Mechanistic models of recruitment variability in fish populations

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Abstract

There are serious concerns worldwide about the decline of exploited fish stocks. The number of fish larvae surviving to be recruited into the adult population each year is fundamental to the long-term stability of a fish stock. Monitoring and predicting recruitment is a crucial component of managing economically important fisheries worldwide. Fish recruitment can vary by an order of magnitude, or more, between years, and the larval stage is a key determining factor. Fish larvae are born into an extremely variable environment, with high mortality rates, and so it is not surprising that the number surviving to join the adult population is highly variable.

This thesis presents simple stochastic, mechanistic larval growth models, developed and utilised to investigate recruitment probabilities and variability. The models are mechanistic in that they are based on consideration of the key ecological processes at work, and not on statistical regression analyses or similar techniques. At the heart of the thesis lies a stochastic drift-diffusion model for the growth of an individual larva. Further mathematical and ecological complexity is built up through consideration of both the temporal and spatial heterogeneity of larval food sources, primarily zooplankton. Results illustrate the impact of stochasticity in the timing of peak food abundance, and the patchiness of the prey, on recruitment variability.

The idea of non-constant variance in recruitment is also investigated, with the aim of testing its practical relevance to fisheries management. It is demonstrated that the currently available stock-recruitment time series are at least one order of magnitude too short to reliably fit such models. Management implications are illustrated using simple models and published recruitment data for two exploited stocks.

The work developed within this thesis highlights the importance of stochasticity in fish larval growth and recruitment, and the power of simple mechanistic models in examining these ideas.

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This thesis is composed of original research conducted by myself, under the supervision of Dr Jon Pitchford and Dr Joe Horwood. All information sources have been acknowledged. No part of this thesis has been submitted for a degree at any other university.

Unless specified below, I performed all literature research, programming, analysis, and writing of the thesis chapters. The following chapters of the thesis have been published in or submitted to peer-review journals. I am the first author on all papers, but have received feedback and corrections from my co-authors.

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Chapter 1

Introduction

The fish in our oceans are not an infinite resource. Unlike in other areas of food production, such as farming, we can do little in the short term to replace or rejuvenate stocks that have been depleted by fishing (Needle, 2002). Exploited species have been declining steadily since the start of fishing (Beaugrand and Kirby, 2010), with up to 90% of the large predatory fish being lost since the beginning of industrial fishing (Myers and Worm, 2003). North Atlantic cod stocks halved from 1.6 million tonnes in 1980 to 0.8 million tonnes in 2000 (Brander, 2003). Due to the dramatic decline in commercially important species such as cod, the potential causes and factors influencing the decline in fish stocks are now subject to urgent scrutiny (Platt et al., 2003). Recovery of depleted marine, demersal, commercial fish stocks has seen only small success worldwide (Horwood et al., 2006), despite strict fishing measures being in place in several cases.

In addition to the long term decline in numbers, fish populations also exhibit pronounced fluctuations in abundance which make planning suitable long term strategies for fisheries management very difficult (Beaugrand and Kirby, 2010).

In this Introduction, we will define and discuss recruitment in fish populations, the recruitment models used in fisheries management, and the factors affecting variability in recruitment. The importance of plankton in the marine ecosystem, and for fish recruitment in particular, will be addressed and discussed. Some of the modelling techniques implemented in the thesis will also be introduced.

1.1 Recruitment in fish populations

Whether fish populations can replace the stock removed by fishing is dependent on recruitment. Recruitment in fish populations is defined as the number of individuals which survive from the egg stage to a certain later stage in their life history. Not all fish ecologists agree on the exact choice of age or stage that defines recruitment; coral reef fish ecologists usually refer to recruitment as the settlement of pelagic larvae from the plankton, while salmon biologists most often define recruitment as the return of juveniles to the adult spawning ground (Myers, 2002). Marine fisheries biologists usually refer to recruitment as the first age when fishing (or sometimes spawning) occurs (Fogarty et al., 1991; Myers, 2002). In this thesis we define recruitment as growth to some mathematically defined threshold size e.g. size at metamorphosis.

Monitoring and predicting recruitment is a crucial component of managing economically important fisheries around the world. The importance of recruitment in fish population dynamics has been recognised since the turn of the previous century (Hjort, 1914).

1.1.1 The stock recruitment relationship

“The most important and generally most difficult problem in biological assessment of fisheries is the relationship between stock and recruitment” (Hilborn and Walters (1992) p.241)

The stock recruitment relationship is fundamental to the scientific approach to fisheries management (ICES, 2006), and is the basis for estimating key parameters used in the modelling and management of fish populations, such as carrying capacity, maximum reproductive rate, and maximum sustainable yield (Myers, 2002). Here, “stock” is defined as spawning stock biomass, which is often deemed to be the most useful measure of a stock (Shepherd and Cushing, 1990) as it is usually the only life history stage that can be controlled through management (Hilborn and Walters, 1992). Understanding the stock recruitment relationship for a population is key to avoiding recruitment overfishing (Myers and Barrowman, 1996).

Below I describe the two most common proposed stock recruitment relationships regularly fitted to fisheries data.

The Beverton-Holt stock recruitment model

The Beverton-Holt stock recruitment model (Beverton and Holt, 1992) is based on separating pre-recruitment mortality into its density-independent and density-dependent parts (Koslow, 1992). That is,

$$\frac{dN}{dt} = -M_0 N - M_1 N^2, \tag{1.1}$$

where $N(t)$ is the number of larval/juvenile fish in a single cohort, M_0 is the density-independent mortality rate, and M_1 is the density-dependent mortality rate (Walters and Martell, 2004). If we then consider $N_T = R$ to be the number of recruits aged T, equation (1.1) can be solved to give

$$N_T = R = \frac{N_0 \exp(-M_0 T)}{1 + (M_1/M_0)(1 - \exp(-M_0 T))N_0},$$

where N_0 is the initial number of eggs or larvae (Walters and Martell, 2004). By grouping parameters, this model can be written in the more familiar form

$$R = \frac{\alpha S}{1 + \beta S},$$

where α is the maximum average survival rate independent of density effects, and β represents the effects of density-dependence. Note this relationship is now in terms of the spawning stock size, S, which is often used as a proxy for the initial number of eggs.

The Ricker stock recruitment model

The Ricker stock recruitment model (Ricker, 1954) assumes that the density-dependent mortality rate is proportional to the initial stock abundance (Walters and Martell, 2004). The model takes the form

$$R = S \exp\left(a\left(1 - \frac{S}{b}\right)\right), \tag{1.2}$$

where e^a is the slope of the curve at the origin, and b is the value of S at which $R = S$ (Hilborn and Walters, 1992). Unlike the Beverton-Holt stock recruitment model, equation (1.2) exhibits declining recruitment at high stock sizes, i.e. it is dome shaped (Hilborn and Walters, 1992).

Figure 1.1 shows the Beverton-Holt and Ricker stock recruitment models fitted to data for Irish Sea cod and North Sea herring. Data are from the ICES Fish Stock Assessment Summary Database, available at www.ices.dk. Recruitment data were scaled by the maximum observed recruitment, and spawning stock biomass data by the maximum observed spawning stock biomass. In Figure 1.1a) the difference in shape between the two models is clearly observable (with the Ricker curve exhibiting declining recruitment as stock size increases), but Figure 1.1b) also demonstrates that the models can look very similar to each other, depending on the parameter values. It has been suggested that a Beverton-Holt curve may apply when a stock experiences high food availability, and that a Ricker curve may apply in stocks with low food availability (Johansen, 2007; Olsen et al., 2011).

1.1.2 Recruitment variability

Large variability in recruitment is usually the most notable feature of stock-recruits data (Cushing, 1968; Koslow, 1992; Needle, 2002; Myers, 2002; Shepherd and Cushing, 1990). Recruitment can vary by one or two orders of magnitude, and the reasons for this are not well understood (Shepherd and Cushing, 1990). Because recruitment data are so typically variable, it is very difficult, if not impossible, to determine even

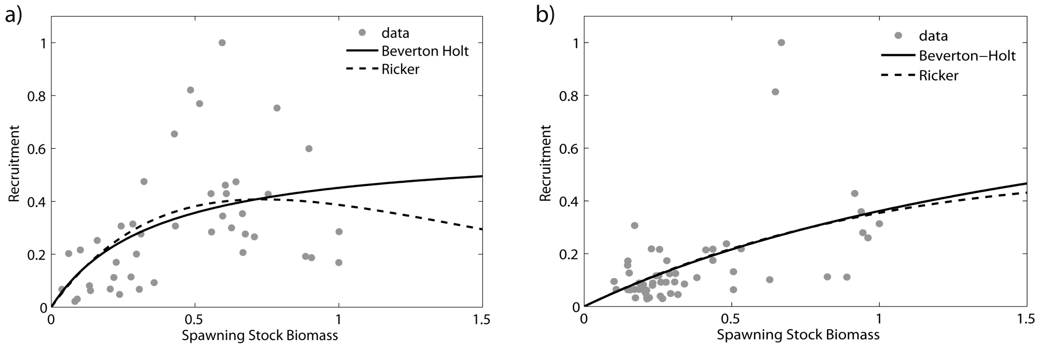

Figure 1.1: *The Beverton-Holt and Ricker stock recruitment models fitted to data for a) Irish Sea cod and b) North Sea herring. Recruitment data were scaled by the maximum observed recruitment, and spawning stock biomass data by the maximum observed spawning stock biomass. Data are from the ICES Fish Stock Assessment Summary Database, available at www.ices.dk.*

the shape of the underlying stock recruitment relationship (Koslow, 1992). In Figure 1.1 we can see the large fluctuations of the stock-recruitment data around the fitted model curves. Figure 1.2 shows recruitment numbers for Irish Sea cod and North Sea herring over nearly 50 years. We can see that recruitment numbers vary by over two orders of magnitude over the period. Data are from the ICES Fish Stock Assessment Summary Database, available at www.ices.dk.

Essentially, the interplay of life history characteristics (such as growth rates) and environmental variability determines fluctuations in recruitment (Fogarty et al., 2001). It is generally accepted that recruitment is mainly determined in the larval stage (Cushing, 1975), and that the main source of recruitment variability is the large interannual variability in the density-independent mortality experienced during the pelagic egg and larval life history stages (Myers, 2002). However there are several different theories concerning the cause of this variability in larval mortality.

The first theory pertaining to recruitment variability was Hjort's "Critical Period" hypothesis (Hjort, 1914). This proposed that recruitment is determined in the early larval stage. After absorption of the yolk sac, larvae must find suitable feeding conditions, otherwise they suffer massive mortality and order-of-magnitude losses in numbers in a short amount of time (Houde, 2008). Although recruitment is now viewed as the result of a mix of complex processes, the Critical Period hypothesis still highlights an important factor determining recruitment variability, and several other linked theories have developed from it.

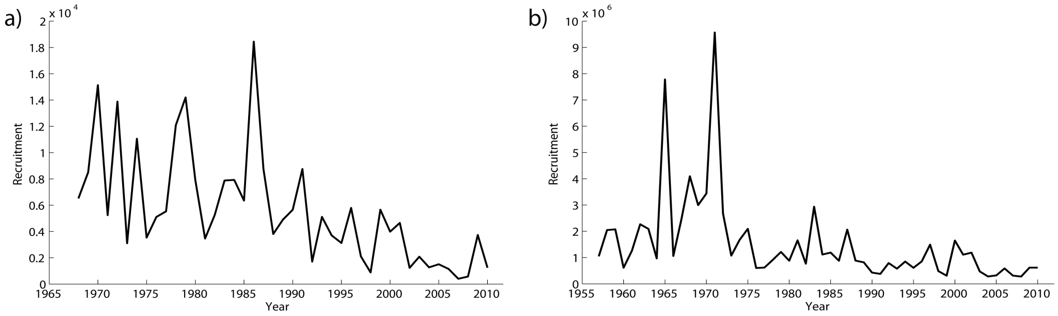

Figure 1.2: *Recruitment numbers for a) Irish Sea cod, and b) North Sea herring. Data are from the ICES Fish Stock Assessment Summary Database, available at www.ices.dk.*

The match/mismatch hypothesis

Fish larvae are reliant on zooplankton (primarily copepods) for their main source of food. The match/mismatch hypothesis was first proposed by Cushing (1975) and suggests that larval growth, survival and consequently recruitment are dependent on the temporal matching of spawning periods with periods of high food availability. If the abundance peaks of larvae and their zooplankton prey are temporally close then recruitment will be higher, due to either the susceptibility of first-feeding larvae to starvation, or because larvae with low food availability will grow more slowly and thus will be more vulnerable to predation (Mertz and Myers, 1994). In fact it is thought by some that fast growth is a precondition for high survival in fish larvae (Kristiansen et al., 2011).

In turn, zooplankton are dependent on phytoplankton for their source of food. The phytoplankton production system can be thought of as predictable on average (for example spring and autumn blooms, (Henson et al., 2009)), but is variable from year to year (Buckley et al., 2010). The variability in the timing of phytoplankton blooms is governed by climatic factors such as wind strength and radiation (Cushing, 1975), and on upwelling and mixing (Henson et al., 2009). These factors are notably variable.

An illustration of the match/mismatch hypothesis can be found in Figure 1.3. Under "match" conditions, the hatching of larvae occurs temporally close enough to the peak in prey abundance. Under "mismatch" conditions, the larvae hatch too early to take advantage of increased prey availability. A mismatch may also occur if larvae hatch too late and miss the peak in prey abundance.

Evidence supporting the match/mismatch hypothesis has been found in both empirical (Horwood et al., 2000) and modelling studies (Mertz and Myers, 1994). For example, Beaugrand et al. (2003) constructed a Plankton Index of larval cod survival, which found that 48% of the fluctuations in plankton quantity and quality could explain the variability seen in cod recruitment in the period 1958-1999 (Beaugrand et al., 2003). Similarly, Beaugrand and Kirby (2010) found that their Plankton Index could explain 46.24% of the variability in their cod recruitment data.

The growth/mortality hypothesis

A theory closely linked to the match/mismatch hypothesis and Hjort's Critical Period hypothesis is the growth/mortality hypothesis (Cushing and Horwood, 1994; Rice et al., 1993). According to this hypothesis, larvae which grow quickly through a "mortality window" have a survival advantage over those that do not (Campana, 1996). As much as 99.99% of larvae die before reaching metamorphosis (Campana, 1996), and rapid growth through the larval stage is thought to increase survival probabilities due to an increased ability to forage for prey and avoid predators (Cushing and Horwood, 1994). Growth rates determine the duration of the period during which

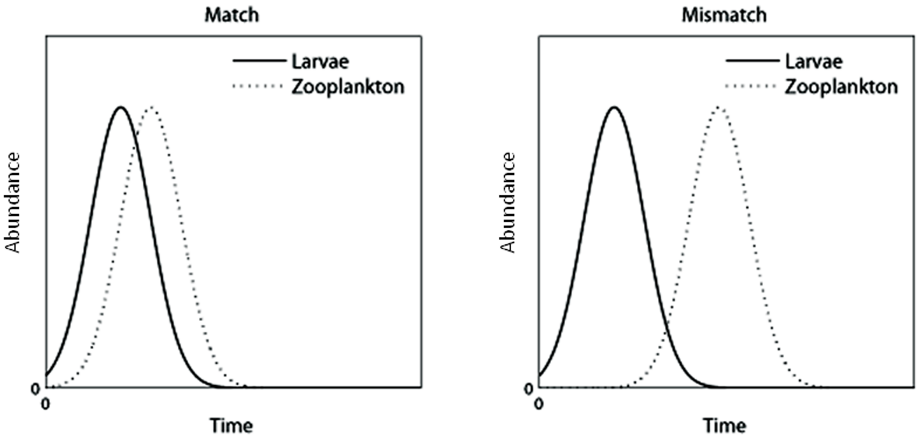

Figure 1.3: *An illustration of the match/mismatch hypothesis. Under "match" conditions, the hatching of larvae occurs temporally close enough to the peak in prey abundance. Under "mismatch" conditions, the larvae hatch too early to take advantage of increased prey availability. A mismatch may also occur if larvae hatch too late and miss the peak in prey abundance. Based on Figure 2 of Mertz and Myers (1994).*

larvae are vulnerable to gape-limited predators (Fogarty et al., 1991).

Other theories attempting to explain recruitment variability include the member-vagrant hypothesis (Iles and Sinclair, 1982), the Stable Ocean hypothesis (Lasker, 1981), and the "Optimum Environmental Window" model (Cury and Roy, 1989). The work in this thesis concentrates on a combination of the growth/mortality and match/mismatch hypotheses.

1.2 Stochastic models of larval fish growth and recruitment

Larvae are small relative to the spatial scales of prey heterogeneity and to the turbulent fluid flow at these spatial scales (Pitchford and Brindley, 2001). They also have only local knowledge of their immediate environment, limited by a visual perceptive distance of around one body length (Pitchford et al., 2003), and they are subject to massive mortality, with a newly hatched individual's probability of survival to metamorphosis being $O(1\%)$ or less (Chambers and Trippel, 1997) driven by typical mortality rates of 10% per day in the larval stage (Cushing and Horwood, 1994). These factors are likely to strongly influence the observed variability in the stock-recruitment relationships which underpin fisheries management.

Deterministic models of recruitment can provide important insights into fish population dynamics in the face of exploitation (Fogarty, 1993). However, because the key natural phenomena are inherently stochastic, deterministic models can be argued to be inappropriate for quantifying recruitment. Rather, stochastic models should be constructed to arrive at recruitment probabilities (Pitchford and Brindley, 2001) and investigate recruitment variability (Fogarty et al., 1991; Fogarty, 1993). Not including the "unpredictable" environmental noise in fisheries models can lead (and has led) to erroneous predictions of the behaviour of exploited stocks, and may have contributed to the deterioration of these stocks (Keyl and Wolff, 2008).

Recent models have treated the recruitment process as a hitting-time (the minimum time taken to reach a certain threshold value) problem for stochastic differential equations (Lv and Pitchford, 2007; Pitchford et al., 2005), showing that environmental stochasticity induced by turbulence and spatial heterogeneity can be beneficial to recruitment. The differences between the predictions from deterministic and stochastic models are particularly great when growth rates are small and mortality rates are large, which is precisely the environment inhabited by fish larvae (Pitchford et al., 2005).

1.2.1 A stochastic differential equation for fish larval growth

To model larval growth we adopt the stochastic model of Pitchford et al. (2005). The model takes the form of a stochastic differential equation (Oksendal, 2000), that is,

$$dM(t) = r(t)dt + \sigma dB(t), \quad M(0) = 0,$$

where $M(t)$ is the mass of an individual fish larva at time t, $r(t)$ is the instanteous deterministic growth rate of the larva at time t, and $B(t)$ is a Brownian noise process with variance σ^2. This growth model is used, in various forms, throughout this thesis. We use an individual-level growth model since the mechanisms governing survival and recruitment in larval fish operate at the level of the individual (Rice et al., 1993).

We define a fixed recruitment mass M_{rec} at which the individual larva is considered to be recruited to its next life history stage. To calculate recruitment probabilities we first determine the distribution $f_{t_{rec}}(t)$ of hitting times t_{rec} where

$$t_{rec} = \inf \{t > 0 : M(t) = M_{rec}\}.$$

In Chapters 2 and 3, as in Burrow et al. (2008) and Pitchford et al. (2005), mortality is represented as a size-independent Poisson process with rate μ, so that an individual fish larva has a probability $\exp(-\mu t_{rec})$ of surviving to M_{rec}. Thus, the probability of an individual being recruited by time t is

$$P_{rec}(t) = \int_0^{t_{rec}} f_{t_{rec}}(t) \exp(-\mu t) dt.$$

1.3 The importance of plankton

We have already hinted at the importance of plankton in the marine ecosystem in Section 1.1.2. Plankton are small pelagic organisms which float and drift in the various water layers of the ocean (Raymont, 1963). The plankton can be roughly split into two groups - the phytoplankton, which are photosynthesising species, and the zooplankton, small animals who feed on other plankton.

Phytoplankton are crucially important to the ocean ecosystems and the global carbon cycle as a whole. They represent the first link in the ocean food chain from inorganic to organic substances and are the primary producers of the ocean (Raymont, 1963). Phytoplankton populations in temperate waters display large temporal fluctuations, most notably in the form of spring blooms. These rapid population explosions are caused by increases in temperature, light availability and nutrient mixing (Sverdrup, 1953; Truscott and Brindley, 1994). Winter storms mix up the nutrient rich bottom layer of the ocean into the upper layers. As spring arrives, the ocean stratifies, and the increasing light levels and day lengths (and therefore increased ability to photosynthesize) allow the phytoplankton to exploit the now nutrient rich upper layers they reside in. These temporary blooms last for around a month and present a large boost to the food supply of their predators, the zooplankton. This increase in food availability in turn leads to an increase in the abundance of zooplankton populations.

Large fluctuations in the timing and intensity of phytoplankton blooms have been noted in both the Atlantic and Pacific oceans (Platt et al., 2007). Henson et al. (2009) observed that the timing of the onset of phytoplankton blooms can vary by 15 to 50 days in the North Atlantic, with the largest variability seen in the transition zone between the subpolar and subtropical regions. The timing of onset of the spring phytoplankton bloom in the North Sea can vary interannually by up to six weeks (Cushing and Horwood, 1994). This variability in phytoplankton dynamics will cause variability in zooplankton dynamics, and thus stochasticity in the food available for fish larvae to prey upon. Thus, fluctuations in the plankton have a large effect on the survival and recruitment of fish larvae, but how variability at one trophic level relates to fluctuations in higher levels is not well understood (Runge, 1988; Runge et al., 2010).

1.3.1 Plankton patchiness and Lévy processes

Zooplankton populations are not only temporally heterogeneous, they also exhibit spatial heterogeneity. Plankton patches exist on a range of scales (Pitchford and Brindley, 2001). Concentrations of these larval prey organisms are thought to be low on average, with dense patches exceeding the average densities by several orders of magnitude (van der Meeren and Naess, 1993).

The general approach of Lv and Pitchford (2007) and Pitchford et al. (2005), which assumes that individual-based variability can be captured at the population level by a diffusion equation, may not be universally appropriate. In particular, diffusion-based models may not be able to capture sudden jumps in growth caused by rare chance encounters with particularly favourable patches of prey. It has been demonstrated that larval prey are not randomly distributed in space, the distribution is in fact closer to a patchy negative-binomial distribution (Young et al., 2009). Larval fish may be dependent on finding dense patches of prey in order to survive to recruitment (Young et al., 2009).

Important clues as to how the diffusion-based approach of Lv and Pitchford (2007) and Pitchford et al. (2005) could better account for planktonic heterogeneity have been provided by recent research on Lévy walks, with attempts to develop a single framework in which to study plankton patchiness (Lough and Broughton, 2007) and non-Brownian motion of predators in heterogeneous stochastic environments (Sims et al., 2008). A Lévy walk is a random walk with step lengths taken from an appropriate heavy tailed distribution (Edwards et al., 2007), allowing very large steps ("jumps") to occur. Brownian motion is recovered as a special case (Bartumeus, 2007; Plank and James, 2008; Viswanathan et al., 2000).

Results from analytical and simulation models (Bartumeus et al., 2002, 2005; Viswanathan et al., 1999), supported by empirical data (Sims et al., 2008) suggest that a naive predator (one with only limited knowledge of its local environment) following a stochastic foraging strategy in a patchy prey environment can optimise its mean rate of prey encounters by following a Lévy walk. Furthermore, simulation results (Sims et al., 2008) suggest that a fitness benefit is conferred by following a Lévy foraging strategy the exponent of which matches that of the underlying prey distribution. These results are not supported by Benhamou (2007), who compares Lévy walks with composite random walks generated by a forager taking smaller steps when it perceives itself to be within a prey patch. Benhamou (2007) shows firstly that a composite random walk can outperform a Lévy walk in a patchy environment, and secondly that data sampled from composite random walks may resemble those from a Lévy walk, leading to possible problems in interpretation. Plank and Codling (2009) and Petrovskii et al. (2011) provide further evidence that non-Lévy movement paths can be mis-identified as being a Lévy walk, and vice versa. Variation in diffusive movement between individuals may lead to the appearance of superdiffusive movement at the population level (Petrovskii et al., 2011).

Important questions also arise concerning pattern versus process in our understanding of animal movements: if a forager exploits a patchy prey environment by changing its movement strategy in response to its perceived prey field, then its movements will appear to be a stochastic Lévy walk foraging strategy when in fact they simply reflect the underlying prey distribution (Benhamou, 2007; Plank and James, 2008). The analyses of Humphries et al. (2010) suggest that in fact individuals may switch between Lévy and Brownian walks depending on the prey field they experience. Lévy movements are found to be associated with low prey availability, and Brownian movements with abundant prey (Humphries et al., 2010).

Whether Lévy or Brownian movements are most effective in increasing mean encounter rates with prey may not be the important question in some circumstances. When viewed in an evolutionary context, the mean prey encounter rate may be equal between the two strategies, but a Lévy-like foraging strategy may be advantageous to the forager due to its effect on the variance of encounter rates (James et al., 2010; Preston et al., 2010).

1.4 Thesis overview

In this thesis I develop simple stochastic growth models for fish larvae, with the aim of exploring the roles of several different factors in recruitment probabilities and recruitment variability.

In Chapter 2, the model of Pitchford et al. (2005) is extended to include non-

Gaussian jumps in growth, representing rare chance encounters with particularly favourable patches of prey. We present two theoretical results. Firstly, if jumps are of a fixed size and occur as a Poisson process (embedded within a drift-diffusion), recruitment is effectively described by a drift-diffusion process alone. Secondly, in the absence of diffusion, and for “patchy” jumps (of negative binomial size with Pareto inter-arrivals), the encounter process becomes superdiffusive. To synthesise these results we conduct a strategic simulation study where “patchy” jumps are embedded in a drift-diffusion process. We conclude that Lévy-like predator foraging strategies can have a significantly positive effect on recruitment at the population level.

In Chapter 3, the role of prey availability and the match/mismatch hypothesis is explored. Two strategic models of zooplankton dynamics are introduced, a two-stage step-function model, and a Gaussian-shape model. Since the strong seasonal forcing in temperate waters means the environment (in this case the abundance of prey) is to some extent predictable on average but is variable from year to year (Buckley et al., 2010), the role of stochasticity in the timing and length of increases in zooplankton abundance is explored, and the consequences for recruitment are discussed. Finally, a simple genetic algorithm is employed to explore the fitness landscape of the Gaussian model in relation to larval hatching day, to determine whether fish can evolve an optimal spawning strategy in a very random environment. We draw four main conclusions.

1. Stochasticity in individual growth is more beneficial to recruitment when larvae experience high food availability early on in their growth.

2. When the timing of peak prey abundance is stochastic, recruitment probabilities are greatest for hatching days just before the expected timing of peak prey abundance.

3. When the timing of periods of high prey density is held fixed, the evolved optimum hatching day becomes earlier as the length of the high density period increases.

4. When both the timing and length of the periods of high density are allowed to (co-)vary, we find no evidence of strong selection pressure for specific hatching days, only for a hatching “window” around the expected prey peak.

In Chapter 4, we explore the idea of non-constant variance in recruitment. We examine the work of Minto et al. (2008), to investigate the proposition that recruitment variance is increased at low stock sizes, with the aim of establishing its practical use in fisheries management. We demonstrate that the current stock-recruitment time series available are not long enough to accurately fit a heteroscedastic (non-constant variance) model, and in particular that they are not long enough to establish in which direction recruitment variance changes with stock size. We go on to show that in some cases, there is very little, if any, practical difference between maximum sustainable yield values calculated from the heteroscedastic model and from a standard Beverton-Holt model. We also demonstrate that, due to the nature of the heteroscedastic model, it is not always possible to calculate a value for maximum sustainable yield.

In Chapter 5 we extend the work carried out in Chapter 3 to include an extra trophic level - phytoplankon. This allows us to synthesize the ideas of Chapters 2, 3 and 4. We aim to examine how variability in the timing of phytoplankton blooms travels up the food chain to influence fish larval recruitment. The second aim of the chapter is to explore the role of zooplankton patchiness in fish larval recruitment. Two contact rate based models of fish larval growth are developed. The first assumes that a larva encounters patches of prey, and subsequently items of prey within that patch, as a Poisson process. The second assumes a negative-binomial distribution of zooplankton. The growth models are coupled to a dynamical phytoplankton-zooplankton model, via predation on the zooplankton by the larvae. We demonstrate that for certain parameter values the two growth models are roughly equivalent, and produce similar recruitment distributions.

We find that recruitment probabilities are reduced as the patch length scale increases. Our results for a stochastically forced phytoplankton bloom suggest that not only does a patchy environment seem to decrease the maximum achievable recruitment, but it also means larval hatching must be more precisely timed to achieve this maximum. For high larval densities, we are able to observe the predation of the larvae on the zooplankton, and the subsequent effects on the phytoplankton dynamics. In these cases the feedback between the trophic layers may play an important role in determining recruitment.

The thesis concludes with a synthesis and discussion of the results presented in the chapters described above, and a look forward to future directions of this research.

Chapter 2

Lévy processes, saltatory foraging, and superdiffusion

It is well established that resource variability generated by spatial patchiness and turbulence is an important influence on the growth and recruitment of planktonic fish larvae. Empirical data show fractal-like prey distributions, and simulations indicate that scale-invariant foraging strategies may be optimal. Here we show how larval growth and recruitment in a turbulent environment can be formulated as a hitting time problem for a jump-diffusion process. We present two theoretical results. Firstly, if jumps are of a fixed size and occur as a Poisson process (embedded within a drift-diffusion), recruitment is effectively described by a diffusion process alone. Secondly, in the absence of diffusion, and for "patchy" jumps (of negative binomial size with Pareto inter-arrivals), the encounter process becomes superdiffusive. To synthesise these results we conduct a strategic simulation study where "patchy" jumps are embedded in a drift-diffusion process. We conclude that Lévy-like predator foraging strategies can have a significantly positive effect on recruitment at the population level.

2.1 Introduction

Planktonic fish larvae may be broadly described as being small, stupid, and dead. These assertions can be made more concrete: larvae are small relative to the spatial scales of prey heterogeneity and to the turbulent fluid flow at these spatial scales (Pitchford and Brindley, 2001); they have only local knowledge of their immediate environment, limited by a visual perceptive distance of around one body length (Pitchford et al., 2003); and they are subject to massive mortality, with a newly hatched individual's probability of survival to metamorphosis being $O(1\%)$ or less (Chambers and Trippel, 1997) driven by typical mortality rates of 10% per day in the larval stage (Cushing and Horwood, 1994). These factors are likely to strongly influence the extreme observed variability in the stock-recruitment relationships which underpin fisheries management.

Because the key natural phenomena are inherently stochastic, deterministic models can be argued to be inappropriate for quantifying recruitment (defined here as growth to some threshold size e.g. size at metamorphosis). Rather, stochastic models must be constructed to arrive at recruitment probabilities (Pitchford and Brindley, 2001). Recent recruitment models have treated this process as a hitting-time problem for stochastic differential equations (Lv and Pitchford, 2007; Pitchford et al., 2005), showing that environmental stochasticity induced by turbulence and spatial heterogeneity can be beneficial to recruitment. The differences between the predictions from deterministic and stochastic models are particularly great when growth rates are small and mortality rates are large, which is precisely the environment inhabited by fish larvae (Pitchford et al., 2005).

The general approach of Lv and Pitchford (2007) and Pitchford et al. (2005), which assumes that individual-based variability can be captured at the population level by a diffusion equation, may not be universally appropriate. In particular, diffusion-based models cannot necessarily capture sudden jumps caused by rare chance encounters with particularly favourable patches of prey (there are parallels to the phenomenon of unpredictable shocks affecting the value of economic markets (Applebaum, 2004)).

The Lévy-Khintchine formula provides a generic mathematical description for an infinitely divisible continuous time stochastic process as a combination of diffusion-with-drift interspersed with probabilistic jumps (Applebaum, 2004).

Important clues as to how the diffusion-based approach of Lv and Pitchford (2007) and Pitchford et al. (2005) could better account for recruitment variability have been provided by recent research on Lévy walks (LWs), with attempts to develop a single framework in which to study plankton patchiness (Lough and Broughton, 2007) and non-Brownian motion of predators in heterogeneous stochastic environments (Sims et al., 2008). A LW is a random walk with step lengths taken from an appropriate heavy tailed distribution (Edwards et al., 2007), allowing very large steps ("jumps") to occur. The probability density function (pdf) for a LW typically takes the form of a power law; for example, $P(l_j) \sim l_j^{-\mu}$, with $1 < \mu \leq 3$ where l_j is the step length and μ is the Lévy exponent (Sims et al., 2008). Brownian motion is recovered as a special case for $\mu > 3$ (Bartumeus, 2007; Plank and James, 2008; Viswanathan et al., 2000). Alternative parameterisations may be more amenable to mathematical progress (see Section 3).

Results from analytical and simulation models (Bartumeus et al., 2002, 2005; Viswanathan et al., 1999), supported by empirical data (Sims et al., 2008) suggest that a naive predator following a stochastic foraging strategy in a patchy prey environment can optimise its mean rate of prey encounters by following a LW. Furthermore, simulation results (Sims et al., 2008) suggest that a fitness benefit is conferred by following a Lévy foraging strategy the exponent of which matches that of the underlying spatial prey distribution. These results are not supported by Benhamou (2007), who compares LWs with composite random walks (CWs) generated by a forager taking smaller steps when it perceives itself to be within a prey patch. Benhamou (2007) shows firstly that a CW can outperform a LW in a patchy environment, and secondly that data sampled from CWs may resemble those from a LW, leading to possible problems in interpretation. Important questions also arise concerning pattern versus process in our understanding of animal movements: if a forager exploits a patchy prey environment by changing its movement strategy in response to its perceived prey field, then its movements will appear to be a stochastic LW foraging strategy when in fact they simply reflect the underlying prey distribution (Benhamou, 2007; Plank and James, 2008).

This study seeks to provide a mathematical basis for the treatment of non-diffusive phenomena in descriptions of planktonic foraging. In Section 2.2 we address the question of whether a reformulation of the recruitment problem can account for locally rare but beneficial conditions using a jump-diffusion process. In Section 2.3 we are motivated by the saltatory (pause-travel) foraging behaviour of planktonic fish larvae (e.g., cod (Ruzicka and Gallager, 2006)). We use a deliberately simple analytical model to ask whether a saltatory strategy in a patchy environment is optimal, and whether there is a mathematical basis for the notion that predator and prey exponents should match. Our approach utilises analytically tractable Pareto distributions for step lengths and inter-arrival times (James et al., 2005). Furthermore, the simplicity of the model means that pattern and process are transparently independent. The resulting individual-based model exhibits superdiffusivity; the variance of the process does not scale linearly with time.

The results in Section 2.3 support Benhamou (2007) and Pitchford and Brindley (2001) in showing that Lévy foraging is not a generically optimal strategy. However, when synthesised within the Lévy process jump-diffusion framework of Section 2.2, the results of simple simulations lead us to argue in Section 2.4 that saltatory LW foraging may be a beneficial strategy when scaled up to the population level. We show that superdiffusivity can in principle increase recruitment probability due to the risk sensitivity associated with foraging in a high mortality environment. However, the ecological details peculiar to each foraging scenario (and therefore their simulation) are likely to be factors of major importance.

2.2 Hitting times for jump diffusion processes and applications to recruitment

Pitchford et al. (2005) and Lv and Pitchford (2007) show that including Gaussian white noise (representing individual and environmental variability) in the growth rate of planktonic fish larvae always increases the probability of maturation (defined here as growth to the recruitment threshold size). Pitchford et al. (2005) describe the gain in mass $M(t)$ of an individual larva at time t as

$$M(t) = rt + \sigma B(t), \qquad M(0) = 0, \tag{2.1}$$

so that each larva grows as a drift-diffusion process with mean rate r and with variance σ^2 (that is, $B(t)$ is a Brownian noise process with variance σ^2).

Because it forms a basis for our subsequent analysis, the model of (2.1) deserves careful consideration, especially regarding linearity in time t and the possibility of negative growth. Modifying the drift term r to account for concave (Von Bertalanffy growth) or convex (geometric) growth, and allowing different scaling of the noise term σ, does not qualitatively affect the results for recruitment probabilities (Lv and Pitchford, 2007). Equation (2.1) admits the possibility of $M(t)$ becoming negative. However, if $M(t)$ is interpreted as a measure of gain in mass from an initial non-zero state M_0, then $M(t) < 0$ does not necessarily imply that the overall mass is negative. The probability of $M(t) < -M_0$ (implying negative mass) for some $t < \infty$ is $\exp\left(\frac{-2rM_0}{\sigma^2}\right)$ (assuming no absorbing barrier at M_{mat}). The possibility that $M(t) < 0$ is addressed fully in Appendix A.

In light of the Lévy-Khintchine formula (Applebaum, 2004) and the patchy nature of plankton distributions (Lough and Broughton, 2007), we quantify the effects of adding non-Gaussian (Lévy) noise which could represent prey patchiness, turbulence, or any other processes causing temporal and spatial heterogeneity. Consider the simplest case, where the Lévy measure v (essentially the measure of non-Gaussian part of the stochastic process) takes the form $v = \lambda\delta_h$, with $\lambda > 0$ and δ_h a Dirac delta function centered at $h \in R\backslash\{0\}$ (Applebaum, 2004). This gives a new growth equation,

$$M(t) = r't + \sigma B(t) + N(t), \qquad M(0) = 0, \tag{2.2}$$

where $r' = r - \int_{(0,1]} xv(dx)$ is the effective growth rate, σ^2 is the variance of the Brownian motion $B(t)$, and $N(t)$ is a Poisson random variable of intensity λ taking values in $\{nh, n \in N\}$, with

$$P(N(t) = nh) = e^{-\lambda t} \frac{(\lambda t)^n}{n!}.$$

Equation (2.2) describes a fish larva growing with drift r' and variance σ^2, between jump discontinuities of size h, caused by encountering rare but favourable patches of prey which occur at random times $(T_n, n \in N)$, $T_n \sim \text{Exp}(\lambda)$.

As in Pitchford et al. (2005) we are interested in the probability of a fish larva reaching maturation. We first determine the distribution of the time to maturation, t_{mat}, where

$$t_{mat} = \inf\{t > 0 : M(t) = M_{mat}\}.$$

M_{mat} is defined to be the fixed recruitment mass and t_{mat} is defined as a hitting time (Condamin et al., 2007). Using Theorem 1.1 of Pakes (1996), the hitting time density for equation (2.2) can be shown to be

$$f_{t_{mat}}(t) = \frac{M_{mat}}{t} \sum_{n=0}^{\infty} \frac{e^{-\lambda t}}{\sqrt{2\pi\sigma^2 t}} \frac{(\lambda t)^n}{n!} \exp\left[\frac{-(M_{mat} - n|h| - rt)^2}{2\sigma^2 t}\right].$$

Although alternative possibilities exist ((Cushing and Horwood, 1994; Pepin et al., 2003)), a size-independent mortality process is appropriate and parsimonious (see Pitchford et al. (2005)) i.e. mortality occurs as a Poisson process with rate μ, so that an individual fish larva has a probability $\exp(-\mu t_{mat})$ of surviving to M_{mat}. Hence the probability of an individual reaching maturity is

$$\begin{aligned} P_{mat}(r, \sigma, \lambda, h) &= \int_0^{\infty} f_{t_{mat}}(t) \exp(-\mu t) dt \qquad (2.3) \\ &= \frac{M_{mat}}{\sqrt{2\pi\sigma^2}} \int_0^{\infty} \frac{e^{-(\mu+\lambda)t}}{\sqrt{t^3}} \sum_{n=0}^{\infty} \frac{(\lambda t)^n}{n!} \exp\left[\frac{-(M_{mat} - n|h| - rt)^2}{2\sigma^2 t}\right] \text{dt}. \end{aligned}$$

To investigate the effects of the additional Lévy noise in the linear growth model, the recruitment probability is plotted against mortality rate μ for a pure drift-diffusion growth process, a mixed drift-diffusion-jump growth process, and a pure Poisson jump growth process (Figure 2.1). The equation for the recruitment probability for the mixed drift-diffusion-jump growth process is given by equation (2.3), and the equation for the pure drift-diffusion process is given by Equation (8) in Pitchford et al. (2005). The probability of maturation for a pure Poisson jump growth process, with intensity λ and jump size h, is

$$P_{mat}(\lambda, h) = \left(\frac{\lambda}{\lambda + \mu}\right)^{\frac{M_{mat}}{h}}.$$

The analytical results in Figure 2.1 were confirmed using explicit individual-based simulations of 100,000 individuals generated using an Euler-Maruyama scheme between exponentially-distributed fixed-size jumps.

The results in Figure 2.1 indicate that, at the scale of larval fish growth, the addition of Lévy noise (in the form of constant size jumps) is unlikely to affect the probability of maturation when the mean and variance of the overall growth process are held fixed. In other words, at the ecologically relevant scale, the input from the jump process becomes essentially diffusive and standard stochastic differential equation (SDE) techniques can be applied. The following section shows that this is a consequence of the choice of jump process, and that more realistic foraging models can result in non-diffusive processes at the population level, with concomitant consequences for recruitment.

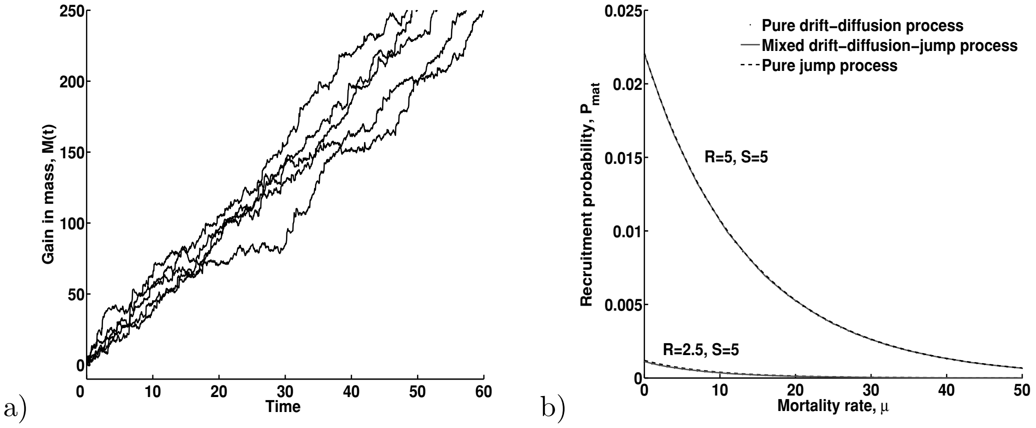

Figure 2.1: *a) Example growth trajectories for individuals growing with a drift-diffusion process between exponentially-distributed fixed-size jumps. Parameters used here were* $r = 2.5$, $\sigma^2 = 12.5$, $h = 5$, $\lambda = 0.5$. *b) The probability of reaching maturity against mortality rate* μ, *for a pure drift-diffusion growth process, a mixed drift-diffusion-jump growth process, and a pure Poisson jump growth process. The mean at time t for all processes was fixed to be Rt, and the variance* S^2t. *For the drift-diffusion process the parameters used were (R=5)* r=5, σ=5; *and (R=2.5)* r=2.5 *and* σ=5. *For the mixed drift-diffusion-jump process the parameters used were, (R=5)* r=2.5, $\sigma=\sqrt{12.5}$, h=5, λ=0.5; *and (R=2.5)* r=1.25, $\sigma=\sqrt{12.5}$, h=10, λ=0.125. *For the pure jump process the parameters used were (R=5)* h=5, λ=1; *and (R=2.5)* h=10, λ=0.25.

2.3 An individual-based model for the encounter process of a saltatory forager

The analytical and numerical results in Section 2.2 indicate that simply describing individual-based growth and recruitment as a hitting time problem for a jump-diffusion process does not necessarily scale up to have an impact at the ecological or management levels. However, the assumption that jumps occur with a fixed magnitude is unrealistic and may be unnecessarily restrictive, because the resulting model resembles a diffusive process over ecologically relevant time scales. The individual-based model formulated below provides theoretical evidence that diffusive models may be inappropriate; for a saltatory forager following a LW in a patchy environment, it is demonstrated that the growth process is superdiffusive.

Consider a naive predator (e.g., planktonic fish larva) foraging in a patchy environment where food items (e.g., copepods) are distributed patchily in space according to a Pareto distribution with parameter r_2 (Johnson et al., 1994). The predator performs a saltatory foraging strategy, moving between search locations at a fixed constant speed. These movements have lengths governed by a Pareto distribution with parameter r_1, i.e., the step lengths are such that the predator follows a LW for $r_1 \leq 2$. We assume that the predator consumes all items of food it finds within each search location before moving on to its next foraging location, and that this consumption is instantaneous (i.e. there is a negligible handling time). These assumptions are useful for analytical tractability, and could be relaxed in numerical simulations.

Although we assume a three dimensional isotropic prey distribution, the foraging process can be regarded as taking place in one spatial dimension (c.f. (Plank and James, 2008)). This is not a restrictive assumption because the movement process is one dimensional from the forager's point of view and Lévy exponents are conserved when dimensionality is reduced via projection (Sims et al., 2008) (Suppl. Mat.). In order to understand how the spatial distribution of predator foraging locations and prey items may be interrelated, we parameterise the probability distributions such that the expected number of foraging locations and the mean–field prey density remain fixed, and only the degree of heterogeneity (of forager movements, prey distribution, or both) varies. This focuses attention on the foraging strategy employed, rather than any mean-field properties. Note that this does not imply a fixed prey field. Conditional on a fixed mean-field density, the number of prey items at each location is independent of all other locations.

We seek to understand the distribution of $X(t)$, the total number of prey items encountered by a stochastic forager in fixed time t. Let $N(t)$ be the number of foraging locations visited in time t, and let δ describe the size of each foraging location (typically the perceptive radius of the forager (Pitchford and Brindley, 2001)). Because the forager travels with constant speed, the time τ between foraging intervals follows a Pareto distribution with parameters r_1 and α_1. Hence the probability density of τ is given by

$$\mathrm{f}(\tau) = \frac{r_1 \alpha_1^{r_1}}{(\alpha_1 + \tau)^{r_1+1}}, \quad (\tau > 0).$$

It follows that (James et al., 2005)

$$N(t) \sim \text{negative binomial}\left(r = r_1, p = \frac{\alpha_1}{\alpha_1 + t}\right),$$

with probability mass function

$$\mathrm{f}(n) = \binom{r+n-1}{n} p^r (1-p)^n, \quad (n = 0, 1, \ldots).$$

For foraging location i, let the number of encounters with prey be Y_i, i.e, Y_i is the number of prey items contained within a sphere of radius δ. Because the prey are distributed according to a Pareto distribution with parameters r_2 and α_2, the distance η between prey items has density function

$$\mathrm{f}(\eta) = \frac{r_2 \alpha_2^{r_2}}{(\alpha_2 + \eta)^{r_2+1}}, \quad (\eta > 0)$$

and it follows that

$$Y_i \sim \text{negative binomial}\left(r = r_2, p = \frac{\alpha_2}{\alpha_2 + \delta}\right).$$

Hence the probability mass function of Y_i is

$$\mathrm{f}(y) = \binom{r+y-1}{y} p^r (1-p)^y, \quad (y = 0, 1, \ldots).$$

We make the natural assumption that the Y_i are independent and identically distributed. There is an implicit, but practically reasonable assumption here that foraging locations do not overlap (MacKenzie and Kiorboe, 1995). The fact that the perceptive field of a larva is better described as a narrow "wedge" further strengthens this assumption (Galbraith et al., 2004). The probability generating functions of N and Y_i can then be derived as

$$G_N(s) = \left(\frac{\alpha_1}{\alpha_1 + [1-s]t}\right)^{r_1},$$

$$G_Y(s) = \left(\frac{\alpha_2}{\alpha_2 + [1-s]\delta}\right)^{r_2}.$$

It follows that $\mathrm{E}(N) = r_1 t/\alpha_1$ and $\mathrm{E}(Y_i) = r_2\delta/\alpha_2$.

Because the total number of prey encountered in time t is simply

$$X = Y_1 + Y_2 + \cdots + Y_N,$$

it follows that the generating function of X is

$$G_X(s) = G_N\{G_Y(s)\} = \alpha_1^{r_1}\left[t - t\left(\frac{\alpha_2}{\alpha_2 - [1-s]\delta}\right)^{r_2} + \alpha_1\right]^{-r_1}.$$

Let $\lambda_1 = r_1/\alpha_1$ and $\lambda_2 = r_2/\alpha_2$. By parameterising in terms of $r_1, r_2, \lambda_1, \lambda_2$, we are able to vary the parameters r_1 and r_2 whilst $\mathrm{E}(N) = \lambda_1 t$ and $\mathrm{E}(Y_i) = \lambda_2\delta$ (mean–field properties) remain fixed. It can then readily be shown that

$$\begin{aligned}\mathrm{E}(X) &= \lambda_1\lambda_2\delta t,\\ \mathrm{Var}(X) &= \lambda_1\lambda_2^2\delta^2 t^2\left(\frac{1}{r_1} + \frac{1}{r_2 t} + \frac{1}{t} + \frac{1}{\lambda_2\delta t}\right).\end{aligned}$$

The implications of these results are discussed in more detail in Section 4, but the most basic message here is that the expected encounter rate depends only on the mean–field properties of the predator movement and prey distribution, not on the details of their distribution (i.e., $E(X)$ is independent of r_1 and r_2). This precisely mirrors the results of Pitchford and Brindley (2001) and Pitchford et al. (2003) for cruise predators: for both cruise and saltatory foragers, heterogeneity in the predator's movement strategy, or in the prey distribution, or both, do not affect mean prey encounter rates. Hence a constant speed predator receives no average benefit by altering its foraging trajectory (although changes in speed can of course influence encounter rates and movement costs (Pitchford et al., 2003)).

The variance in the encounter rate is superdiffusive ($\mathrm{Var}(X) \propto t^\rho$, $1 < \rho < 2$). Because the model in this section relates to encounter rate rather than time to maturity, it is not straightforward to incorporate mortality and formulate a model for recruitment probability as in Section 2.2. In Section 2.4.1, we incorporate the features of the "patchy" jump process that leads to superdiffusion into an idealised simulation of a jump-diffusion process. The consequences for recruitment are then discussed.

2.4 Discussion

The analytical results in Sections 2.2 and 2.3 raise important issues regarding both the inclusion of stochasticity in mathematical models, and the ecological and evolutionary processes underpinning our ideas of planktonic foraging.

2.4.1 Superdiffusive models of recruitment

Motivated by Sections 2.2 and 2.3, Figure 2.2 shows the results of simulating a jump-diffusion process with Pareto interarrival times between jumps (simulating a saltatory predator) and with negative-binomially distributed jump sizes (simulating a patchy prey distribution). Parameter values are again chosen based on those of Pitchford et al. (2005) so far as possible, and mortality rate μ is fixed at 0.1. The mean growth rate of the overall stochastic process is $R = r + \lambda_1 \lambda_2$. Consistent with Section 2.2, $R = 5$, $r = 2.5$ and $M_{mat} = 200$. Results are shown for a range of r_1 and r_2, to capture the dependence of recruitment probabilities on both the foraging strategy of the predator and the patchiness of the prey distribution. A minimum exponent value $r_i = 2$ is imposed because smaller values correspond to infinite variance and are therefore difficult to justify with empirical data. The results are calculated from simulations of 10,000 individuals using an Euler-Maruyama scheme between Pareto-distributed negative-binomial-sized jumps.

Figure 2.2a) depicts five example individual growth trajectories for $r_1 = 2$, $r_2 = 2$, illustrating the non-diffusive nature of the underlying process. The consequences at the population level are shown in Figure 2.2b); recruitment probability is seen to increase with decreasing exponent r_1. The role of the prey distribution, captured by prey exponent r_2, appears to be less important (given that the mean-field prey concentration is constant across all simulations). However, whilst illustrating the general principle, the simulations in Figure 2.2 ought to be regarded as strategic. The Pareto formulation in Section 2.3 allows many small jumps rather than enforcing a minimum jump size. This may be inappropriate for some predators (although the factors of turbulence and wedge-shaped perceptive fields may ameliorate this criticism; the assumption that foraging locations are disjoint is likely to be reasonable (MacKenzie and Kiorboe, 1995)). Practical applications of this modelling framework would require context-specific consideration of underlying processes such as turbulence, swimming speeds and handling times and are beyond the scope of this study.

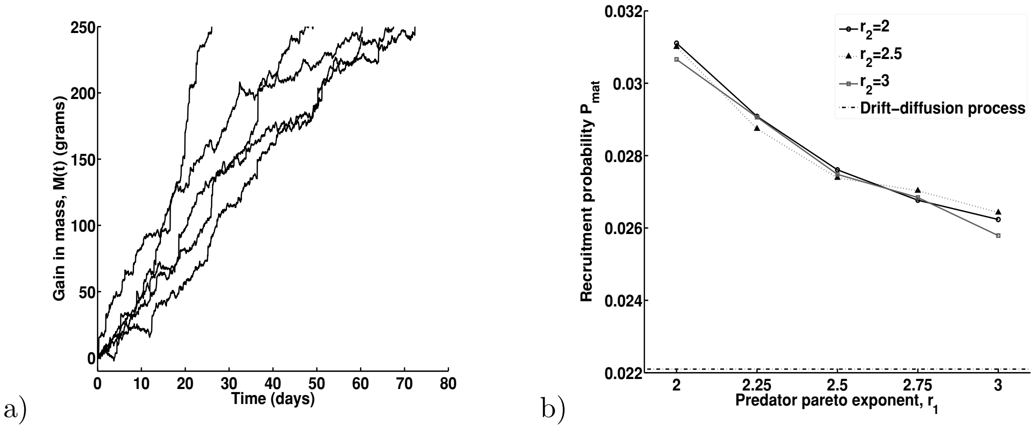

Figure 2.2: *a) Example superdiffusive growth trajectories for individuals growing with a drift-diffusion process between negative binomially distributed jumps at Pareto distributed inter-arrival times. Parameters used here were* $r = 2.5$*,* $\sigma^2 = 12.5$*,* $r_1 = 2$*,* $\alpha_1 = 2$*,* $r_2 = 2$*,* $p = 2/7$*. b) The probability of reaching maturity against predator Pareto exponent,* r_1*, for a range of values of prey patchiness,* r_2*. Mass at maturation was fixed at* 200*, and mortality rate at* 0.1*. The mean at time* t *for all processes was fixed to be* $Rt = (r+\lambda_1\lambda_2)t = 5t$ *(see Sections 2.2 and 2.3 for definitions of variables).*

2.4.2 Foraging behaviour

Important messages arise from the encounter process modelled in Section 2.3. By employing increasingly non-diffusive Lévy-type movements (i.e., decreasing r_1), the predator can increase the variability in its encounter rate. Decreasing r_2 increases the variability in encounter rates at the individual level. In other words, although individual mean encounter rates are not affected, prey patchiness and Lévy foraging increase the variability in the gain an individual forager experiences. This echoes the results of Pitchford and Brindley (2001), and it is possible to combine the results presented here with those of Benhamou (2007) and Pitchford and Brindley (2001) to make some definite statements regarding stochastic foraging. Where simulations show a fitness benefit (an increase in mean encounter rate) in Lévy foraging over RW foraging, then the benefit does not arise solely as a consequence of predator movement and prey patchiness. Rather, where any benefit exists, it must arise in conjunction with other processes within the simulations. Details such as predators' behavioural responses to prey, how prey regeneration is handled, and how prey patchiness is statistically maintained after a predation event, are likely candidates. Such processes warrant greater attention to biological and ecological detail in order to build a more comprehensive picture of "optimal" foraging.

Predator movement and prey heterogeneity alone are not sufficient to favour Lévy foraging. Benhamou (2007) suggests that, where LW are observed in data (and provided these have not been misidentified (Edwards et al., 2007; Sims et al., 2007, 2008)), this is likely to be a confusion of pattern and process or a superposition of different movement strategies operating at different spatial scales. There is, however, another possibility which may be of particular importance for marine plankton (zooplankton or larval and juvenile fish) subject to high levels of mortality and turbulence. Pitchford et al. (2005) show that stochasticity, manifested by a large variance in individual prey encounter rate, is beneficial to the growth and recruitment of organisms which grow slowly and whose survival to the next life history stage is unlikely (see (Lv and Pitchford, 2007) for nonlinear generalisations of this simple model). Such foragers, whose knowledge of their turbulent environment is necessarily local in both space and time, have a strong evolutionary pressure to increase their encounter variance (i.e., to follow a classic "risk sensitive" foraging strategy). It is not the object of this paper to quantify the evolutionary consequences of risk sensitivity, but we note that the model of evolutionarily stable strategies under uncertain trade-offs in Currey et al. (2007) provides an appropriate framework. The deterministic energy costs of faster swimming must be balanced against the stochastic benefits of increased mean and variance in encounter rate, which can be quantified using the mathematics in Section 2.3 (saltatory predators) or Pitchford and Brindley (2001) (cruise predators).

The individual-based foraging model presented here is highly idealised, but this is necessary to disentangle the "pattern versus process" arguments described in (Benhamou, 2007). In particular, the model implies that the forager will not interact with any prey it meets whilst moving between foraging locations. Adapting the model to account for such possibilities inevitably leads one to consider more cruise-like foraging strategies where the theories of Benhamou (2007), Pitchford and Brindley (2001), and Viswanathan et al. (2000) are more appropriate. We note that, compared to a saltatory forager, cruise predation is unlikely to be an effective way to leave regions of low prey density, i.e., to escape low quality habitats. The ability to leave regions of low yield in favour of a small chance of finding a higher yield location is likely to be of particular importance to risk sensitive foragers. Therefore, although some of the complex behaviours observed in saltatory foraging are missing (Ruzicka and Gallager, 2006), our model can be claimed to capture and quantify the fundamental processes.

2.4.3 Summary

This study attempts to synthesise observational evidence of the non-diffusive distribution of planktonic predators and their prey in the natural environment with existing stochastic models, thereby characterising important ecological processes at the population level. We show that, when generalising from SDE to jump-diffusion process, the individual-level processes which generate the jump distribution can give rise to superdiffusivity.

The model of saltatory foraging in Section 2.3 agrees with previous models of cruise predators in questioning whether there is a generic advantage, in terms of mean encounter rate, for a naive predator to move according to a LW. Furthermore, we find no theoretical support for matching between exponents governing predator and prey distributions in maximising mean prey encounter rates. However, when interpreted in the context of a risk sensitive foraging strategy in a patchy environment, Figure 2.2 shows that saltatory foragers may be at a significant advantage. Accurately quantifying this advantage requires more careful consideration of the ecological details (minimum jump size, prey regeneration, predator perceptive field and behaviour, handling time etc.). These form the subject of ongoing work.

Chapter 3

The importance of variable timing and abundance of prey for fish larval recruitment

Fish recruitment can vary by an order of magnitude between years, and the larval stage is a key determining factor. Zooplankton, the main source of larval food, are temporally and spatially heterogeneous, and this could contribute to recruitment variability and ultimately stock sustainability. Here we use simple stochastic models of larval growth and zooplankton dynamics, together with an evolutionary algorithm, to investigate the role of transient peaks in zooplankton abundance and the match/mismatch hypothesis in recruitment success and variability. We draw four main conclusions. 1. Stochasticity in individual growth is more beneficial to recruitment when larvae experience high food availability early on in their growth. 2. When the timing of peak prey abundance is stochastic, recruitment probabilities are greatest for hatching days just before the expected timing of peak prey abundance. 3. When the timing of periods of high prey density is held fixed, the evolved optimum hatching day becomes earlier as the length of the high density period increases. 4. When both the timing and length of the periods of high density are allowed to (co-)vary, we find

no evidence of strong selection pressure for specific hatching days, only for a hatching "window" around the expected prey peak.

3.1 Introduction

The number of fish larvae recruited into the adult population each year is fundamental to the long-term stability of a fish stock (Chambers and Trippel, 1997). Large variability in recruitment is ubiquitous (Cushing, 1968; Koslow, 1992; Needle, 2002; Shepherd and Cushing, 1990). It is believed that recruitment success and variability is largely determined during the larval stage (Brander et al., 2001; Horwood et al., 2000). Fish larvae are born into an extremely variable environment with high mortality rates (Chambers and Trippel, 1997; Cushing and Horwood, 1994) and so it is not surprising that the number of larvae surviving long enough to be recruited into the adult population is stochastic. Much emphasis is placed on predicting annual recruitment, and consequently understanding the processes governing recruitment variability.

The currently available stock and recruitment data are limited (see, for example, Koslow (1992)) primarily in the length of the time series for individual stocks; therefore emphasis should be placed on understanding and studying the biological and dynamical processes underlying recruitment variability. It may in fact be far more important to understand the causes of recruitment variability, rather than attempting to predict with any degree of accuracy the number of recruits arising from a given stock in a given year (Needle, 2002). Mechanistic process-based models are thus a useful tool in exploring and understanding recruitment variability.

Fish larvae are reliant on zooplankton (primarily copepods) for their main source of food. The match/mismatch hypothesis was first proposed by Cushing (1975) and suggests that larval growth, survival and consequently recruitment are dependent on the temporal matching of spawning periods with periods of high food availability. This suggests that investigating the links between larval and plankton population dynamics is fundamental in furthering our understanding of larval recruitment success. Zooplankton are heterogeneous in both time (influenced by seasonal phytoplankton blooms) and space (patchily distributed) and this could contribute to recruitment variability.

The match/mismatch hypothesis has been explored previously using simple mathematical models (for example see (Biktashev et al., 2003; James et al., 2003; Mertz and Myers, 1994)). However, most studies use deterministic models of larval growth and plankton abundances. We argue that deterministic models may be inappropriate for modelling the recruitment process, since the key underlying factors are inherently stochastic (Burrow et al., 2008; Pitchford et al., 2005). Here we develop the simple stochastic larval growth model of Pitchford et al. (2005) to allow for the inclusion of the effects of variable prey concentrations on recruitment success and variability. Two strategic models of zooplankton dynamics are introduced, a two-stage step-function model, and a Gaussian-shape model. Since the strong seasonal forcing in temperate waters means the environment (in this case the abundance of prey) is to some extent predictable on average but is variable from year to year (Buckley et al., 2010), the role of stochasticity in the timing and length of increases in zooplankton abundance is explored, and the consequences for recruitment are discussed.

Finally, a simple genetic algorithm is employed to explore the fitness landscape of the Gaussian model in relation to larval hatching day, to determine whether fish can evolve an optimal spawning strategy in a very random environment.

3.2 Methods

3.2.1 A simple stochastic model for fish larval growth

To model larval growth we adopt the stochastic growth model of Pitchford et al. (2005). The model takes the form

$$dM(t) = r(t)dt + \sigma dB(t), \quad M(0) = 0, \tag{3.1}$$

where $M(t)$ is the mass of an individual fish larva at time t, $r(t)$ is the instanteous deterministic growth rate of the larva at time t, and $B(t)$ is a Brownian noise process with variance σ^2. We define a fixed recruitment mass M_{rec} at which the individual larva is considered to be recruited to its next life history stage. To calculate recruitment probabilities we first determine the distribution $f_{t_{rec}}(t)$ of hitting times t_{rec} where

$$t_{rec} = \inf \left\{ t > 0 : M(t) = M_{rec} \right\}.$$

As in Burrow et al. (2008) and Pitchford et al. (2005) mortality is represented as a size-independent Poisson process with rate μ, so that an individual fish larva has a probability $\exp(-\mu t_{rec})$ of surviving to M_{rec} (a value of $\mu = 0.1$ is used for all results). Thus, the probability of an individual being recruited by time t is

$$P_{rec}(t) = \int_0^{t_{rec}} f_{t_{rec}}(t) \exp(-\mu t) dt.$$

3.2.2 A step-function model for zooplankton dynamics

We wish to introduce the simplest possible model for the underlying prey (i.e. zooplankton) population dynamics. It is acceptable to assume that an increase in prey population density would lead to an increase in the growth rate of a fish larva. We introduce a strategic step-function zooplankton dynamics (Z-dynamics) model in the form of a “jump” in the deterministic larval growth rate $r(t)$. In our strategic Z-dynamics model there are two states, “low density” and “high density”. We define r_1 to be the lower value of r, and r_2 the higher. We also define t_1 to be the time at which r switches from r_1, to r_2, i.e. the time the period of high density starts, and t_2 to be the time the period of high density ends (Figure 3.1(a)).

To quantify the effect of a match/mismatch between spawning and peak prey abundance, a period of high prey density is fixed to start on Day 40 and to persist for 40 days, with a batch of larvae hatching on a set day, from Day 0 to Day 100. A length of 40 days is used as an example broadly representative of natural systems; the results hold qualitatively for any length of period. Recruitment probabilities are calculated for each hatching day both analytically and numerically. To calculate recruitment probabilities numerically we use a fixed step Euler-Maruyama scheme (Higham, 2001) to simulate 10,000 fish larvae growing according to equation (3.1) and record hitting times for the fixed recruitment mass M_{rec}, which is fixed to be 200 for all results presented in this chapter (the parameters and variables used in the models presented here are non-dimensional, however for applications they could be considered dimensional, using mg for mass, for example). The average hitting time for that hatching day is then calculated as

$$P_{rec} = \frac{1}{n} \sum_{i=1}^{n} \exp(-\mu t_{rec,i}),$$

where $n = 10{,}000$ is the number of simulated larvae, and $t_{rec,i}$ is the hitting time of larva i. The results for stochastic larval growth, with $\sigma = 5$, are compared to those for deterministic larval growth (i.e. $\sigma = 0$ in equation (3.1)).

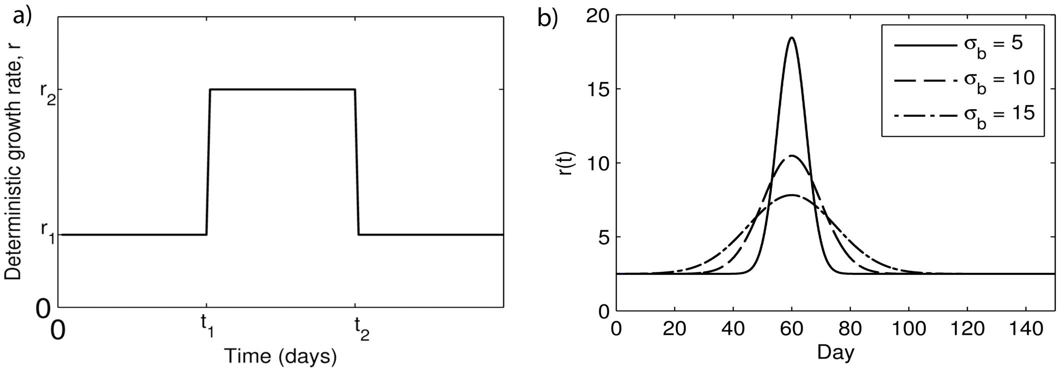

Figure 3.1: *a) Step-function representation of zooplankton dynamics in the stochastic larval growth model. r is the deterministic growth rate of a fish larva. b) Example Gaussian representations of zooplankton population dynamics in the stochastic larval growth model.* $r(t)$ *is the deterministic growth rate of a fish larva.* μ_b*= 60 and h=0 for all three examples.*

3.2.3 A Gaussian model for zooplankton dynamics

We consider the step-function model to be a good first approximation model for zooplankton population dynamics; however, it is unrealistic to assume that there are only two levels of zooplankton densities in the ocean, and that there is such a sharp transition between the two. We wish to consider a more realistic, smooth model for the Z-dynamics, and one which can naturally be extended to include stochasticity in zooplankton abundances and correlations between the timing and length of periods of high density. We now let $r(t)$ take a Gaussian form, i.e.

$$r(t) = r_1 + \frac{A}{\sigma_b\sqrt{2\pi}} \exp\left\{-\frac{(t+h-\mu_b)^2}{2\sigma_b^2}\right\}, \tag{3.2}$$

where r_1 is the larval growth rate at the lowest zooplankton density (i.e. the lowest value of $r(t)$), μ_b is the time at which the peak zooplankton density occurs, σ_b is the standard deviation of the Z-dynamic (this gives a measure of the length of the period of increased prey abundance), A is the area under the curve of the Z-dynamic, and h is the hatching day of the larvae. Figure 3.1b) shows three example Z-dynamics, for three different values of σ_b. The area under the curve of the Z-dynamic is held constant at 200 (ecologically this represents the total amount of zooplankton being constant across different Z-dynamics shapes, to allow comparison), and $h = 0$, in all cases.

We compare the recruitment probabilities for larvae growing deterministically (σ_b $= 0$) against larvae growing stochastically ($\sigma_b = 5$), for fixed values of μ_b and σ_b. This allows comparison with the results of our step-function Z-dynamic model. Larvae are hatched on a certain day over a 100 day period, and growth is simulated and recruitment probabilities calculated as described in the previous subsection.

Next we consider the effects of μ_b and σ_b being stochastic. In real ocean systems, the spring or autumn phytoplankton bloom will not occur on exactly the same day every year (Mertz and Myers, 1994; Brander et al., 2001), and consequently the timing of peak zooplankton density will also vary. We wish to investigate when a batch of larvae should hatch in order to maximise their recruitment success when the timing of peak prey abundance is stochastic. To do this, μ_b and σ_b are now considered to be random variables with $\mu_b \sim N(\mu_{\mu_b}, \sigma_{\mu_b})$ and $\sigma_b \sim N(\mu_{\sigma_b}, \sigma_{\sigma_b})$.

For each hatching day, 1000 random samples of μ_b and σ_b are generated. For each pair of samples of μ_b and σ_b, the growth trajectories of 1000 larvae were simulated using an Euler-Maruyama scheme, and the recruitment probabilities calculated as described in the previous subsection. This is effectively generating recruitment data over a 1000 year period with the annual plankton bloom occurring on a random day each year, within a certain spawning window. The duration of a phytoplankton bloom (and the associated period of high zooplankton population density) may be correlated to its timing (Keller et al., 2001), and so we wish to investigate the effect of a correlation between μ_b and σ_b on our recruitment results. To simulate correlated μ_b and σ_b variables, we first generate two standard normal variables X_1 and X_2. We then define

$$\begin{aligned} \mu_b &= \sigma_{\mu_b} X_1 + \mu_{\mu_b}, \\ \sigma_b &= \sigma_{\sigma_b}(\rho X_1 + \sqrt{1-\rho^2} X_2) + \mu_{\sigma_b}. \end{aligned} \tag{3.3}$$

It is easy to show that $E(\mu_b) = \mu_{\mu_b}$, $E(\sigma_b) = \mu_{\sigma_b}$, $\mathrm{Var}(\mu_b) = \sigma_{\mu_b}$, and $\mathrm{Var}(\sigma_b) = \sigma_{\sigma_b}$. Since any linear transformation of a normal random variable is also normal (Rice, 1995), we then have $\mu_b \sim N(\mu_{\mu_b}, \sigma_{\mu_b})$ and $\sigma_b \sim N(\mu_{\sigma_b}, \sigma_{\sigma_b})$. Thus, μ_b and σ_b are normally distributed random variables with correlation ρ. To investigate the effects of both early periods of high prey density being shorter and being longer we simulated positive and negative correlations respectively between μ_b and σ_b.

3.2.4 A genetic algorithm for optimal hatching day

To explore the possibility of optimal hatching days in this stochastic environment we implement a simple genetic algorithm; 200 parent individuals each produce 50 offspring, which inherit their parent's spawning day h (the day the offspring of that adult are hatched) plus or minus some noise (up to 1% of h). The fittest 200 offspring are then selected to become the next generation of adults based on the fastest hitting times. The genetic algorithm was run for 200 generations, or until the population appeared to have converged if this occurred sooner. We deemed the algorithm to have converged if the mean and variance of the evolved hatching days of the population had changed by less than 1% in successive generations. Note that this genetic algorithm does not purport to be an accurate and detailed reconstruction of the evolution of hatching strategies. Rather, it is a systematic attempt to explore the evolutionary stability of hatching strategies in a stochastic environment, and to infer what behaviours (if any) may be favourably selected.

3.3 Results

3.3.1 A step-function model for zooplankton dynamics

We calculate recruitment probabilities analytically for the deterministic ($\sigma = 0$) growth case first. We have the simple growth equation $dM/dt = r(t)$, where $r(t)$ is a step function as shown in Figure 3.1. This gives us

$$M(t) = M_0 + \int_0^t r(s)ds = \begin{cases} M_0 + r_1 t, & \text{if} \quad t < t_1 \\ M_0 + r_1 t + (r_2 - r_1)(t - t_1), & \text{if} \quad t_1 \le t < t_2 \\ M_0 + r_1 t + (r_2 - r_1)(t_2 - t_1), & \text{if} \quad t > t_2. \end{cases}$$

The logic behind the derivation of these results is shown schematically in Figure 3.2. From above, $M_{rec} = M_0 + \int_0^{t_{rec}} r(s)ds$. It is trivial to rearrange to find expressions for t_{rec}. The recruitment probability is then $P_{rec} = \exp(-\mu t_{rec})$. It is worth noting that the hitting times and recruitment probabilities above are for a larva hatching on Day 0, relative to t_1. The results are simple to adjust for larvae hatching at other times.

Using methods exactly analogous to the deterministic growth case, we can derive the following hitting time distribution for the stochastic growth case,

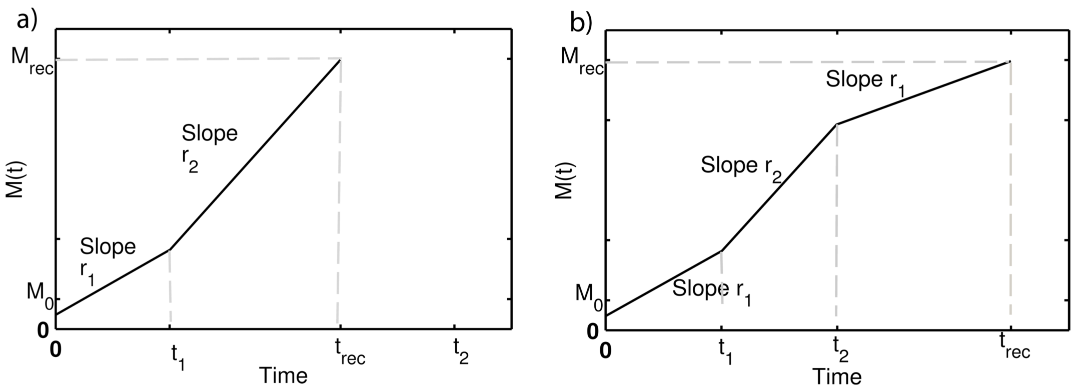

Figure 3.2: *Schematic representations of the growth of a fish larva of size $M(t)$, growing deterministically according to $dM(t)/dt = r(t)$, where $r(t)$ is a step function as described in the text (and shown in Figure 3.1(a)). a) The larva reaches recruitment mass M_{rec} during the r_2 stage of the step function, b) the larva reaches recruitment mass M_{rec} during the second r_1 stage of the step function.*

$$f_{t_{rec}}(t) = \begin{cases} f^1_{t_{rec}}(t) = f(0, r_1, t), & \text{for t} < \text{t}_1, \\ f^2_{t_{rec}}(t) = \displaystyle\int_{-\infty}^{M_{rec}} f(x, r_2, t - t_1) g(x, r_1, t_1)\, dx, & \\ & \text{for t}_1 \leq \text{t} < \text{t}_2, \\ f^3_{t_{rec}}(t) = \displaystyle\int_{-\infty}^{M_{rec}} \int_{-\infty}^{M_{rec}} f(y, r_1, t - t_2) g(x, r_1, M_{rec}, t_1) & \\ \qquad \times g(y - x, r_2, M_{rec} - x, t_2)\, dx\, dy, & \\ & \text{for t} \geq \text{t}_2, \end{cases}$$

where

$$f(x, r, t) = \frac{M_{rec} - x}{\sqrt{2\pi\sigma^2 t^3}} \exp\left\{ -\frac{(M_{rec} - x - rt)^2}{2\sigma^2 t} \right\}$$

is the hitting time distribution for individuals with initial size x and instantaneous growth rate r, and

$$g(t,r,x) = \frac{1}{\sqrt{2\pi\sigma^2 t}}\left[\exp\left\{-\frac{(rt-x)^2}{2\sigma^2 t}\right\} - \exp\left\{\frac{2rM_{rec}}{\sigma^2}\right\}\exp\left\{-\frac{(2M_{rec}-x+rt)^2}{2\sigma^2 t}\right\}\right].$$

is the size distribution at time t of individuals with instantaneous growth rate r who have not reached size M yet. We can then define the recruitment probability to be

$$P_{rec} = \int_0^{t_1} f^1_{t_{rec}}(t)dt + \int_{t_1}^{t_2} f^2_{t_{rec}}(t)dt + \int_{t_2}^{\infty} f^3_{t_{rec}}(t)dt. \tag{3.4}$$

As in the deterministic growth case, equation (3.4) is the recruitment probability for a larva hatched on Day 0 (in relation to time t_1). It is again trivial to adjust the equation for a larva hatching at a later time. Equation (3.4) cannot be integrated analytically. However is it simple to integrate numerically using mathematical software - for example, Matlab. To verify our analytical results, recruitment probabilities were also calculated numerically, as described in the Methods section. The results for recruitment are shown in Figure 3.3. In both the stochastic and the deterministic ($\sigma = 0$) growth cases, hatching around the start of the period of high prey availability greatly increases the recruitment probability. For all hatching days, recruitment probabilities are greater for the stochastic growth case than for the deterministic growth case (see (Lv and Pitchford, 2007) and (Pitchford et al., 2005) for examples and discussion of the general role of stochasticity leading to increased recruitment probabilities).

What is interesting, however, is that stochasticity does not provide an equal benefit for all hatching days. To illustrate this point, compare the larvae born on Days 35 and 55. In the deterministic growth case, both batches experience the same length of high prey density between hatching and recruitment, and thus have the same recruitment probability (the parameter values used here mean that a deterministically growing larva will reach recruitment in 30 days; the larvae hatched on Day 35 are thus recruited during the period of high prey density and so do not experience its

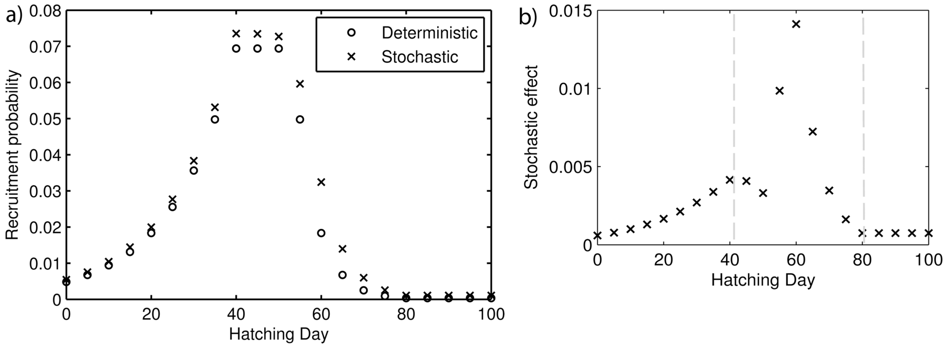

Figure 3.3: *Recruitment results for the strategic bloom model, for a fixed bloom of length 40 days, beginning on Day 40. Circles represent larvae growing deterministically, crosses stochastically. b) The benefit of stochasticity on recruitment, calculated as the stochastic recruitment probability minus the deterministic recruitment probability.*

entire length). In the stochastic case, the larvae hatched on Day 55 have a greater recruitment probability than those born on Day 35, despite the fact that those hatched on Day 35 could theoretically experience the full 40 days of high prey density, whereas those hatched on Day 55 can only experience a maximum of 25 days of increased prey availability and thus increased growth rate. The addition of the stochastic term means that an individual hatched on Day 55 has the possibility of reaching recruitment mass before the period of lower prey concentration begins, that is it will only experience the higher prey concentration. An individual hatched on Day 35 cannot avoid the period of lower prey concentrations because this occurs at the beginning of its larval growth phase.

Examining the hitting time distributions for the hatching days in question (Figure 3.4) provides further insight. Despite having equal mean hitting times, the hitting time distribution for larvae hatched on Day 55 is more positively skewed than that of the larvae hatched on Day 35, that is more individuals hatched on Day 55 have a short hitting time than those hatched on Day 35. The nonlinearity of the Poisson

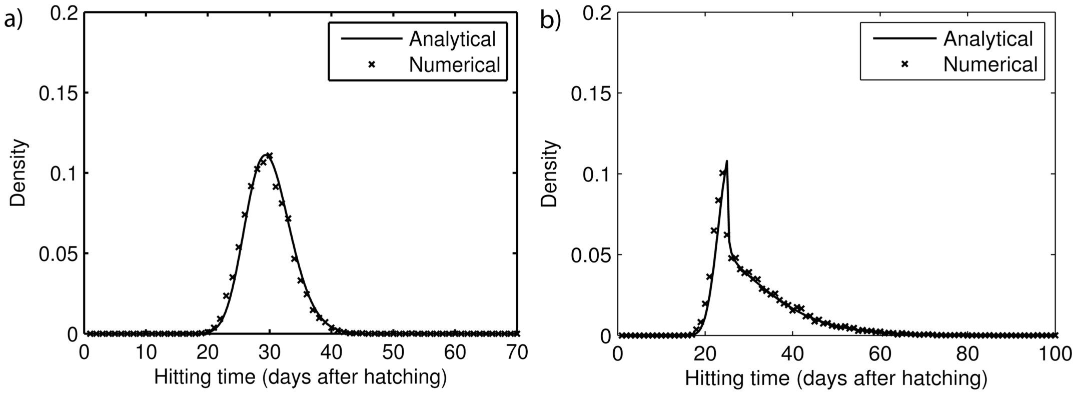

Figure 3.4: *Hitting time distributions for larvae hatching on a) Day 35 and b) Day 55, for the step-function Z-dynamic model, from equation (3). Numerical results were calculated from simulations of 10,000 individuals.*

mortality process means more weight is put on lower hitting times, thus increased positive skewness of the hitting time distribution leads to a higher mean recruitment probability. This stochastic effect is even more pronounced in the comparison of larvae hatched on Days 20 and 60 (Figure 3.3).

3.3.2 A Gaussian model for zooplankton dynamics

As previously, our simple growth equation is $dM(t) = r(t)dt + \sigma dW(t)$, where in this case $r(t)$ takes the form (3.2). We can calculate recruitment probabilities analytically in the deterministic, $\sigma = 0$, case. Integrating the growth equation gives

$$M_{rec} = r_1 t_{rec} + \frac{A}{\sigma_b\sqrt{2\pi}} \int_0^{t_{rec}} \exp\left\{-\frac{(t+h-\mu_b)^2}{2\sigma_b^2}\right\} dt.$$

A simple change of variables allows integration, giving

$$M_{rec} = r_1 t_{rec} + \frac{A}{2}\left[\operatorname{erf}\left(\frac{t+h-\mu_b}{\sigma_b\sqrt{2}}\right) - \operatorname{erf}\left(\frac{h-\mu_b}{\sigma_b\sqrt{2}}\right)\right],$$

from which t_{rec} can readily be evaluated using (for example) the ‘fzero’ function in Matlab. Results for stochastic larval growth are calculated numerically, as described previously.

Figure 3.5 shows the recruitment probabilities for larvae growing deterministically and larvae growing stochastically, for μ_b=60 and σ_b=15. We can see that the results are very similar to the results for the step-function model; stochasticity always has a positive effect on recruitment, and the addition of stochasticity has a greater effect on recruitment success after the peak prey density, in comparison to before it.

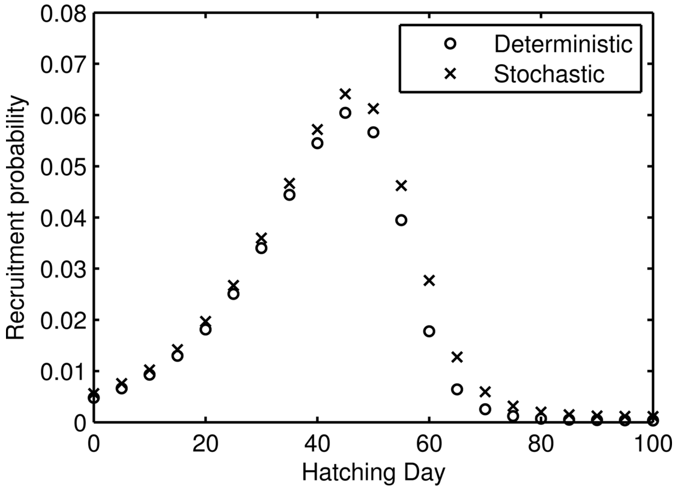

Figure 3.5: *Recruitment probabilities for larvae growing deterministically (circles) and stochastically (crosses), with $r(t)$ taking the form (2). σ_b=15, μ_b = 60. For the stochastic results each point is the average of 10,000 individual recruitment probabilities.*

Figure 3.6 shows the recruitment probabilities for stochastic timing and length of the peak zooplankton density, with $\mu_b \sim N(50, 10)$ and $\sigma_b \sim N(20, 5)$. Each box plot represents 1000 instances of μ_b and σ_b, with recruitment probabilities averaged over 1000 stochastically growing larvae for each instance. The black dots mark the mean recruitment probability for each hatching day. The mean and median recruitment probabilities are maximised on hatching days shortly before the expected timing of the peak in zooplankton abundance. Recruitment variability is greatest for those hatching days when the mean recruitment probability is greatest (the hatching days

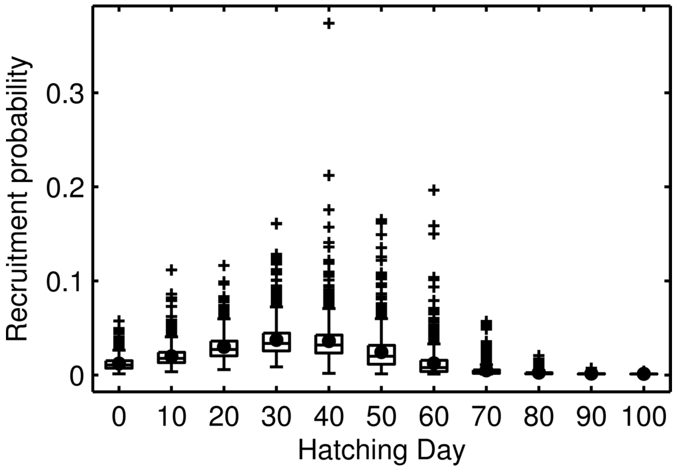

Figure 3.6: *Recruitment probabilities for stochastic peak zooplankton density time* (μ_b) *and length* (σ_b) *for* $\mu_b \sim N(50, 10)$ *and* $\sigma_b \sim N(20, 5)$*. Each box plot represents 1000 random draws of* μ_b *and* σ_b*, with recruitment probabilities averaged over 1000 stochastically growing larvae for each draw of* μ_b *and* σ_b*. The black dots mark the mean recruitment probability for each hatching day.*

around the expected peak zooplankton abundance).

Figure 3.7 shows the recruitment probabilities for correlated peak bloom time (μ_b) and bloom length (σ_b). As in Figure 3.6, each box plot represents 1000 instances of μ_b, with recruitment probabilities averaged over 1000 stochastically growing larvae for each instance of μ_b. The black dots mark the mean recruitment probability for each hatching day. For the mean and median recruitment probabilities, the results in Figure 3.7 are qualitatively equivalent to those in Figure 3.6; the optimum time for a larva to hatch is slightly before the expected timing of the peak in zooplankton abundance. However the results do differ for recruitment variability. When the timing of the peak in zooplankton abundance and the length of time for which zooplankton abundance is high are positively correlated (earlier blooms are shorter), recruitment variability is higher for early spawning, whereas the opposite is true when the timing and length of peak zooplankton abundance are negatively correlated.

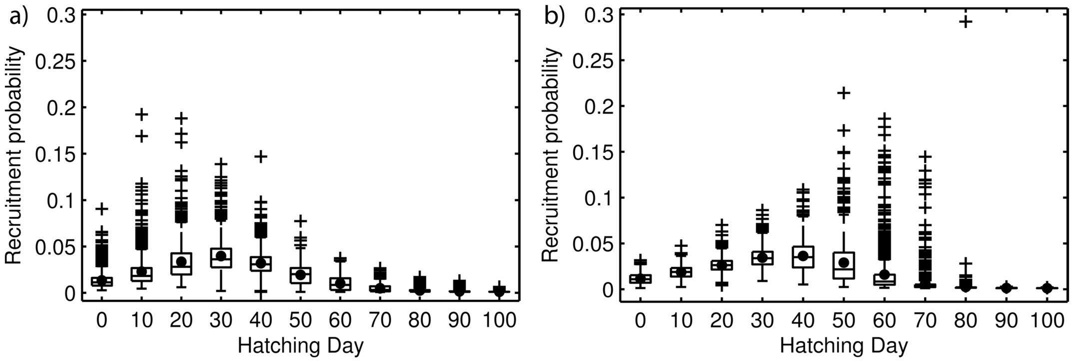

Figure 3.7: *Recruitment probabilities for stochastic correlated peak bloom time (μ_b) and bloom length (σ_b) for: a) positive correlation (ρ = 0.7), and b) negative correlation (ρ =-0.7). $\mu_b \sim N(50, 10)$ and $\sigma_b \sim N(20, 5)$. Each box plot represents 1000 random draws of μ_b and σ_b, with recruitment probabilities averaged over 1000 stochastically growing larvae for each draw of μ_b and σ_b. The black dots mark the mean recruitment probability for each hatching day.*

3.3.3 A genetic algorithm for optimal hatching day

The results of our genetic algorithm indicate that if the timing and length of the peak prey density are deterministic, there is a clear negative relationship between length of the period of peak prey abundance and optimal hatching day, i.e. the longer the period of high prey density, the earlier the optimal hatching day (Figure 3.8). For comparison, optimal hatching days were also calculated from the original Gaussian Z-dynamics model. For each value of σ_b, recruitment probabilities were calculated for fish larvae hatching on each day, and the day with the greatest recruitment probability was taken to be the optimal hatching day. A fixed value of μ_b =50 was used in both the genetic algorithm and the Gaussian Z-dynamics model, for this comparison. We can see that the results from the original Gaussian Z-dynamics model qualitatively match those from the genetic algorithm (Figure 3.8).

When the timing and length of the period of high prey density are stochastic, there is no clear convergence of the genetic algorithm. These model results indicate that there may be relatively weak selection pressure for specific hatching days in highly stochastic environments, so long as the larvae hatch within a window around the time of the increase in prey abundance.

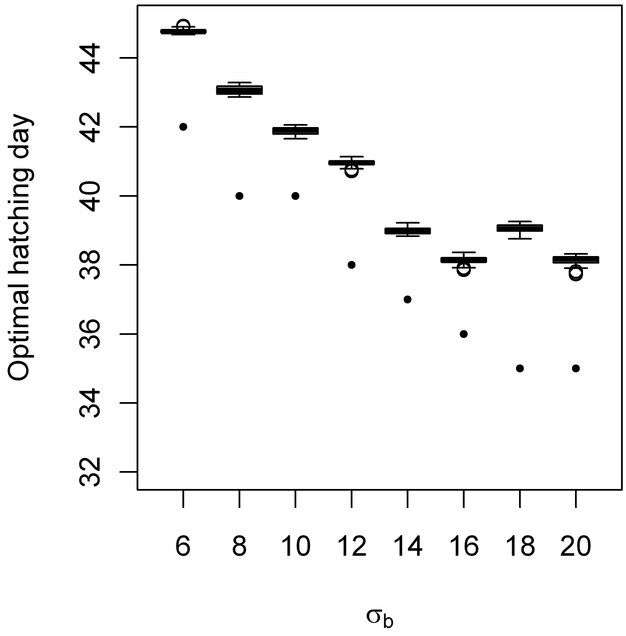

Figure 3.8: *Optimal hatching days evolved from the simple genetic algorithm described in the text (box plots), and the hatching days with the greatest recruitment probabilities, for fish larvae growing under the Gaussian Z-dynamics model (black dots), for different values of* σ_b*. The environment is fixed with* $\mu_b = 50$ *in both.*

3.4 Discussion

We have demonstrated that simple strategic mechanistic models, coupling fish larval growth to zooplankton population dynamics, can give insight into the processes effecting larval recruitment success and variability. Our results have interesting implications for the match/mismatch hypothesis. As discussed in (Burrow et al., 2008) and (Pitchford et al., 2005), fish larvae live in an extremely volatile and variable environment, and so it is very likely that stochastic models are more able to capture the important factors at work in the growth of fish larvae than their deterministic counterparts.

The results from the step-function Z-dynamics model indicate that the amount by which an individual larva's recruitment probability is increased due to environmental stochasticity is dependent on when the larva hatches relative to the peak prey abundance. In a stochastic environment, to maximise chances of survival to recruitment, a fish larva ideally wants to be born into a period of high prey availability and potentially suffer low prey abundances later, rather than vice versa. When stochasticity in the timing of high zooplankton densities is introduced in a possibly more realistic Gaussian Z-dynamics model, our results suggest that recruitment probabilities are "optimised" when larvae hatch slightly before the expected time of peak zooplankton density. This result is supported by empirical studies; Buckley and Durbin (2006) found that the peak hatching period of both cod and haddock on the Georges Bank was ahead of the peak abundance of their copepod prey. Platt et al. (2003) hypothesize that most haddock larvae off the eastern continental shelf of Nova Scotia hatch before the spring plankton bloom, and that early blooms thus result in higher recruitment due to a greater temporal overlap between the larvae and their prey. Their empirical findings support this theory, reporting that early blooms were correlated with high recruitment. Wright and Bailey (1996) also found that hatching of the sandeel *Ammodytes marinus* in the Shetland waters preceded the peak in prey availability.

It may appear at first glance that the results from the step-function Z-dynamics model and the Gaussian Z-dynamics model are contradictory; the step-function model suggests that, if an adult fish cannot time its spawning with enough accuracy so that its larvae hatch on the day with greatest recruitment probability, then it should spawn later rather than earlier, whereas the Gaussian model suggests the opposite. However, these are not contradictory results. In fact, examination of Gaussian model with fixed parameters (Figure 3.5) leads to the same conclusion drawn from the step-function model. It is the inclusion of stochasticity in the timing of the peak zooplankton abundance that alters the optimum spawning strategy from “better late than early” to a “better early than late”. If we make the parameter t_1 a random variable in the step-function model, we see results qualitatively similar to those from the stochastic Gaussian model. This is a further demonstration of the importance of including stochastic effects in models of fish larval growth.

So what of recruitment variability? In the results of our stochastic Gaussian Z-dynamics model, we see large recruitment variability, with around an order of magnitude difference between the lowest and highest recruitment probabilities. This is in agreement with observations from nature (for example North Sea cod (Horwood et al., 2000)).

A pattern in recruitment variability is observed in our model results when the duration of a period of high zooplankton density is linked to its timing. When parameters are correlated so that early periods of high density are shorter, variability is greater for hatching days before the expected peak density day. When early blooms periods of high density are longer, variability is greater for hatching days after the expected peak density day. This has interesting consequences for spawning strategies: if an adult fish wishes to maximise both the mean and variance of its offspring’s recruitment (a risk spreading strategy (Real, 1980; Reddingius and den Boer, 1970)) then this is more achievable in an environment where early periods of high prey density are shorter. In real systems, the correlation between bloom timing and length may be dependent on season, temperature, and/or many other factors.

It has been proposed that the duration of the spawning/hatching period can also have a substantial effect on recruitment variability (Mertz and Myers, 1994). Protracted spawning can be viewed as a risk-spreading strategy, attempting to reduce the variance in offspring survival (Biktashev et al., 2003; Wright and Trippel, 2009). It may be that there is a stronger selection pressure for hatching period than for hatching day, but we did not see evidence for this in our model. This is most likely due to the fact we have no competition between individual larvae, and no top-down effects of the larvae on the zooplankton population. Future modelling work will include competition for food and top-down effects of the larval growth dynamics on the plankton dynamics, which may be very important (James et al., 2003). The bottom-up effect of phytoplankton population dynamics on zooplankton abundances could also play an important role in the recruitment process. Spatial heterogeneity in prey could also have an effect on recruitment variability.

Whilst it may be argued that the models presented in this study are very simple, we have demonstrated that strategic mechanistic models can improve our understanding of the processes governing recruitment success, and recruitment variability in particular. Notably, we have demonstrated that although there may exist an optimal window for hatching, in the very random environment that fish larvae survive in, selective pressures may not be strong enough to evolve an optimal hatching day. Studying models such as these alongside more data-analytic approaches will give a more thorough understanding of the fundamental processes affecting recruitment and its variability.

Chapter 4

Variable variability: consequences for fisheries management?

Recent analyses propose that the key processes in regulating the size of fish stocks are stochastic rather than deterministic, characterised by increased recruitment variance at low stock sizes (heteroscedasticity). Here we investigate the consequences of this idea, with the aim of testing its practical relevance to fisheries management. We argue that stock-recruitment time series are at least one order of magnitude too short to reliably fit heteroscedastic models; indeed they are typically insufficient even to establish in which direction recruitment variance changes with stock size. Management implications are illustrated using simple models and published recruitment data for two exploited stocks. For North Sea herring heteroscedasticity appears negligible, with no practical difference between maximum sustainable yield (MSY) values calculated using a heteroscedastic model versus a standard Beverton-Holt model. In contrast, for North Sea cod heteroscedastic models result in highly volatile (and sometimes nonexistent) MSY estimates which are likely to seriously overestimate levels of sustainable harvest. Statistical models of this type are useful to elucidate broad-scale

regulatory processes, but a better mechanistic understanding is necessary before they can be used in a management setting.

4.1 Introduction

Traditionally, studies of population regulation in fisheries have sought underlying deterministic processes. More recently it has been recognised that the ecosystem complexity and environmental uncertainty may render such simple explanations inadequate; stochastic (random) factors may be at least as important. For example, Shepherd and Cushing (1990) acknowledge that deterministic mechanisms such as density dependent growth or fecundity can explain the weak regulation needed to prevent stocks exploding at low mortality rates. However, they have more difficulty finding a deterministic mechanism explaining the strong regulation necessary to prevent stocks collapsing at high mortality rates (Shepherd and Cushing, 1990). They hypothesise a stochastic regulatory process characterized by increased variance in recruitment at low stock sizes. Shepherd and Cushing (1990) were unable to statistically prove their hypothesis using stock-recruit time series, as these datasets were, at the time, too short (characteristically around 30 years). Garrod (1983) also attempted to find increased variance at low stock sizes, but failed.

As time series data for fish stocks have increased in length and statistical techniques have developed, Minto et al. (2008) reinvestigated the idea by extending the Deriso-Schnute stock recruitment model (Deriso, 1980; Schnute, 1985) to include heteroscedastic (non-constant) variance in recruitment. They employed a meta-analysis of 147 fish stocks to demonstrate an inverse relationship between survival variability (a proxy for recruitment variability) and stock size. This conclusion could have important consequences for fisheries management, particularly that of over-fished stocks which already have increased survival variability (Hsieh et al., 2006; Anderson et al., 2008) (these two processes may in fact be linked).

The study presented here asks whether the heteroscedastic relationship is of practical importance in the context of parameterising stock-recruitment relationships and improving management. We first show that, when using data to parameterise stochastic models, the variability predicted by the best-fitting parameters is large enough to make their estimation highly uncertain. Put simply, even if the parameters of a stochastic model are "known" with great precision, the randomness they predict may make it impossible to recover these known values from data in any meaningful time frame. We go on to examine the possible management consequences of this fact using simple maximum sustainable yield models.

4.2 Heteroscedastic model

Minto et al. (2008) define a new stock-recruitment relationship in which the variance is a function of population abundance. The model takes the form

$$\ln\left(\frac{R}{S}\right) \sim N(\mu, \sigma^2), \text{ with } \mu = \ln\alpha + \frac{1}{\gamma}\ln(1-\gamma\beta S), \;\; \sigma^2 = \exp(\eta_0 + \eta_1 S), \tag{4.1}$$

where R is defined to be the number of juvenile fish recruited to the adult population each year and S the spawning stock biomass. The parameter γ allows the underlying stock-recruitment relationship to switch between several standard models: γ =-1,000 gives a model with essentially no density dependence, γ =-2 a Cushing-like model,γ =-1 a Beverton-Holt model, γ =0 a Ricker model, and γ =1 a Schaefer model (Minto et al., 2008). The parameter η_1 is defined as the coefficient of heteroscedasticity, indicating to what extent, and in which direction, the variance changes with stock density in a population.

A binomial test on the individual species fits supports the negative trend in η_1 values seen by Minto et al. (2008), finding a statistically significant number of negative η_1 estimates (see Appendix B). However, we wish to establish whether the idea of heterosceadasticity in recruitment can be of practical use in fisheries management. To determine this, we first examine the sensitivity of parameter estimates in the heteroscedastic relationship to the size of the data set used to generate these estimates. We then use simple population models to calculate maximum sustainable yields to determine whether the use of a heteroscedastic model in place of a more conventional model (the well known Beverton-Holt model is used here) has any effect on management limits. We use data from two example stocks, North Sea cod (*Gadus morhua*) and North Sea herring (*Clupea harengus*). These stocks were chosen because the time series available display a large range of spawning stock size values, and both have been overfished to very low levels.

4.3 Model fitting

To establish whether the heteroscedastic model (4.1) could be useful in single stock management, we first determine whether parameters can be accurately estimated for realistic sizes of data sets.

We first fit the heteroscedastic model to stock and recruitment data for North Sea cod and North Sea herring, to find what we will henceforth refer to as the "true" parameter values for our two example stocks. These "true" parameter values are given at the top of Table C.1 (Appendix C). The original data are from the ICES Working Group 2007. We use maximum likelihood methods for the model fitting. The log-likelihood function for the heteroscedastic model is

$$\ell_M(\alpha, \beta, \eta_0, \eta_1) = -\frac{n}{2}\ln(2\pi) - \frac{1}{2}\sum_{i=1}^{n}(\eta_0 + \eta_1 S) - \sum_{i=1}^{n} \frac{ln\left(\frac{R_i}{S_i}\right) - f\left(\frac{R_i}{S_i}\right)}{\exp(\eta_0 + \eta_1 S)},$$

where R_i are the recruitment data points, S_i are the spawning stock biomass (SSB) data points, and

$$f\left(\frac{R_i}{S_i}\right) = \ln(\alpha) - \ln(1 + \beta S_i).$$

We have chosen γ =-1 for our analyses here (representing an underlying Beverton-Holt stock recruitment relationship); however, the results hold qualitatively for other values of γ. Parameters were estimated using the `optim` function in R (R Development Core Team, 2007). Both spawning stock biomass (SSB) and recruitment are scaled by their maximum values, as in Minto et al. (2008). The maximum values for the ICES Working Group 2007 data were 252747 tonnes (SSB) and 2.567×10^9 recruits for North Sea cod, and 2183501 tonnes (SSB) and 1.09×10^8 recruits for North Sea herring.

Next, we use the spawning stock data from the ICES Working Group 2007, the heteroscedastic model (4.1), and the true parameter values, to simulate new recruitment data for each species. We then re-fit the heteroscedastic model to the new simulated data, to obtain parameter estimates $\hat{\alpha}$, $\hat{\beta}$, $\hat{\eta_0}$, and $\hat{\eta_1}$ (which are estimates of our true parameter values, since we used these to generate the data). The size of the data set is increased by replicating the spawning stock data then generating recruitment data from the new, larger stock data set (this does not result in replicates of recruits data because the heteroscedastic model used to simulate the data is stochastic). The minimal data set size used is that of the data themselves (43 and 47 data points for cod and herring, respectively); these are compared to estimates from data sets with sizes increased by one, two and three orders of magnitude. The process of generating recruitment data and fitting the heteroscedastic model to obtain parameter estimates is repeated 10 times for each size of data set.

Figure 4.1 shows the η_1 parameter estimates for North Sea cod and herring, for four different size data sets. Parameter estimates for all dataset sizes are given in Appendix C. It is clear from Figure 4.1 that for data sets smaller than *c.*4000 observations in magnitude, it is not possible to accurately recover the "true" η_1 parameter value used to generate the data. What is particularly important is that for the currently available number of data (usually around 40 to 50 years of data, with each year corresponding to one data point) it may not be possible to recover the sign of the heteroscedastic coefficient η_1. This possibility is demonstrated in Figure 4.1a); the "true" η_1 values is positive, however not all the estimates for it are positive. The parameter estimates for the remaining parameters, $\hat{\alpha}$, $\hat{\beta}$, and $\hat{\eta_0}$ also display large variability for small data sets (see additional figures and tables in Appendix C).

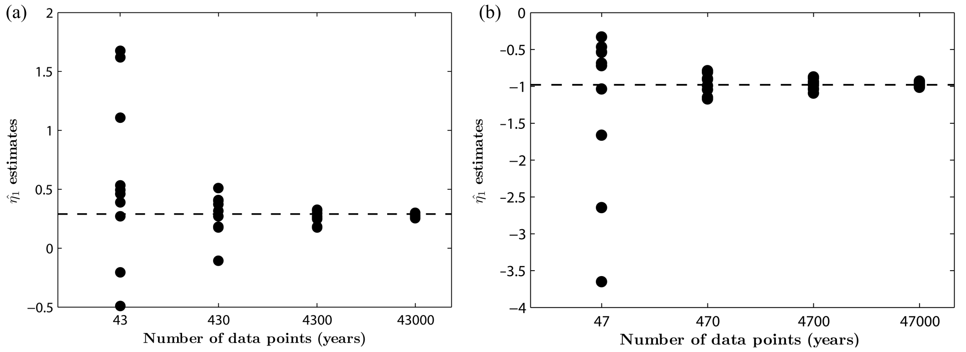

Figure 4.1: η_1 *parameter estimates (dots) for a) North Sea cod, and b) North Sea herring. Parameters were estimated using the* `optim` *function in R (R Development Core Team, 2007). The "true" values of* η_1 *are shown by the dashed lines.*

4.4 Consequences for management

When asking whether the heteroscedastic model is useful in fisheries management, the consequences of the parameter estimate variability shown in Figure 4.1 must be taken into account. Figure 4.2 shows the expected stock recruitment curves for the North Sea cod and herring stocks, using the "true" parameter values found in the previous section (a Beverton-Holt model was also fitted to the North Sea cod and herring data to give "true" parameter values for this model). The dashed lines represent the expected recruitment from a fitted Beverton-Holt stock recruitment model[1], and the solid lines are the expected recruitment from the heteroscedastic model (4.1). The derivation of the expected recruitment for both models is given in Appendix B.

In the case of North Sea cod, the inclusion of heteroscedasticity in the stock-recruitment model leads to a depensatory expected stock-recruitment curve, in comparison to the compensatory Beverton-Holt model. In the case of North Sea herring, the inclusion of heteroscedasticity leads to a slightly over-compensatory expected stock-recruitment curve (this is difficult to see in the figure; however, the maximum

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[1] Note the expected recruitment is not simply the Beverton-Holt model, as we assume log-normally distributed noise. See Appendix B for the derivation of the expected recruitment plotted here.

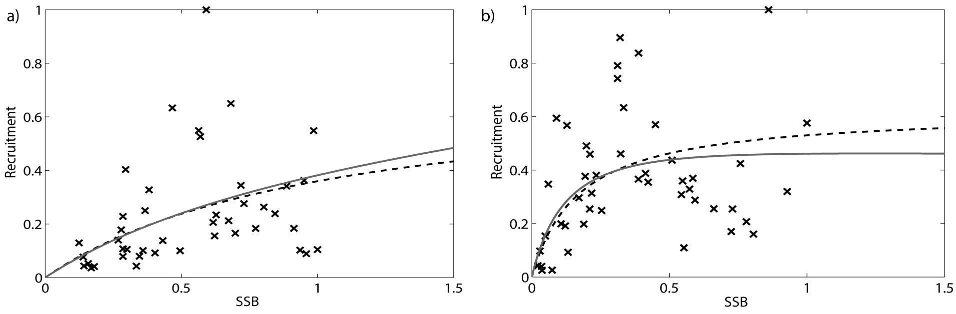

Figure 4.2: *Stock recruitment curves for a) North Sea cod, and b) North Sea herring. The dashed lines are the expected recruitment for a Beverton-Holt stock-recruitment model (assuming log-normal noise), the solid lines the expected recruitment from the heteroscedastic model (4.1). See Appendix B for the derivation of the expected recruitments plotted here. Crosses are the data from the ICES Working Group 2007.*

recruitment does occur at around S = 1.25). For North Sea cod, the heteroscedastic model predicts higher expected recruitment than the Beverton-Holt model at high stock levels. For North Sea herring, the Beverton-Holt model predicts higher expected recruitment than the heteroscedastic model at high stock levels. For both stocks, both models predict similar recruitment at low stock levels.

To allow comparison with the heteroscedastic model, we also fit a standard Beverton-Holt model to the simulated data (the Beverton-Holt model is fitted to the same simulated data as the heteroscedastic model, that is, the underlying data is heteroscedastic, however the fitted Beverton-Holt model assumes constant variance). The purpose of this is to establish whether there is any practical difference between fitting a heteroscedastic model or a constant-variance model, when the underlying data are heteroscedastic. The parameter estimates for the Beverton-Holt model are tabulated in Appendix C.

Using the parameter estimates in Tables C.1 and C.2 (see Appendix C) and simple population management models, we can calculate the maximum sustainable yield (MSY) (Begon et al., 1996) for each model. The simple population model for a

Beverton-Holt model takes the form

$$S_{t+1} = S_t + \frac{\alpha S_t}{1+\beta S_t} \exp\left(\frac{\sigma^2}{2}\right) - \mu S_t - H, \tag{4.2}$$

where S_t is the spawning stock size in year t, μ is the natural mortality rate (assumed to be 0.3 for all results), and H is the fixed MSY harvested from the stock each year. This management model assumes that the expected recruitment each year is simply that derived from an underlying Beverton-Holt recruitment function, and does not account for heteroscedasticity. This model gives a MSY of

$$H_{MSY} = \frac{\tilde{\alpha} + \mu - 2\sqrt{\tilde{\alpha}\mu}}{\beta},$$

where $\tilde{\alpha} = \alpha \exp\left(\frac{\sigma^2}{2}\right)$. The calculated MSY values for each parameter set are given in Table C.6 (Appendix C).

We now compare the above MSY values with those for a heteroscedastic management population model of the form

$$S_{t+1} = S_t + \frac{\alpha S_t}{1+\beta S_t} \exp\left(\frac{\exp(\eta_0 + \eta_1 S_t)}{2}\right) - \mu S_t - H. \tag{4.3}$$

We cannot find an analytical closed form expression for the MSY from this model. In fact, due to the nature of this model, a MSY does not always exist. If we assume equilibrium ($S_{t+1} = S_t = S$), then

$$H(S) = \frac{\alpha S}{1+\beta S} \exp\left(\frac{\exp(\eta_0 + \eta_1 S)}{2}\right) - \mu S. \tag{4.4}$$

For $\eta_1 < 0$ a MSY can be found in the standard way. However, for $\eta_1 > 0$, $H(S)$ (4.4) will tend to infinity for large values of S. Under the usual method for finding a MSY (finding the maximum value of H for which $S > 0$), this would suggest the MSY is infinitely large, which is clearly wrong.

For certain sets of parameter values we can find a local maximum H_{MSY} before the function tends to infinity (Figure 4.3a). However, for other sets of parameter values, this local maximum does not exist and we cannot calculate a MSY (Figure

4.3b). This indicates that the management model (4.3) is only valid for cases where $\hat{\eta_1} < 0$.

For the case of North Sea herring, we can see (Table C.6, Appendix C) that the calculated MSY values do not differ greatly between the Beverton-Holt and heteroscedastic models. This indicates that there may be no management benefit to using the hetereoscedastic model over a more conventional stock recruitment model.

For North Sea cod, we are only able to calculate MSY values for three out of the ten parameter sets (plus the "true" parameter set) for the heteroscedastic model. In all these cases, the MSY value for the heteroscedastic model is greater than that for the Beverton-Holt model. This may be cause for concern if the correct MSY value for the stock is lower (in fact the "true" MSY value is the lowest of the values we were able to calculate).

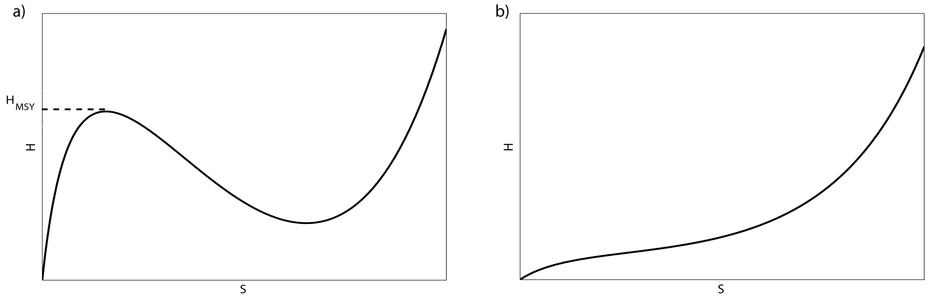

Figure 4.3: *Schematic representations of the two different forms the function $H(S)$ (equation 4.4) can take for the heteroscedastic population management model, when $\eta_1 > 0$. In case a) a local maximum can be found and defined as the MSY. In case b), no local maximum can be found, and consequently no MSY can be defined.*

4.5 Discussion

In the continuing search for regulatory processes in fish populations, Shepherd and Cushing (1990) and Minto et al. (2008) advocate a stochastic regulatory mechanism;

that fish recruitment is heteroscedastic, with recruitment variability increasing with decreasing stock size. By investigating whether a heteroscedastic stock-recruitment model could be used in single stock management, we argue that the available stock-recruit time series for individual populations are not long enough to accurately estimate parameter values for the heteroscedastic model (4.1).

Minto et al. (2008) find a consistent trend in negative η_1 values (the coefficient of heteroscedasticity), which supports an inverse relationship between recruitment variability and stock size, and an inverse relationship between survival variability and the strength of density dependence. A binomial test on Minto *et al.*'s single species fits supports this relationship as a general principle. However, if it is not possible to recover the true value or sign of η_1 for a single stock, as we have demonstrated, it may be inappropriate or even dangerous to use the heteroscedastic model of Minto et al. (2008) in a management setting.

Minto et al. (2008) attempt to overcome the problem of short time series by combining data (by species) from different populations using a meta analysis to increase the power of their statistical analysis. However, this implicitly assumes that all stocks of a particular species will have the same heteroscedastic coefficient. It may not be reasonable to assume that two stocks from very different parts of the world will experience the same environmental conditions and regulatory processes. Consequently, using a meta-analytic approach to fitting this, or any other, stock recruitment model may not be appropriate for use in single stock management and quota setting.

Our MSY results are intended as strategic illustrations of the fact that that these details can be important; they are not specific recommendations for the harvesting of particular stocks. We demonstrate that the heteroscedastic model with $\eta_1 > 0$ can produce indefinitely (and therefore unrealistically) high MSYs (Figure 4.3). We have found no evidence of biological models to suggest how this might occur, and the extreme properties are exhibited well outside the range of current observations. We would suggest that model fits with an estimated $\eta_1 > 0$ are discounted in a management context at least until such mechanisms are better supported. Even in the cases where an MSY can be defined for the heteroscedastic management model, the estimated MSY values were higher than those for the simple management model, which is also cause for concern. The stock recruitment plots in Figure 4.2 show the two models converging at the origin, which implies that heteroscedasticity does not mean stocks can be fished at a higher rate (the slope at the origin is closely related to the maximum harvest rate before extinction). In contrast, for the case where $\eta_1 < 0$ (the example of North Sea herring is presented here) there is little, if any, difference between the MSYs calculated using a fitted heteroscedastic model and a fitted Beverton-Holt model. This indicates, that even if the underlying recruitment process is heteroscedastic, there may be little benefit in fitting the more complicated model.

The work of Minto et al. (2008) is statistically sound, interesting, and potentially important ecologically. It is especially valuable in elucidating the importance of factors which, by their very nature, are random: any rational management strategy must take such factors into account if it is to be sustainable. However, such models may not yet be of practical use to fisheries managers. We propose that developing and studying mechanistic models of the recruitment process can build a broader understanding of the factors causing and controlling recruitment variability. Such models, which may include elements of the widely advocated ecosystem approach (Jennings and Rice, 2011), may provide us with evidence of the mechanisms causing high variability at low stock sizes, thereby leading to more reliable ways of incorporating stochasticity into fisheries management.

Chapter 5

Phytoplankton blooms, zooplankton patchiness, and fish recruitment

Plankton populations display heterogeneity in both space and time. Fish larvae are dependent primarily on zooplankton for their source of food, and the availability of food has a considerable effect on larval growth and survival. Consequently variability in the plankton is widely believed to contribute to the large fluctuations observed in fish larval recruitment.

Here, the roles of temporal heterogeneity, caused by temporal variation in their phytoplankton food, and spatial heterogeneity, in the form of patchiness, in zooplankton abundances in determining recruitment variability are explored. A simple stochastic larval growth model is coupled to an excitable media model of phytoplankton and zooplankton densities. Phytoplankton blooms are forced, causing a peak in zooplankton abundances to follow. Within the model, larval growth rates are dependent on the mean and variance of encounter rates with zooplankton prey, which in turn are dependent on the spatial structure of the prey field. Two models of zooplankton patchiness are introduced. In the first, patches of prey, and prey within those patches, are encountered as a Poisson process. In the second, individual prey items are assumed to be distributed according to a negative-binomial distribution.

We demonstrate that increased patchiness decreases recruitment probabilities, and that patchiness has a greater effect on recruitment after the peak in zooplankton abundance. We also find evidence that increased spawning stock size can decrease recruitment variability for some hatching days, but increase it for others. For higher larval densities predation by the larvae had a considerable effect on the zooplankton dynamics, and subsequently on the phytoplankton dynamics. This verifies that the feedback between the trophic layers can play an important role in determining recruitment. We conclude that spatial heterogeneity in the prey field is as important as temporal heterogeneity in determining recruitment variability.

5.1 Introduction

Variability in food availability is widely believed to have a considerable effect on both the growth and survival of larval fish (van der Meeren and Naess, 1993). Variation in these vital rates is implicated in large fluctuations in recruitment and year-class strength (Houde, 1997). Fish larvae rely primarily on zooplankton, such as copepods and copepod nauplii, for their source of food. Both the abundance and spatial structure of plankton populations are affected by environmental and atmospheric conditions, such as stratification and turbulence, which creates an unpredictable prey field for fish larvae (van der Meeren and Naess, 1993).

Zooplankton are dependent on phytoplankton for their source of food. Large fluctuations in the timing and intensity of phytoplankton blooms have been noted in both the Atlantic and Pacific oceans (Platt et al., 2007). Henson et al. (2009) observed that the timing of the onset of phytoplankton blooms can vary by 15 to 50 days in the North Atlantic, with the largest variability seen in the transition zone between the subpolar and subtropical regions. The timing of onset of the spring phytoplankton bloom in the North Sea can vary interannually by up to six weeks (Cushing and Horwood, 1994). This variability in phytoplankton dynamics will cause variability in zooplankton dynamics, but how variability at one trophic level relates to fluctuations in higher levels is not well understood (Runge, 1988; Runge et al., 2010). Prey availability may be a necessary condition for determining larval growth and survival, but recruitment is the result of a combination of complex processes which may enhance or counteract the links between primary production and larval survival (Runge et al., 2010).

As well as displaying temporal heterogeneity, zooplankton populations are also unevenly distributed in space (Letcher and Rice, 1997). They are known to exhibit patchiness over a range of spatial scales, from less than 10m up to tens of km (Currie et al., 1998; Pitchford and Brindley, 2001; Tokarev et al., 1998). This patchiness will affect the encounter rates been fish larvae and their prey, which in turn will have an effect on their individual growth rates (Letcher and Rice, 1997), and thus on their survival and recruitment. Zooplankton patchiness is the result of many physical processes interacting with many biological processes (Pinel-Alloul, 1995), thus making it challenging to understand and predict.

The spatial distribution of zooplankton is often modelled using a Poisson distribution (Lough and Broughton, 2007; Young et al., 2009), as other patchier distributions are often more difficult to specify and work with mathematically (Rothschild, 1991). However recent studies have shown the distribution of zooplankton is more aggregated than predicted by a Poisson distribution, and a more overdispersed negative-binomial distribution is more appropriate for modelling (Lough and Broughton, 2007; Young et al., 2009).

In this chapter we explore the role of temporal variability in phytoplankton densities, and spatial heterogeneity of zooplankton populations, on the recruitment of fish larvae. We employ two simple stochastic models for fish larval growth, which are coupled to an excitable media model of phytoplankton-zooplankton dynamics. The role of patchiness in zooplankton densities is first explored using the Poisson patch encounter model of Pitchford and Brindley (2001), and secondly by developing a larval growth model when the prey field is overdispersed, using a negative-binomial distribution for encounters between fish larvae and their prey. We examine the effect of variability in the timing of phytoplankton blooms by making the time of initiation of the bloom a random variable.

Alongside this, we look for evidence of heterscedasticity (non-constant variance, see Chapter 4) in fish larval recruitment by varying the initial density of larvae in the system (this is used as a proxy for spawning stock size).

5.2 Methods

5.2.1 Two models for fish larval growth in a patchy environment

Model 1

The first model we use for fish larval growth is the simple stochastic differential equation of Pitchford et al. (2005), adapted to allow the inclusion of contact rates with prey in different (homogeneous or patchy) environments. For an individual larva of mass $M(t)$ at time t,

$$dM(t) = \min(r(Z,M)dt + \sigma(Z,M)dB(t), r_L M(t)dt) \quad M(0) = M_0 \tag{5.1}$$

where the deterministic instantaneous growth rate, $r(Z,M)$, and the variance of the white noise process, $\sigma^2(Z,M)$ are calculated from the contact rate model of Pitchford and Brindley (2001). The model represents a larva foraging in a patchy prey environment, where patches, and prey within patches, are encountered according to a Poisson process. The maximal growth rate of an individual larva is represented by r_L.

Let us define V to be the fraction of the whole volume taken up by prey patches. We assume that prey only occur in patches, so that $(1 - V)$ is the proportion of the volume devoid of prey (Pitchford and Brindley, 2001). An individual fish larva will encounter a prey patch as a Poisson process with rate α. Once inside a patch, the larva will encounter individual prey items as a Poisson process with rate γ. If we denote X to be the number of prey consumed by a larva in one day, it can be shown (Pitchford and Brindley, 2001) that

$$\begin{aligned} E(X) &= T_D \frac{\gamma V}{1 + \gamma V \tau}, \\ Var(X) &\approx \gamma T_D V \left(1 + \frac{2\gamma(1 - V)}{(\alpha + \beta)} \right), \end{aligned}$$

where T_D is the proportion of a day a larva spends foraging, τ is the handling time of a predation event (this is set to zero to derive an approximation for the variance of the encounter rate (Pitchford and Brindley, 2001)), and β is the rate parameter of the Poisson process governing a larva within a patch leaving that patch. It is worth noting that the expected number of prey consumed in one day is independent of the parameters α and β; patchiness only plays a role through the parameter V. We can then define

$$r(Z, M) = \beta(M)E(X) - AM^B,$$

$$\sigma(Z, M) = \beta(M)(Var(X))^{1/2},$$

where $\beta(M) = \beta_{max} - (\beta_{max} - \beta_{min})e^{-jM}$ is a function representing how efficiently prey is converted to larval biomass (Pitchford and Brindley, 2001), and the term AM^B represents the metabolic costs of foraging.

We use the turbulent contact rate model of Rothschild and Osborn (1988) to determine the values of parameters α and γ. Fish larvae are small relative to the spatial scales of turbulence affecting plankton patchiness, and contact rates between larvae and their prey are thus in part determined by turbulence. From (Rothschild and Osborn, 1988) and (Pitchford and Brindley, 2001), we can define

$$\gamma = Z\pi R^2 \frac{u^2 + 3v^2 + 4w_R^2}{3(v^2 + w_R^2)^{1/2}},$$

where u and v are the swimming speeds of a prey organism and a fish larva respectively, and Z is the number of prey organisms per unit volume. w_R is the root-mean-square turbulent velocity on the R length scale, where R is the fish larva's perceptive distance. We assume that an encounter occurs when the distance between a larva and a prey organism falls below R (Pitchford and Brindley, 2001). As in Pitchford and Brindley (2001), we will assume that the zooplankton prey are non-motile, that is $u = 0$.

Similarly, if we regard prey patches as spheres of radius L (henceforth referred to as the patch length scale), we can also define

$$\alpha = d\pi L^2 \frac{3v^2 + 4w_L^2}{3(v^2 + w_L^2)^{1/2}},$$

where d is the number of patches per unit volume, and we assume that patches are non-motile. The turbulent velocities follow the simple expression

$$w_a = 1.9(\epsilon a)^{1/3}$$

for the relevant length scales $a = R$ and $a = L$ (Pitchford and Brindley, 2001), and where ϵ is the turbulent kinetic energy dissipation rate (Rothschild and Osborn, 1988). We note that the value given for ϵ in Table 5.1 is not the value used by Rothschild and Osborn (1988) and Pitchford and Brindley (2001). These studies used the value given in the abstract of MacKenzie and Kiorboe (1995) ($\epsilon = 7.4 \times 10^{-8}$ m^{2}s^{-3}), which is incorrect and does not match the values given for depth and wind velocity in their methods, and the formula given by MacKenzie and Leggett (1993). The corrected value[1] for ϵ, calculated from the formula of MacKenzie and Leggett (1993) and using values of 20m for depth and 6 ms^{-1} for wind speed, is 6.29×10^{-5} m^{2}s^{-3}.

As in previous chapters, we define a fixed recruitment mass M_{rec} at which the individual larva is considered to be recruited to its next life history stage. Mortality

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[1] Thank you to Dr Mark Preston for pointing out the incorrect parameter value.

is modelled as a time (age) dependent process, with the number $N(t)$ of larvae alive at time t being given by (James et al., 2003)

$$N(t) = N_0(1 + bt)^{-\mu_L/b}. \tag{5.2}$$

Figure 5.1 displays the dependence of recruitment on the average density of prey in the environment, and on the degree of patchiness. Recruitment is shown as a function of food supply for the deterministic growth case ($\sigma = 0$), and for stochastic growth in a homogeneous prey field, and in patchy prey fields with prey distributed according to a Poisson process, in patches of length scales 10m, 20m, and 30m. Parameter values used are given in Table 5.1. Each recruitment probability was calculated from simulations of 10,000 individuals, growing according to an Euler-Maruyama scheme of equation (5.1), with a time step of 0.05 days. Food supply (zooplankton density) was held constant for each simulation.

Model 2

As discussed in Section 5.1, it has been found that the spatial distribution of zooplankton is better represented by a negative-binomial distribution than a Poisson distribution (Lough and Broughton, 2007; Young et al., 2009). Our first model of larval growth assumed the patches of zooplankton followed a Poisson distribution, and that individual plankton within patches were distributed according to a Poisson process. We now wish to develop a model assuming a negative-binomial distribution of individual zooplankton, to assess what consequences this might have for the recruitment of fish larvae.

If we assume that individual zooplankton are distributed according to a negative-binomial distribution, then the number of prey encountered by a fish larva in a unit of time ($X(t)$), will be a negative-binomial random variable. The probability mass function for a negative-binomial distribution with parameters r and p is often written in the form (Johnson et al., 1992),

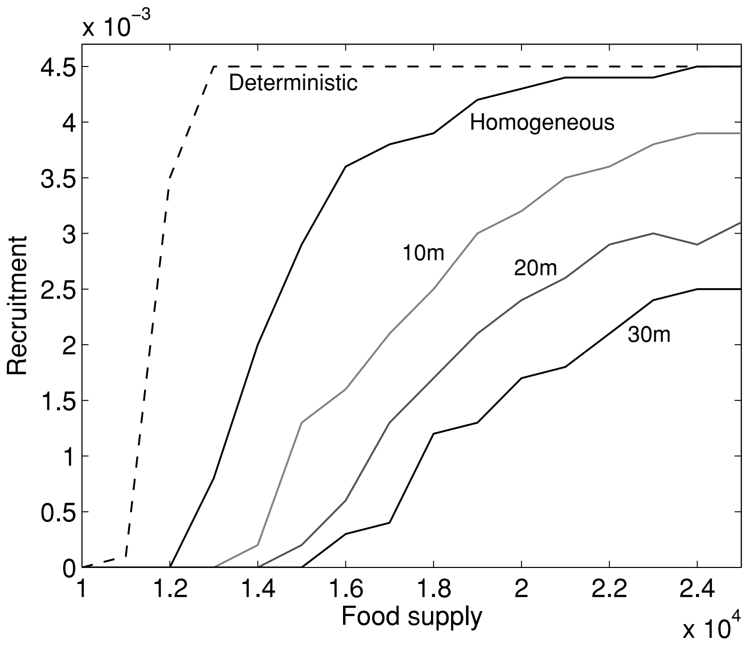

Figure 5.1: *Recruitment against food supply, for the deterministic growth case, and for stochastic growth in a homogeneous prey field, and in patchy prey fields with patches distributed according to a Poisson process, and prey distributed within patches according to a Poisson process, in patches of length scales 10m, 20m, and 30m. Each recruitment probability was calculated from simulations of 10,000 individuals, growing according to an Euler-Maruyama scheme of equation (5.1). Food supply (mean field zooplankton density) was held constant for each simulation.*

$$P(X = x) = \binom{r + x - 1}{r - 1} \left(\frac{p}{1+p}\right)^x \left(\frac{1}{1+p}\right)^r .$$

However, for this application we adopt a more suitable parameterisation, that is (Bolker, 2007),

$$P(X = x|\theta, k) = \frac{\Gamma(k + x)}{\Gamma(k)x!} \left(\frac{k}{k+\theta}\right)^k \left(\frac{\theta}{k+\theta}\right)^x ,$$

where $\theta = E(X)$ and k is defined as the “overdispersion” parameter. A smaller k implies a patchier distribution. It is worth noting that here $Var(X) = \theta + \theta^2/k$, that is the variance is always greater than the mean of the distribution. This is in contrast to the Poisson distribution, which has equal mean and variance.

The fish larval growth model now takes the form,

$$M(t + dt) = M(t) + \min(\beta(M(t))\xi(t) - AM^B, r_L M(t)dt) \quad M(0) = M_0, \qquad (5.3)$$

where, as in Model 1, $\beta(M(t))$ is a function representing how efficiently prey is converted to larval biomass (Pitchford and Brindley, 2001), the term AM^B represents the metabolic costs of foraging, and $\xi(t)$ is a negative-binomial random variable with mean $\theta = T_D \frac{\gamma}{1+\gamma\tau}$ (with γ and T_D as in Model 1), and variance $\theta + \theta^2/k$. Mortality again follows equation (5.2), and recruitment is defined as growth to a fixed size M_{rec}.

Figure 5.2 displays the dependence of recruitment on the average density of prey in the environment, and on the degree of overdispersion. Recruitment is shown as a function of food supply for growth in a near-Poisson prey field (k=100), and in prey fields with increasing degrees of overdispersion (k=10 and k=5). Parameter values used are given in Table 5.1. Each recruitment probability was calculated from simulations of 10,000 individuals, growing according to a fixed time step scheme of equation (5.3), with a time step of 0.05 days. Food supply (mean field zooplankton density) was held constant for each simulation.

5.2.2 Model equivalence

Models 1 and 2 are close to equivalent for certain choices of parameter values. We have already defined the expected encounter rate within each model to be equal, and thus we would see very similar growth trajectories if the variance of the encounter rates were also close to equal.

The variance of the encounter rate of Model 2 (negative binomial prey field) is $\theta + \theta^2/k$, where θ is the expected encounter rate and k is the overdispersion parameter. Let us denote the encounter rate variance of Model 1 by Ψ. For equal variance we therefore require $\Psi = \theta + \theta^2/k$.

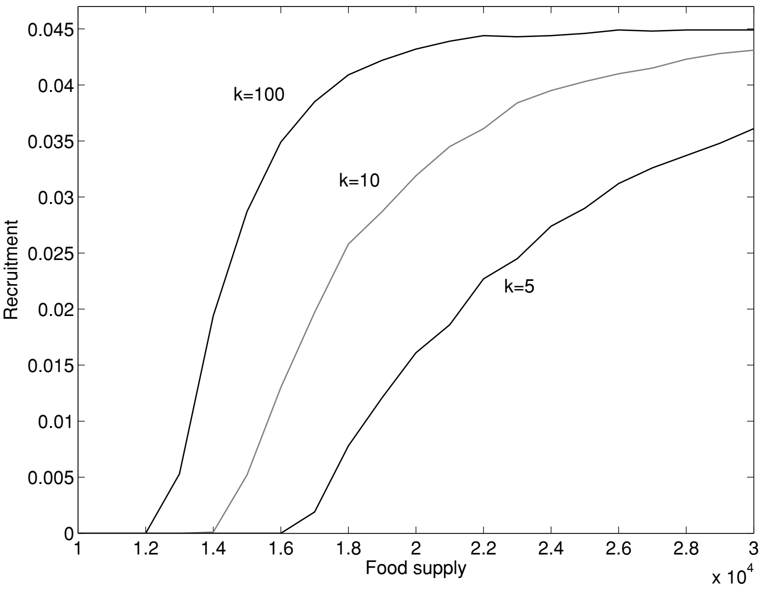

Figure 5.2: *Recruitment against food supply, for growth in a prey field of negative-binomially distributed zooplankton, for a near-Poisson prey field (k=100), and in prey fields with increasing degrees of overdispersion (k=10 and k=5). Parameter values used are given in Table 5.1. Each recruitment probability was calculated from simulations of 10,000 individuals, growing according to a fixed time step scheme of equation (5.3). Food supply (mean field zooplankton density) was held constant for each simulation.*

For a homogeneous prey field in Model 1, $V = 1$, and consequently the mean and the variance of the encounter rate are equal. This implies that $\theta = \theta + \theta^2/k$, which is true as $k \to \infty$. Therefore, for large values of k, $k = 100$ for example, the recruitment results for Model 2 will be very similar to those for Model 1 with $V = 1$. In fact, for $k > 10$ it is difficult to tell the negative-binomial distribution apart from a Poisson distribution (Bolker, 2007).

For $V < 1$ in Model 1, the variance of the encounter rate has a more complicated formulation; however, we can still expect the results to look similar for the two

Models for certain values of k. In fact, for $V < 1$, the prey field in Model 1 is also overdispersed, since patchiness increases the variance of the encounter rate so that it is greater than the mean.

5.2.3 A coupled phytoplankton-zooplankton model

To model primary and secondary production we adopt the excitable media model of Truscott and Brindley (1994). The model takes the form

$$\begin{aligned} \frac{dP}{dt} &= r_p P\left(1-\frac{P}{P_{max}}\right) - r_z Z\frac{P^2}{P^{*2}+P^2}, \\ \frac{dZ}{dt} &= \delta_z r_z Z\frac{P^2}{P^{*2}+P^2} - \mu_z Z - R_{total}, \end{aligned} \tag{5.4}$$

where P and Z represent the densities of phytoplankton and zooplankton respectively. r_p is the maximum growth rate and P_{max} the carrying capacity of the phytoplankton population, r_z is the maximum specific predation rate of zooplankton on phytoplankton, P^* governs how quickly this maximum is attained as the prey (phytoplankton) density increases, and δ_z is the ratio of biomass consumed to biomass of new zooplankton produced (Truscott and Brindley, 1994). The removal of zooplankton by predation by fish larvae is represented by R_{total}. Units and parameter values used in the simulations presented in this chapter are given in Table 5.1.

The Truscott and Brindley model (5.4) was designed to investigate the triggering of red tides and spring blooms in plankton systems. An excitable media model was used as Truscott and Brindley (1994) deemed that the irreducible characteristics of red tide events (the existence of two stable population levels of phytoplankton, rapid outbreaks followed by slow relaxation, the existence of a trigger mechanism, and a cyclic nature) matched the main properties of excitable media (Murray, 1993). The trigger mechanism explored by Truscott and Brindley (1994) came from the interaction of the growth rate of phytoplankton and the grazing rate of the zooplankton. A Holling Type-III predation function was chosen since it allows the triggering of blooms, and is justifiable since zooplankton (in particular copepods) are known to exhibit the foraging behaviour associated with the Holling Type-III grazing function. A Holling Type-II function was discarded as the lower stable equilibrium value for the phytoplankton population is at $P = 0$ (Truscott and Brindley, 1994). In fact, any bloom triggered in a Holling Type-II model would result in the extinction of the phytoplankton population at the end of the bloom. Figure 5.3 shows example trajectories for the phytoplankton-zooplankton system. The parameter values used are given in Table 5.1. A phytoplankton bloom is forced by increasing the growth rate r_p from a starting value of 0.3 d^{-1} to a value of 0.5 d^{-1}, at a rate of 0.005 $d^{-1}d^{-1}$, on Day 20.

Note that equation (5.4) is a model for the mean field density of phytoplankton and zooplankton. The spatial structure of the zooplankton population is accounted for only within the larval growth models.

The larval growth and plankton models are linked via predation on the zooplankton population by the fish larvae. As described in the previous subsection, the mean and variance of the encounter rates of fish larvae with their zooplankton prey are dependent on $Z(t)$, the density of zooplankton at time t. For Model 1, the number of zooplankton removed by predation (R_{total}) in a unit time is given by

$$R_{total} = \sum_{i=1}^{N} E(X(t))_i + (Var(X(t))_i)^{1/2}\xi_i(t),$$

where $E(X)_i$ and $Var(X)_i$ are the mean and variance of the encounter rate, defined in Section 5.2.1, for larva i (out of N) and the ξ_is are the values picked from the standard random normal distribution at that point in the simulation.

For Model 2,

$$R_{total} = \sum_{i=1}^{N} \eta_i(t),$$

where the η_i are the values picked from a negative binomial distribution with parameters θ and k, defined in Section 5.2.1.

We wish to evaluate the effect of variable phytoplankton abundances travelling up through the trophic levels to determine fish larval recruitment, and how this effect varies depending on when the larvae hatch in reference to the phytoplankton bloom (the match/mismatch hypothesis (Cushing, 1975); see Chapter 4 and (Burrow et al., 2011)). We force a phytoplankton bloom by increasing the growth rate r_p from a starting value of 0.3 d^{-1} to a value of 0.5 d^{-1}, at a rate of 0.005 $d^{-1}d^{-1}$, on Day 20 of a 250 day period. A batch of larvae then hatches on one specific hatch day from Day 0 to Day 250, and their recruitment success is calculated by counting what fraction of the initial number of larvae reach recruitment mass M_{rec} before dying.

As discussed in the introduction to this chapter, the onset of a phytoplankton bloom can vary interannually by as much as six weeks. To investigate what effect this variability in bloom timing can have on the variability of fish larval recruitment, and

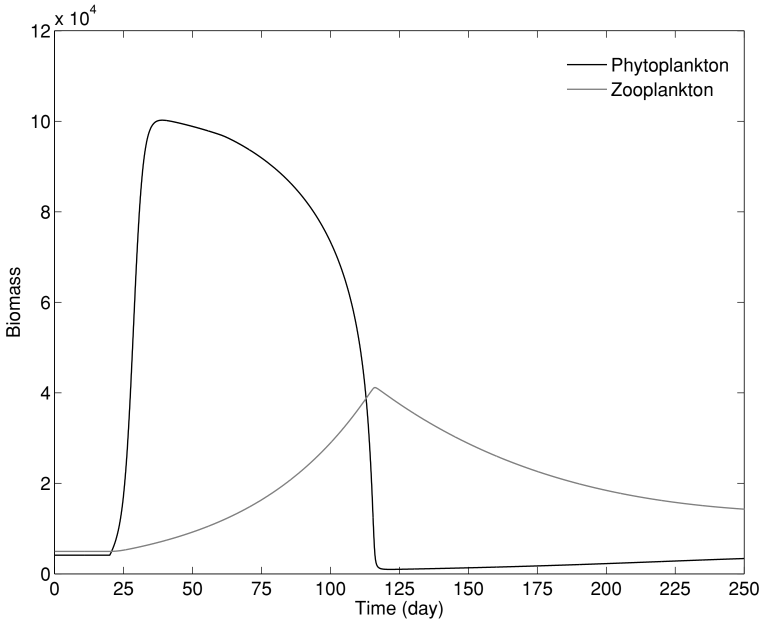

Figure 5.3: *An example of a phytoplankton bloom in the P-Z model, in the absence of fish larvae. A bloom was triggered by increasing the phytoplankton growth rate* r_p *from a starting value of 0.3* d^{-1} *to a value of 0.5* d^{-1}*, at a rate of 0.005* d^{-1}*, on Day 20.*

how this depends on when the larvae hatch, the forcing of the phytoplankton bloom is made stochastic. We introduce a second independent variable, a "force day", which is picked from a normal distribution with mean 40 and variance 10, and the phytoplankton growth rate r_p is increased as described in the previous paragraph. This gives a realistic range of around 60-70 days on which the onset of the phytoplankton bloom will occur. The value of the force day is constrained to be greater than zero (if a force day < 0 is picked, that force day is set to be Day 0).

For each hatching day (every tenth day over a 250 day period), 1000 random samples of the force day are generated. For each force day, the growth trajectories of 1000 larvae were simulated using an Euler-Maruyama scheme, or a fixed time step scheme (for growth Models 1 and 2 respectively), and the recruitment probabilities calculated as described above. This is effectively generating recruitment data over a 1000 year period (assuming statistically stationary conditions) with the annual plankton bloom occurring on a random day each year, within a constrained spawning window.

5.3 Results

5.3.1 The role of timing of hatching

Figure 5.4 shows results for fish larvae growing according to Model 1, in a homogeneous prey field (V=1), and patchy prey fields with patch length scale of 10m and 20m, for different initial larval densities. Figure 5.6 shows the results for fish larvae growing according to Model 2, for three different values of the overdispersion parameter k. A phytoplankton bloom was forced on Day 20 in all cases. Results were calculated by simulating 1000 individual larvae growing and predating on a zooplankton population, which in turn feed on a phytoplankton population. Examples of the phytoplankton-zooplankton dynamics underlying Figures 5.4 and 5.6 are shown in Figures 5.5 and 5.7, for a homogeneous prey field, with larvae hatching on Days 50, 100 and 150, with initial larval densities of 1 larva m^{-1}, 10 larvae m^{-1}, and 50 larvae

m^{-1}.

Figures 5.4 and 5.6 indicate that there is an optimum hatching window during which recruitment is greater than zero. As anticipated from examination of Figure 5.1, recruitment numbers in patchy environments are always lower than in a homogeneous environment. Patchiness in the prey field has a more negative effect for larval hatching after the peak in prey availability.

The results also demonstrate that the initial larval density can have an effect on recruitment. For both models we see a decline in the length of the optimal hatching window as initial larval density increases. This is consistent with the results shown in Fig. 6 of James et al. (2003).

5.3.2 Variability in bloom timing

Figures 5.8 and 5.9 shows the recruitment probabilities for stochastic onset of plankton blooms, with the day of initiation of bloom forcing being drawn from a normal distribution with mean 40 and variance 10. Each box plot represents 1000 instances of the stochastic force day, with recruitment probabilities averaged over 1000 larvae growing according to Model 1 (5.1) for each instance. The black dots mark the mean recruitment probability for each hatching day. Figures 5.8a) and 5.9a) are for larvae growing in a homogeneous prey environment, with initial larval densities of $N_0 = 1$ and $N_0 = 50$ respectively. Figures 5.8b) and 5.9b) are for larvae growing in a patchy prey environment with a patch length scale of 20m, with initial larval densities of $N_0 = 1$ and $N_0 = 50$ respectively.

For larvae growing in a homogeneous environment, with an initial density of 1 larva m^{-3}, the highest mean recruitment is achieved by those hatching on Days 130-150. For larvae growing in a patchy environment with patch length scale 20m, the highest mean recruitment is achieved by those hatching in Day 130, with the mean recruitment being lower for the hatch days on either side. If a phytoplankton bloom is forced on the expected force day (i.e. Day 40), the corresponding peak in zooplankton density occurs around Day 130. A patchy environment seems to not only decrease the

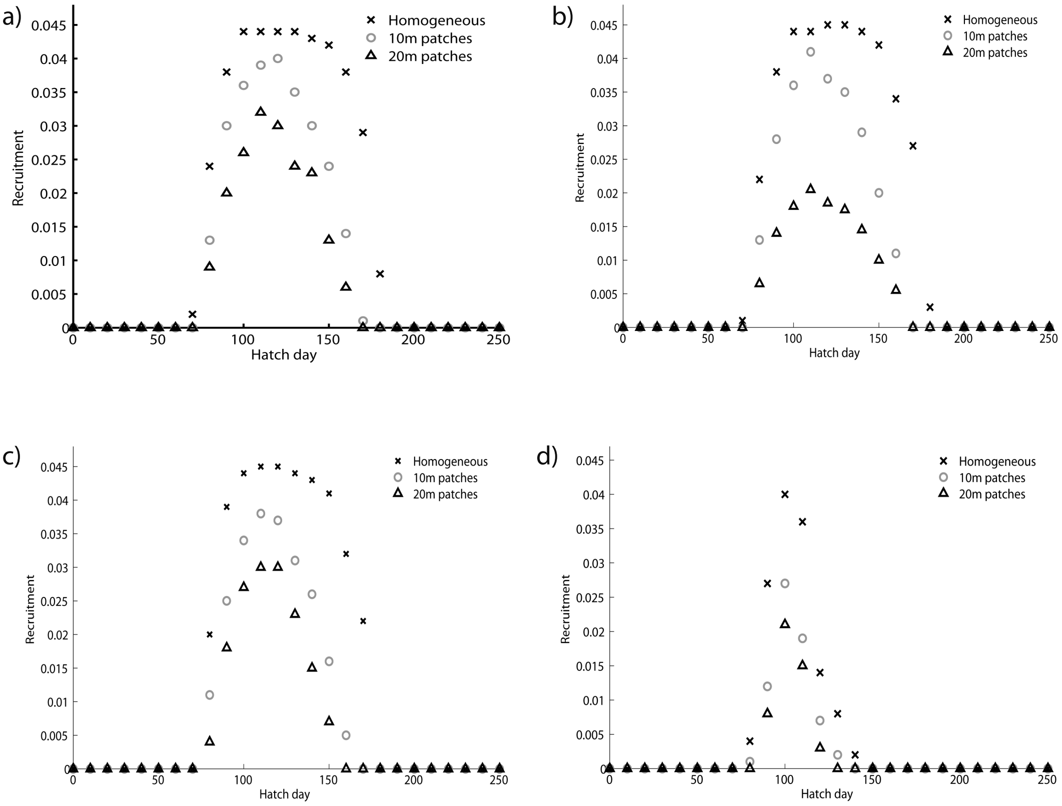

Figure 5.4: *Recruitment values for larvae growing in a homogeneous environment (crosses), larvae growing in a patchy environment with a patch length scale of 10m (circles, and larvae growing in a patchy environment with a patch length scale of 20m (triangles). Initial larval density* N_0 *was a) 1 larva* m^{-3}*, b) 5 larva* m^{-3}*,, c) 10 larvae* m^{-3}*, d) 50 larvae* m^{-3}*. A phytoplankton bloom was forced by increasing the phytoplankton growth rate on Day 20 (see Figure 5.5 for the plankton dynamics). Results were calculated by simulating 1000 individual larvae growing and predating on a zooplankton population, which in turn feed on a phytoplankton population.*

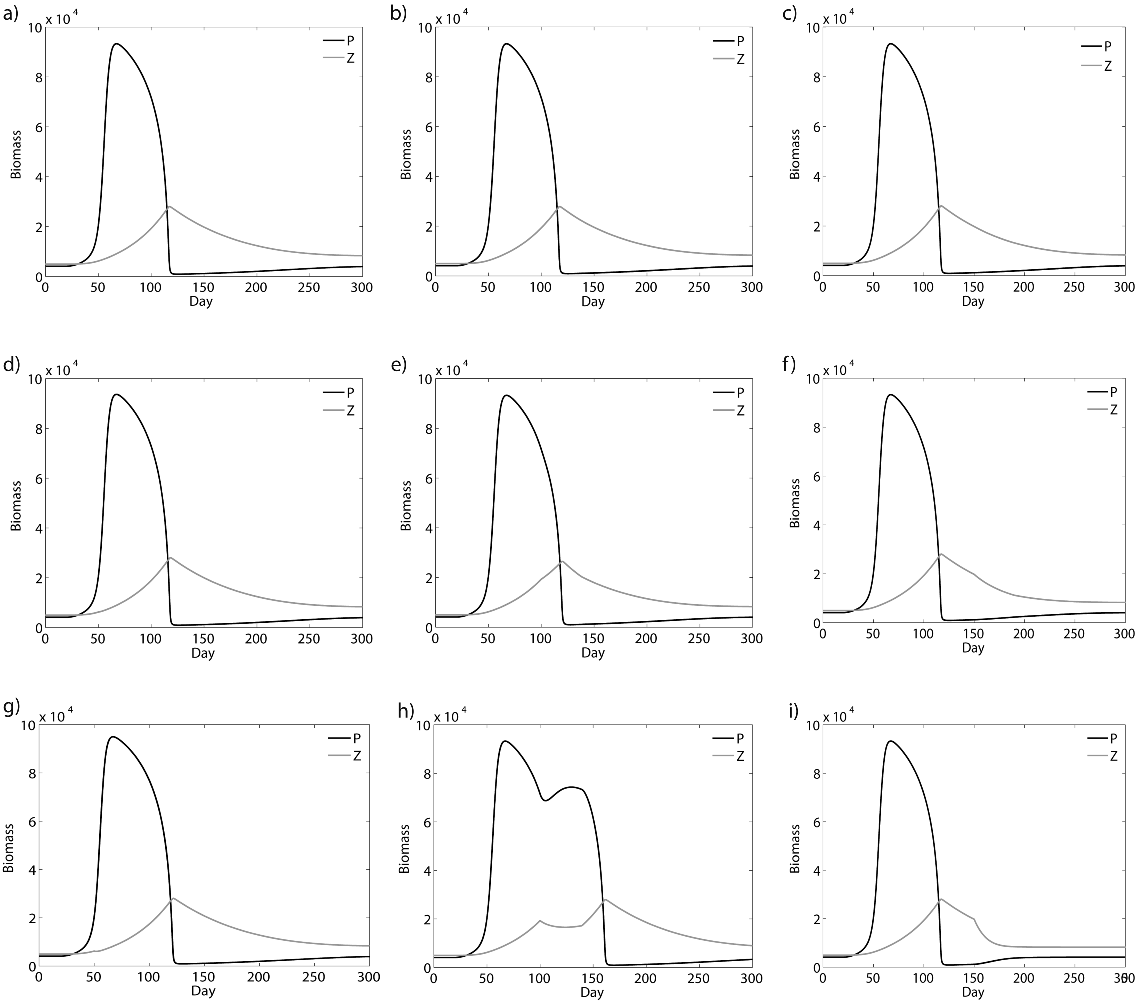

Figure 5.5: *Phytoplankton (P) and zooplankton (Z) trajectories for a selection of the results shown in Figure 5.4. A phytoplankton bloom was forced by increasing the phytoplankton growth rate on Day 20. a)-c) show the P-Z trajectories for an initial density of 1 larva* m^{-3}*, d)-f) for an initial density of 10 larvae* m^{-3}*, and g)-i) for an initial density of 50 larvae* m^{-3}*. The batches of larvae were introduced on either Day 50 (a),d),g)), Day 100 (b),e),h)) or Day 150 (c),f),i)).*

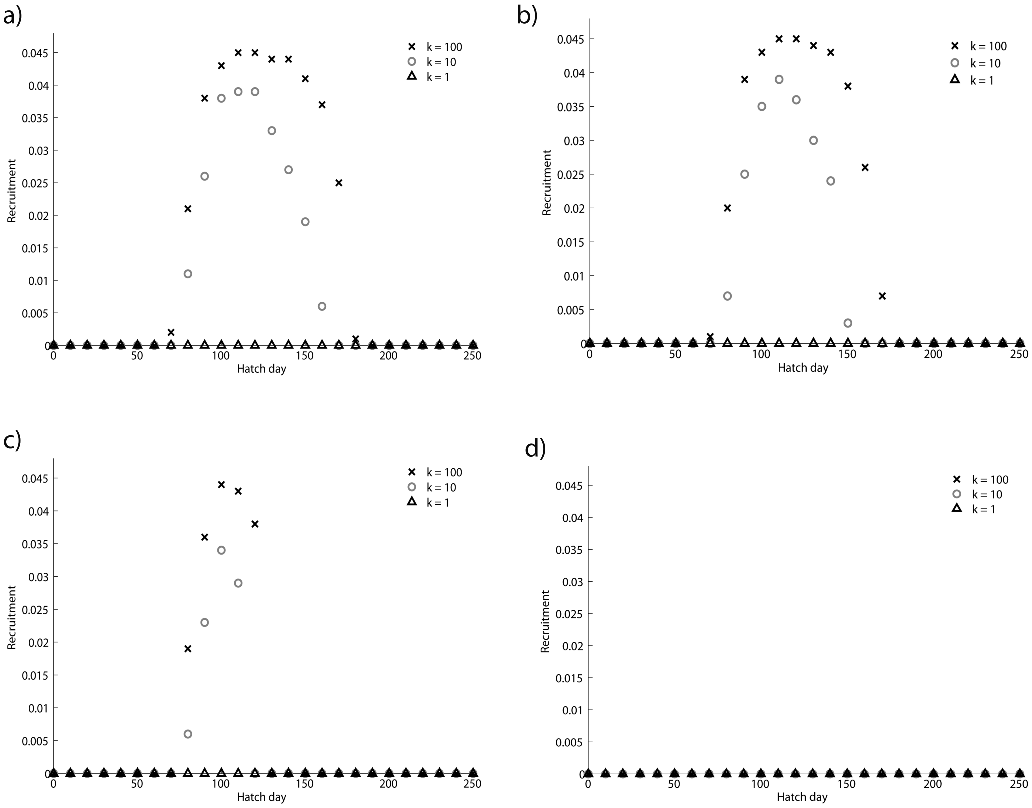

Figure 5.6: *Recruitment values for larvae growing in an overdispersed, negative-binomially distributed prey field, for different values of the overdispersion paramater k. A smaller value of k indicates a greater degree of patchiness. Initial larval density N_0 was a) 1 larva m^3, b) 5 larvae m^{-3}, c) 10 larvae m^{-3}, d) 50 larvae m^{-3}. A phytoplankton bloom was forced by increasing the phytoplankton growth rate on Day 20 (see Figure 5.7 for the plankton dynamics). Results were calculated by simulating 1000 individual larvae growing and predating on a zooplankton population, which in turn feed on a phytoplankton population.*

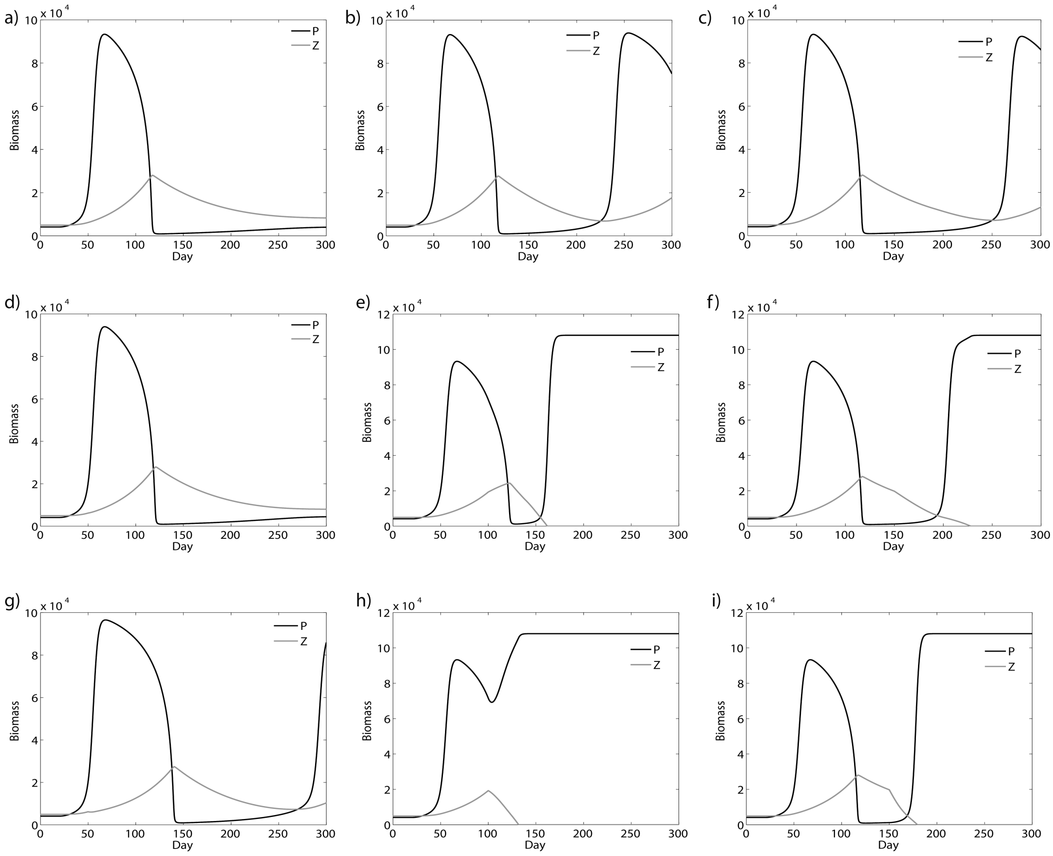

Figure 5.7: *Phytoplankton (P) and zooplankton (Z) trajectories for a selection of the results shown in Figure 5.6. A phytoplankton bloom was forced by increasing the phytoplankton growth rate on Day 20. a)-c) show the P-Z trajectories for an initial density of 1 larva m*$^{-3}$*, d)-f) for an initial density of 10 larvae m*$^{-3}$*, and g)-i) for an initial density of 50 larvae m*$^{-3}$*. The batches of larvae were introduced on either Day 50 (a),d),g)), Day 100 (b),e),h)) or Day 150 (c),f),i)).*

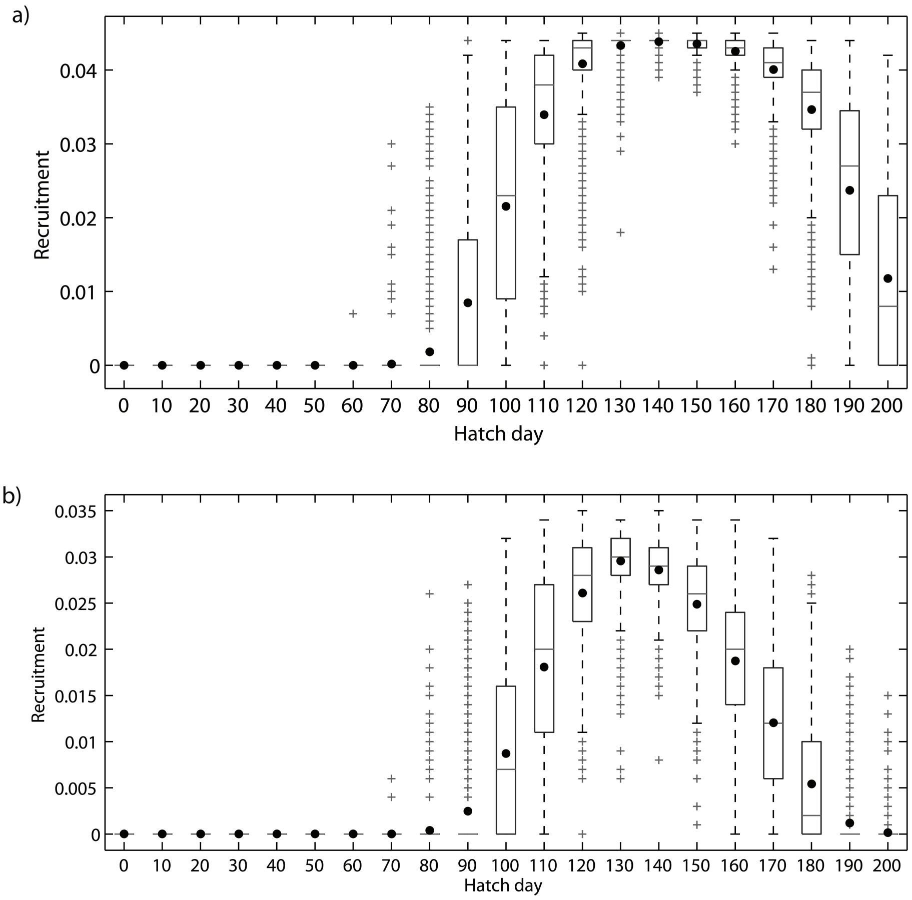

Figure 5.8: *Recruitment results for initial larval density of 1* m^{-3}*, for a) a homogeneous prey field (*$V = 1$*), b) a patchy prey field with* $V = 0.5$*,* $L = 20$*. A phytoplankton bloom was forced, with the day of initiation of bloom forcing being drawn from a normal distribution with mean 40 and variance 10. Each box plot represents 1000 instances of the stochastic force day, with recruitment probabilities averaged over 1000 larvae growing according to Model 1 (5.1) for each instance. The black dots mark the mean recruitment probability for each hatching day.*

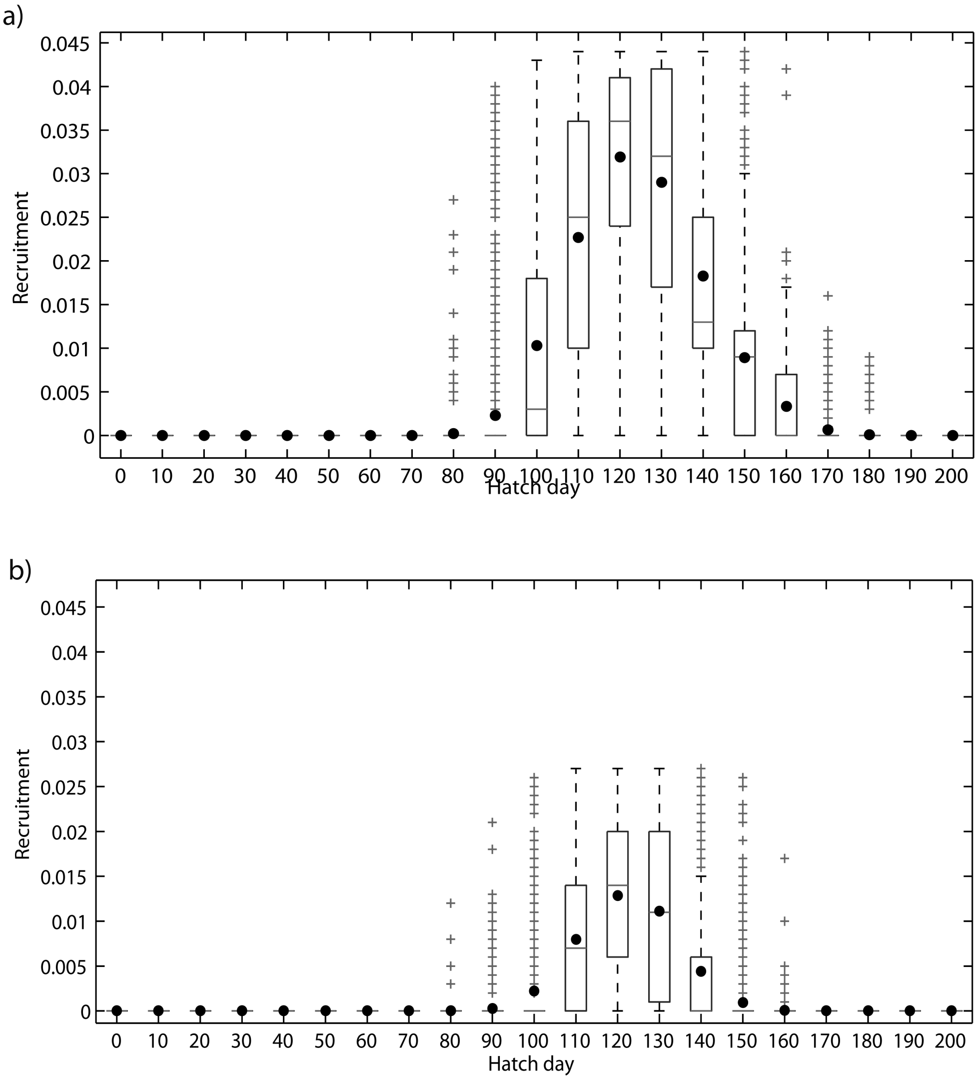

Figure 5.9: *Recruitment results for initial larval density of 50 m^{-3}, for a) a homogeneous prey field ($V = 1$), b) a patchy prey field with $V = 0.5$, $L = 20$. A phytoplankton bloom was forced, with the day of initiation of bloom forcing being drawn from a normal distribution with mean 40 and variance 10. Each box plot represents 1000 instances of the stochastic force day, with recruitment probabilities averaged over 1000 larvae growing according to Model 1 (5.1) for each instance. The black dots mark the mean recruitment probability for each hatching day.*

maximum achievable recruitment, it also means larval hatching must be more precisely timed to achieve this maximum. Recruitment variability is also higher around the peak hatch days in the patchy environment. This result holds for both initial larval densities simulated.

For an initial larval density of 50 larvae m^{-3}, the highest mean recruitment has shifted and is achieved by those hatching on Day 120. The highest mean recruitment is also lower than that for an initial larval density of 1 larva m^{-3}, and the period over which high recruitment is achieved is shorter. Recruitment variability around the optimal hatching day is much higher than in the case of low larval density, but is reduced for hatching days later than the optimum. Patchiness in the prey field decreases recruitment similarly to the results in Figure 5.8b).

The corresponding results for Model 2 with an initial larval density of 1 larva m^{-3} are shown in Figure 5.10. As in the previous results, a phytoplankton bloom was forced, with the day of initiation of bloom forcing being drawn from a normal distribution with mean 40 and variance 10. Each box plot represents 1000 instances of the stochastic force day, with recruitment probabilities averaged over 1000 larvae growing according to Model 2 (5.3) for each instance. The black dots mark the mean recruitment probability for each hatching day. Recruitment probabilities were calculated for a near-homogeneous environment with $k = 100$ (Figure 5.10a) and for an overdispersed, patchy environment with $k = 10$ (Figure 5.10b).

5.4 Discussion

By coupling a stochastic larval growth model to a dynamic phytoplankton-zooplankton model we have examined the roles of variability in phytoplankton bloom timing and heterogeneity in the spatial distribution of zooplankton in the recruitment of fish larvae.

When zooplankton patchiness is modelled as a Poisson encounter process, with larvae encountering patches of prey, and prey within those patches, as a Poisson

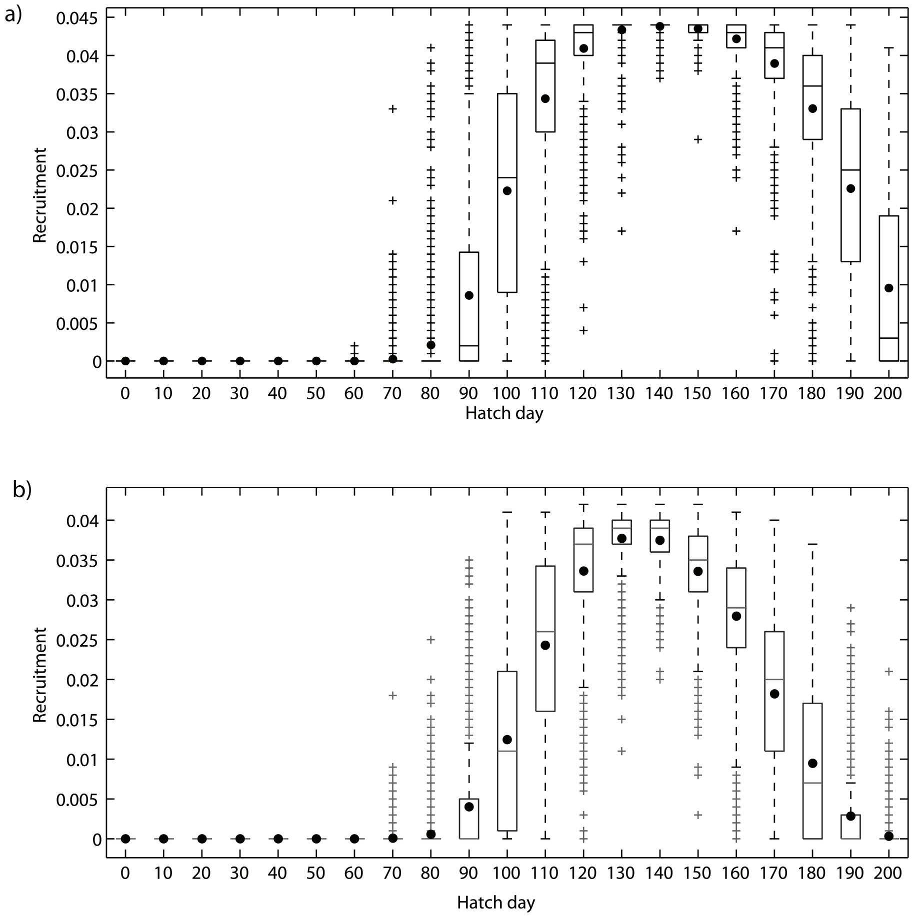

Figure 5.10: *Recruitment results for initial larval density of 1 larva* m^{-3}*, for larvae growing in an overdispersed, negative-binomially distributed prey field, for different values of the overdispersion paramater* k*. In a)* $k = 100$*, in b)* $k = 10$*. A phytoplankton bloom was forced, with the day of initiation of bloom forcing being drawn from a normal distribution with mean 40 and variance 10. Each box plot represents 1000 instances of the stochastic force day, with recruitment probabilities averaged over 1000 larvae growing according to Model 2 (5.3) for each instance. The black dots mark the mean recruitment probability for each hatching day.*

process, we find that recruitment probabilities are reduced as the patch length scale increases. Our results for a stochastically forced phytoplankton bloom suggest not only that a patchy environment seems to decrease the maximum achievable recruitment, but it also means larval hatching must be more precisely timed to achieve this maximum.

These results for recruitment in a patchy environment are perhaps more in line with what we would expect from observational data. In the case of a homogeneous prey field, there is a clear hatching period for optimal recruitment, and recruitment variability is much lower for this period, in comparison to other hatch days. If this were the case in real ocean systems, we might expect that fish populations would have evolved their spawning strategy so as to allow their larvae to hatch within this 20 day window, and as a consequence we would not see the order of magnitude variability in recruitment that we do observe. For the patchy environment, the optimal hatching window is smaller, and recruitment variability within this window is of the magnitude observed in real data. These results indicate that spatial heterogeneity in the prey field is as important in determining fish larval recruitment as temporal heterogeneity.

An important aim of the research carried out in this chapter was to look for possible evidence of heteroscedasticity (non-constant variance, see Chapter 4) in fish recruitment. We hoped to find evidence of increased recruitment variability at low stock sizes, as was proposed by Shepherd and Cushing (1990) and Minto et al. (2008). Taking initial larval density as a proxy for spawning stock biomass, we found clear evidence that spawning stock size does effect recruitment probabilities and variability, however, the story from our results is not clear cut. We found that mean recruitment probabilities in a variable environment were reduced for high initial larval densities (50 larvae m^{-3}). Recruitment variability was in fact increased around the optimal hatching day, and was only less than that for the low initial larval density (1 larva m^{-3}) for hatching days some time after the optimum, where recruitment probabilities were very low overall. We have confirmed that spawning stock biomass may affect recruitment variability, but we may have to use more than one proxy to delve deeper into the story. Length of spawning period may be linked to the size of the spawning stock, and it has been proposed that the duration of the spawning/hatching period can have a substantial effect on recruitment variability (Mertz and Myers, 1994).

As larval density increased, the hatching of and predation by the fish larvae had a greater effect on the plankton dynamics. For low initial larval densities (N_0=1,5), the larvae had little, if any, effect on the zooplankton, and therefore phytoplankton, dynamics (Figure 5.5). For these cases, the feedback effects between the trophic layers were negligable, and thus the results for recruitment will be similar to those in Chapter 4 (and Burrow et al. (2011)), with the exception of the effect of patchiness.

For higher larval densities (N_0=10,50), predation by the larvae had a considerable effect on the zooplankton dynamics (Figure 5.5), and subsequently on the phytoplankton dynamics. In these cases the feedback between the trophic layers may have played an important role in determining recruitment, and may explain the marked difference in recruitment probabilities between the cases for N_0=1 and N_0=50.

Results for growth in an overdispersed, negative-binomially distributed prey field (Model 2) were very similar to those for growth in a Poisson patchy environment. This could indicate that at the scale of larval growth and recruitment, it is the presence of patchiness, rather than the specific distribution of these patches, that is important. It should be noted, however, that the values we used for the over-dispersion parameter k are not indicative of very overdispersed distributions. In fact, for $k > 10$ it is difficult to tell the negative-binomial distribution apart from a Poisson distribution (Bolker, 2007), and by its nature (the variance of the encounter rate being greater than the mean when the volume taken up by patches is less than 1), the Poisson patch encounter model is also overdispersive. The equivalence of the two larval growth models was discussed in Section 5.2.2.

In contrast, the effect of larval hatching on the plankton dynamics was more pronounced for Model 2 than Model 1. Even at low intial larval densities, the hatching of larvae triggered a second plankton bloom (Figure 5.7). For higher initial densities, the zooplankton population was completely depleted, leading to an explosion in the phytoplankton abundances. The difference in the effects of larval hatching on the plankton in the two models may be due to the explicit use of a negative-binomial distribution in Model 2 (thus giving an integer number of zooplankton encountered and consumed in a unit time). The extreme effect of larval predation on the plankton dynamics using Model 2 indicates we should be cautious in our use of Model 2 in investigating the effects of zooplankton spatial distributions on fish recruitment. Second phytoplankton blooms occuring shortly after the first are extremely rare, if not unheard of, so the behaviour of the coupled model is not realistic. More work and thought may be needed to model zooplankton populations using a negative-binomial distribution.

It may be interesting to explore the consequences for recruitment for a value of $k \leq 1$ (k is often less than one in ecological applications (Bolker, 2007)), but, as demonstrated in Figure 5.2, recruitment numbers were zero for $k = 1$, and would also be zero for $k < 1$. However, when fitting negative-binomial distributions to data in their study of plankton micropatchiness, Lough and Broughton (2007) found values of k ranging from -26 up to 46, but no values for which $|k| \leq 1$. We can therefore consider the values of k used in this chapter to be within a realistic range.

The results in this chapter demonstrate the important roles of both temporal and spatial heterogeneity in the determination of larval fish recruitment. This approach to modelling variability in recruitment is complementary to the Ecosystem Approach to Fisheries (Cury et al., 2005; Jennings and Rice, 2011). We have demonstrated that plankton dynamics and trophic interactions are key determinants of recruitment variability; that is, we have demonstrated the importance of considering other ecosystem elements when evaluating recruitment variability.

Parameter (larval growth)	Value	Units	Parameter (Plankton)	Value	Units
β_{min}	0.135	-	r_P	0.3 - 0.5	d^{-1}
β_{max}	0.480	-	r_Z	0.7	d^{-1}
j	0.002	-	P^*	5700	$\mu g N m^{-3}$
M_0	33.0	μg	P_{max}	108000	$\mu g N m^{-3}$
M_{rec}	3165.0	μg	δ_Z	0.05	-
A	2.60	μg^{1-B}	P_0	4117.2	$\mu g N m^{-3}$
B	0.67	-	Z_0	4950.3	$\mu g N m^{-3}$
r_L	0.12	d^{-1}	μ_Z	0.012	d^{-1}
ϵ	6.29×10^{-5}	$m^2 s^{-3}$	P_0	4117.2	$\mu g N m^{-3}$
v	1.5 l	m	Z_0	4950.3	$\mu g N m^{-3}$
R	$0.75l$	m			
l	$(2.01 \times 10^{-3}) M^{0.2234}$	m			
μ_L	0.089	d^{-1}			
b	0.005	d^{-1}			

Table 5.1: *Parameters used in the models and numerical simulations*

Chapter 6

Concluding Remarks

6.1 Summary of results

Using simple mechanistic models, this thesis has examined the role of various factors in the determination of recruitment probabilities and recruitment variability.

In **Chapter 2** we attempted to synthesise observational evidence of the non-diffusive distribution of planktonic predators and their prey in the natural environment with existing stochastic models, thereby characterising important ecological processes at the population level. We demonstrated that, when generalising from a stochastic differential equation to a jump-diffusion process, the individual-level processes which generated the jump distribution could give rise to superdiffusivity.

The model of saltatory foraging in Section 2.3 agrees with previous models of cruise predators in questioning whether there is a generic advantage, in terms of mean encounter rate, for a naive predator to move according to a Lévy walk. Furthermore, we found no theoretical support for matching between exponents governing predator and prey distributions in maximising mean prey encounter rates. However, when interpreted in the context of a risk sensitive foraging strategy in a patchy environment, our results showed that saltatory foragers may be at a significant advantage.

The results of coupling a fish larval growth model to a variable zooplankton model in **Chapter 3** had interesting implications for the match/mismatch hypothesis (Cushing, 1975). The results from the step-function Z-dynamics model indicated that the amount by which an individual larva's recruitment probability is increased due to environmental stochasticity is dependent on when the larva hatches relative to the peak prey abundance.

When stochasticity in the timing of high zooplankton densities was introduced in a possibly more realistic Gaussian Z-dynamics model, our results suggested that recruitment probabilities are "optimised" when larvae hatch slightly before the expected time of peak zooplankton density. This result is supported by several empirical studies (Buckley and Durbin, 2006; Platt et al., 2003; Wright and Bailey, 1996).

A pattern in recruitment variability was observed in our model results when the duration of a period of high zooplankton density was linked to its timing. When parameters were correlated so that early periods of high density were shorter, variability was greater for hatching days before the expected peak density day. When early blooms periods of high density were longer, variability was greater for hatching days after the expected peak density day. This has interesting consequences for spawning strategies: if an adult fish wishes to maximise both the mean and variance of its offsprings' recruitment (a risk spreading strategy (Real, 1980; Reddingius and den Boer, 1970)) then this is more achievable in an environment where early periods of high prey density are shorter.

In **Chapter 4** we turned to examine the hypothesis of increased recruitment variability at low stock sizes (a type of heteroscedasticity, or non-constant variance). By investigating whether a heteroscedastic stock-recruitment model could be used in single stock management, we demonstrated that the available stock-recruit time series for individual populations are not long enough to accurately estimate parameter values for such a model.

We also demonstrated that we should be cautious in applying the heteroscedastic model in a fisheries management setting. In the case where $\eta_1 < 0$ (see Chapter 4 for model details) there was little, if any, difference between the MSYs calculated using a fitted heteroscedastic model and a fitted Beverton-Holt model. In this case, this indicates that even if the underlying recruitment process is heteroscedastic, there is no benefit in fitting the more complicated model for use in simple management strategies.

We established that it may not be possible even to calculate a value for MSY when $\eta_1 > 0$, due to the properties of the heteroscedastic model. This again highlights important limitations in a management setting. In the cases where an MSY could be defined for the heteroscedastic management model, the estimated MSY values were higher than those for the simple management model, which is also cause for concern.

The research conducted in **Chapter 5** built on that of Chapter 3. A third trophic level - phytoplankton - was introduced, utilising the excitable media model of Truscott and Brindley (1994). We examined the roles of variability in phytoplankton bloom timing and heterogeneity in the spatial distribution of zooplankton in the recruitment of fish larvae.

When zooplankton patchiness was modelled as a Poisson encounter process, with larvae encountering patches of prey, and prey within those patches, as a Poisson process, we found that recruitment probabilities were reduced as the patch length scale increased. Our results for a stochastically forced phytoplankton bloom suggested that not only does a patchy environment seem to decrease the maximum achievable recruitment, but it also means larval hatching must be more precisely timed to achieve this maximum. Our results indicated that spatial heterogeneity in the prey field is as important in determining fish larval recruitment as temporal heterogeneity.

For higher larval densities, we were able to observe the predation of the larvae on the zooplankton, and the subsequent effects on the phytoplankton dynamics. In these cases the feedback between the trophic layers may have played an important role in determining recruitment, and may explain the marked difference in recruitment probabilities between the cases for low and high larval densities.

Results for growth in an overdispersed, negative-binomially distributed prey field were very similar to those for growth in a Poisson patchy environment. This could indicate that at the scale of larval growth and recruitment, it is the presence of patchiness, rather than the specific distribution of these patches, that is important. It should be noted, however, that the values we used for the over-dispersion parameter k are not indicative of very overdispersed distributions. In fact, for $k > 10$ it is difficult to tell the negative-binomial distribution apart from a Poisson distribution (Bolker, 2007), and by its nature (the variance of the encounter rate being greater than the mean when the volume taken up by patches is less than 1), the Poisson patch encounter model is also overdispersive.

6.2 Relevance to fisheries management

The models presented in this thesis are theoretical and may seem quite removed from practical fisheries management. However, we believe the findings of this thesis, and in particular the methods and models used, are relevant to the management of fisheries. It is our belief that mechanistic models of this type are key to understanding the factors underpinning fish stock stability and variability.

Standard stock recruitment models, such as the Beverton-Holt and Ricker models, have been central to fisheries modelling and management for decades. However, these models were intended to portray factors controlling the long-term dynamics of populations, not to provide short-term recruitment predictions (Fogarty et al., 1991). In particular, considering the variability among individuals may reveal insights regarding the processes shaping year class strength that are not available from analyses of population parameters and the dynamics of the averages (Rice et al., 1993).

Our approach to modelling variability in recruitment is complementary to the Ecosystem Approach to Fisheries (Cury et al., 2005; Jennings and Rice, 2011). We have demonstrated that plankton dynamics and trophic interactions are key determinants of recruitment variability; that is, we have demonstrated the importance of considering other ecosystem elements when evaluating recruitment variability.

Strong evidence exists for systematic changes in plankton abundances and community structure worldwide over recent decades (Hays et al., 2005), changes which may increase and amplify with climate change. Improved technology allows us to collect high resolution data on the changes in phytoplankton abundances and distributions (Platt et al., 2007). Mechanistic models, such as those presented in this thesis, can allow researchers to investigate how changes in the plankton will affect fish populations.

A collective approach combining studies of mechanistic models, observational evidence and statistics, and data-driven models could be a great advantage in the build up to the review of the European Common Fisheries Policy in 2012 (European Commission, 2011).

6.3 Further research

There are two directions in which the research presented in this thesis could be developed in the future. The first is the introduction of a spawning period into the models coupling larval growth to plankton dynamics. It has been proposed that the duration of the spawning/hatching period can have a substantial effect on recruitment variability (Mertz and Myers, 1994). There is growing evidence that phenotypic characteristics, such as size and age, influence the timing and duration of spawning, and the quality of the eggs produced (Wright and Trippel, 2009). Older, repeat spawners are thought to spawn earlier and over a longer period than younger first time spawners (Wright and Trippel, 2009). Protracted spawning can be viewed as a risk-spreading strategy, attempting to reduce the variance in offspring survival (Biktashev et al., 2003; Wright and Trippel, 2009).

Fishing reduces spawning stock biomass and skews the age distribution of a stock towards earlier maturation at younger and smaller sizes (Anderson et al., 2008; Beaugrand and Kirby, 2010). It is not unrealistic to propose that reducing a fish stock by removing older, larger adults will reduce the length of the spawning season of that stock, and perhaps delay the start of the season. This could have a large effect of recruitment variability, and may be a cause of the increased recruitment variability at low stock sizes observed by Minto et al. (2008). Therefore, one obvious further development of the models presented in this thesis (the models used in Chapter 5, for example) would be to include a “spawning period” in constrast to the “point spawning” currently implemented in the models. This may provide more evidence for, and go some way towards explaining, increased recruitment variability at low stock sizes.

The second extension would be to investigate the effects of temperature on larval growth and plankton dynamics. It is vitally important to study the effects of temperature on fish recruitment, as Global Circulation Models predict significant warming across the globe under increasing levels of greenhouse gases (IPCC, 2007).

Changes in climate and temperature may effect fish recruitment both directly through physiological processes, and indirectly by changing the composition of zooplankton communities, which are the main food source for fish larvae (Olsen et al., 2011). Through these two mechanisms, increasing global temperatures could have a doubly negative effect on gadoid fish survival (Beaugrand et al., 2003). Firstly, temperature is positively correlated to metabolic and energetic costs (Beaugrand et al., 2003), so an increase in temperature would result in increased foraging and feeding costs for fish larvae. Plankton fluctuations have also been shown to be highly correlated to sea surface temperature changes, with the availability of plankton prey decreasing with increasing temperatures (Beaugrand et al., 2003). In fact, the analyses of Beaugrand and Kirby (2010) suggest that the indirect effect of temperature through plankton is likely a stronger determinant of recruitment than the direct effects on fish physiology. The models in this thesis have proved to be very efficient for testing the effects of plankton changes on fish recruitment, thus making them suitable for addressing questions relating temperature to recruitment.

Temperature and climate change may also link back to the first suggested extension of the models presented in this thesis. It is thought that temperature could affect both the age and maturity and spawning times in fish stocks (Drinkwater, 2005). There are therefore several ways temperature could be included in our models of larval growth and recruitment, thus allowing us to investigate the potential effects of climate change on fish larval recruitment.

Appendix A

A double barrier hitting time problem

To address the possibility of negative mass in the model of Pitchford et al. (2005), we can redefine the recruitment problem as a double barrier hitting time problem. The gain in mass equation

$$M(t) = rt + \sigma B(t), \qquad M(0) = 0,$$

still holds, however in addition to the absorbing barrier at M_{mat}, we now place another absorbing barrier at $-M_0$, where M_0 is defined to be the initial mass of a single planktonic fish larva. We wish to find the hitting time distribution for M_{mat} given that the growth trajectory $M(t)$ does not hit the barrier at $-M_0$ earlier. Using the methods of (Lin, 1998), we can derive this distribution:

$$f_{\hat{t}_{mat}}(t) = \exp\left\{\frac{M_{mat}r}{\sigma^2} - \frac{1}{2}\left(\frac{r}{\sigma}\right)^2 t\right\} \sum_{n=-\infty}^{\infty} g(t; b_n),$$

where

$$g(t;x) = \frac{x}{\sqrt{2\pi t^3}}\, e^{-\frac{x^2}{2t}}, \quad b_n = \frac{1}{\sigma}\left(2n[M_{mat} + M_0] + M_{mat}\right),$$

and

$$\hat{t}_{mat} = \inf(t > 0 : M(t) = M_{mat} |\, M(s) > -M_0,\ 0 \leq s \leq t)$$

is the redefined hitting time. Taking the same simple mortality model as Pitchford et al. (2005), we can arrive at the probability of maturation,

$$\begin{aligned} P_{mat}(r,\sigma) &= \int_0^\infty f_{\hat{t}_{mat}}(t)\exp(-\mu t)dt \\ &= \int_0^\infty \exp\left\{\frac{M_{mat}r}{\sigma^2} - \frac{1}{2}\left(\frac{r}{\sigma}\right)^2 t - \mu t\right\} \sum_{n=-\infty}^{\infty} g(t;b_n)\, dt. \end{aligned}$$

We can now repeat the results of Pitchford et al. (2005), to assess whether the inclusion of an absorbing barrier at “zero” alters the conclusions. Figure A.1 shows the results for the double barrier hitting time problem, for an initial mass of $M_0 = 2$ (a) and b) and $M_0 = 10$ (c) and d) in comparison to the single barrier problem.

For an initial larval mass of $M_0 = 2$ the addition of the second absorbing barrier can change the results of Pitchford et al. (2005), especially in the $r = 2.5$ case: stochasticity is not necessarily beneficial to recruitment because it increases the probability of absorption at the lower barrier. For $M_0 = 10$, the additional barrier does not significantly affect the results for $r = 5$, and has only a small effect on the results for $r = 2.5$.

The effect of the lower absorbing barrier is highly dependent on the value of M_0, even within a small range (as shown in Figure A.2). The parameters used in this paper are chosen to be broadly representative of a fish larva reaching recruitment mass after an average of 40 days (Pitchford et al., 2005). Values for M_0 (relative to a fixed $M_{mat} = 200$) in the literature can range over at least two orders of magnitude e.g. $M_0 = 0.12$ for bay anchovy *Anchoa mitchilli* larvae reaching metamorphosis in 32 days, $M_0 = 22.3$ for European plaice *Pleuronectes platessa* larvae reaching metamorphosis in 100 days (Froese and Pauly, 2000) (www.fishbase.org). For species and ecological scenarios where the starvation of larvae is known to be an ecologically relevant process, the possibility of absorption at the lower barrier can be included using the above methods. However, our overall conclusions regarding the role of

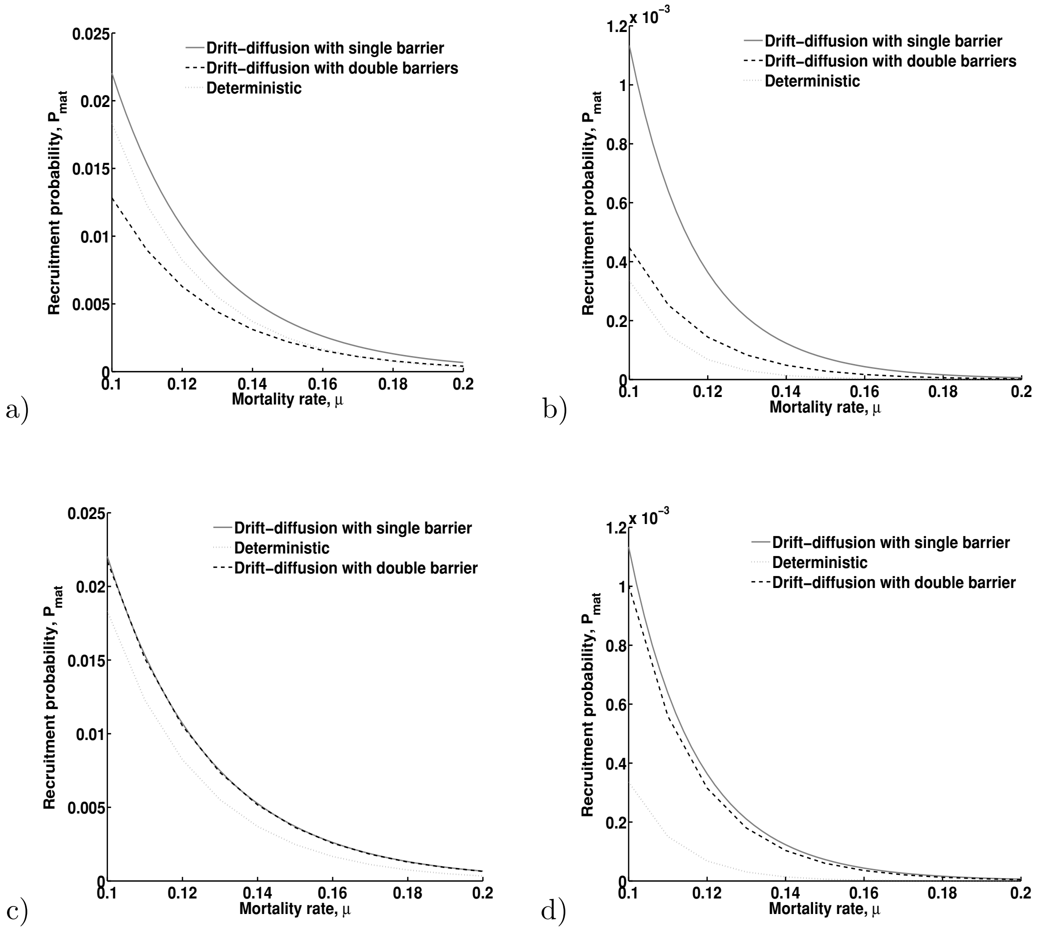

Figure A.1: *Examples of the effect of an additional absorbing barrier on the probability of recruitment, for the drift-diffusion model of Pitchford et al. (2005). In all graphs* $\sigma=5$ *and a)* $M_0=2$, $r=5$, *b)* $M_0=2$, $r=2.5$, *c)* $M_0=10$, $r=5$, *d)* $M_0=10$, $r=2.5$.

superdiffusive growth in the recruitment process are qualitatively unaffected.

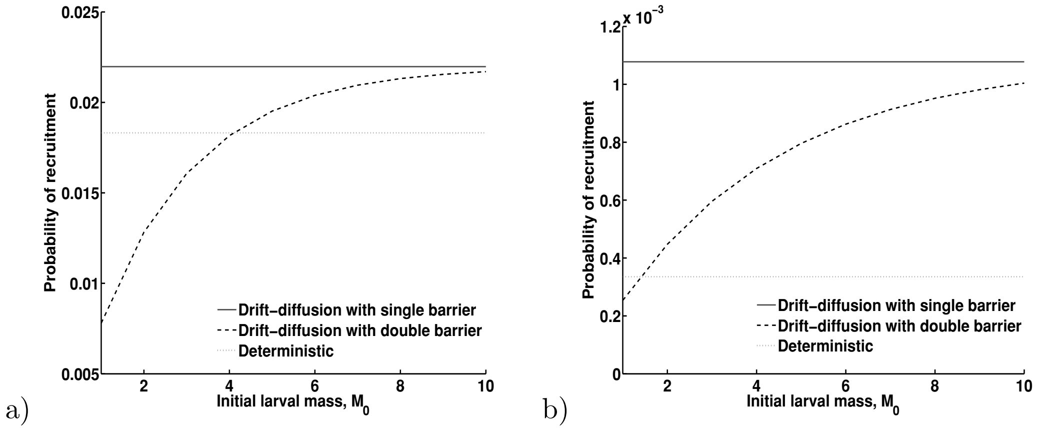

Figure A.2: *The dependence of the probability of recruitment on initial larval mass* M_0 *for the double barrier hitting time problem. In both graphs* μ*=0.1,* σ*=5 and a)* r*=5, b)* r*=2.5.*

Appendix B

Binomial test and derivation of expected recruitment

B.1 Binomial test

We carry out a binomial test (Siegel and Jr., 1988) to assess whether Minto et al. (2008) found a statistically significant number of negative η_1 values in their single species analysis. η_1 is the coefficient of heteroscedasticity (non-constant variance), and indictates which direction recruitment variance changes with stock size.

A total number of 148 η_1 values were fitted to single species data sets. For an underlying Beverton-Holt model ($\gamma = -1$ in equation (1)), 87 negative η_1 values were found. For an underlying Ricker model ($\gamma = 0$ in equation (1)), 101 negative η_1 values were found. For an underlying Schaefer model ($\gamma = 1$ in equation (1)), 104 negative η_1 values were found.

A one-sided binomial test is performed in R (R Development Core Team, 2007), giving p-values of 0.01976, 5.3×10^{-6}, and 4.4×10^{-7}, for the underlying Beverton-Holt, Ricker and Schaefer models respectively. This demonstrates that the number of negative η_1 values found is significant at the 5% level for the underlying Beverton-Holt model, and significant at the 1% level for the underlying Ricker and Schaefer models.

B.2 Derivation of expected recruitment

Following Minto et al. (2008) we suppose that the survival index $\ln(R/S)$ is normally distributed with mean $\mu = \ln(\alpha) - \ln(1 + \beta S)$ and variance σ^2 ($= \exp(\eta_0 + \eta_1 S)$ for the heteroscedastic model). This implies

$$\ln\left(\frac{R}{S}\right) \sim \text{logN}(\mu, \sigma^2).$$

Then, by the properties of the log-normal distribution,

$$\mathbf{E}\left(\frac{R}{S}\right) = \exp\left(\mu + \frac{\sigma^2}{2}\right).$$

Thus for a fixed stock size S the expected recruitment, $\mathbf{E}(R)$, is

$$\begin{aligned} \mathbf{E}(R) &= S\exp\left(\ln(\alpha) - \ln(1+\beta S) + \frac{\sigma^2}{2}\right) \\ &= \frac{\alpha S}{1+\beta S}\exp\left(\frac{\sigma^2}{2}\right) \end{aligned}$$

for a Beverton-Holt recruitment model with constant variance, and

$$\begin{aligned} \mathbf{E}(R) &= S\exp\left(\ln(\alpha) - \ln(1+\beta S) + \frac{\exp(\eta_0 + \eta_1 S)}{2}\right) \\ &= \frac{\alpha S}{1+\beta S}\exp\left(\frac{\exp(\eta_0 + \eta_1 S)}{2}\right) \end{aligned}$$

for the heteroscedastic recruitment model.

Appendix C

Parameter estimates and additional figures

C.1 Parameter estimates

	Cod				Herring			
	$\hat{\alpha}$	$\hat{\beta}$	$\hat{\eta_0}$	$\hat{\eta_1}$	$\hat{\alpha}$	$\hat{\beta}$	$\hat{\eta_0}$	$\hat{\eta_1}$
“true”	0.55	0.86	-0.96	0.29	3.21	6.77	-0.53	-0.98
1	0.677	0.0186	-2.419	-0.206	2.584	4.511	-0.940	-0.720
2	0.703	0.193	-3.427	1.676	3.271	7.264	-0.945	-1.038
3	0.8	0.343	-3.527	1.621	6.228	12.173	-0.737	-0.532
4	0.535	0.394	-0.667	-0.491	4.632	11.743	-0.791	-0.684
5	0.651	0.994	-1.119	0.533	2.130	3.368	-0.879	-0.536
6	0.496	0.552	-1.312	0.461	3.077	6.445	-0.351	-0.329
7	0.743	1.683	-1.473	1.107	2.651	5.399	-0.760	-0.463
8	0.695	0.952	-0.925	0.270	4.192	7.869	0.225	-3.650
9	0.451	0.522	-1.139	0.493	2.242	3.878	-0.562	-1.663
10	0.439	0.574	-0.943	0.390	3.220	7.168	0.204	-2.644

Table C.1: *“True” parameter values and parameter estimates for the heteroscedastic stock-recruitment model (equation (4.1) in main text), for North Sea cod and herring. Each cod data set had 43 data points (years), corresponding to the size of the original North Sea cod data set. Each herring data set had 47 data points (years), corresponding to the size of the original North Sea herring data set. Parameters were estimated using the* `optim` *function in R (R Development Core Team, 2007).*

	Cod			Herring		
	$\hat{\alpha}$	$\hat{\beta}$	$\hat{\sigma}$	$\hat{\alpha}$	$\hat{\beta}$	$\hat{\sigma}$
"true"	0.55	0.29	-	3.21	6.77	-
1	0.681	0.029	0.283	2.561	4.425	0.551
2	0.693	0.157	0.293	3.509	8.219	0.524
3	0.808	0.370	0.278	6.446	12.870	0.629
4	0.556	0.488	0.632	4.701	12.031	0.598
5	0.667	1.080	0.662	2.177	3.546	0.585
6	0.492	0.531	0.588	3.135	6.687	0.791
7	0.867	2.441	0.654	2.646	5.379	0.629
8	0.679	0.875	0.678	3.045	4.467	0.645
9	0.434	0.421	0.647	2.114	3.440	0.577
10	0.430	0.518	0.694	4.897	13.660	0.733

Table C.2: *Parameter estimates for the Beverton-Holt stock-recruitment model (with dummy variance parameter σ^2) for North Sea cod and herring. The Beverton-Holt model was fitted to the ten generated heteroscedastic datasets, hence there is not a "true" value for the variance parameter σ. Each cod data set had 43 data points (years), corresponding to the size of the original North Sea cod data set. Each herring data set had 47 data points (years), corresponding to the size of the original North Sea herring data set. Parameters were estimated using the* `optim` *function in R (R Development Core Team, 2007).*

	Cod				Herring			
	$\hat{\alpha}$	$\hat{\beta}$	$\hat{\eta}_0$	$\hat{\eta}_1$	$\hat{\alpha}$	$\hat{\beta}$	$\hat{\eta}_0$	$\hat{\eta}_1$
"true"	0.55	0.86	-0.96	0.29	3.21	6.77	-0.53	-0.98
1	0.569	1.082	-0.841	-0.106	3.261	6.633	-0.610	-0.790
2	0.562	0.730	-0.829	0.180	2.912	6.287	-0.469	-1.172
3	0.494	0.586	-1.044	0.372	3.295	7.428	-0.576	-0.895
4	0.614	1.097	-1.047	0.403	3.223	6.557	-0.545	-0.905
5	0.542	0.828	-0.911	0.181	2.707	5.425	-0.526	-0.989
6	0.555	0.792	-1.002	0.408	2.725	5.351	-0.380	-1.045
7	0.575	0.908	-1.123	0.510	3.447	7.163	-0.645	-0.902
8	0.592	0.972	-0.977	0.272	3.536	7.866	-0.474	-1.150
9	0.540	0.881	-0.907	0.176	3.262	6.668	-0.641	-0.793
10	0.601	0.987	-1.049	0.318	2.791	5.578	-0.773	-0.811

Table C.3: *"True" parameter values and parameter estimates for the Minto stock-recruitment model (equation (4.1) in main text), for North Sea cod and herring. Each cod data set had 430 data points (years), and each herring data set had 470 data points (years). Parameters were estimated using the* `optim` *function in R (R Development Core Team, 2007).*

	Cod				Herring			
	$\hat{\alpha}$	$\hat{\beta}$	$\hat{\eta_0}$	$\hat{\eta_1}$	$\hat{\alpha}$	$\hat{\beta}$	$\hat{\eta_0}$	$\hat{\eta_1}$
“true”	0.55	0.86	-0.96	0.29	3.21	6.77	-0.53	-0.98
1	0.535	0.828	-0.955	0.259	3.090	6.420	-0.566	-0.948
2	0.544	0.829	-1.006	0.272	3.306	7.085	-0.509	-1.093
3	0.546	0.818	-0.992	0.328	3.304	6.990	-0.488	-1.031
4	0.560	0.915	-0.940	0.297	3.258	6.936	-0.538	-0.983
5	0.550	0.910	-0.990	0.323	3.305	7.137	-0.512	-0.932
6	0.562	0.900	-0.920	0.182	3.295	7.278	-0.517	-0.963
7	0.567	0.951	-1.020	0.292	3.098	6.429	-0.509	-1.043
8	0.579	1.014	-0.946	0.247	3.172	6.568	-0.586	-0.888
9	0.533	0.793	-0.958	0.319	3.263	6.952	-0.586	-0.871
10	0.557	0.886	-0.864	0.176	3.156	6.620	-0.508	-0.948

Table C.4: *“True” parameter values and parameter estimates for the Minto stock-recruitment model (equation (4.1) in main text), for North Sea cod and herring. Each cod data set had 4300 data points (years), and each herring data set had 4700 data points (years). Parameters were estimated using the* `optim` *function in R (R Development Core Team, 2007).*

	Cod				Herring			
	$\hat{\alpha}$	$\hat{\beta}$	$\hat{\eta_0}$	$\hat{\eta_1}$	$\hat{\alpha}$	$\hat{\beta}$	$\hat{\eta_0}$	$\hat{\eta_1}$
"true"	0.55	0.86	-0.96	0.29	3.21	6.77	-0.53	-0.98
1	0.548	0.854	-0.962	0.279	3.220	6.830	-0.531	-0.970
2	0.553	0.873	-0.935	0.271	3.170	6.631	-0.512	-1.010
3	0.556	0.892	-0.947	0.255	3.129	6.770	-0.514	-0.990
4	0.560	0.915	-0.937	0.260	3.220	6.790	-0.554	-0.947
5	0.553	0.866	-0.963	0.300	3.240	6.680	-0.523	-0.980
6	0.554	0.883	-0.970	0.282	3.196	6.741	-0.533	-0.989
7	0.547	0.854	-0.949	0.271	3.223	6.770	-0.529	-0.975
8	0.555	0.873	-0.931	0.258	3.147	6.600	-0.520	-0.997
9	0.556	0.893	-0.959	0.273	3.259	6.930	-0.518	-0.974
10	0.556	0.899	-0.940	0.260	3.169	6.670	-0.547	-0.929

Table C.5: *"True" parameter values and parameter estimates for the Minto stock-recruitment model (equation (4.1) in main text), for North Sea cod and herring. Each cod data set had 43000 data points (years), and each herring data set had 47000 data points (years). Parameters were estimated using the* `optim` *function in R (R Development Core Team, 2007).*

	Cod		Herring	
	Beverton-Holt	Heteroscedastic	Beverton-Holt	Heteroscedastic
“true”	-	0.328	-	0.306
1	2.985	4.320	0.314	0.307
2	0.584	NA	0.259	0.266
3	0.367	NA	0.395	0.403
4	0.170	0.382	0.276	0.281
5	0.122	NA	0.317	0.315
6	0.089	NA	0.347	0.349
7	0.098	NA	0.290	0.288
8	0.162	0.493	0.432	0.381
9	0.080	NA	0.310	0.287
10	0.071	NA	0.214	0.321

Table C.6: *Maximum sustainable yields for North Sea cod and North Sea herring, for the Beverton-Holt and heteroscedastic parameter estimates and management models.*

C.2 Additional figures

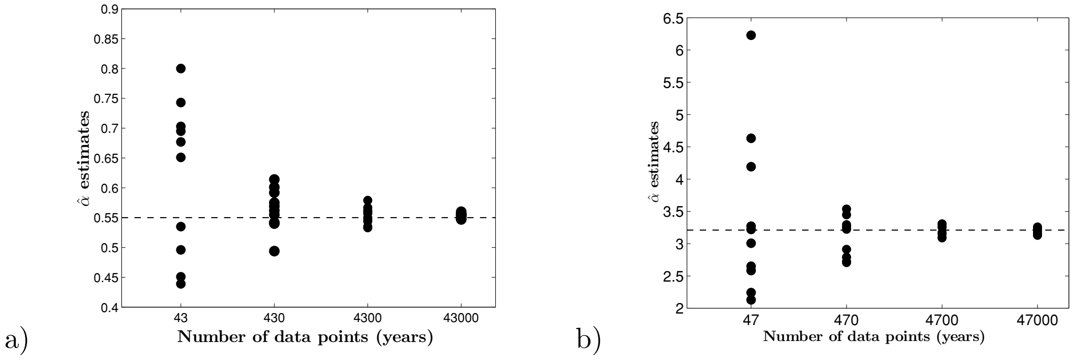

Figure C.1: *α parameter estimates (dots) for a) North Sea cod and b) North Sea herring. Parameters were estimated using the* `optim` *function in R (R Development Core Team, 2007). The real values of α are shown by the dashed line.*

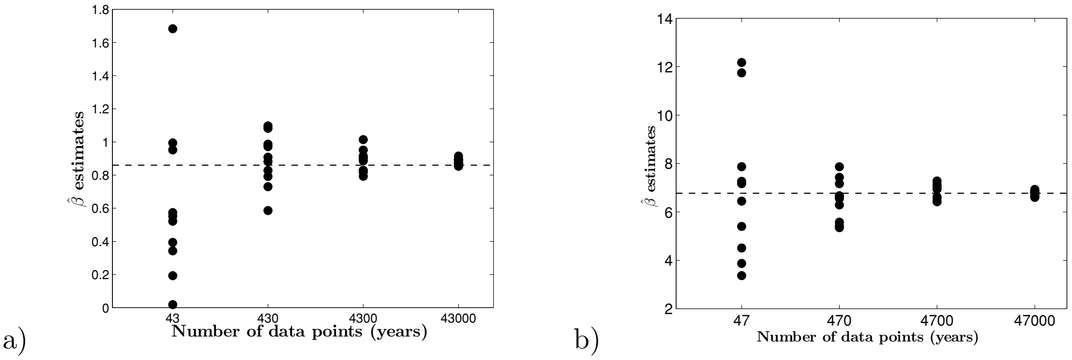

Figure C.2: *β parameter estimates (dots) for a) North Sea cod and b) North Sea herring. Parameters were estimated using the* `optim` *function in R (R Development Core Team, 2007). The real values of β are shown by the dashed line.*

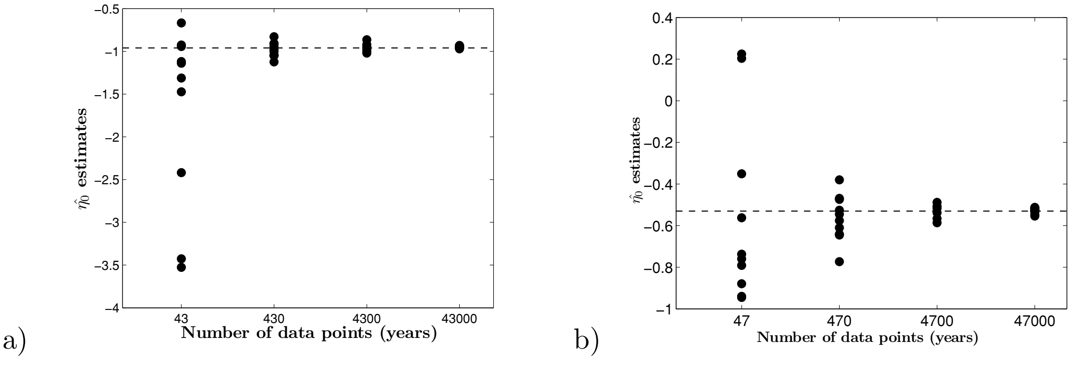

Figure C.3: *η_0 parameter estimates (dots) for a) North Sea cod and b) North Sea herring. Parameters were estimated using the* `optim` *function in R (R Development Core Team, 2007). The real values of η_0 are shown by the dashed line.*

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