stage oocytes. Instead, vitellogenic oocytes became atretic and were reabsorbed (Pollock 1984). Unlike our study, Pollock (1984) found that non-migratory A. australis had a similar GSI to migratory fish during the spawning season, thus, non-migratory fish waste a considerable amount of their energy reserves in unnecessary gonad development. Pollock (1984) hypothesized that perhaps the trigger for participation in spawning migration occurs at a very late stage in the reproductive period for A. australis. No evidence was found for spawning omission in male A. australis. All male A. australis over the age of 2 years migrated to the spawning grounds and only immature fish and mature non-reproductive females remained in the estuary.

2.5.3 Spawning omission in male C. auratus from the Kaipara Harbour?

Currently, there is no definitive microscopic characteristic to measure spawning omission in male fish. Non-reproductive mature males are usually identified by their small testes during the gonad maturation season (Rideout et al. 2000; Yaragina 2010). All male C. auratus captured within the harbour in this study had very small testes with a mean GSI of ≤1. However, despite the small size of the testes the majority (86–100%) of males contained mature sperm during November–December, and males with ripe sperm were captured from November to June inside the harbour. Many of these males were classified as stage 4b (i.e., they had small testes filled with mature sperm and there was little sign of spermatogenesis still occurring). It is not known whether these males had returned to the harbour after spawning early in the season or if they had failed to undergo spermatogenesis this year and just contained some residual sperm from the previous spawning season. Similarly, Rideout et al. (2000) identified potentially mature non-reproductive male G. morhua that possessed small amounts of residual sperm but showed little sign of spermatogenesis in January when the majority of the population had completed spermatogenesis. However, these authors
acknowledged that it was possible that these ‘non-reproductive’ males may have a delayed reproductive development and may still have completed spermatogenesis prior to the spawning season.

2.5.4 Implications of spawning omission in *C. auratus* for fisheries management

The occurrence of spawning omission in *C. auratus* may have important implications for fisheries management. Although this is the first record of spawning omission in *C. auratus*, the phenomenon is difficult to detect and it is possible that spawning omission may be relatively common in this species. Furthermore, intensive commercial fishing targeted at spawning aggregations may provide artificial selection pressure that advantages spawning omission in the population. Non-reproductive individuals that do not migrate to spawning areas are likely to be subjected to less fishing pressure than spawning individuals, whose spawning aggregations are easily targeted by commercial trawlers (Livingston *et al.* 1997). If spawning omission is a genetically determined trait, then the incidence rate is likely to increase over time in populations where the spawning aggregations are heavily fished.

If spawning omission is a widespread phenomenon in *C. auratus* populations, then stock-recruitment models that predict the reproductive output based on the annual spawning of the entire adult population are likely to overestimate the reproductive output. The discovery that *C. auratus* does not spawn inside the Kaipara Harbour is particularly important for fisheries management in New Zealand. Research on otolith microchemistry signatures indicates that the Kaipara Harbour is a critical nursery area for juvenile *C. auratus* with up to 98% of all west coast North Island adult *C. auratus* spending their first year in the harbour (Morrison 2008). Thus, spawning aggregations outside the Kaipara Harbour are likely to be the source of recruitment for *C. auratus* populations over a very broad geographic area. Spawning aggregations outside west coast New Zealand harbours are heavily targeted by commercial trawlers and current biomass estimates for west coast *C. auratus* stocks are 6–14% of virgin biomass, well below the biomass required to attain a maximum sustainable yield (Davies *et al.* 2006). Over-exploitation of local spawning
aggregations outside the Kaipara Harbour is likely to have widespread consequences, reducing the biomass of the entire west coast North Island C. auratus stock.

Similarly, Hamer et al. (2011) found that C. auratus across a broad geographic range in South Australia were largely dependent on recruits originating from one harbour. Over 70% of 4–5+ year-old C. auratus captured along approximately 800 km of coastline originated from Port Phillip Bay. The dependency of some broad-scale C. auratus populations on recruitment from localised areas makes these populations very vulnerable to over-exploitation and there is an urgent need for careful management of these fisheries.
Chapter 3

Environmental influences on the larval recruitment dynamics of snapper, *Chrysophrys auratus*

This chapter has been published as:

3.1 Abstract

Recruitment success in demersal fish species that settle in estuaries after a pelagic larval duration in coastal waters is dependent on; 1) abiotic and biotic variables that promote good survival, and 2) local environmental conditions that facilitate and direct the transport of larvae to settlement habitats. In this study we described the patterns of larval abundance, pelagic larval duration and settlement of a commercially important sparid, *Chrysophrys auratus*, in northern New Zealand over two years, and investigated the relationships between pelagic larval duration or daily settler abundance and various environmental variables. Pelagic larval duration varied from 17–33 days and the successful spawning period that produced settled juveniles varied from 29–109 days among our four sites. The average temperature during the pelagic larval duration was >18 °C for 91% of fish captured. Significant correlations between daily settler abundance and environmental variables varied among sites and between years, however, temperature, tidal range and on-shore winds were most strongly correlated with settlement, explaining up to 38% of the variability in settler abundance. The present results suggested that, in some locations, high water temperatures, large tides and on-shore winds are likely to increase recruitment success in *C. auratus*. 
3.2 Introduction

For many marine fish species, variability in larval abundance can have major impacts on the subsequent abundance of juveniles, often producing 10 to 100 fold differences in interannual recruitment (Bradford 1992; Mertz and Myers 1995; Pope and Macer 1996; Houde 2009). Identification of the factors that control variability in fish stock abundances has been a major focus for fisheries scientists for over 100 years (Hjort 1914). It is now generally accepted that recruitment variability (defined in this paper as variability in the abundance of 0+ year fish) is not governed by a single mechanism or factor, but is influenced by many variables such as water temperature, hydrodynamics, prey availability, predation and larval growth, and their complex interactions (Fogarty et al. 1991; Houde 2009).

For demersal fish species that settle in estuaries after a pelagic larval duration (PLD) in coastal waters, recruitment success is dependent on; 1) abiotic and biotic variables that promote good survival, and 2) local environmental conditions (e.g., currents, winds, orientation cues), which facilitate and direct the transport of larvae to settlement habitats (Jenkins et al. 1997). Late-stage larval fish are not passive particles; they are often capable of sustained, directional travel utilizing specific orientation cues (Leis 2006; Dixson et al. 2008; Radford et al. 2012). However, environmental variables are still likely to have a major influence on patterns of larval dispersal. Prior to the development of swimming ability, early-stage larvae may be transported large distances by prevailing currents or winds as relatively passive particles (Jenkins et al. 1997; Jenkins et al. 1999), and late-stage larvae have been shown to utilise tidal fronts (Kingsford et al. 1991; Kingsford and Suthers 1996), tidal streams (Churchill et al. 1999; Forward Jr et al. 1999), selective tidal stream transport (Rijnsdorp et al. 1985; Rowe and Epifanio 1994) and boundary layers (Breitburg et al. 1995) to ensure their entry and retention in estuaries. In this study we use the term “successful spawning period” to describe the spawning period that produced fish that managed to survive the PLD and settle in juvenile habitats.

The use of otolith microstructure aging techniques in larval recruitment studies has allowed researchers to investigate the influence of environmental variables on the recruitment
success of fishes on a fine temporal scale. Fish otoliths are metabolically inert and grow throughout the lifetime of the fish by the addition of successive layers of aragonitic calcium carbonate (Campana 1999). These layers are usually formed either daily or annually, providing a permanent record of the life history of the fish, which can be used to estimate age and growth, and for dating major physiological events such as hatch date and settlement date (Shima and Swearer 2009). This information can be combined with environmental data to identify the environmental conditions that occurred during the PLD of individual fish, and the possible influence of environmental conditions on the dispersal and recruitment success of the fish.

*Chrysophrys auratus* (formerly *Pagrus auratus*) (Sparidae: Perciformes), commonly known as snapper, is widely distributed throughout the warm temperate waters of New Zealand and Australia (Gomon et al. 2008; Ministry of Fisheries 2010). It is a highly-prized fish that supports significant commercial, recreational and customary (indigenous) fisheries in New Zealand and Australia. In 2009–2010, the total allowable commercial catch (TACC) for *C. auratus* in New Zealand was 6357 tonnes (t), generating NZ$36 million in export earnings (Seafood Industry Council 2011). Australia has a smaller commercial fishery for *C. auratus* with 2106 t harvested in 2009–2010, worth AU$14 million (Australian Bureau of Agricultural and Resource Economics 2011).

In early spring, adult *C. auratus* often aggregate outside harbours, bays and estuaries to spawn (Crossland 1977a; Scott et al. 1993; Jackson 2007). Spawning aggregations of *C. auratus* are known to occur outside the Kaipara and Manukau Harbours on the west coast of the North Island (Smith et al. 1978), and throughout much of the Hauraki Gulf on the east coast of the North Island (Zeldis and Francis 1998). Fish spawn daily during the spawning season, which occurs from late spring to early autumn (October–March) in New Zealand, with peak spawning occurring in November–December (Crossland 1977a; Scott et al. 1993; Sim-Smith et al. 2012b). Larvae hatch at a relatively small size (2.1 mm standard length (SL), Pankhurst et al. 1991) and spend 18–32 days in the plankton (Francis 1994b; Fowler and Jennings 2003) before settling in the shallow waters of estuaries and bays at 9–14 mm SL (Miskiewicz 1986; Trnski 2002; Hamer and Jenkins 2004). In New Zealand, *C. auratus* appear
to prefer to settle in shallow areas containing biogenic structure e.g., seagrass (*Zostera muellieri*) or horse mussels (*Atrina zelandica*) beds, as high densities of 0+ year juveniles have been found associated with these habitats (Schwarz et al. 2006; Morrison et al. 2007; Usmar 2009).

The Kaipara Harbour is the largest estuary in the southern hemisphere encompassing an area of ~947 km$^2$ (Fahy et al. 1990). Otolith microchemistry research indicates that the Kaipara Harbour is a critical nursery area for juvenile *C. auratus*, with up to 98% of the population of this fish on the west coast of the North Island spending their 0+ year in the Kaipara Harbour (Morrison 2008). These results highlight the need to understand the factors that influence the recruitment of *C. auratus* within the Kaipara Harbour, to ensure the protection of the west coast North Island stock (SNA8), which comprises 20% of the total New Zealand TACC for this species (Ministry for Primary Industries 2012).

Interannual recruitment variability of *C. auratus* is high (Francis 1995; Coutin et al. 2003; Hamer and Jenkins 2004; Fowler et al. 2007) and there is good evidence that recruitment variability of 0+ year fish is strongly correlated with variability in the abundance of *C. auratus* larvae (Hamer et al. 2010). Previous research indicates that water temperature (Francis 1993; Francis et al. 1997) and prey availability (Zeldis et al. 2005; Murphy et al. 2012) can be important influences on interannual variability in the abundance of *C. auratus* larvae and new recruits. On a finer temporal scale, intraannual variation in recruitment may provide us with additional information on the local environmental variables that influence recruitment. Research on other fish species has shown that daily settlement patterns may be related to temperature (Findlay and Allen 2002; Bergenius et al. 2005; Lemberget et al. 2009), the lunar cycle and tidal amplitude (Findlay and Allen 2002; D’Alessandro et al. 2007; Vallès et al. 2009), winds (Jenkins et al. 1997; Findlay and Allen 2002; Raventos and MacPherson 2005) and solar radiation (Bergenius et al. 2005), however, the relationship between environmental variables and daily settlement has not been investigated for *C. auratus*. Thus, the overall aim of this study was to gain a greater understanding of the factors that influence recruitment variability of *C. auratus*. Specifically, the aims of this study were to; 1) describe the patterns of larval abundance, PLD and settlement of *C. auratus* at
four harbours in northern New Zealand (Kaipara, Manukau, Mahurangi and Huruhi) using otolith microstructure and fish abundance data, and 2) determine whether recruitment to settlement habitats is correlated with local environmental variables that may facilitate higher larval survival or transport to settlement habitats.

3.3 Materials and methods

3.3.1 Field collection
Sampling was conducted in four harbours around northern New Zealand; the Kaipara, Manukau, Mahurangi and Huruhi Harbours (Fig. 3.1). These harbours were chosen because they were situated within the two most important snapper-stock regions (east Auckland (SNA1) and west coast (SNA8)), and because initial pilot surveys found that newly-settled *C. auratus* could be reliably captured within these harbours. The Kaipara and Manukau Harbours are the two largest harbours on the west coast of the North Island. Currents in these two large harbours are strongly influenced by wind and tides, with current speeds at times exceeding 2 m s\(^{-1}\) at the harbour entrances (Heath *et al.* 1977; Haggit *et al.* 2008). The Mahurangi and Huruhi Harbours are situated on the east coast of the North Island. The Mahurangi Harbour is a small (25 km\(^2\)), sheltered harbour located within the Hauraki Gulf, while Huruhi Harbour is a sheltered bay (0.5 km\(^2\)) located within Great Mercury Island, which lies offshore of the outer Coromandel Peninsula.

Ichthyoplankton sampling was conducted at the entrance to the Kaipara and Huruhi Harbours (Fig. 3.1) between 23 November 2010 and 10 March 2011 to determine the temporal abundance of *C. auratus* larvae among sampling occasions and over the flood tide, as previous studies have shown that ichthyoplankton abundance can vary significantly with tidal phase (Kingsford and Suthers 1996; Vargas *et al.* 2003). Sampling was conducted throughout the night flood tide at fortnightly intervals in the Kaipara Harbour and at monthly intervals in Great Mercury Bay. Sampling was conducted during the night because catch rates for *C. auratus* larvae are greater at night (Murphy *et al.* 2011). The water depth at both sites was between 19 and 28 m. Stepped, oblique plankton tows were conducted
every 30 mins throughout the flood tide using a 1 mm mesh plankton net with a 1 m² square opening. The net was a box-pyramid design with a 1:10 mouth area: mesh area ratio. The water column from approximately 1 m above the seafloor to the sea surface was divided into 4 m depth strata. The net was towed at a speed of approximately 0.8 m s⁻¹ for 2 mins in each strata so that the overall tow time was typically between 10 and 15 mins. A General Oceanics flowmeter (model 2030, General Oceanics Inc., Miami, Florida, USA) was strung across the opening of the net to determine the volume of water filtered in each tow (mean ± S.E. = 588 ± 12 m³). Upon recovery of the net the material from the cod end of the net was immediately sorted and any ichthyoplankton found were preserved in 95% ethanol. All other material from the cod end was preserved in 70% ethanol and sorted later in the laboratory under a dissection microscope to ensure that no ichthyoplankton had been missed. *Chrysophrys auratus* larvae were identified following descriptions by Niera *et al.* (1998). Larval densities were standardized to the number per 1000 m³.

Newly recruited *C. auratus* were collected from the Kaipara, Manukau, Mahurangi and Huruhi Harbours between December and May in 2009/2010 and 2010/2011. In 2009/2010 sampling was conducted over a three hour period during the day, one and a half hours either side of low tide. Fish from the Mahurangi Harbour site were collected from the centre of the harbour in water depths of approximately 3 m using a beam trawl that had a 4 m long beam, from which was suspended a 3 m wide x 4 m long main net constructed of 12 mm stretched mesh, and a 1 m long cod end constructed of 8 mm stretched mesh. Fish from the other sites were collected from shallow subtidal waters (<1.5 m) using an 11 m long beach seine net with a 2.3 m drop and a 4 m long cod end. The net was constructed of 12 mm stretched mesh in the main section and 6.8 mm stretched mesh in the cod end. Three to five haphazardly placed, non-overlapping hauls were made in order to collect at least 50 *C. auratus* per sampling occasion. Despite repeated sampling attempts only 33 *C. auratus* in total were collected from the Manukau Harbour site owing to their low abundance at that site. In 2009/2010, the Kaipara Harbour site was sampled on three occasions (18 February, 1 March, 23 April) from site 1 and once from site 2 (26 March), the Manukau Harbour site was sampled on three occasions (3 and 25 April, 15 May), and the Mahurangi and Huruhi Harbour sites were each sampled once (9 February and 29 April, respectively) (Fig. 3.1).
Figure 3.1. Map of the North Island, New Zealand, showing the sampling locations. The inset maps show the position of the sampling sites for *C. auratus* larvae (stars) and juveniles (triangles) within each location. In the Kaipara Harbour the black triangle is site 1 and the grey triangle is site 2.
In 2010/2011 newly recruited *C. auratus* were sampled from the Kaipara Harbour at fortnightly intervals and the Huruhi Harbour at monthly intervals, using a purpose-built benthic sled that was towed behind an inflatable boat. The sled had a 1 m wide x 0.5 m high opening that was constructed from galvanized steel tubing, to which was attached a 3 m long net made from 3.8 mm stretched mesh. The use of the sled instead of the beach seine allowed sampling to be conducted in water deeper than 1.5 m. Eighteen, non-overlapping, five minute tows were conducted within an approximately 4 km² area in the shallow sandflats in the centre of the Kaipara Harbour near site 1 on each sampling occasion (1 December, 7 and 26 January, 11 and 28 February, 15 March). At Huruhi Harbour, only 12 tows were conducted throughout the harbour on each sampling occasion (9 December, 11 January, 7 February, 10 March), owing to the much smaller size of the harbour. Upon capture, fish were immediately stored on ice and then frozen at -80 °C upon return to the laboratory.

### 3.3.2 Otolith preparation and analysis

The formation of daily otolith increments has been validated for *C. auratus* for fish up to 160 days old (Francis 1994b; Fowler and Jennings 2003). All *C. auratus* captured were measured for standard length (SL) and weighed to the nearest 0.01 g. Both sagittal otoliths were extracted from at least fifty randomly chosen fish from each sampling occasion if sufficient fish were available. Fish sampled for their otoliths were sub-sampled from the catch of 3–5 net hauls per sampling occasion in 2009/2010 and 4–12 hauls in 2010/2011. The otoliths were placed in pre-weighed eppendorf vials and cleaned by soaking in a 15% H₂O₂ solution buffered with 4 g NaOH L⁻¹ for 24 h. The otoliths were rinsed three times in Millipore water (18 MQ), air dried, and then weighed to nearest 0.00001 g.

Thin, transverse sections of the otoliths of at least twenty randomly chosen fish per sampling occasion were prepared following the methods of Campana (2010). Briefly, sections were prepared by grinding and polishing from both the rostral and antirostral ends of the otolith, using a range of diamond sandpaper (Diamond Edge Ltd, Auckland, New Zealand) and diamond lapping film (6–35 µm) (Allied High Tech Products Ltd, Rancho...
Larval recruitment dynamics of *Chrysophrys auratus*

Dominguez, California, USA). For the first grind the otolith was fixed onto the edge of a glass microscope slide with thermoplastic glue (Crystalbond™509, Aremco Products Inc., Valley Cottage, New York, USA), positioned with core of the otolith in line with the edge of the slide, and hand sanded until the core was reached. For the second grind the ground surface of the otolith was attached to the centre of the microscope slide with Crystalbond™. The other end of the otolith was hand sanded until a thin section of the otolith containing the core was obtained.

Digital images were taken of each otolith section using a Meiji Techno ML5000 compound microscope (Meiji Techno, Japan) fitted with a Leica DFC420 digital camera that was connected to Leica Application Suite (LAS) imaging software (Leica Microsystems, Wetzlar, Germany). Images were captured at ×200–600 magnification and daily increments were counted and measured from the core to the otolith edge along the sagitta-subcupular meshwork fibre (SMF) zone (Fig. 3.2). Francis *et al.* (1992b) found that *C. auratus* sagittae were most easily interpreted along the SMF zone, which is a darker zone that runs from the core to the proximal surface between the sulcus and the ventral apex. Immersion oil (Ondina oil 68, Shell Company of Australia, Melbourne, Victoria), was used to enhance the resolution of the increments. Otoliths were read on two separate occasions by C. Sim-Smith. If the counts differed by more than 5% the otolith was re-read a third time. If the counts still differed by more than 5% after the third reading the otolith was rejected, otherwise, the mean of the two closest counts was used as the best estimate of the number of increments. Readings were made blind with respect to the metadata associated with the otoliths.

Age at capture and larval duration were recorded for each fish. The larval duration was determined as the number of increments between the core and the settlement mark plus two because the first increment is formed 2–3 days after hatching (Fowler and Jennings 2003). The settlement mark was identified as a prominent dark ring that is caused by an abrupt decrease in increment width and a change in optical density of the otolith (Fig. 3.2). Immediately outside the settlement mark the increments become broader, lighter in colour and more widely spaced (Fowler and Jennings 2003). Date of spawning was calculated by subtracting the age at capture plus four days from the date of capture because the average
Figure 3.2. a) Thin transverse section of a sagittal otolith from a 49 mm (SL) *C. auratus* showing the position of the SMF zone along which daily increments are counted. b) High magnification image of the otolith core showing the larval rings and the settlement mark. c) A sagittal otolith from a 5.9 mm (SL) *C. auratus* larva showing 11 daily rings.
duration between spawning and hatching is two days (Crossland 1980; Pankhurst et al. 1991; Battaglene and Talbot 1992) and the first increment in *C. auratus* is not formed until larvae are three-day-old (Fowler and Jennings 2003). In total, the otoliths of 315 *C. auratus* were read: 140 juveniles from 2009/2010, and 55 larvae and 120 juveniles from 2010/2011.

### 3.3.3 Environmental data

Daily sea surface temperature (SST) data were obtained from the Group for High Resolution Sea Surface Temperature (GHR SST) L4 dataset that was provided by the Australian Bureau of Meteorology as part of National Oceanic and Atmospheric Administration’s (NOAA) Environmental Research Division's Data Access Program (ERDDAP, ver. 1.36) (Simons 2011). The SST satellite analyses have a 9 km resolution and a 0.42 °C standard deviation when compared with observed SST buoy readings (Beggs et al. 2011). SST data were obtained for the coastal waters just outside the harbour entrances of all four sites.

Daily rainfall, solar radiation, wind speed and wind directional data were acquired from New Zealand’s National Climate Database (National Institute of Water and Atmospheric Research 2011) for the closest meteorological stations to the four study sites. Solar radiation (MJ m⁻²) and wind data were acquired from Dargaville (61 km due north of the entrance to the Kaipara Harbour), Slipper Island (50 km south of Huruhi Harbour), Auckland airport (adjacent to the Manukau Harbour) and Warkworth (10 km northwest of Mahurangi Harbour). Wind speed (m s⁻¹) and directional (degrees) data were combined into two orthogonal vectors that represented onshore-offshore and along-shore winds following the methods of Bergenius et al. (2005). The vectors were derived by adding 30° to the wind directions to make the along-shore wind component parallel to the coastline, separately applying cosine and sine functions to the modified daily wind directions to obtain the along-shore and cross-shore components, respectively, and then multiplying by the daily wind speed. Positive and negative along-shore vectors represented winds from the northwest and southeast, respectively, whereas, positive and negative cross-shore vectors represented winds from the northeast and southwest, respectively. Daily total rainfall data (mm day⁻¹) were acquired from Mairetahi (21 km southeast of the Kaipara Harbour), Whitianga (27 km
southwest of Huruhi Harbour), Waiuku (26 km south of the Manukau Harbour) and Warkworth (10 km northwest of Mahurangi Harbour).

### 3.3.4 Statistical analyses

All statistical analyses were performed using R software (ver. 2.15.0, R Foundation for Statistical Computing, Vienna). A two-way Analysis of Variance (ANOVA) was used to determine the effect of month and incoming tidal hour on the abundance of *C. auratus* larvae after larval abundance had been natural log ($x+1$) transformed to meet the assumptions of normality and homogeneity of variance.

The mean size of *C. auratus* larvae during January and February were compared using a Welch two-sample $t$-test. Insufficient larvae were caught during December and March to include these months in the analysis. Larval size data were natural log transformed to meet the assumptions of homogeneity of variance and normality. The mean size of larvae over the six hour tidal period sampled was compared with a one-way ANOVA.

The relationships between PLD and average daily environmental variables during the PLD (SST, rainfall ($\log_{10} (x+1)$ transformed), along-shore winds, cross-shore winds and solar radiation) were modeled separately for each site using multiple linear regressions. Environmental variables were checked to ensure that there was no collinearity among variables. The minimum adequate model was obtained by dropping environmental variables one at a time from the full model in a stepwise approach, and comparing the Akaike Information Criterion (AIC) values. Each data set was checked for extreme outliers and data points that had a Cook’s distance of $>1$ were excluded from the analysis (Montgomery and Peck 1992), because the outcome of multiple regression analyses are very susceptible to outliers.

The relationship between daily abundance of settlers and the environmental variables for the previous day (along-shore winds, cross-shore winds, total daily rainfall ($\log_{10} (x+1)$ transformed), SST and daily tidal range) was modeled separately for each harbour using a generalized linear model (GLM) with Poisson errors. The GLM transforms the data with a log
function because count data cannot be negative. Settler abundance was compared to the environmental variables of the previous day to allow time for larvae to be transported to settlement areas and settle. Time lags of 0 and 2 days were also investigated, but a time lag of 1 day produced the most significant correlations. Environmental variables were checked to ensure that there was no collinearity among variables and any extreme outliers were removed from the analyses. The minimum adequate model was obtained by dropping environmental variables one at a time from the full model in a stepwise approach, and comparing the AIC values. The amount of variability explained by the final model was assessed using a Pseudo $R^2$ (Zuur et al. 2009).

$$Pseudo \ R^2 = \frac{null \ deviance - residual \ deviance}{null \ deviance} \times 100$$  \text{(Equation 1)}

3.4 Results

3.4.1 Environmental variables

Changes in SST between November and March were similar for all four sites, increasing from approximately 15 °C in November to around 21–22 °C in February. Averages, maxima and minima for SST, solar radiation and winds were generally similar among sites and between years. 2010/2011 had a higher maximum daily rainfall than 2009/2010 at the Kaipara and Huruhi sites (Table 3.1). Wind predominantly came from the SW quarter (41–53% of days) for all harbours in 2009/2010. In 2010/2011, NE was the predominant wind direction in the Kaipara Harbour (33%), and SW was the predominant wind direction in Huruhi Harbour (40%).
3.4.2 Temporal abundance of *C. auratus* larvae

In total, 71 *C. auratus* larvae and 1424 juveniles were captured that ranged in size from 3.5–96.3 mm SL (Table 3.2). No *C. auratus* larvae were captured in the Kaipara Harbour on any of the seven plankton sampling occasions. *Chrysophrys auratus* larvae were captured from Huruhu Harbour between December 2010 and March 2011, with 94% of larvae captured in January and February. Larval abundance was significantly different among months ($F_{3,39} = 28.55, P < 0.0001$) with a peak abundance of 12 ± 2 S.E. larvae 1000 m$^{-3}$ recorded in January (Fig. 3.3). Larval abundance was not significantly different among the hours over the incoming tidal period ($F_{5,39} = 0.81, P = 0.55$). Larvae ranged in size from 3.5–11.6 mm SL with an average of 6.4 ± 0.2 S.E. mm SL, and ranged in age from 11–30 days. Larval size did not vary significantly between January and February ($t_{45} = 1.68, P = 0.10$) or among the hours over the incoming tidal period ($F_{5,58} = 1.76, P=0.14$).

**Figure 3.3.** Mean abundance (± S.E.) of *C. auratus* larvae in Huruhu Harbour, northeastern New Zealand, between December 2010 and March 2011. Larval abundances have been standardized to the number per 1000 m$^3$. 
Table 3.1. Daily means ± S.E., minima and maxima of environmental variables from November 2009 to March 2010 in the Kaipara, Huruhi, Manukau and Mahurangi Harbours, and from November 2010 to March 2011 in the Kaipara and Huruhi Harbours.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Year</th>
<th>Harbour</th>
<th>Mean ± S.E.</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>SST (°C)</td>
<td>2009/2010</td>
<td>Kaipara</td>
<td>19.0 ± 0.1</td>
<td>15.8</td>
<td>20.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Huruhi</td>
<td>19.1 ± 0.2</td>
<td>15.4</td>
<td>21.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Manukau</td>
<td>18.7 ± 0.1</td>
<td>14.8</td>
<td>21.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mahurangi</td>
<td>19.4 ± 0.2</td>
<td>15.6</td>
<td>21.9</td>
</tr>
<tr>
<td></td>
<td>2010/2011</td>
<td>Kaipara</td>
<td>19.2 ± 0.1</td>
<td>15.3</td>
<td>21.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Huruhi</td>
<td>19.7 ± 0.2</td>
<td>15.5</td>
<td>22.3</td>
</tr>
<tr>
<td>Rainfall (mm day⁻¹)</td>
<td>2009/2010</td>
<td>Kaipara</td>
<td>1.6 ± 0.6</td>
<td>0</td>
<td>79.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Huruhi</td>
<td>2.7 ± 0.9</td>
<td>0</td>
<td>121.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Manukau</td>
<td>2.0 ± 0.4</td>
<td>0</td>
<td>33.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mahurangi</td>
<td>1.9 ± 0.6</td>
<td>0</td>
<td>73.0</td>
</tr>
<tr>
<td></td>
<td>2010/2011</td>
<td>Kaipara</td>
<td>3.5 ± 1.2</td>
<td>0</td>
<td>116.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Huruhi</td>
<td>7.0 ± 2.1</td>
<td>0</td>
<td>219.6</td>
</tr>
<tr>
<td>Radiation (MJ m⁻²)</td>
<td>2009/2010</td>
<td>Kaipara</td>
<td>21.8 ± 0.5</td>
<td>3.9</td>
<td>33.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Huruhi</td>
<td>21.4 ± 0.6</td>
<td>3.0</td>
<td>35.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Manukau</td>
<td>21.6 ± 0.6</td>
<td>3.5</td>
<td>34.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mahurangi</td>
<td>20.3 ± 0.5</td>
<td>4.0</td>
<td>31.1</td>
</tr>
<tr>
<td></td>
<td>2010/2011</td>
<td>Kaipara</td>
<td>21.2 ± 0.6</td>
<td>3.8</td>
<td>33.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Huruhi</td>
<td>21.9 ± 0.7</td>
<td>3.0</td>
<td>34.9</td>
</tr>
<tr>
<td>Wind speed (m s⁻¹)</td>
<td>2009/2010</td>
<td>Kaipara</td>
<td>4.2 ± 0.1</td>
<td>0.5</td>
<td>13.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Huruhi</td>
<td>5.6 ± 0.1</td>
<td>0.3</td>
<td>15.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Manukau</td>
<td>5.1 ± 0.1</td>
<td>0.1</td>
<td>12.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mahurangi</td>
<td>4.2 ± 0.1</td>
<td>0.3</td>
<td>12.0</td>
</tr>
<tr>
<td></td>
<td>2010/2011</td>
<td>Kaipara</td>
<td>3.8 ± 0.1</td>
<td>0.3</td>
<td>19.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Huruhi</td>
<td>5.3 ± 0.1</td>
<td>0.3</td>
<td>22.0</td>
</tr>
</tbody>
</table>
Table 3.2. Sampling dates, overall sample size ($n_1$), and size range (SL) of larval and juvenile *C. auratus* captured from the Kaipara, Huruhi, Manukau and Mahurangi Harbours in 2009/2010 and 2010/2011, and the sub-sample size ($n_2$) and size range of fish that were measured for their daily otolith increments. Mean standard lengths ± S.E. are given in parentheses.

<table>
<thead>
<tr>
<th>Year</th>
<th>Site</th>
<th>Life stage</th>
<th>Sample date</th>
<th>Overall sample $n_1$</th>
<th>SL (mm)</th>
<th>Fish sampled for their otoliths $n_2$</th>
<th>SL (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2009/2010</td>
<td>Kaipara</td>
<td>juvenile</td>
<td>18 February</td>
<td>452</td>
<td>18.9–53.5 (33.5 ± 0.3)</td>
<td>20</td>
<td>20.4–53.5 (37.4 ± 1.4)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>juvenile</td>
<td>1 March</td>
<td>291</td>
<td>27.2–62.8 (44.5 ± 0.4)</td>
<td>22</td>
<td>34.1–62.8 (47.3 ± 1.5)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>juvenile</td>
<td>26 March</td>
<td>88</td>
<td>28.2–64.1 (44.7 ± 0.7)</td>
<td>20</td>
<td>37.6–64.1 (45.9 ± 1.6)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>juvenile</td>
<td>22 April</td>
<td>50</td>
<td>43.9–77.8 (57.7 ± 1.0)</td>
<td>20</td>
<td>48.1–70.8 (59.4 ± 1.3)</td>
</tr>
<tr>
<td></td>
<td>Huruhi</td>
<td>juvenile</td>
<td>29 April</td>
<td>171</td>
<td>13.9–75.7 (38.2 ± 0.7)</td>
<td>27</td>
<td>14.3–75.7 (39.3 ± 1.9)</td>
</tr>
<tr>
<td></td>
<td>Manukau</td>
<td>juvenile</td>
<td>3 April</td>
<td>23</td>
<td>20.2–96.3 (44.4 ± 3.8)</td>
<td>17</td>
<td>20.2–96.3 (45.0 ± 3.6)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>juvenile</td>
<td>24 April</td>
<td>6</td>
<td>37.3–50.1 (44.5 ± 2.3)</td>
<td>3</td>
<td>37.6–49.3 (44.8 ± 2.6)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>juvenile</td>
<td>15 May</td>
<td>4</td>
<td>38.4–60.1 (50.0 ± 5.2)</td>
<td>4</td>
<td>38.4–60.1 (50.0 ± 5.2)</td>
</tr>
<tr>
<td></td>
<td>Mahurangi</td>
<td>juvenile</td>
<td>9 February</td>
<td>60</td>
<td>13.4–44.2 (27.8 ± 0.9)</td>
<td>35</td>
<td>14.6–44.2 (28.9 ± 1.0)</td>
</tr>
<tr>
<td>2010/2011</td>
<td>Kaipara</td>
<td>juvenile</td>
<td>26 January</td>
<td>18</td>
<td>11.0–54.0 (16.2 ± 2.5)</td>
<td>17</td>
<td>11.0–54.0 (16.4 ± 2.6)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>juvenile</td>
<td>11 February</td>
<td>26</td>
<td>10.6–30.0 (15.3 ± 0.8)</td>
<td>22</td>
<td>10.6–30.0 (15.5 ± 1.0)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>juvenile</td>
<td>28 February</td>
<td>11</td>
<td>13.5–81.1 (43.0 ± 6.9)</td>
<td>10</td>
<td>13.5–81.8 (40.7 ± 7.2)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>juvenile</td>
<td>15 March</td>
<td>11</td>
<td>28.7–76.3 (46.5 ± 4.6)</td>
<td>9</td>
<td>38.0–76.3 (49.4 ± 5.0)</td>
</tr>
<tr>
<td></td>
<td>Huruhi</td>
<td>larva</td>
<td>9 December</td>
<td>1</td>
<td>7.3</td>
<td>1</td>
<td>7.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>juvenile</td>
<td>9 December</td>
<td>9</td>
<td>9.5–15.4 (11.9 ± 0.7)</td>
<td>9</td>
<td>9.5–15.4 (11.9 ± 0.7)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>larvae</td>
<td>11 January</td>
<td>35</td>
<td>4.0–11.0 (6.0 ± 0.2)</td>
<td>27</td>
<td>4.4–11.0 (6.0 ± 0.3)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>juvenile</td>
<td>11 January</td>
<td>87</td>
<td>11.0–26.8 (13.8 ± 0.3)</td>
<td>20</td>
<td>11.0–21.5 (13.5 ± 0.5)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>larvae</td>
<td>7 February</td>
<td>32</td>
<td>3.5–11.6 (6.9 ± 0.4)</td>
<td>25</td>
<td>3.5–11.6 (6.8 ± 0.4)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>juvenile</td>
<td>7 February</td>
<td>39</td>
<td>10.7–26.0 (13.7 ± 0.4)</td>
<td>21</td>
<td>10.7–17.7 (12.9 ± 0.4)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>larvae</td>
<td>10 March</td>
<td>3</td>
<td>11.0 (11.0 ± 0)</td>
<td>2</td>
<td>11.0 (11.0 ± 0)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>juvenile</td>
<td>10 March</td>
<td>78</td>
<td>10.0–68.1 (36.4 ± 1.7)</td>
<td>23</td>
<td>10.0–68.1 (29.2 ± 3.5)</td>
</tr>
</tbody>
</table>
3.4.3 Successful spawning and settlement periods for *C. auratus*

Duration and timing of the successful spawning period (spawning that produced settled juveniles) varied among sites and between years (Table 3.3, Fig. 3.4). The successful spawning period in the Kaipara Harbour in 2009/2010 was particularly constricted (29 days), despite the fact that fish were captured on four different occasions over a two month period, and from two different sites. The successful spawning periods at the other three harbour sites lasted 2–3 months, although the timing of the successful spawning period varied among these sites (Fig. 3.4). The successful spawning period in the Mahurangi Harbour site was only recorded between November and December, however, it is possible that the successful spawning period was longer, as sampling in the Mahurangi Harbour was conducted in early February, and therefore, any fish spawned from January onwards would not have been caught. In 2010/2011, the successful spawning periods of *C. auratus* in both the Kaipara and Huruhi Harbours commenced earlier in the season and were longer in duration than their respective periods in 2009/2010 (Table 3.3, Fig. 3.4).

**Table 3.3.** Successful spawning period and settlement period for *C. auratus* in the Kaipara, Huruhi, Manukau and Mahurangi Harbours from 2009–2011.

<table>
<thead>
<tr>
<th>Site</th>
<th>Successful spawning period</th>
<th>Settlement period</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Start date</td>
<td>End date</td>
</tr>
<tr>
<td>Huruhi</td>
<td>13/12/2009</td>
<td>16/03/2010</td>
</tr>
</tbody>
</table>
Figure 3.4. Successful spawning and settlement periods for *C. auratus* in the Kaipara, Huruhi, Manukau and Mahurangi Harbour sites in 2009/2010 and for the Kaipara and Huruhi Harbour sites in 2010/2011. In the Kaipara Harbour in 2009/2010, fish were captured from site 1 on the 18/02/2010, 1/03/2010 and 22/04/2010, and from site 2 on the 26/03/2010. Spawning and settlement dates are back-calculated from daily otolith increments of 0+ year fish.
The average SST during the PLD was >18 °C for 91% of the *C. auratus* recruits captured in this study (Fig. 3.5) suggesting that there may be a temperature threshold, below which, the survival of larvae is very poor.

The PLD for *C. auratus* determined by pre-settlement otolith increments ranged from 17–33 days with a mean of 21.2 days ± 0.1 S.E. Given the low variability in the PLD, the range of the settlement period was very similar to the range of the successful spawning period (Fig. 3.4).

**Figure 3.5.** Relationship between the percentage of total *C. auratus* recruits captured and the average SST (°C) during the PLD.
3.4.4 Correlations between environmental variables and pelagic larval duration

Few significant correlations were found between PLD and the environmental variables modeled. PLD was found to be significantly negatively correlated with SST in the Mahurangi Harbour site in 2009/2010 ($F_{1, 32} = 5.93, P = 0.02$) and the Huruhi Harbour site in 2010/2011 ($F_{1, 64} = 11.77, P = 0.001$), with SST explaining 16% of the variability in PLD at both sites. PLD was also found to be significantly positively correlated with along-shore winds in the Huruhi Harbour site in 2009/2010 ($F_{1, 20} = 5.31, P = 0.03$), with along-shore winds explaining 21% of the variability (Fig. 3.6). PLD was not found to be related to average daily rainfall, solar radiation or cross-shore winds during the PLD.

3.4.5 Correlations between environmental variables and daily settlement

A number of significant correlations were found between the daily settlement and some of the environmental variables for the previous day, which explained between 10–38% of the variability in settlement (Table 3.4). Settlement of *C. auratus* in the Kaipara Harbour was negatively correlated with cross-shore winds and positively correlated with tidal range in 2009/2010, but was only positively correlated with SST in 2010/2011. Settlement of *C. auratus* in the Mahurangi Harbour in 2009/2010 was strongly positively correlated with tidal range, and less strongly positively correlated with SST. Likewise, settlement of *C. auratus* in Huruhi Harbour was positively correlated with SST in 2009/2010, but was not correlated with any of the environmental variables modeled in 2010/2011. Settlement of *C. auratus* in the Manukau Harbour was negatively correlated with along-shore winds, and weakly positively correlated with cross-shore winds (Fig. 3.7 & Table 3.4). No relationship between settlement and daily rainfall was found at any of the sites.
Figure 3.6. Significant relationships between the PLD of *C. auratus* and average daily environmental variables during the PLD. Positive and negative along-shore winds represented winds from the northwest and southeast, respectively.
Figure 3.7. Significant relationships between daily abundance of *C. auratus* settlers and the environmental variables for the previous day, estimated by GLMs with Poisson errors. Positive and negative along-shore winds represented winds from the northwest and southeast respectively, whereas, positive and negative cross-shore winds represented winds from the northeast and southwest, respectively.
Table 3.4. Results of the GLM models fitted between the number of *C. auratus* settlers per day and the environmental variables of the previous day. Only variables retained in the minimum adequate model are shown. None of the environmental variables modelled significantly affected the abundance of settlers in Huruhi Harbour in 2010/2011. Cross = cross-shore winds, along = along-shore winds.

<table>
<thead>
<tr>
<th>Site</th>
<th>Year</th>
<th>Model null deviance (df)</th>
<th>Model residual deviance (df)</th>
<th>Pseudo $R^2$ (%)</th>
<th>Environmental variables</th>
<th>Deviance</th>
<th>Reduction in deviance</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kaipara</td>
<td>2009/2010</td>
<td>63.65 (33)</td>
<td>44.3 (31)</td>
<td>30</td>
<td>cross</td>
<td>49.66</td>
<td>13.99</td>
<td>0.0002</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>tide</td>
<td>44.32</td>
<td>5.34</td>
<td>0.02</td>
</tr>
<tr>
<td>Huruhi</td>
<td>2009/2010</td>
<td>68.56 (74)</td>
<td>61.41 (73)</td>
<td>10</td>
<td>SST</td>
<td>61.41</td>
<td>7.15</td>
<td>0.008</td>
</tr>
<tr>
<td>Mahurangi</td>
<td>2009/2010</td>
<td>63.32 (49)</td>
<td>39.50 (47)</td>
<td>38</td>
<td>tide</td>
<td>46.19</td>
<td>17.13</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>SST</td>
<td>39.50</td>
<td>6.69</td>
<td>0.01</td>
</tr>
<tr>
<td>Manukau</td>
<td>2009/2010</td>
<td>73.92 (68)</td>
<td>63.43 (66)</td>
<td>14</td>
<td>along</td>
<td>67.33</td>
<td>6.59</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>cross</td>
<td>63.43</td>
<td>3.90</td>
<td>0.048</td>
</tr>
<tr>
<td>Kaipara</td>
<td>2010/2011</td>
<td>112.21 (66)</td>
<td>74.37 (65)</td>
<td>34</td>
<td>SST</td>
<td>74.37</td>
<td>37.84</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
3.5 Discussion

3.5.1 Successful spawning periods for *C. auratus*

Reproductive studies show that *C. auratus* spawn daily over a period of up to five months (Scott and Pankhurst 1992; Jackson *et al.* 2010; Sim-Smith *et al.* 2012b), however, results from this study and that of Fowler & Jennings (2003) show that the successful spawning period leading to recruitment is often much shorter than the overall spawning period. In particular, the successful spawning period in the Kaipara Harbour was constricted to only 1 or 2 months, which was much shorter than the successful spawning period at the other three sites. Results from a previous study in the Hauraki Gulf found a much longer successful spawning period of between 3.5 and 5 months for *C. auratus* (Francis 1994b). In 2010/2011, the successful spawning periods of *C. auratus* in both the Kaipara and Huruhi Harbours commenced earlier in the season and were longer in duration than the previous year. Some of the difference in successful spawning periods between the two years may be due to a change in sampling methodology. In 2010/2011 a finer mesh net was used (3.8 mm versus 6.8 mm) and sampling started earlier in spawning season than 2009/2010, which allowed smaller fish to be captured in 2010/2011.

The discrepancy between the overall spawning period and the successful spawning period may be because of different larval survival rates during the spawning period and/or the requirement for larvae of a suitable stage of development to be available when a certain combination of environmental parameters are present (Pineda *et al.* 2010), e.g., onshore winds, to facilitate the transport of larvae to the settlement areas. On-shore transport mechanisms may be particularly important for the *C. auratus* populations in west coast harbours, which are subjected to very strong wind and tidal currents. The results of this study suggest that SST, tidal range and winds may be important factors in the survival and transport of *C. auratus* larvae to settlement habitats, however, significant correlations varied among sites and between years, indicating that relationships are likely to be site specific and may also be affected by other factors, e.g., food availability or predation, that were not investigated in this study. For example, Murphy *et al.* (2012) demonstrated that
larval abundance of *C. auratus* was significantly higher in years that had high zooplankton abundances.

### 3.5.2 The effect of temperature on pelagic larval duration and recruitment

The positive relationship between water temperature and the growth rate of larval fish, and the subsequent reduction in PLD is well described in the literature (e.g. Houde 1989b; Francis 1994b; Benoît *et al.* 2000). When food is abundant, higher temperatures usually result in increased metabolic rates and food consumption in fishes (up to an optimum), leading to an increase in growth rate and usually a reduction in PLD (Benoît *et al.* 2000). Previous research on *C. auratus* has shown that fish with a short PLD (<20 days) grew significantly faster than fish with a long PLD (>24 days) (Sim-Smith *et al.* 2012a). The PLD of *C. auratus* from the Hauraki Gulf, New Zealand, was found to be significantly negatively correlated with average SST between 16 and 21 °C (Francis 1994b). However, in this current study, PLD was only found to be significantly negatively correlated with SST in two of the six models tested, and the correlations were weak ($r^2 = 0.16$). The lack of correlation between PLD and SST in this study may be partially because of the small range in SST during the PLD at most of our sites. Average SST during the PLD only varied by 1.5–3.8 °C in the sites that did not show a significant relationship between PLD and SST, compared to a range of 3.3–5.9 °C in those that did show significant relationships. Assessment of *C. auratus* recruitment data in the Northern Spencer Gulf, Australia between 2000 and 2010 showed a similar lack of correlation between SST and PLD (Fowler 2010).

Temperature can also often explain a substantial proportion of recruitment variability in many species, because it directly and indirectly affects many of the processes that govern recruitment, such as metabolic rate, growth, stage durations, mortality, prey availability and risk of predation (Houde 2008). Abundance of 1+ year *C. auratus* in the Hauraki Gulf, New Zealand, over a ten year period was found to be significantly positively correlated with SST during Feb–June of the previous (0+) year, with SST explaining 79% of the variability in abundance, though the underlying causal relationship is unknown (Francis 1993; Francis *et al.* 1997). However, the relationship between SST and recruitment of *C. auratus* is not
consistent among different populations around New Zealand (M. Francis, NIWA, pers. comm.), and there is little evidence of a relationship between SST and recruitment of 0+ year *C. auratus* in southern Australia (Fowler and Jennings 2003; Fowler 2010; Hamer *et al.* 2010), indicating that other factors also have a significant effect on *C. auratus* recruitment.

Examination of the relationship between SST and settler abundance in this current study generally supports Francis’ (1993) conclusion that SST is an important determinant of recruitment success in *C. auratus*. SST was found to be significantly positively correlated with daily settler abundance in 3 of the 6 models tested in this study, and the average SST during the PLD was >18 °C for more than 91% of the *C. auratus* recruits sampled (Fig. 3.5), despite the fact that *C. auratus* start spawning when SST are around 15 °C (Scott and Pankhurst 1992; Wakefield 2010; Sim-Smith *et al.* 2012b). Similarly, strong recruitment of *C. auratus* in northeastern New Zealand occurred in 1987 and 1988 following an abrupt increase in SST from 17 °C to 18.5–18.8 °C (Francis 1994b). It is likely that *C. auratus* that are spawned before the average water temperatures reach 18 °C experience very high mortality. Results from an aquaculture study on *C. auratus* support this hypothesis, with a high percentage of abnormal egg development at water temperatures <18.5 °C (Fielder and Allan 2003). Although the cultured *C. auratus* broodstock naturally commenced spawning when water temperatures reached 15 °C in this previous study, the average fertilization rates were <60% and average hatch rates were <5% at water temperatures between 15 and 18.5 °C. When the water temperature rose to ≥19 °C, average fertilization and hatch rates were generally >80% (Fielder and Allan 2003).

The use of SST in the present study to represent the water temperatures experienced by larvae needs to be interpreted with caution because the SST resolution was relatively course (9 km) and temperatures in deeper waters may be different to SST. Whereas eggs and yolk-sac larvae are buoyant (Cassie 1956; Pankhurst *et al.* 1991), older larvae utilise waters <40 m deep, although, the majority of *C. auratus* larvae captured from the Hauraki Gulf has been captured from waters <20 m deep (Kingsford 1988). Waters in the inner Hauraki Gulf are often strongly stratified in summer; however, the depth of the mixed layer during summer (December–February) is typically 15–40 m (Zeldis *et al.* 2004; Bury *et al.* 2012) and,
therefore, SST still provides a good proxy for the overall water temperature conditions encountered by *C. auratus* larvae.

Bergenius *et al.* (2005) found that high levels of solar radiation significantly decreased the growth rate and increased the PLD of coral reef surgeonfish (*Acanthurus chirurgus*) larvae. The authors hypothesized that exposure to high levels of solar radiation and ultraviolet light had a negative effect on the development of *A. chirurgus* larvae. In contrast, the results of the present study showed no relationship between the level of solar radiation and the PLD of *C. auratus*. This result is unsurprising given that *C. auratus* larvae are mainly found in the middle of the water column during the day (Murphy *et al.* 2011; J. Zeldis, NIWA, pers. comm.). The negative effects of solar radiation are likely to be greatest in larvae which primarily inhabit the surface layer of waters.

### 3.5.3 Larval abundance and transport to settlement areas

No *C. auratus* larvae were caught entering the Kaipara Harbour despite sampling fortnightly over a three month period. It is unlikely that this was the result of the sampling methodology because *C. auratus* larvae were caught from Huruhi Harbour on all four sampling occasions using the same methods. *Chrysophrys auratus* larvae have been rarely caught in New Zealand in significant numbers, despite the fact that *C. auratus* is one of the most common demersal fish species in northern New Zealand, and they spawn daily over an extended period (Scott *et al.* 1993). Previous studies have shown that the abundance of *C. auratus* larvae is highly variable both temporally and on small spatial scales, with zero or very low catch rates being common despite intensive plankton sampling (Atkinson 1987; Neira and Sporci 2002; Coutin *et al.* 2003; Hamer *et al.* 2010; 2011). For example, the mean abundance of *C. auratus* larvae within Port Phillip Bay varied from 0 to ≤150 larvae 1000 m⁻³ between sites, and standard errors between replicate tows were ≤70% of the mean (Hamer *et al.* 2010).

*Chrysophrys auratus* larvae most likely enter the Kaipara Harbour sometime during their larval period because *C. auratus* do not appear to spawn within the Kaipara Harbour (Sim-
Larval recruitment dynamics of *Chrysophrys auratus*

Smith *et al.* 2012b) and recently settled *C. auratus* (9.5–15 mm SL) were caught in the shallow regions of the harbour from late January onwards. The Kaipara Harbour is strongly tidal with current speeds of up to 2 m s\(^{-1}\) at the harbour entrance (Haggit *et al.* 2008). Given the strong currents in and out of the Kaipara Harbour it is likely that *C. auratus* larvae only enter the harbour late in their larval period when their swimming ability is strongest. Research from an Australian estuary supports this hypothesis, with the majority of *C. auratus* larvae caught entering Lake Macquarie found to be at settlement-stage (mean = 11.1 mm SL) (Miskiewicz 1986). Settlement-stage *C. auratus* larvae have a mean and maximum swimming speed of 0.1 m s\(^{-1}\) and 0.14 m s\(^{-1}\), respectively (Leis and Stobutzki 1999), still an order of magnitude less than the maximum current speeds in the Kaipara Harbour. It is probable that *C. auratus* larvae, like many other fish larvae, use selective tidal stream transport to facilitate their movement into harbours (Rowe and Epifanio 1994; Forward Jr *et al.* 1999; Hare *et al.* 2005). The significant positive correlations between daily settler abundance and tidal range in the Kaipara Harbour and Mahurangi Harbour sites in 2009/2010 support this hypothesis, because larvae utilizing selective tidal stream transport have a greater ability to travel to upstream settlement areas during spring tides. Similarly, settlement of kelp bass (*Paralabrax clathratus*) was found to be positively correlated with tidal range, and the authors hypothesized that internal tidal bores were a likely means of onshore transport for larvae (Findlay and Allen 2002).

Knowledge of spawning locations and local hydrodynamics would greatly assist our understanding of the transport of larvae to settlement habitats. *Chrysophrys auratus* are known to spawn outside the entrances of the Kaipara and Manukau Harbours (Smith *et al.* 1978; Sim-Smith *et al.* 2012b), and throughout much of the Hauraki Gulf, including the area southeast of Mahurangi Harbour (Zeldis *et al.* 2005). We hypothesized that winds blowing from the direction of these known spawning locations towards the harbours would be positively correlated with daily settler abundance. However, we found this only to be the case for settlement of *C. auratus* in the Kaipara Harbour site in 2009/2010, which was significantly higher during periods of strong on-shore (southwest) winds. It is possible that the lack of correlations between winds and daily settlement was because the sampled fish did not originate from the known spawning areas, but originated from a variety of locations.
or within the harbours themselves. *Chrysophrys auratus* do not appear to spawn within the Kaipara Harbour (Sim-Smith *et al.* 2012b), but the extent of spawning activity within the Manukau, Mahurangi or Huruhi Harbours is unknown. Previous research has shown that while settlement of larval fish is sometimes strongly correlated with on-shore winds (Shenker *et al.* 1993; Kingsford and Finn 1997; Findlay and Allen 2002), correlations are often absent or inconsistent (e.g., Robertson *et al.* 1999; Wilson and Meekan 2001; Bergenius *et al.* 2005; Vallès *et al.* 2009). These mixed results suggest that the relationship between settlement and wind is often likely to be more complex than a simple on-shore transport mechanism and is likely to be highly specific to species and location.

*Chrysophrys auratus* larvae were caught from outside Huruhi Harbour from December to March. The hydrodynamics around Great Mercury Island are very different from that of the Kaipara or Manukau Harbours. Great Mercury Bay is a large open embayment with slow currents. The lack of relationship between larval size or abundance and incoming tide period, or between daily settlement and tidal range suggests that tidal currents have little influence on the transport of *C. auratus* larvae to Great Mercury Bay, though it should be noted that under-sampling of very small larvae is likely to have occurred owing to the 1 mm$^2$ mesh size of our plankton net. Similarly, winds were not found to significantly affect daily settler abundance in the Huruhi Harbour site, though along-shore winds (northwest winds) were found to be significantly correlated with PLD. It is possible that winds from the northwest push warmer, plankton rich waters down the coast of the North Island, increasing the abundance of prey in Great Mercury Bay. Larvae down to 3.5 mm SL were caught in Great Mercury Bay, indicating that some *C. auratus* spawning activity occurred close to the bay, and it is possible that larvae are retained near Huruhi Harbour for their entire PLD and are able to reach settlement areas independently without requiring any on-shore transport mechanism.

Estuarine plumes may provide a directional, chemical signal that may be used by fish larvae to locate suitable settlement habitats (Leis *et al.* 2011). During periods of heavy rainfall these estuarine plumes will be detectable over a greater distance, and therefore, it was hypothesised that settlement of fish larvae would be higher following periods of heavy
rainfall. Previous research has demonstrated that *C. auratus* larvae are capable of differentiating between the odors of water collected from different regions of the Kaipara Harbour, and that larvae show a significant preference for water taken from above seagrass beds, their preferred settlement habitat, over water taken from the harbour entrance or artificial seawater (Radford *et al.* 2012). In addition, the abundance of *C. auratus* larvae entering Lake Macquarie, Australia, was found to be positively correlated with rainfall events that occurred in the previous 3–9 days (Trnski 2003), which suggests that larvae may be using olfactory cues in estuary plume water to locate the estuary. However, the results of this current study showed no relationship between rainfall and daily settlement of *C. auratus*. This lack of relationship does not mean that *C. auratus* do not use estuarine plume odor as an orientation cue, but only that there is no detectable difference in the use of the cue after heavy rainfall events.

### 3.5.4 Conclusion

The successful spawning period for *C. auratus* in this study occurred between October and March, with peak spawning occurring in December and January. The overall successful spawning period varied from 29–109 days among our four sites, with the Kaipara Harbour having the shortest successful spawning period. Recruitment to shallow water settlement sites may be influenced by environmental conditions that affect the survival and transport of larvae to settlement areas. Correlations between environmental variables and recruitment are often difficult to identify because recruitment is the result of complex interactions between numerous environmental variables, prey availability and predation. These abiotic and biotic variables affect the growth, mortality and dispersal of larvae, which in turn, influence recruitment variability. While significant correlations between environmental variables and daily settlement in this study were not consistent among sites or between years, they do indicate that SST, tidal range and strong on-shore winds are likely to be important to the recruitment of *C. auratus* to shallow water settlement sites in northern New Zealand.
Chapter 4

Variation in the growth of larval and juvenile snapper, *Chrysophrys auratus* (Sparidae)

This chapter has been published as:

4.1 Abstract

For many fish species, growth and mortality of larvae are closely coupled, with faster-growing larvae generally experiencing higher survivorship in the plankton, which may lead to higher recruitment. Using back-calculated growth trajectories derived from otolith increments we used the modified-Fry model to estimate the growth rate of larvae and early juveniles of the commercially important sparid, *Chrysophrys auratus*, at four sites around northern New Zealand. Back-calculated growth rates were used to test the hypothesis that fish with a short pelagic larval duration (≤20 days) grew faster than did fish with a long pelagic larval duration (>24 days) during both the larval and juvenile periods. At three of the four sites, fish with a short larval duration grew significantly faster during the larval period, and these larvae generally continued to have a larger size-at-age as juveniles up to 70-day-old. Growth rates for both the larval and early juvenile period were also found to vary significantly among the four sites and were found to be unrelated to differences in water temperature. Localised variation in early growth of *C. auratus* among sites may be important in helping to explain differences in their contribution to the recruitment to *C. auratus* populations.
4.2 Introduction

Growth and mortality of the larvae of many fish species appears to be closely coupled and numerous studies have shown that faster-growing larvae generally experience higher survivorship in the plankton (e.g., Meekan and Fortier 1996; Hare and Cowen 1997; Shahidul Islam et al. 2010). Faster-growing larvae often have a shorter pelagic larval duration and are also usually in better condition at the time of settlement, which leads to their subsequent success as juveniles (Searcy and Sponaugle 2001; Shima and Findlay 2002; Sponaugle and Grorud-Colvert 2006) and adults (Moss et al. 2005; Robert et al. 2007; Duffy and Beauchamp 2011). These concepts form the basis of the “Growth-Mortality” hypothesis (Anderson 1988), which states that; 1) larger larvae are less susceptible to predation, 2) faster-growing larvae are less vulnerable to predation as they spend less time as small larvae, and 3) faster-growing larvae reach metamorphosis faster reducing their overall larval mortality rate.

Fish otoliths, which are calcium carbonate structures that are analogous to the inner ear bones of other vertebrates, are commonly used to estimate the age and growth rate of fish. Otoliths are metabolically inert and grow throughout the lifetime of the fish by the addition of successive layers of aragonitic calcium carbonate (Campana 1999). These layers are usually formed daily, providing a permanent record of the life history of the fish, which can be used to estimate age and growth, and for dating major physiological events, such as hatch date and metamorphosis (Shima and Swearer 2009).

Otoliths have frequently been used to provide information on age and length-at-capture of sampled fish, and these data are commonly used in the construction of population-growth models (e.g., von Bertalanffy). However, construction of growth models from age and length-at-capture data only provides a single estimate of growth for each fish and aggregates all fish into a single age group, ignoring differences in growth rate between early and late-spawned fish, and the possibility that size-bias mortality may have occurred in the population (Chambers and Miller 1995). More recently, back-calculation techniques based on the measurement of daily otolith increments have been developed, which provide much more accurate information on the variability in growth between individual fish, and how
growth rates change throughout the life history of a fish (Campana and Jones 1992; Wilson et al. 2009).

Back-calculation of fish size from otolith increments is based on the following three assumptions; 1) the rate of deposition of otoliths increments is consistent, 2) increments can be read with accuracy and precision, and 3) there is a consistent relationship between otolith growth and somatic growth (Wilson et al. 2009). The first two assumptions are typically fulfilled, because many fish species lay down daily increments that can usually be accurately interpreted with careful preparation and practice (Stevenson and Campana 1992). The third assumption of a consistent relationship between otolith increments and somatic growth is more problematic. In general, many fish species show a strong allometric relationship between otolith radius and fish length (Jones 1992), however, uncoupling of otolith growth and somatic growth can sometimes occur (e.g., Secor and Dean 1989; Francis et al. 1993; Barber and Jenkins 2001), with slower-growing fish having larger and heavier otoliths relative to their body length. Early back-calculation growth models, e.g., the body proportional hypothesis (Whitney and Carlander 1956) and the Fraser–Lee linear back-calculation model (Fraser 1916; Lee 1920) did not take into account this growth effect, resulting in significant over-estimation of slow-growing fish. More recently, a number of back-calculation models have been developed to try and account for age, growth and time-varying effects. Wilson et al. (2009) tested five back-calculation models (biological intercept (Campana 1990), modified-Fry (Vigliola et al. 2000), time-varying growth (Sirois et al. 1998), body proportional hypothesis (Whitney and Carlander 1956) and age-effects (Morita and Matsuishi 2001)) by using fish reared under varying growth regimes. The modified–Fry model was found to produce the most accurate length-at-age estimates, with small bias (~5%) in size-at-age estimations, even when age, growth and time-varying effects were present.

*Chrysophrys auratus* (formerly *Pagrus auratus*) (Sparidae: Perciformes), commonly known as snapper, is widely distributed throughout the warm temperate waters of New Zealand and Australia (Ayling and Cox 1982; Gomon et al. 2008). It is a highly prized fish that supports significant commercial, recreational and customary (indigenous) fisheries in New Zealand
and Australia. In early spring, adult *C. auratus* often aggregate outside harbours, bays and estuaries to spawn (Crossland 1977a; Scott *et al.* 1993; Jackson 2007). Spawning aggregations of *C. auratus* are known to occur outside the Kaipara and Manukau Harbours on the western coast of the North Island (Smith *et al.* 1978), and throughout much of the Hauraki Gulf on the eastern coast of the North Island (Zeldis and Francis 1998). Larvae hatch at a relatively small size (2.1 mm standard length (SL), Pankhurst *et al.* 1991) and spend 18–32 days in the plankton (Francis 1994b; Fowler and Jennings 2003) before settling into the shallow waters of estuaries and bays at lengths of 9–14 mm SL (Miskiewicz 1986; Trnski 2002; Hamer and Jenkins 2004).

Growth of *C. auratus* is relatively slow, with fish reaching approximately 11–14 cm fork length (FL) after one year, 16–20 cm FL after two years, and 23–34 cm FL after four years (Longhurst 1958; Paul 1976; Horn 1986; McKenzie *et al.* 1992; Walsh *et al.* 2006). Growth rates have been shown to differ between populations of *C. auratus* on the eastern and western coast of the North Island of New Zealand, with fish from the western coast growing faster than fish from the eastern coast (Longhurst 1958).

Few studies have investigated the growth rate of wild *C. auratus* larvae and early juveniles, although previous studies using the sagittal otoliths of *C. auratus* have shown that this species fulfils the three assumptions required for using otolith growth to estimate somatic growth, namely; 1) larvae and juveniles lay down daily otolith increments, 2) daily increments are resolvable by light microscopy for fish up to 160-day-old, and 3) a strong linear relationship generally exists between otolith growth and somatic growth for 0+ year fish (Francis *et al.* 1993; Fowler and Jennings 2003). In some slow-growing *C. auratus*, uncoupling of otolith and somatic growth can sometimes occur (Francis *et al.* 1993).

Francis (1994a) determined the post-larval growth rate of 0+, 1+, and 2+ year *C. auratus* in the Hauraki Gulf by using age and length-at-capture data. Growth rates of 0+ year fish were approximately linear for their first 5–6 months, and were typically between 0.5–0.9 mm day$^{-1}$ (Francis 1994a). However, this previous study did not provide any information on larval or early juvenile growth rates because the youngest fish captured was 60-day-old. More recently, the biological intercept model (Campana 1990) was used to back-calculate the
growth rate of 0+ year *C. auratus* sampled in South Australia (Fowler and Jennings 2003). Growth rates were found to vary considerably among and within the three years sampled, although the differences were not statistically tested, and the authors hypothesized that the differences in growth rate were likely to be related to variations in water temperature. Localised differences in larval and juvenile growth rates among *C. auratus* may affect their contribution of recruits to adult populations, because it has been demonstrated that faster growth rates in the larval and early juvenile period are correlated with higher survival rates in adult fish (Moss *et al.* 2005; Robert *et al.* 2007; Duffy and Beauchamp 2011). Therefore, the aims of the current study were to; 1) provide information on the early growth of *C. auratus* by using the modified-Fry model to estimate the growth rate of *C. auratus* larvae and early juveniles from four sites around northern New Zealand, and 2) test the hypothesis that fish with a short pelagic larval duration (≤20 days) grow faster than do fish with a long pelagic larval duration (>24 days) during both the larval and juvenile periods.

### 4.3 Materials and methods

#### 4.3.1 Field collection

Newly recruited (0+ year) *C. auratus* were collected from four harbour sites (Kaipara, Manukau, Mahurangi and Huruhi) around northern New Zealand between 9 February and 15 May 2010 (hereafter referred to as 2009/2010), and from two sites (Kaipara and Huruhi) between 9 December 2010 and 15 March 2011 (hereafter referred to as 2010/2011) (Fig. 4.1).
Figure 4.1. Map of the North Island, New Zealand, showing the four sampling locations. The inset maps show the position of the sampling sites for *C. auratus* larvae (stars) and juveniles (triangles) within each location.
In 2009/2010, sampling was conducted over a three hour period during the day, one and a half hours either side of the low tide. Fish from the Mahurangi Harbour site were collected from the centre of the harbour in water depths of approximately 3 m by using a beam trawl that had a 4 m long beam, from which was suspended a 3 m wide x 4 m long main net constructed of 12 mm stretched mesh, and a 1 m long cod end constructed of 8 mm stretched mesh. Fish from the other sites were collected from shallow subtidal waters (<1.5 m) using an 11 m long beach seine net with a 2.3 m drop and a 4 m long cod end. The net was constructed of 12 mm stretched mesh in the main section and 6.8 mm stretched mesh in the cod end. Sufficient haphazardly placed, non-overlapping hauls were made in order to collect at least 50 *C. auratus* per sampling occasion. However, despite repeated sampling attempts, only 33 *C. auratus* in total were collected from the Manukau Harbour site, owing to their low abundance at that site. In 2009/2010, the Kaipara Harbour site was sampled on three occasions (18 February, 1 March, 23 April), the Manukau Harbour site was sampled on three occasions (3 and 25 April, 15 May), and the Mahurangi and Huruhi Harbour sites were each sampled once (9 February and 29 April, respectively).

In 2010/2011, newly recruited *C. auratus* were sampled from the Kaipara Harbour site at fortnightly intervals and the Huruhi Harbour site at monthly intervals, by using a purpose-built benthic sled that was towed behind an inflatable boat. The sled had a 1 m wide x 0.5 m high opening that was constructed from galvanized steel tubing, to which was attached a 3 m long net made from 3.8 mm stretched mesh. The use of the sled instead of the beach seine allowed sampling to be conducted in water deeper than 1.5 m. Eighteen, non-overlapping, five minute tows were conducted within an approximately 4 km² area in the shallow sandflats in the centre of the Kaipara Harbour on each sampling occasion (1 December, 7 and 26 January, 11 and 28 February, 15 March). At Huruhi Harbour, only 12 tows were conducted throughout the harbour on each sampling occasion (9 December, 11 January, 7 February, 10 March), owing to the much smaller size of the harbour (0.5 km²). On capture, fish were immediately stored on ice and then frozen at -80 °C on return to the laboratory.
Ichthyoplankton sampling was conducted at the entrance to the Kaipara and Huruhi Harbours (Fig. 4.1) between the 23 November 2010 and the 10 March 2011. Sampling was conducted throughout the night flood tide at fortnightly intervals in the Kaipara Harbour, and at monthly intervals in Great Mercury Bay. Stepped, oblique plankton tows were conducted every 30 mins throughout the flood tide with a 1 mm mesh net with a 1 m$^2$ square opening. The net was towed at a speed of approximately 0.8 m s$^{-1}$ and the overall tow time was typically between 10 and 15 mins. A General Oceanics flowmeter (model 2030, General Oceanics Inc., Miami, Florida, USA) was strung across the opening of the net to determine the volume of water filtered in each tow. All material from the cod end was preserved in 70% ethanol and sorted in the laboratory under a dissection microscope for ichthyoplankton. *Chrysophrys auratus* larvae were identified following descriptions by Niera et al. (1998).

### 4.3.2 Environmental data

Daily sea surface temperature (SST) data were obtained from the Group for High Resolution Sea Surface Temperature (GHR SST) L4 dataset that was provided by the Australian Bureau of Meteorology as part of National Oceanic and Atmospheric Administration’s (NOAA) Environmental Research Division’s Data Access Program (ERDDAP, ver. 1.36) (Simons 2011). The SST satellite analyses have a 9 km resolution and a 0.42 °C standard deviation when compared with observed SST buoy readings (Beggs et al. 2011). SST data were obtained for the coastal waters just outside the entrances of all four harbours.

### 4.3.3 Otolith preparation and analysis

All *C. auratus* captured were measured for SL and weighed to the nearest 0.01 g. Sagittal otoliths were extracted from at least 50 randomly chosen fish from each sampling occasion, if sufficient fish were available. Fish sampled for their otoliths were sub-sampled from the catch of 3–5 net hauls per sampling occasion in 2009/2010 and 4–12 hauls in 2010/2011. The otoliths were placed in pre-weighed eppendorf vials and cleaned by soaking in a 15%
H$_2$O$_2$ solution buffered with 4 g NaOH L$^{-1}$ for 24 h. The otoliths were rinsed three times in Millipore water (18 MΩ), air dried, and then weighed to the nearest 0.00001 g.

Thin, transverse sections of a sagittal otolith from at least 20 randomly chosen fish per sampling occasion were prepared following the methods of Campana (2010). Briefly, sections were prepared by grinding and polishing from both the rostral and anterostral ends of the otolith with a range of diamond sandpaper (Diamond Edge Ltd, Auckland, New Zealand) and diamond lapping film (6–35 µm) (Allied High Tech Products Ltd, Rancho Dominguez, California, USA). For the first grind the otolith was fixed onto the edge of a glass microscope slide with thermoplastic glue (Crystalbond™509, Aremco Products Inc., Valley Cottage, New York, USA), positioned with the core of the otolith in line with the edge of the slide, and hand sanded until the core was reached. For the second grind the ground surface of the otolith was attached to the centre of the microscope slide with Crystalbond™. The other end of the otolith was hand-sanded until a thin section of the otolith containing the core was obtained.

Digital images were taken of each otolith section using a Meiji Techno ML5000 compound microscope (Meiji Techno, Iruma-gun, Saitama, Japan) fitted with a Leica DFC420 digital camera that was connected to Leica Application Suite (LAS) imaging software (Leica Microsystems, Wetzlar, Germany). Images were captured at ×200–600 magnification and daily increments were counted and measured from the core to the otolith edge along the sagitta-subcupular meshwork fibre (SMF) zone (Fig. 3.2 in Chapter 3). Francis et al. (1992b) found that C. auratus sagittae were most easily interpreted along the SMF zone, which is a darker zone that runs from the core to the proximal surface between the sulcus and the ventral apex. Immersion oil (Ondina oil 68, Shell Company of Australia, Ltd, Melbourne, Victoria, Australia) was used to enhance the resolution of the increments. Otoliths were read on two separate occasions by C. Sim-Smith. If the counts differed by more than 5%, the otolith was re-read a third time. If the counts still differed by more than 5% after the third reading, the otolith was rejected; otherwise, the mean of the two closest counts was used as the best estimate of the number of increments. Readings were made blind with respect to the metadata associated with the otoliths or previous counts.
Date of spawning was calculated by subtracting the number of increments plus four days from the date of capture because the average duration between spawning and hatching is two days (Crossland 1980; Pankhurst et al. 1991; Battaglene and Talbot 1992), and the first increment in *C. auratus* is not formed until larvae are three-day-old (Fowler and Jennings 2003). In total, the otoliths of 315 *C. auratus* were read; including 140 juveniles from 2009/2010, and 55 larvae and 120 juveniles from 2010/2011.

### 4.3.4 Back-calculation of growth rates

Fish size-at-age was back-calculated using the modified Fry model (Vigliola et al. 2000) as follows:

\[ L_i = a + \exp \left( \ln(L_{0p} - a) + \left( \ln(L_{cpt} - a) - \ln(L_{0p} - a) \right) \times \left( \frac{\ln(R_i) - \ln(R_{0p})}{\ln(R_{cpt}) - \ln(R_{0p})} \right) \right) \]  
\[ \text{Eqn. 1} \]

where \( L_i \) = fish length at age \( i \), \( L_{0p} \) = fish length at biological intercept, \( L_{cpt} \) = fish length at capture, \( R_i \) = otolith radius at age \( i \), \( R_{0p} \) = otolith radius at biological intercept, and \( R_{cpt} \) = otolith radius at capture.

\( L_{0p} \), the average length of *C. auratus* at first increment formation was set at 3.03 mm SL, on the basis of measurements of 3-day-old cultured *C. auratus* (Pankhurst et al. 1991), and \( R_{0p} \), the mean radius of the first otolith increment in *C. auratus* from the current study was 3.1 µm.

Constants \( b \) and \( c \) were estimated from the non-linear regression of Equation 2:

\[ L_{cpt} = L_{0p} - bR_{0p}^c + bR_{cpt}^c \]  
\[ \text{Eqn. 2} \]

and the constant \( a \), was determined from Equation 3:

\[ a = L_{0p} - bR_{0p}^c \]  
\[ \text{Eqn. 3} \]
4.3.5 Data analyses

Successful spawn dates in the four sites occurred at different times between 23 November and 16 March in 2009/2010, and between 1 December and 15 March in 2010/2011 (Fig. 3.4 in Chapter 3), when water temperatures varied between 16.9 °C and 21.9 °C. Water temperature strongly affects the growth rate in juvenile *C. auratus* (Francis 1994a), therefore, to reduce variation in SST among sites, only fish spawned in December and January were used in the among-site comparisons (Table 4.1). SST (mean ± S.E.) for December and January was 19.0 ± 0.1 °C for the Kaipara Harbour, 18.5 ± 0.1 °C for Huruhi Harbour, 18.8 ± 0.1 °C for Manukau Harbour, and 19.0 ± 0.1 °C for Mahurangi Harbour in 2009/2010, and 19.5 ± 0.2 °C for the Kaipara Harbour and 19.5 ± 0.1 °C for Huruhi Harbour in 2010/2011. The effect of the mean SST on the mean growth rate during both the larval and juvenile period in 2009/2010 was determined using separate linear mixed effects models (PROC MIXED) using SAS software (ver. 9.3, SAS Institute Inc., Cary, NC, USA). SST was used as the fixed effect and site was used as the random effect. The mean SST was calculated by averaging the daily SST at the four sites during either the larval or juvenile period. The mean growth rate (mm day\(^{-1}\)) was calculated by averaging the daily back-calculated growth rates over the larval or juvenile period. Degrees of freedom were calculated using the Kenward-Roger method (Kenward and Roger 1997), which is appropriate for unequal sample sizes.
Table 4.1. Sampling dates, overall sample size \((n_1)\), and standard length (SL) of \(C.\ auratus\) juveniles and larvae captured from the Kaipara, Huruhi, Manukau and Mahurangi Harbour sites in 2009/2010 and 2010/2011, and the sub-sample size \((n_2)\) and size of fish that were spawned in December and January and used in the growth rate comparisons. Mean ± S.E. are given in parentheses.

<table>
<thead>
<tr>
<th>Year</th>
<th>Site</th>
<th>Sample date</th>
<th>Overall sample (n_1)</th>
<th>SL, range and mean (mm)</th>
<th>December and January spawned fish (n_2)</th>
<th>SL, range and mean (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Juveniles</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2009/2010</td>
<td>Kaipara</td>
<td>18 February</td>
<td>452</td>
<td>18.9–53.5 (33.5 ± 0.3)</td>
<td>19</td>
<td>20.4–53.5 (37.1 ± 1.9)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1 March</td>
<td>291</td>
<td>27.2–62.8 (44.5 ± 0.4)</td>
<td>22</td>
<td>34.1–62.8 (48.1 ± 1.7)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>22 April</td>
<td>50</td>
<td>43.9–77.8 (57.7 ± 1.0)</td>
<td>19</td>
<td>48.1–69.2 (58.3 ± 1.5)</td>
</tr>
<tr>
<td></td>
<td>Huruhi</td>
<td>29 April</td>
<td>171</td>
<td>13.9–75.7 (38.2 ± 0.7)</td>
<td>14</td>
<td>37.8–75.7 (49.4 ± 3.0)</td>
</tr>
<tr>
<td></td>
<td>Manukau</td>
<td>3 April</td>
<td>23</td>
<td>20.2–96.3 (44.4 ± 3.8)</td>
<td>15</td>
<td>30.0–80.2 (46.8 ± 3.5)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>24 April</td>
<td>6</td>
<td>37.3–50.1 (44.5 ± 2.3)</td>
<td>4</td>
<td>37.6–49.3 (44.8 ± 2.6)</td>
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<tr>
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<td></td>
<td>15 May</td>
<td>4</td>
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<td>57.4–60.1 (58.8 ± 1.4)</td>
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<td>17.2–41.6 (28.7 ± 1.3)</td>
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<td>16</td>
<td>11.0–33.0 (14.1 ± 1.3)</td>
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<tr>
<td></td>
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<td>11 February</td>
<td>26</td>
<td>10.6–30.0 (15.3 ± 0.8)</td>
<td>17</td>
<td>10.9–30.0 (16.3 ± 1.2)</td>
</tr>
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<td></td>
<td></td>
<td>28 February</td>
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<td>13.5–81.1 (43.0 ± 6.9)</td>
<td>6</td>
<td>27.2–50.0 (34.6 ± 3.4)</td>
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<td></td>
<td>15 March</td>
<td>11</td>
<td>28.7–76.3 (46.5 ± 4.6)</td>
<td>5</td>
<td>38.0–51.8 (43.5 ± 2.4)</td>
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<tr>
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<td>–</td>
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<tr>
<td></td>
<td></td>
<td>11 January</td>
<td>87</td>
<td>11.0–26.8 (13.8 ± 0.3)</td>
<td>11</td>
<td>11.0–15.7 (12.7 ± 0.4)</td>
</tr>
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<td>14</td>
<td>10.7–17.7 (13.4 ± 0.6)</td>
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<td>17</td>
<td>16.7–46.7 (28.2 ± 2.0)</td>
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<td><strong>Larvae</strong></td>
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<td></td>
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<tr>
<td>2010/2011</td>
<td>Huruhi</td>
<td>9 December</td>
<td>1</td>
<td>7.3</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td></td>
<td>11 January</td>
<td>35</td>
<td>4.0–11.0 (6.0 ± 0.2)</td>
<td>–</td>
<td>–</td>
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<td></td>
<td></td>
<td>7 February</td>
<td>32</td>
<td>3.5–11.6 (6.9 ± 0.4)</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10 March</td>
<td>3</td>
<td>11.0 (11.0 ± 0.0)</td>
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</table>
Growth trajectories of “larval” (5–20-day-old) and “juvenile” (25–70-day-old) *C. auratus* from the Kaipara, Huruhi, Manukau and Mahurangi sites were compared in 2009/2010, and from the Kaipara and Huruhi sites in 2010/2011, using back-calculated length data for every fifth day between 5 and 70 days. The pelagic larval duration (PLD) for our fish ranged from 17 to 33 days; however, for simplicity, we refer to the first 20 days as the larval period because the median PLD for our fish was 21 days and 92% of aged fish had a PLD of <25 days. Growth trajectories of fish from the Kaipara and Huruhi sites were also compared between the two years. Back-calculated SL data were analysed with repeated measures analysis of variances (ANOVA) using a linear mixed effects model (PROC MIXED) available in SAS software. Site or year, age, and the interaction between site and age were used as fixed factors, and fish (within each site) and the interaction between fish and age were used as random factors. A repeated measures ANOVA accounts for the non-independence of repeated measurements from the same fish (Chambers and Miller 1995). Separate repeated measures ANOVAs were conducted for the larval and juvenile durations that compared; 1) the differences in growth among sites within years, and 2) the difference in growth between years in the Kaipara and Huruhi sites. In instances where the variance of the residuals was found to be heterogeneous a weighted variance structure was chosen using log-likelihood tests (see Table 1 in the Appendix for the results of model comparisons). Degrees of freedom were calculated using the Kenward-Roger method (Kenward and Roger 1997). Tukey’s multiple comparison tests were used, where applicable, to compare differences in mean modelled standard length of fish among sites for 5-, 15-, 20-, 25-, 35-,45-, 55- and 70-day-old fish.

To compare the growth rate between fish with short and long PLDs for each site, the larval and juvenile growth trajectories of five fish with a short PLD (≤20 days) were compared with five fish with long PLD (>24 days) by using repeated measures ANOVAs (as above). A separate repeated measures ANOVA was conducted for the larval and juvenile periods for each site-year combination. No comparison was made for fish from the Huruhi Harbour site in 2009/2010 because only one fish had a PLD >24 days. Growth of fish from the Kaipara and Manukau Harbour sites in 2009/2010 were modelled from 5–70-day-old fish and growth of
fish from all other sites were modelled from 5–40-day-old, owing to the small number of fish >40 day-old.

One-way ANOVAs were used to compare differences in PLD among sites using R software (ver. 2.15.0, R Foundation for Statistical Computing, Vienna, Austria). Separate ANOVAs were preformed for 2009/2010 and 2010/2011 because the Mahurangi and Manukau Harbour sites were not resampled in 2010/2011. The data were found to meet the assumptions of normality and homogeneity of variance. Tukey’s multiple comparison tests were used, where applicable, to compare differences in PLD between pairs of sites.

4.4 Results

In total, 71 larvae were captured from Huruhi Harbour and 1336 newly recruited *C. auratus* were captured from all sites (Table 4.1). No larvae were captured from Kaipara Harbour on any of the seven plankton sampling occasions. Overall, the sampled larvae ranged in size between 3.5 mm SL and 11.6 mm SL, and the sampled juveniles ranged in size between 9.5 mm SL and 96.3 mm SL. Of the sampled fish, 208 fish were sub-sampled for growth comparisons (Table 4.1).

4.4.1 Relationship between otolith growth and somatic growth

Otolith radii were strongly positively correlated with SL for all 431 *C. auratus* measured (Fig. 4.2, $r^2 = 0.976$). Although an allometric equation was fitted to the data (Eqn. 2), the regression estimated $c$ to be 1.04, and thus, the relationship between the otolith radius and SL was effectively linear. The strong relationship between the otolith radius and SL demonstrates that otolith growth rates are a good proxy for somatic growth rates of *C. auratus* between 3.5 and 100 mm SL and, therefore, otolith measures are likely to provide a reliable size-at-age measure.
Growth of larval and juvenile Chrysophrys auratus

Figure 4.2. Relationship between otolith radius and standard length of larval and juvenile C. auratus. Otolith radii were measured along the sagittal-subcupular meshwork fibre (SMF) line.

A comparison of the average size-at-age of fish back-calculated by the modified-Fry model for the Huruhi Harbour site in 2010/2011 with the age and length-at-capture of fish shows that the modelled growth rates generally provided good estimates for average fish length, though the model appears to underestimate the size-at-age for older larvae (Fig. 4.3).
4.4.2 Growth of 0–70-day-old *C. auratus*

Initial growth of *C. auratus* larvae was $<0.14$ mm day$^{-1}$, with growth rates decreasing between day 4 and day 6–7. After day 10, growth rates increased rapidly to reach a maximum of between 0.7 and 1.0 mm day$^{-1}$ about day 35–45. Thereafter, growth continued at a similar level, or decreased slightly, up to day 70 (Fig. 4.4).
Figure 4.4. Mean (± S.E.) daily growth rate back-calculated from daily otolith increments for *C. auratus* ≤70-day-old, from (a) the Kaipara, Huruhi, Manukau and Mahurangi Harbour sites in 2009/2010, and (b) the Kaipara and Huruhi Harbour sites in 2010/2011.
4.4.3 Effect of temperature on growth

Differences in average growth rates for *C. auratus* that were spawned in December and January were not related to differences in average SST during the larval period ($F_{1, 103} = 0.99, P = 0.32$). However, during the juvenile period the average growth rate was found to be slightly negatively correlated with average SST ($F_{1, 14} = 6.56, P = 0.02$) (Fig. 4.5).

**Figure 4.5.** The relationship between the mean SST during the (a) larval and (b) juvenile duration of *C. auratus* captured from the Kaipara, Huruhi, Manukau and Mahurangi Harbour sites in 2009/2010, and their mean daily growth rate. Daily growth was back-calculated from daily otolith increments.
### 4.4.4 Differences in growth rates of C. auratus among sites

Results from the repeated measures ANOVAs on estimated size-at-age showed that the modelled growth trajectories of *C. auratus* that were spawned in December and January were significantly different among sites for fish sampled in 2009/2010 for both the larval period ($F_{3,362} = 4.71, P = 0.003$) and the juvenile period ($F_{3,36.7} = 6.88, P = 0.0009$). Tukey’s multiple comparisons showed that fish from the Kaipara Harbour site were significantly longer than those from the Manukau Harbour site between 15- and 70-day-old (Tukey’s $P = 0.0002–0.05$), and those from the Mahurangi Harbour site between 15- and 35-day-old (Tukey’s $P = 0.0003–0.03$), whereas they were not significantly different from the fish from the Huruhi Harbour site. Fish from Huruhi Harbour site were also significantly longer than those from the Manukau Harbour site between 20- and 35-day-old (Tukey’s $P = 0.005–0.046$) and those from the Mahurangi Harbour site between 20- and 25-day-old (Tukey’s $P = 0.009–0.04$) (Fig. 4.6a–h).

In 2010/2011, the growth trajectories for fish from the Kaipara and Huruhi Harbours were not significantly different for the larval period ($F_{1,235} = 1.37, P = 0.24$), but were significantly different for the juvenile period ($F_{1,84.9} = 11.51, P = 0.001$). Tukey’s multiple comparisons showed that fish from Huruhi Harbour were significantly longer than those from Kaipara Harbour at 25–35-day-old (Tukey’s $P = 0.001–0.01$), however, they were not significantly different for any other age tested (Fig. 4.7a–d).

The modelled growth trajectories of *C. auratus* from the Kaipara Harbour site that were spawned in December and January were not significantly different between 2009/2010 and 2010/2011 for both the larval period ($F_{1,345} = 0.01, P = 0.92$) and the juvenile period examined ($F_{1,102} = 0, P = 1.0$). Similarly, the growth trajectories of *C. auratus* from the Huruhi Harbour site that were spawned in December and January were not significantly different between 2009/2010 and 2010/2011 for both the larval period ($F_{1,166} = 0.01, P = 0.91$) and the juvenile period ($F_{1,14.7} = 2.87, P = 0.11$).
Figure 4.6. Individual back-calculated growth trajectories from daily otolith increments for larval and juvenile *C. auratus* from the (a–b) Kaipara Harbour site, (c–d) Huruhi Harbour site, (e–f) Manukau Harbour site, and (g–h) Mahurangi Harbour site in 2009/2010.
4.4.5 Differences in pelagic larval duration among sites

The PLD for *C. auratus*, determined from pre-settlement otolith increments, ranged from 17 to 33 days with an overall median PLD of 21 days. PLD was generally most consistent in fish from the Kaipara Harbour site (mean = 20.9 ± 0.2 S.E.) and most variable in fish from the Manukau Harbour site (mean = 22.7 ± 0.8 S.E.) (Fig. 4.8). PLDs were significantly different among sites in 2009/2010 ($F_{3, 123} = 5.58$, $P = 0.001$), with fish from the Manukau Harbour site having a significantly longer PLD than fish from the Kaipara Harbour site (Tukey’s $P = 0.007$) and fish from the Huruhi Harbour site (Tukey’s $P = 0.008$). PLD was not significantly different between the Kaipara and Huruhi Harbour sites in 2010/2011 ($F_{1, 93} = 0.47$, $P = 0.49$).
4.4.6 Differences in growth between larvae with short and long pelagic larval durations

In three of our four sites, *C. auratus* with a short PLD grew significantly faster than those with a long PLD, during both their larval and juvenile period. Fish with a short PLD were significantly bigger than were those with a long PLD from 15- to 70-day-old in Kaipara Harbour site in 2009/2010 (Tukey’s *P* <0.0001–0.008), from 15- to 60-day-old in the Manukau Harbour site in 2009/2010 (Tukey’s *P* = 0.02–0.0008) and from 15- to 40-day-old in the Huruhui Harbour site in 2010/2011 (Tukey’s *P* = 0.01–0.0003) (Fig. 4.9 & Table 4.2). In the Kaipara Harbour site in 2010/2011, fish with a short PLD grew significantly faster than did
those with a long PLD for the larval period, but not for the juvenile period. Conversely, in the Mahurangi Harbour site, growth of fish was not significantly different during the larval period, but fish with a short PLD had significantly faster growth than did those with a long PLD during the juvenile period (Fig. 4.9 & Table 4.2).

**Table 4.2.** Results of repeated-measures ANOVAs, comparing the difference in growth rates between fish with short (≤20 days) and long (>24 days) pelagic larval durations from sites in the Kaipara, Huruhi, Manukau and Mahurangi Harbours in 2009/2010 and 2010/2011. *P* values in bold indicate a significant difference at *P*<0.05.

<table>
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<tr>
<th>Year</th>
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<th></th>
<th>Juveniles</th>
<th></th>
</tr>
</thead>
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<td></td>
<td></td>
<td><em>F</em></td>
<td><em>df</em></td>
<td><em>P</em></td>
</tr>
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<td>10.73</td>
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<td>1, 28</td>
<td>0.04</td>
<td>2.21</td>
</tr>
<tr>
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<td>Huruhi</td>
<td>5.17</td>
<td>1, 32</td>
<td>0.03</td>
<td>37.76</td>
</tr>
</tbody>
</table>
Figure 4.9. Individual growth trajectories of *C. auratus* with short (≤20 days) and long (>24 days) pelagic larval durations from the (a) Kaipara Harbour site in 2009/2010, (b) Manukau Harbour site in 2009/2010, (c) Mahurangi Harbour site in 2009/2010, (d) Kaipara Harbour site in 2010/2011, and (e) Huruhi Harbour site in 2010/2011. Note that the scale of the x-axis varies among graphs.
4.5 Discussion

The current study is the first one to determine the growth trajectories of larval and early juvenile \textit{C. auratus} from otolith increments, by using the modified-Fry growth model, and to statistically compare growth trajectories among different sites and years. Back-calculated length data provide detailed information on how growth rates of individual fish change over time, unlike the traditional age- and length-at-capture data, which only provide a single measurement per fish. We chose to use the modified-Fry model because it has been shown to be least biased in the presence of age, growth or time-varying effects, and to produce more accurate length-at-age estimates than does the biological intercept model, the time-varying growth model, the body proportional hypothesis model or the age-effects model (Vigliola \textit{et al.} 2000; Wilson \textit{et al.} 2009; Perez and Munch 2013). The modified-Fry model generally provided good estimates for the early growth of \textit{C. auratus}, though it appeared to underestimate the size-at-age for older larvae. The early growth of \textit{C. auratus} may be better modelled by a stepped growth model e.g., (Günther \textit{et al.} 2012), which allows for a change in the SL–otolith radius relationship between the larval and juvenile stages. However, we captured too few settlement-stage larvae in this study to accurately determine if there is a change in relationship between SL and otolith radius relationship at settlement for \textit{C. auratus}.

4.5.1 Growth of 0–70-day-old \textit{C. auratus}

Growth of newly hatched \textit{C. auratus} was slow between days 4 and 7, which corresponds to the period between the absorption of the yolk sac (day 3) and first feeding (day 4–6) (Pankhurst \textit{et al.} 1991; Battaglene and Talbot 1992). Thereafter, the growth rate of the fish rapidly increased to a maximum of between 0.7 and 1.0 mm day$^{-1}$ by day 35–45, before levelling out or decreasing slightly. These growth rates are comparable to the growth rates of older \textit{C. auratus} (60–200-day-old) from the Hauraki Gulf estimated from age- and length-at-capture data, which varied from a minimum of 0.35 mm day$^{-1}$ to a maximum of 1.0 mm day$^{-1}$ (Francis 1994a).
Growth of larval and juvenile *Chrysophrys auratus*

Fowler and Jennings (2003) constructed back-calculated growth trajectories for a small number of *C. auratus* from the Spencer Gulf, South Australia, by using the biological intercept model. The growth trajectory for *C. auratus* from the Spencer Gulf during 2002 was very similar to the growth trajectories in the current study, with fish from Spencer Gulf reaching a maximum growth rate of 0.8 mm day$^{-1}$ by 25–35-day-old, and then remaining between 0.6 and 0.8 mm day$^{-1}$ until approximately 80-day-old. However, growth trajectories of fish from Spencer Gulf in the preceding two years increased more rapidly, reached a higher maximum (1.2 mm day$^{-1}$), and remained elevated for longer, than did either fish from the Spencer Gulf in 2002 or fish from the current study in New Zealand. Higher SST in the Spencer Gulf in 2000 and 2001 may explain the difference in growth rates between *C. auratus* from the current study and that from Fowler and Jennings (2003). SST in the Spencer Gulf in 2000 and 2001 were around 22–23 °C during the month of spawning, whereas daily SST in the current study were between 17 °C and 21 °C during the spawning months (December and January). Water temperature has been shown to strongly affect the early growth rates of *C. auratus* and Francis (1994a) found that, in many cases, growth rates of 0+ year *C. auratus* were strongly positively correlated with SST, with SST explaining 25–77% of the variability in growth rate. However, Fowler (2010) did not find a consistent relationship between growth of larval *C. auratus* from Northern Spencer Gulf and SST over a 10 year period. Similarly, in the current study, differences in larval growth were not related to average SST, and differences in juvenile growth were only weakly correlated with SST indicating that other factors may also have an important influence on the growth of *C. auratus*.

4.5.2 The relationship between growth and pelagic larval duration in *C. auratus*

The PLDs of *C. auratus* in the current study were very similar to those of *C. auratus* previously observed in the Hauraki Gulf, northeastern New Zealand (18–32 days) (Francis 1994b) and South Australia (18–28 days) (Fowler and Jennings 2003). The consistent and relatively small range in the PLD in all three studies indicates that *C. auratus* does not exhibit delayed metamorphosis, and that variability in PLD is more likely to be a result of variations
in growth. Furthermore, in the current study, fish with a long PLD did not show a period of depressed growth late in their larval period, which is an indication of delayed metamorphosis (Victor 1986). In three of our four sites, fish with a short PLD were found to grow significantly faster than were fish with a long PLD. This result concurs with other studies that have also shown that PLD was inversely related to growth in larval fish (Denit and Sponaugle 2004; Green and Fisher 2004; Sponaugle et al. 2006).

Chrysophrys auratus that had a short PLD and grew fast as larvae generally continued to grow faster as juveniles than did fish with a long PLD. It is possible that differences in growth rates are due to genetic or nutritional differences among fish, which continue to confer growth advantages to juvenile fish after they transition from the pelagic environment to the benthic habitat. The majority of research on larval growth in fish has shown that individuals that grow faster as larvae are able to maintain faster growth rates as juveniles (e.g., Tupper and Boutilier 1995; Vigliola and Meekan 2002; McCormick and Hoey 2004). However, this is not always the case because growth of larval Pleuronectes americanus was found to be either uncorrelated or negatively correlated with juvenile growth rates in the first month following metamorphosis (Bertram et al. 1993; 1997). Similarly, in the current study, not all slow-growing larvae remained as slow-growing juveniles. In some cases, individuals that grew slowly as larvae showed accelerated growth during the juvenile period (Fig. 4.9b & 4.9d), demonstrating that growth compensation may occur in some individuals despite the lack of growth compensation overall in a juvenile cohort.

4.5.3 Differences in pelagic larval duration and growth rates among sites
Pelagic larval duration and growth were found to vary significantly among sites in the current study. Fish from the Manukau Harbour site had a more variable and longer median PLD, and also grew significantly slower than did fish from the Kaipara or Huruhi Harbour sites over the larval and juvenile periods. The slower growth and longer PLD suggest that environmental conditions for growth during the larval and early juvenile periods were likely to be less favourable and potentially more spatially and/or temporally variable at the Manukau Harbour site than they were at the other sites.
Growth rates of fish are usually positively correlated with SST (up to a thermal maximum) (Blaxter 1992) and SST has been shown to be positively correlated with growth rates of juvenile *C. auratus* (Francis 1994a). However, differences in larval growth in the current study were not found to be related to average SST, and surprisingly, juvenile growth was found to be slightly negatively correlated with SST. The weak negative relationship between SST and juvenile growth is likely to be a coincidental correlation rather than a causative factor, and could be driven by fish from the Kaipara Harbour site showing some of the faster growth rates while experiencing the lowest water temperatures (Fig. 4.5). Similarly, Fowler (2010) did not find a consistent relationship between growth of larval *C. auratus* from Northern Spencer Gulf and SST over a 10 year period. It is unlikely that the SST experienced by fish in the current study (≤22 °C) were too high for *C. auratus* because the optimal growth temperature for cultured *C. auratus* larvae and post-larvae was found to be 24 °C (Fielder *et al.* 2005; 2008).

It is possible that differences in growth rates among our sites were due to differences in food availability at the sites. Food availability is thought to be critical for the growth and survival of *C. auratus* larvae. For example, the abundance of *C. auratus* larvae in the Hauraki Gulf, north-eastern New Zealand, did not correspond with SST or late-stage egg abundance, but instead was found to be correlated with phytoplankton and zooplankton densities (Zeldis *et al.* 2005). The presence, in our study, of seagrass only at the two sites that supported the highest growth rates in *C. auratus* may also be an indication of higher food availability at those sites, because previous research has shown that the abundance of prey species for juvenile fish within seagrass beds is significantly higher than in adjacent areas of bare substrate (e.g., Lubbers *et al.* 1990; Connolly 1997; Nakamura and Sano 2005). However, further research is required to determine whether differences in growth rates among sites are due to differences in prey abundances associated with juvenile habitat type.
4.5.4 Conclusion

The results from the current study have shown that the modified Fry model can be used to provide a good estimation of the daily growth rate of *C. auratus*, with the possible exception of the late larval stage. Growth was found to be related to PLD, with fish with a short PLD generally showing faster growth during both the larval and early juvenile periods, than fish with a long PLD. Growth rates from the late larval period onward were also found to vary significantly among our four sampling sites. There was no clear relationship between growth of fish at each of the sampling sites and the corresponding water temperatures. The higher growth rates of fish from the Kaipara and Huruhi Harbour sites may be because of higher prey availability at these sites; however, further research is needed to confirm this. There is strong evidence demonstrating that faster-growing larvae have a higher survival rate (e.g., Meekan and Fortier 1996; Takasuka *et al.* 2003; Nielsen and Munk 2004). Variation in larval survival rates can have major impacts on the subsequent abundance of juvenile fish (e.g., Bradford 1992; Mertz and Myers 1995), often producing 10- to 100-fold differences in interannual recruitment (Pope and Macer 1996; Houde 2009). These findings are important for fisheries management because previous research indicates that even small differences in growth rates of larvae can ultimately lead to large fluctuations in recruitment and population size (Houde 1989a; Campana 1996).
5.1 Abstract

Larval and early juvenile fish living in temperate environments with limited food resources face conflicting metabolic demands. To optimise their survival probability, fish must balance the need to out-grow predators by maximising their growth, whilst also accumulating sufficient energy reserves to sustain them through winter when food is scarce. We tested the hypothesis that resource allocation in the sparid, *Chrysophrys auratus*, changed from maximising growth to maximising energy storage over their first summer–autumn (i.e., directly after settlement) by measuring recent growth rates from peripheral otolith increments, and lipid, protein and carbohydrate concentrations in fish over three months. Lipid concentrations showed the greatest change over the growing season, being three-fold higher in mid-autumn than in summer. Growth rates showed the opposite trend, being significantly lower in mid-autumn than in summer. The relationships between growth rate and lipid or protein concentrations were consistent with a shift in resource-allocation from growth to storage. During summer and early autumn, growth rates were independent of protein or lipid concentrations, but during mid-autumn there were significant positive
correlations between the variables. Lipid, protein or carbohydrate concentrations were independent of fish size, indicating that the shift in resource-allocation from growth to storage is time-dependent rather than size-dependent. These results indicate that the accumulation of sufficient energy reserves for winter is determined by the timing of settlement and subsequent feeding conditions, which together are likely to affect the interannual variability in recruitment of this commercially important species.

5.2 Introduction

Larval and early juvenile temperate fishes face competing demands for nutritional resources during their first summer/autumn. Smaller fish are more vulnerable to predation and numerous studies have demonstrated that faster-growing and larger fish have a higher probability of survival (e.g., Meekan and Fortier 1996; Hare and Cowen 1997; Takasuka et al. 2003; Shahidul Islam et al. 2010). However, fish must also accumulate sufficient energy reserves to sustain them over their first winter when food is relatively scarce, and other studies have shown that survival of 0+ year fish is positively related to energy accumulation prior to winter (Huss et al. 2008; Heermann et al. 2009). Thus, in order to maximise their chances of survival, fish must balance the amount of available energy that they allocate to growth with the accumulation of energy reserves (Post and Parkinson 2001; Díaz et al. 2009).

The relationship between growth and energy storage in fish is complex and is affected by numerous factors including fish size (Post and Parkinson 2001; Sogard and Spencer 2004), water temperature (Sogard and Spencer 2004), season (Hurst and Conover 2003; Biro et al. 2005; Huss et al. 2008) and food availability (Sogard and Spencer 2004; Jacobs et al. 2012). Fish primarily store energy reserves as proteins, lipid and carbohydrates. During periods of starvation, fish metabolize their carbohydrates first, then their storage lipids, and finally their protein reserves (Ferron and Leggett 1994; Frommel and Clemmesen 2009). Numerous studies have found that growth rates of juvenile fish are significantly positively correlated with their lipid (Amara et al. 2007; Frommel and Clemmesen 2009; Copeland et al. 2010) and protein (Foster et al. 1993; Frommel and Clemmesen 2009) concentrations. However,
other studies have found no correlation between growth and energy reserves (Suthers 1992; Peck et al. 2003). A lack of correlation between growth and energy reserves may be because of uneven resource allocation to the two variables over time and/or as the fish grow. Initially, it is advantageous for small fish to maximise their growth rate in order to out-grow predators, and several studies have shown that smaller fish allocate proportionally more energy towards growth than larger fish (Post and Parkinson 2001; Sogard and Spencer 2004; Biro et al. 2005). Energy allocation has also been shown to vary temporally in fish that live in seasonal environments. In early summer, 0+ year fish use nearly all their available energy to maximise their growth rates, with little accumulation of energy reserves (Hurst and Conover 2003; Biro et al. 2005; Huss et al. 2008). During autumn, the opposite occurs with fish directing their energy toward accumulation of energy reserves in preparation for the winter months when food is scarce (Hurst and Conover 2003; Biro et al. 2005; Huss et al. 2008).

The aim of this study was to investigate the relationship between growth and energy reserves in 0+ year Chrysophrys auratus (Sparidae: Perciformes), a commercially important fish in New Zealand and Australia. Interannual variability in recruitment of C. auratus is high (Francis 1993; Coutin et al. 2003; Fowler et al. 2007) and research indicates that early growth and survival rates of C. auratus have a large influence on the subsequent success of the year-class (Fowler and Jennings 2003; Hamer et al. 2010). An understanding of the relationship between growth and energy reserves in C. auratus may provide us with a greater understanding of the factors that influence recruitment variability. Specifically, our objectives were to determine whether; 1) the resource allocation in C. auratus changed from maximising growth to maximising energy storage over the course of their first growing season (summer–autumn), and 2) if recent growth rates in 0+ year fish, determined by peripheral otolith increments, were correlated with protein, lipid or carbohydrate reserves.
5.3 Materials and Methods

5.3.1 Field collection

Newly recruited *C. auratus* were collected from shallow subtidal sandflats in the centre of the Kaipara Harbour, New Zealand on the 18 February, 1 March and 22 April 2010 (Fig. 5.1). Unfortunately, a sampling trip scheduled for late March had to be cancelled because of rough weather, and therefore the time periods between the sampling events are uneven (11 and 52 days). For simplicity, however, we refer to the three sampling events by their month. Sampling was conducted over a three hour period, one and a half hours either side of low tide. Fish were collected using an 11 m long beach seine net with a 2.3 m drop and a 4 m long cod end. The net was constructed of 12 mm stretched mesh in the main section and 6.8 mm stretched mesh in the cod end. Three to five haphazardly placed, non-overlapping hauls were made in order to collect at least 50 *C. auratus* per sampling occasion. Upon capture, fish were immediately stored on ice and then frozen at -80 °C on return to the laboratory.

![Figure 5.1](image.png)

Figure 5.1. Map of the Kaipara Harbour, northwestern New Zealand, showing the approximate location of the sampling site (triangle).
5.3.2 Biochemical analyses

Twenty randomly chosen *C. auratus* per month were taken for biochemical analyses of lipid, protein and carbohydrates. Fish were randomly chosen from the total catch of 3–5 net hauls per sampling occasion. Fish were wet weighed to the nearest 0.01 g, measured for standard length (SL), dissected to remove their sagittal otoliths, stomach and intestines, freeze-dried for 24 hours, and then re-weighed to obtain a gutted dry weight (DW). The white muscle tissue directly below the dorsal fin was removed from either side of the fish. White muscle was chosen for the analyses because snapper are primarily composed of protein (~18% wet weight, WW) and lipid (~5% WW) (Vlieg 1988), with the majority of protein stored in the muscle (Ferron and Leggett 1994; FAO 2005). Furthermore, white muscle was analysed so that our results were comparable to other biochemical studies of *C. auratus* (e.g., Majed et al. 2002) and the closely related *Pagrus major* (e.g., Chatzifotis and Takeuchi 1997). Viscera were not included in any of the biochemical analyses, because gut contents can sometimes be responsible for up to 95% of whole body lipid measurements in small fish (Lochmann et al. 1996).

Three replicate ~15 mg pieces of muscle tissue, including the attached skin, were weighed for lipid analysis. The remaining white muscle tissue was pulverized to dust using a mortar and pestle after the skin had been removed, thoroughly mixed, and divided into six weighed replicate aliquots (~5 mg each); three aliquots were used for the protein analysis and three aliquots were used for the carbohydrate analysis. Only one or two replicates per biochemical constituent were used for some fish because they were too small to provide sufficient muscle tissue for three replicates. The mortar and pestle were thoroughly cleaned between processing samples from each fish.

Total protein was quantified by the bicinchoninic acid (BCA) method (Smith et al. 1985) using a Micro BCA Protein Assay Kit (Thermo Scientific Pierce, Waltham, Massachusetts) with bovine serum albumin as the reference protein. Total lipid was quantified using a modified Bligh and Dyer (1959) one-phase methanol/chloroform/water extraction. Total carbohydrate were quantified using the phenol-sulfuric acid method (Dubois et al. 1956) with a D-glucose standard.
5.3.3 Otolith analyses

Otolith increment widths of \( \leq 160 \)-day-old *C. auratus* have been shown to provide accurate estimates of the early growth rates of *C. auratus* (Francis 1994b; Fowler and Jennings 2003; Sim-Smith et al. 2012a). A thin, transverse section of a randomly selected sagittal otolith was prepared for each fish. Detailed methods on the preparation of transverse sections are given in Chapter 3. Digital images were taken of each otolith section using a Meiji Techno ML5000 compound microscope (Meiji Techno, Iruma-gun, Saitama, Japan) fitted with a Leica DFC420 digital camera that was connected to Leica Application Suite (LAS) imaging software (Leica Microsystems, Wetzlar, Germany). Images were captured at \( \times 200 \)–400 magnification and daily increment widths were measured along the sagitta-subcupular meshwork fibre (SMF) zone (Fig. 3.2 in Chapter 3), because *C. auratus* sagittae are most easily interpreted along this zone (Francis et al. 1992a). The width of the peripheral increments for the 14 days prior to capture were used as a measure of recent growth. Suthers (1992) recommended that peripheral increments for the previous 14 days be used as a conservative measure of recent growth, which is supported by subsequent research showing a 2–14-day lag between changes in food ration and otolith increment widths (Suthers et al. 1999; Massou et al. 2002; Tonkin et al. 2008).

5.3.4 Data analyses

The effect of month on the lipid, protein and carbohydrate content of *C. auratus* was examined using separate linear mixed-effects models (PROC MIXED) available in SAS software (ver. 9.3, SAS Institute Inc., Cary, NC, USA.). The percentage concentrations of lipid, protein and carbohydrates were arcsine-square root transformed, which is appropriate for percentage data (Crawley 2007). Month and SL were used as fixed factors and fish (within month) was used as a random factor. Concentrations of protein, lipid and carbohydrates in fish are often positively correlated with size (e.g., Post and Parkinson 2001; Sogard and Spencer 2004), and therefore, SL was included as a fixed factor in the model to account for any effect of size on the biochemical constituents. In instances where the variance of the residuals was found to be heterogeneous, a weighted variance structure was chosen using
log-likelihood tests. Degrees of freedom were calculated using the Kenward and Roger’s method, which is appropriate for unequal sample sizes (Kenward and Roger 1997). Tukey’s multiple comparison tests were used, where applicable, to compare differences in mean lipid, protein or carbohydrate content among months. Reported mean values and standard errors have been back-transformed from the arcsine-square root transformed data.

The effect of month on growth rate (estimated by the mean daily otolith increment) was determined using an Analysis of Covariance (ANCOVA) in R software (ver. 2.15.0, R Foundation for Statistical Computing, Vienna, Austria), using SL as the covariate. There was no interaction between month and SL, indicating that the data met the assumption of homogenous slopes. Growth rate was log_{10} transformed to meet the assumptions of normality and homogeneity of variance. Tukey’s multiple comparison tests were used to compare the differences in mean growth rate among months.

Correlations between mean daily otolith increment width for individual fish and the measures of each of the three biochemical constituents (i.e., lipid, protein and carbohydrate concentrations) were analysed using linear regressions in R software. Separate linear regressions were performed for each biochemical constituent and for each month. The data met the assumptions of normality and homogeneity of variance.

5.4 Results

5.4.1 Biochemical composition of C. auratus

The SL of sampled fish ranged from 24.0 mm to 69.3 mm. Mean SL increased from 38.2 ± 1.8 mm in mid February, to 47.0 ± 1.6 in early March, to 56.6 ± 1.3 in late April. Concentrations of protein in sampled fish ranged between 36.6 and 69.8 %DW (mean ± S.E. = 54.8 ± 0.5 %DW), concentrations of lipid ranged between 0.0 and 7.0 %DW (mean ± S.E. = 3.1 ± 0.2 %DW), and concentrations of carbohydrates ranged between 0.3 and 2.3 %DW (mean ± S.E. = 0.6 ± 0.02 %DW).
5.4.2 Changes in resource allocation over the growing season

The results of the linear mixed-effects models showed significant differences in lipid ($F_{2, 36.7} = 70.82, P <0.0001$) and protein ($F_{2, 37.5} = 75.60, P <0.0001$) concentrations in *C. auratus* among months. Tukey’s multiple comparisons showed that lipid concentrations were significantly higher in late April ($P <0.0001$) than in mid February or early March, while protein concentrations were significantly higher in early March ($P <0.0001$) than in mid February or late April. Carbohydrate concentrations were not significantly different among months ($F_{2, 38.9} = 1.71, P = 0.19$) (Fig. 5.2). There were no significant effects of SL on lipid ($F_{1, 41.8} = 3.68, P = 0.06$), protein ($F_{1, 53.9} = 0.08, P = 0.78$) or carbohydrate ($F_{1, 47.7} = 0.29, P = 0.59$) concentrations (Fig. 5.3).

Mean daily otolith increments were significantly different among months ($F_{2, 56} = 405.63, P <0.0001$). There was no significant difference between the mean daily increment in mid February and early March (Tukey’s HSD test, $P = 0.07$), but the mean daily increment in mid February and early March were significantly larger than in late April (Tukey’s HSD test, $P <0.0001$) (Fig. 5.2a).

5.4.3 Relationship between growth rate and energy reserves in individual fish

The relationship between recent growth rate (estimated by daily otolith increments) and biochemical constituents in 0+ year *C. auratus* changed over time. During mid February and early March there was no significant relationship between the growth rates of fish and lipid or protein concentrations. However, during late April, growth rates were significantly positively correlated with lipid ($F_{1, 18} = 11.69, P <0.01$) and protein ($F_{1, 18} = 12.09, P <0.01$) concentrations (Fig. 5.4). There were no significant correlations between carbohydrate concentrations in *C. auratus* and growth rates during any of the three months (Fig. 5.4).
Figure 5.2. Measures of mean (± 95% confidence intervals) a) lipid, b) protein, and c) carbohydrate content (% DW) in the white muscle tissue of 0+ year *Chrysophrys auratus* from February to April (grey bars), and a) daily otolith increment ± S.E. (black line). Months with an asterisk are significantly different (*P* < 0.05) from other months.
Figure 5.3. Relationship between standard length of 0+ year *Chrysophrys auratus* captured from February to April 2010 and the arcsine-square root transformed concentration (% DW) of *a*) lipids, *b*) proteins, and *c*) carbohydrates in their white muscle tissue.
Figure 5.4. Relationship between a) lipid, b) protein, or c) carbohydrate content of *Chrysophrys auratus* between February and April, and daily otolith increment averaged over the previous 14 days. Regression lines indicate a significant correlation between the biochemical constituent and daily otolith increment at \( P < 0.05 \).
Discussion

The results of this current study showed that 0+ year *C. auratus* increased the quantity of lipid in their muscle tissue by over three-fold between late summer (mid February–early March) and autumn (late April), while growth rates showed the opposite trend, being significantly higher in mid February and early March than in late April. Given the unequal time periods between the sampling dates, it would be expected that the biochemical content and growth rates of fish sampled in mid February and early March would be more similar to one another than to fish sampled in late April. Nevertheless, these results are still consistent with other studies that show that 0+ year fish, which are vulnerable to size-dependent predation and over-winter starvation mortality, demonstrate different resource-allocation strategies over the growing season (Metcalfe *et al.* 2002; Hurst and Conover 2003; Jacobs *et al.* 2012). Initially, small fish utilise all their available energy for growth rather than for the accumulation of energy reserves in order to out-grow predators. As winter approaches, fish switch from maximising growth to the accumulation of energy reserves, primarily lipids, which will provide energy reserves during winter when food is scarce. For example, resource allocation in 0+ year striped bass (*Morone saxatilis*) changed over their first growing season. During summer, fish allocated 92% of their available energy to non-lipid somatic growth, whereas between autumn and early winter, fish allocated an increasing proportion of their available energy to lipid storage (12% and 40%, respectively) (Hurst and Conover 2003).

The relationship between recent growth and energy reserves in individual *C. auratus* changed over the growing season. During mid February and early March there was no relationship between growth and energy reserves, but during late April, when water temperatures and growth rates were lower, there was a positive correlation between growth and lipid concentrations, and also, growth and protein concentrations. These results concur with Huss *et al.* (2008) who predicted that 0+ year fish that were subjected to the conflicting demands of size-dependent predation and over-winter starvation would demonstrate little correlation between growth and energy reserves early in the growing season when fish were maximising growth, but fish would show a positive correlation between growth and energy reserves late in the growing season when they allocated more
resources to energy reserves. The positive correlation between growth rates and protein or lipid concentrations in late April indicates that growth is still important to these fish, and that fish were allocating energy both to growth and energy storage. It is probable that this positive correlation will be lost later in the year, when growth rates slow even further and more energy is allocated to storage. Food availability has also been shown to influence the relationship between growth and energy reserves. When food is unlimited, fish will maximise both growth and energy reserves, resulting in a positive correlation between the two variables. However, when food is limited there is a trade-off between growth and energy reserves, which may result in a lack of correlation between the two variables (Sogard and Spencer 2004; Jacobs et al. 2012).

A number of studies have used biochemical indicators (protein or lipid concentrations) as estimates of growth, with varying degrees of success (e.g., Suthers 1992; Peck et al. 2003; Frommel and Clemmesen 2009). The results of this study and others (Hurst and Conover 2003; Biro et al. 2005) demonstrate that there is a strong temporal effect on the relationship between growth and energy reserves in juvenile fish living in seasonal environments. Furthermore, the relationship between growth and energy reserves has been shown to be affected by food availability (Sogard and Spencer 2004) and predation risk (Biro et al. 2005). Thus, if biochemical indicators are used to predict growth, care needs to be taken to ensure that the relationship between growth and the biochemical indicator does not change over the study period.

In contrast to a number of studies that have demonstrated that lipid and protein concentrations increased with increasing fish size (Post and Parkinson 2001; Sogard and Spencer 2004; Biro et al. 2005), we found that lipid, protein and carbohydrate concentrations showed no significant correlation with SL. Similarly, Díaz et al. (2009) found no correlation between lipid, protein or carbohydrate concentrations and SL in horse mackerel (Trachurus trachurus) larvae. The relationship between lipid concentration and SL has been shown to be affected by food availability, fish size and the presence of predators (Biro et al. 2005). Cultured rainbow trout (Onchorhynchus mykiss) fed to satiation and reared without predators showed a clear positive correlation between lipid concentrations
and fish size. However, lipid concentrations in similar-sized wild fish were much lower and nearly independent of size (Biro et al. 2005). The authors proposed that lipid concentrations would remain low and independent of SL in juvenile fish that were at risk from size-dependent predation until they reached a certain “predation-free” size. Thereafter, lipid concentrations would increase proportionally with SL as increasing energy was allocated to lipid reserves to sustain them over the winter months. The results of this current study only partially concur with Biro et al.’s (2005) hypothesis. We found that lipid concentrations did remain low and independent of SL during mid February and early March when fish were small and growth rates were high, however, lipid concentrations in late April remained independent of size, despite the significant increase in concentration. The switch in resource allocation in the current study appears to be time-dependent rather than size-dependent. If lipid accumulation was size-dependent then we would expect to see similar lipid concentrations in similar-sized fish regardless of their capture date, however, 50–60 mm SL fish captured in late April had much higher lipid concentrations than 50–60 mm SL fish captured in early March.

The switch in resource allocation from growth to storage in C. auratus may be triggered by a decrease in water temperature. Mean (± s.e.) sea surface temperature in the Kaipara Harbour for the fortnight preceding sampling were similar for February (19.7 ± 0.1 °C) and March (20.4 ± 0.04 °C), but decreased to 18.8 ± 0.1 °C in late April. Although water temperature has been shown to affect the relationship between growth and energy storage (Sogard and Spencer 2004), it does not solely determine the partitioning of resources to growth versus storage, indicating that the change in resource allocation is not simply a metabolic response to temperature. For example, sablefish (Anoplopoma fimbria) reared at low temperatures did not always allocated more energy towards lipid storage than fish reared at high temperatures, and small sablefish were found to allocate more energy towards growth than larger fish, irrespective of water temperature (Sogard and Spencer 2004). Similarly, small gulf menhaden (Brevoortia patronus) continued to allocate the majority of their resources towards growth in late autumn, whereas larger juveniles switched to allocate the majority of their resources towards lipid storage (Deegan 1986).
Thus, it appears that in these two examples the requirement to out-grow predators is more important than the accumulation of energy reserves.

Over-winter mortality of 0+ year fish is likely to be higher in years that have an early onset of winter or poor feeding conditions during this brief growing season, because fish will have less time to accumulate sufficient energy reserves to sustain them through the winter. This hypothesis may explain the strong positive correlation ($r^2 = 0.94$) that Francis (1993) found between the abundance of 1+ year $C$. auratus and the mean April–June SST of the previous (0+) year. We found that lipid concentrations in $C$. auratus during mid February and early March were very low (<1.5% DW), making them very vulnerable to starvation mortality if food was scarce during this relatively short time period. A number of studies have shown that prior to the switch in resource allocation from growth to storage, lipid concentrations in juvenile fish were just above the minimum concentration required for survival (Post and Parkinson 2001; Biro et al. 2005; Huss et al. 2008), and that over-winter mortality was inversely related to lipid content in 0+ year fish (Schultz and Conover 1997; Biro et al. 2004).

Changes in protein and carbohydrate concentration in $C$. auratus did not follow the same pattern as lipid concentrations. Protein concentrations were significantly higher in March than the other two months, although the reason for this is unclear. Carbohydrate concentrations did not differ significantly among the months. Carbohydrates account for a very small percentage of the energy reserves in fish, and are primarily used by fish to meet their short-term energy requirements (Ferron and Leggett 1994).

In conclusion, the results of this study show a clear shift in resource-allocation in 0+ year $C$. auratus over their first growing season. Initially, small fish allocated nearly all their available energy into maximising their growth, and lipid concentrations were low and independent of SL. In autumn (late April), there was a significant decrease in growth rate coupled with a significant increase in lipid concentration. The trigger for the shift in resource-allocation from growth to storage appears to be time-dependent and/or temperature-dependent rather than size-dependent. Changes in resource allocation in $C$. auratus throughout their first growing season may have important impacts on recruitment variability, and may help to explain why the abundance of 1+ year fish is strongly correlated with late autumn–winter
water temperatures of the previous year (Francis 1993). Over-winter mortality of 0+ year fish is likely to be higher in years that have an early onset of winter or poor feeding conditions during this brief growing season, because fish will have less time to accumulate sufficient energy reserves to sustain them through the winter.
Chapter 6

General Discussion

The results of the research presented in this thesis provide new information on the reproductive biology, larval recruitment and settlement dynamics, and early growth of *C. auratus* in northern New Zealand. An understanding of the factors that influence the early life history of *C. auratus* is critical for effective management of fisheries for this species because it appears that interannual variability in year-class strength is largely determined by factors that affect the abundance of larvae and early juveniles (Hamer and Jenkins 2007; Hamer et al. 2010).

6.1 Spawning behaviour and larval supply

The reproductive biology of *C. auratus* appears to be highly flexible and the timing of spawning, size at sexual maturity and spawning locations varies considerably among geographic locations (Scott and Pankhurst 1992; Wakefield 2006; Jackson et al. 2010; Stewart et al. 2010). Adult fish often form transient spawning aggregations in the same locations each year (Zeldis et al. 2005; Jackson and Moran 2012), which may occur inside (Hamer et al. 2011) or outside harbours, estuaries and bays (Crossland 1977a; Jackson 2007; Wakefield et al. 2011), or in coastal waters ≤100 m deep (Moran et al. 2003). Spawning aggregations in the Hauraki Gulf, northeastern New Zealand, were found to be correlated with regions of high primary productivity (Zeldis et al. 2005) suggesting that adult fish choose spawning locations that can support high feeding rates in larvae. Results from this current study show that almost all spawning activity in *C. auratus* found in the Kaipara Harbour region occurs outside the harbour, despite the presence of an extensive population of adult fish within the harbour. Gonadosomatic indices of male and female *C. auratus* captured within the harbour remained ≤1 throughout the year, and female *C. auratus* with
vitellogenic or hydrated oocytes were rarely caught within the harbour. Furthermore, a notable proportion (17–38%) of the female *C. auratus* caught within the harbour during November and December had begun to reabsorb their vitellogenic oocytes prior to the commencement of spawning. In contrast, adult fish caught outside the harbour showed normal reproductive development, with peak spawning occurring in spring.

Spawning aggregations of *C. auratus* are thought to comprise both local, resident fish and migratory fish from distant populations (Crossland 1982; MacDonald 1982; Fowler *et al.* 2007), and it is hypothesized that the resident population of *C. auratus* in the Kaipara Harbour segregates during the spawning season, with spawning individuals migrating out to the coast in early spring to join spawning aggregations, and non-spawning individuals remaining inside the harbour. Further research combining the tagging of individual fish and histological gonad analyses is required to determine whether fish participating in spawning aggregations originate from within the Kaipara Harbour, from the surrounding coastal waters, or from both sources.

The causal factors for spawning omission in *C. auratus* are unknown. Spawning omission in fishes can be caused by a number of factors including poor nutrition (Burton and Idler 1987; Rijnsdorp 1990; Skjæraasen *et al.* 2009), low temperatures (Pawson *et al.* 2000; Pörtner *et al.* 2001), shortage of mates (Trippel and Harvey 1990), and exposure to pollutants (McFarlane and Franzin 1978). Alternatively, fish may opt to channel their energy into growth and survival instead of reproduction to increase their future reproductive success (Jørgensen *et al.* 2006). The stomachs of most fish sampled from within the harbour were observed to be full of food, suggesting that poor nutrition is unlikely to be an issue for *C. auratus* in the Kaipara Harbour. The majority (91%) of the sexually mature *C. auratus* population captured inside the harbour were young fish (2–6 years-of-age) and it is more likely that these fish used their consumed energy to maximise their growth and survival, rather than their reproductive output. This is consistent with an energy-allocation model proposed by Jørgensen *et al.* (2006), which predicted that spawning omission in the Atlantic cod, *Gadus morhua*, was more likely in; 1) younger fish, 2) when fishing mortality at the spawning grounds was high, 3) when fishing mortality at the feeding grounds was low, 4)
when natural mortality was low, and, 5) when the energetic costs associated with migration and spawning were high.

The occurrence of spawning omission in *C. auratus* may have important implications for fisheries management. Although this study is the first record of spawning omission in *C. auratus*, the phenomenon is difficult to detect because it requires careful examination of histological preparations of gonads, and it is possible that spawning omission may be a relatively common occurrence in this species. If spawning omission is a widespread phenomenon in *C. auratus* populations, then stock-recruitment models that predict the reproductive output based on the annual spawning of the entire adult population are likely to overestimate the reproductive output. Furthermore, the discovery that *C. auratus* does not spawn inside the Kaipara Harbour is particularly important for fisheries management of this commercially important fish stock in New Zealand. Previous research on otolith microchemistry signatures indicates that the Kaipara Harbour is a critical nursery area for juvenile *C. auratus*, with up to 98% of all west coast North Island adult *C. auratus* spending their first year in the Kaipara Harbour (Morrison 2008). Spawning aggregations outside the Kaipara Harbour are likely to be the primary source of recruitment for *C. auratus* to the harbour, which in turn, is the main supply of fishery recruits to the entire west coast fishery (SNA8). Over-exploitation of local spawning aggregations outside the Kaipara Harbour is likely to have widespread consequences, reducing the biomass of *C. auratus* over a broad geographic area.

### 6.2 Larval transport to settlement habitats

*Chrysophrys auratus* larvae frequently settle in the shallow waters of estuaries and bays at 9–14 mm SL (Miskiewicz 1986; Trnski 2002; Hamer and Jenkins 2004). It is most likely that *C. auratus* enter the Kaipara Harbour sometime during their late larval period when their swimming and sensory abilities are well developed (Leis 2006; Montgomery *et al.* 2006). In this current study, recently settled *C. auratus* (10.6–15.0 mm SL) were caught in the shallow regions of the harbour from late January 2011 onwards. However, despite extensive sampling with fortnightly plankton tows between late November 2010 and late February
2011, no *C. auratus* larvae were captured entering the Kaipara Harbour. There are two possible explanations for the absence of *C. auratus* larvae during this plankton sampling in the Kaipara Harbour; 1) larvae may enter the harbour in discrete pulses of short duration, which were missed by the fortnightly sampling events, or 2) larvae travel into the harbour near the seabed, perhaps utilizing the slower water currents within the boundary layer near the seafloor, and thus, were not sampled by the plankton net, which only sampled the water column from ~1 m above the seabed to the surface. The latter is a more likely explanation because Trnski (2002) found that settlement-stage *C. auratus* that were captured in the plankton and then released inside an estuary nearly always headed down towards the seabed upon release, and then swam slowly just above the seabed.

The successful spawning period leading to recruitment in the Kaipara Harbour was found to be constricted to 1–2 months in this study, despite *C. auratus* spawning over a period of up to four months in the harbour (Sim-Smith *et al.* 2012b). The discrepancy between the overall spawning period and the successful spawning period observed in this study may be because of; 1) different larval survival rates during the spawning period, and/or 2) the requirement for larvae of a suitable stage of development to be available when a certain combination of environmental parameters are present, to facilitate the transport of larvae to the settlement habitats within the harbour. Significant positive correlations were found between daily settler abundance and tidal range (of the previous day) in the Kaipara and Mahurangi Harbours in 2009/2010, and on-shore winds (of the previous day) in the Kaipara Harbour in 2009/2010, explaining up to 38% of the variability in daily settler abundance. These results suggest that the transport of larvae to settlement habitats is assisted by large tides and on-shore winds. However, these environmental factors were not found to be correlated with daily settler abundance in the following year, or in the Manukau or Huruhi Harbours. The inability to detect any further correlations may be due to the relatively low numbers of fish that were sampled in the current study, or a result of interannual variability in the transport processes for larvae.

The environmental factors that influence larval recruitment dynamics in Huruhi Harbour, on Great Mercury Island, off the east coast of the North Island, appear to be very different
from those that affect the larval recruitment dynamics in large estuaries such as the Kaipara Harbour. Huruhi Harbour is a small bay adjacent to Great Mercury Bay, which is a large open embayment with slow currents. The lack of relationship between larval size or abundance and incoming tide period, or between daily settlement and tidal range or winds suggests that tidal currents and winds have little influence on the transport of *C. auratus* larvae to Huruhi Harbour. Larvae between 3.5–11.6 mm SL were caught in Great Mercury Bay indicating that some *C. auratus* spawning activity occurred close to the bay, and it is possible that larvae are retained near Huruhi Harbour for their entire pelagic larval duration and are able to reach settlement areas independently without requiring any on-shore transport mechanism.

There is some evidence indicating that the movement of *C. auratus* to settlement areas is not solely via passive transport processes but may also be facilitated by larval behaviour, such as their response to olfactory cues and hydrodynamic features. It has been demonstrated that *C. auratus* larvae can differentiate between water sources collected from different regions of the Kaipara Harbour, and that larvae show a significant preference for water taken from seagrass beds, their preferred settlement habitat, over water taken from the harbour entrance or artificial seawater (Radford et al. 2012). In addition, the abundance of *C. auratus* larvae entering Lake Macquarie, Australia, was found to be positively correlated with rainfall events that occurred in the previous 3–9 days, which suggests that larvae could be using olfactory cues in estuary plume water to locate the estuaries (Trnski 2003). *Chrysophrys auratus* larvae were also found to aggregate outside Lake Macquarie at the edge of the tidal plume and travel into the estuary with the plume edge (Trnski 2003). It is probable that *C. auratus* larvae, like many other fish larvae, use selective tidal stream transport to facilitate their movement and retention into harbours (Rowe and Epifanio 1994; Forward Jr et al. 1999; Hare et al. 2005).
6.3 Larval survival

The pelagic larval duration of *C. auratus* in this current study varied from 17–33 days, which is very similar to that of *C. auratus* previously observed in the Hauraki Gulf (18–32 days) (Francis 1994b) and South Australia (18–28 days) (Fowler and Jennings 2003). The consistent and relatively small range in pelagic larval duration in all three studies suggests that *C. auratus* has a limited physiological ability to delay settlement. The fate of fish that reach settlement-stage far away from inshore settlement habitats is unknown. It is possible that they can settle in deeper, coastal waters because 0+ year *C. auratus* have been found out to the edge of the continental shelf (Moran *et al.* 2003).

Water temperature appears to be an important determinant for the survival of *C. auratus* larvae in New Zealand. SST was found to be significantly positively correlated with daily settler abundance in three of the six statistical models tested from data derived in this study. The average SST during the pelagic larval duration was >18 °C for more than 91% of the *C. auratus* recruits sampled, despite the fact that *C. auratus* start spawning when SST are around 15 °C (Scott and Pankhurst 1992; Wakefield 2010; Sim-Smith *et al.* 2012b). Similarly, cultured *C. auratus* had a very high percentage of abnormal egg development when they spawned in water temperatures <18.5 °C (Fielder and Allan 2003). It appears that *C. auratus* that are spawned before the average water temperatures reach 18 °C often experience very high mortality. However, high larval survival rates appear to be possible at water temperatures <18 °C, because very high abundances of *C. auratus* larvae (30–32 fish 100 m⁻³) were recorded in the Hauraki Gulf in November–December 1987 when average water temperatures were 16.6–17.3 °C (Zeldis *et al.* 2005). Furthermore, larval abundances in 1987/1988 were 4–30-fold higher than abundances in the two previous years, despite similar monthly water temperatures for all three years. Prey densities were also much higher in 1987/1988 than in the two previous years, and the authors hypothesized that higher food availability in 1987/1988 resulted in a much higher survival rate of larvae (Zeldis *et al.* 2005).
6.4 Growth rates of larval and early juveniles

Growth rates are often used as a measure of the nutritional condition of fish larvae (Suthers 1998) because the growth and mortality of larvae are closely coupled in many fish species (Meekan and Fortier 1996; Hare and Cowen 1997; Shahidul Islam et al. 2010). Faster-growing larvae generally have a shorter pelagic larval duration (Denit and Sponaugle 2004; Green and Fisher 2004; Sponaugle et al. 2006), higher survivorship in the plankton (Meekan and Fortier 1996; Hare and Cowen 1997; Shahidul Islam et al. 2010), and are also usually in better condition at the time of settlement, which leads to their subsequent success as juveniles (Searcy and Sponaugle 2001; Shima and Findlay 2002; Sponaugle and Grorud-Colvert 2006) and adults (Moss et al. 2005; Robert et al. 2007; Duffy and Beauchamp 2011).

Results from this current study demonstrate that in three of the four harbours that were sampled, *C. auratus* larvae with a short pelagic larval duration were found to grow significantly faster than fish with a long pelagic larval duration, and generally continued to grow faster as juveniles. Similarly, the majority of research on larval growth in fish has shown that individuals which grow faster as larvae are able to maintain faster growth rates as juveniles (e.g., Tupper and Boutilier 1995; Vigliola and Meekan 2002; McCormick and Hoey 2004). It is possible that differences in growth rates are caused by genetic or nutritional differences among fish, which continue to confer growth advantages to juvenile fish after they transition from the pelagic environment to the benthic habitat.

Larval and early juvenile growth rates were found to vary significantly among the four harbour sites, with *C. auratus* from the Kaipara and Huruhi Harbours growing significantly faster than fish from the Manukau or Mahurangi Harbours. Differences in growth rates among the four sites were found to be unrelated to differences in water temperature. Instead, it is hypothesized that the differences in growth rates among the sites were due to differences in food availability between each of the sites. Food availability is thought to be critical for the growth and survival of *C. auratus* larvae and previous studies have shown that the abundance of the larvae of this species is correlated with prey abundance (Zeldis et al. 2005; Murphy et al. 2012). The presence of seagrass only at the Kaipara and Huruhi Harbour sites may be an indicator of higher food availability at these sites for juvenile *C.
Numerous studies have found that the abundance of prey species for juvenile fishes within seagrass beds is significantly higher than the abundance of prey in adjacent areas of bare substrate (e.g., Lubbers et al. 1990; Connolly 1997; Nakamura and Sano 2005). The growth of juvenile fish that inhabit seagrass beds has also been shown to be higher than the growth of con-specifics inhabiting unvegetated areas (Levin et al. 1997; Stunz et al. 2002; Heck Jr et al. 2003), and it is thought that this elevated growth is the result of higher food abundance within seagrass beds (Sogard 1992; Levin et al. 1997). Further research in this area should focus on the comparison of growth rates of C. auratus at multiple seagrass and non-seagrass sites, the quantification of pelagic and benthic prey species at the sites, and diet analyses of the fish, to determine whether growth of C. auratus is faster within seagrass beds, and whether this faster growth is due to higher food availability.

6.5 Resource allocation in early juveniles

Resource allocation between growth and energy storage in 0+ year C. auratus was found to change over their first summer-autumn. During February and March growth rates were high and lipid concentrations in the muscle tissue were very low in 0+ year C. auratus, but during April growth rates halved and lipid concentrations increased by three-fold. These results are consistent with other studies that show that 0+ year fish, which are vulnerable to size-dependent predation and over-winter starvation mortality, demonstrate different resource-allocation strategies over the growing season (Metcalfe et al. 2002; Hurst and Conover 2003; Jacobs et al. 2012). Initially, small fish utilise all their available energy for growth rather than for the accumulation of energy reserves in order to out-grow predators. As winter approaches, fish switch from maximising growth to the accumulation of energy reserves, primarily lipids, which will provide energy reserves during winter when food is scarce. For example, resource allocation in 0+ year striped bass (Morone saxatilis) changed over their first growing season. During summer, fish allocated 92% of their available energy to non-lipid somatic growth, whereas between autumn and early winter fish allocated an increasing proportion of their available energy to lipid storage (12% and 40%, respectively) (Hurst and Conover 2003).
Lipid concentrations in *C. auratus* prior to the switch in resource allocation from growth to storage were very low (<1.5% DW), making them vulnerable to starvation mortality. Over-winter mortality of 0+ year *C. auratus* is likely to be higher in years that have an early onset of winter or poor food availability, because fish will have less time to accumulate sufficient energy reserves. This hypothesis may help explain the strong positive correlation that Francis (1993) found between the abundance of 1+ year *C. auratus* and the mean April–June SST of the previous (0+) year. The ability to predict recruitment to the *C. auratus* fishery several years in advance, based on a simple measure such as SST, has the potential to greatly assist the management of the fishery. Future work should focus on confirming the relationships between growth rate, lipid reserves, food abundance, SST and over-winter mortality in 0+ year cohorts of *C. auratus*.

### 6.6 Conclusion

The behaviour, diet and habitat usage by 0+ year *C. auratus* has been found to vary greatly among different geographic localities (Trnski 2002; Fowler and Jennings 2003; Morrison et al. 2007; Saunders et al. 2012; Usmar 2012). Historically, research on *C. auratus* in New Zealand has primarily focused on the Hauraki Gulf region and very little is known about the biology of *C. auratus* in other New Zealand regions. One of the overall objectives of this study was to increase our understanding of the factors that influence the early life history of *C. auratus* in the Kaipara Harbour, a critical nursery area for *C. auratus*. This study has provided new information on the spawning dynamics, recruitment and growth of *C. auratus* in the Kaipara Harbour, and demonstrates that these variables can differ significantly from *C. auratus* populations on the northeast coast of New Zealand. This information can be used to assist in the fisheries management of this important commercial species, and to provide appropriate protection for critical habitats, such as the Kaipara Harbour, against environmental degradation.
## Appendix

**Table 1.** Results of the log-likelihood tests in Chapter 4 for difference repeated measures ANOVA model variance structures of tested (equal variances (EV), separate intercept variances per site (SI), separate slope variances per site (SS) and separate intercept and slope variances per site (SIS)). *P* values in bold indicate a significantly better model fit at *P*<0.05.

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