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PhD thesis

Modelling the Shetland Sandeel Stock

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Declaration:

I declare this thesis represents, except where a note is made to the contrary, work carried out by myself. The text was composed by myself.

Elvira Severina Poloczanska

September 2001

"Daisy, Daisy, give me your answer do ...."

Hal, 2001

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ABSTRACT

Young sandeels (0- and 1-group fish) form a substantial part of the total stock biomass at Shetland. As well as forming the basis for a local fishery at Shetland, they are also an extremely important prey item for many seabird species which breed around Shetland coasts. Improving our understanding of recruitment dynamics is vital for managing the Shetland fishery whilst minimizing adverse affects on breeding seabirds. Therefore, this thesis has concentrated on analyzing recruitment patterns and developing models to simulate hypothetical recruitment scenarios.

Various models were developed and/or parameterised to simulate recruitment. Firstly, as there appeared to be no clearly defined stock-recruit relationship, time series models were applied to expose and improve understanding of patterns in the data. However, the relationship between stock and recruitment cannot be ignored if spawning stock biomass changes through exploitation. Therefore, Shepherd (1982) and Ricker (1954, 1975) stock-recruit models are parameterised using bootstrap analysis. For the Shepherd model, which is the more complex of the two, bootstrap analysis identified models which could be considered as "constant recruitment" models - that is no influence of spawning stock biomass on recruitment.

It was found that four very low recruit years, which occurred in the late 1980s when spawning stock biomass was generally high or moderate, were strongly influencing model fit. This prompted the question: are these low recruit years typical of the range of recruitment for the given spawning stock biomasses or can they be considered outliers? In the face of uncertainty (although there is no biological reasoning) these data points were removed and the stock-recruit models re-parameterised. This enabled curves with 95% confidence intervals to be parameterised for both stock-recruit models (Shepherd & Ricker). The autoregressive model parameterised earlier was combined with the stock-recruit models so recruitment in any year was expressed as a function of SSB and of recruitment in the previous year.

Wright (1996) presents evidence that, in some years, there may be a net input of recruits that originated from outside the Shetland system. This will obscure the stock-recruit relationship at Shetland as not all the recruits originate from the local spawning stock and may account for the difficulties in defining stock-recruit relationships. External recruitment may also may have implications for the persistence of the stock and for breeding seabirds. As the frequency and size of

external recruitment to the Shetland stock is unquantified, it was assumed that the stock-recruit relationship at Shetland (local recruitment) was similar to that in other areas of the North Sea. Ricker models were fitted to the North Sea stock and the mean curve was scaled down for use with the Shetland data. This was used to develop models to simulate both local and external recruitment at Shetland.

During the late 1980s, when sandeel recruitment was extremely low, many seabird colonies at Shetland showed reduced or complete breeding failure. Breeding Arctic terns and kittiwakes are considered among the most vulnerable to sandeel availability. A function of potential kittiwake breeding success against sandeel biomass was developed as an indicator of possible affects of fishery management on seabird breeding success.

The performance of the all recruitment models developed were tested under a range of input fishing mortality rates. With a fishery operating on all age classes, the models indicated that a substantial catch (31,000 tonnes), could potentially be landed each year with little adverse affect on recruitment or breeding seabirds. Simulations were rerun without exploitation of 0-group sandeels. This was assumed to mimic the present strategy of closing the fishery for June and July to avoid competition with breeding seabirds. It was found that a mean catch from the models in range of 37,000-51,000 tonnes (depending on the recruitment model) may have little affect on recruitment to the stock and on breeding seabirds. This was higher then the mean catches from the models with a fishery operating on all age-classes. The model with independent external recruitment model can support high levels of exploitation by the fishery with little adverse affect on potential breeding success of kittiwakes. However, the underlying local stock size decreases as exploitation increases but this is masked by external recruitment - if external larval transport mechanisms cease then the local stock may be at too low a level to be self-sustaining.

In summary, a number of models were developed to simulate potential recruitment dynamics for sandeels at Shetland – including models with external recruitment. Simulations varying fishing mortality rate indicated a fishery that does not exploit 0-group fish could sustain higher catches with little adverse affect on kittiwake breeding success. Depending on the recruitment model selected, optimal catches occur in the range 37,000-51,000 tonnes for this fishery.

CHAPTER 1

GENERAL INTRODUCTION

1.1 Industrial Fisheries

In industrial fisheries, such as the Shetland sandeel fishery, the catch is not intended for direct human consumption but is generally reduced to fishmeal and fish oil. These fisheries tend to target small pelagic or semi-demersal shoaling fish such as anchovies (*Engraulis* sp.), sardines (*Sardinops* sp.), mackerel (*Sprattus* sp.), herring (*Clupea* sp.) and sandeels (*Ammodytes* sp.). The first large-scale industrial fisheries developed along the west coasts of the Americas and Africa, where major up-welling systems of cold, nutrient-rich waters support large stocks of small planktivorous fish which are dominated by one or a few schooling species. In the North Sea, industrial fisheries developed during the 1950s for small species like sandeel (*Ammodytes* sp.), sprat (*Sprattus sprattus*) and Norway pout (*Trisopterus esmarkii*), and increased dramatically in the following decades (Figure 1.1).

A large proportion of fishmeal is used for farming and aquaculture purposes for example, in feed for poultry and pigs and in food pellets for salmon and shrimp farming (Fischer *et al.*, 1997). The aquaculture industry has grown rapidly in the past decade (more then doubled in weight and value) as catches of wild fish decline (Fischer *et al.*, 1997, Naylor *et al.*, 2000). Although, potentially, fish farming should relieve pressure on wild fish stocks this is not necessarily the case, especially for species that form the basis of the industrial fisheries (Naylor *et al.*, 2000). For terrestrial animals, the ratio between industrial fish used and meat produced is low, however the biomass of fish required as fishmeal in aquaculture is often greater then the biomass of farmed product produced (Fischer *et al.*, 1997). For example, the production of 1 tonne of farmed salmon uses approximately 3.16 tonnes of wild fish as fishmeal (Naylor *et al.*, 2000). The rapidly expanding aquaculture industry, together with terrestrial farming, is placing increasing demands on the industrial fisheries.

The stock-recruit relationship is an important concept for fisheries management, this assumes there is a relationship between the size of the spawning stock (spawning stock biomass: SSB) in any particular year and the average number of recruits produced by that spawning that enter the stock. Industrial fish species tend to be short-lived fish with a low age at reproductive maturity and high natural mortality rates. Inter-annual recruitment may be extremely variable depending on environmental conditions. As environmental factors have a strong influence on stock size, it is often difficult to define a stock-recruit relationship which provides understanding of the underlying dynamics of recruitment for management purposes.

The early maturation and selective fishing of industrial fish species may enhance the ability of certain populations to show some recovery after a prolonged decline (Hutchings, 2000). As such, industrial fisheries are difficult to regulate and often are not regulated as tightly as the more valuable (monetary value of catches) whitefish fisheries. This has already been demonstrated by the "collapse" of various industrial fisheries throughout the globe bought about by overfishing. Probably, one of the best known examples of industrial overfishing is the Peruvian anchoveta, *Engraulis ringens*, fishery (Troadec *et al.*, 1980).

Other examples of industrial fishery collapses include the capelin *Mallotus villosus* fishery in the Barents Sea (Beverton, 1990), the sardine *Sardinops caerulea* fishery in the California current (Troadec *et al.*, 1980; Beverton, 1990; Schwartzlose *et al.*, 1999), the sardinella *Sardinella aurita* fishery off Ghana and the Ivory coast (Troadec *et al.*, 1980) and the pilchard *Sardinops ocellata* fishery in the Benguela system off Namibia (Troadec *et al.*, 1980; Beverton, 1990; Schwartzlose *et al.*, 1999). In all of these cases, the associated fishery was implicated in the stock collapse and environmental effects were thought to play an important part. Often, breeding failures of local seabird colonies occurred and long-term declines in seabird populations may be apparent (see Troadec *et al.*, 1980; Furness, 1982; Crawford, 1991, Anker-Nilssen *et al.*, 1997; Crawford & Jahncke, 1999).

1.2 Biology of Sandeels

Sandeels are small, shoaling fish (up to 25-45 cm length depending in species) that are found throughout the North Sea (Macer, 1966; Reay, 1970). Five species of sandeel occur in the North Sea – *Ammodytes marinus*, *A. tobianus*, *Hyperplus lanceolatus*, *H. immaculatus* and *Gymnammodytes semisquamatus* (Macer, 1966; Langham, 1971b; Wright & Bailey, 1993). Of these five species *A. marinus*, the lesser sandeel (Figure 1.2), is the most abundant (Langham, 1971b) comprising of over 90% of sandeel fishery catches (Macer, 1966; Goodlad & Napier, 1997). In view of the predominance of *A. marinus* in fishery landings, any future references to sandeel in this thesis will be concerned only with *A. marinus* unless indicated otherwise.

1.2.1 Habitat requirements

Sandeels are probably the most abundant fish in the North Sea accounting for between 10-15% of the total fish biomass (Yang, 1982; Daan *et al.*, 1990; Sparholt, 1990). The distribution of sandeels is patchy, they commonly occur in great numbers in shallow coastal waters and on sandbanks. Sandeels do not have a swim bladder for buoyancy therefore, in order to remain in the water column, energetically costly swimming movements must be sustained (Reay, 1970). Sandeels are morphologically adapted for burying in the sediment and spend a considerable part of the year buried in the sand. Lying buried just below the surface of the sea bed may conserve energy and also may provide some protection from predation (Reay, 1970).

Sediment grain size together with the strength of currents over the seabed will affect aeration of the sediment and consequently the supply of oxygen to buried fish. This will influence the distribution of sandeels, because of these habitat requirements adult sandeels are restricted to appropriate areas of the seabed (Reay, 1970; Wright *et al.*, 2000). Depth is also an important factor, with few sandeels found below 70m, probably due to the decline in water movement with increasing depth (Wright *et al.*, 2000). Sandeels inhabit a narrow range of 'sand' sediment compositions therefore, by analysing seabed characteristics, it should be possible to predict where sandeels are found (or not) in the North Sea (Wright *et al.*, 2000). Major sandeel fishing grounds in the North Sea, such as the Dogger and Norfolk Banks, are all areas of coarse sand sediments preferred by sandeels (Wright *et al.*, 2000).

1.2.2 Life Cycle – spawning and pre-recruit

Sandeels are short-lived fish (up to 8 years) that have both a larval dispersive stage and an adult site-attached stage in their life cycle (Figure 1.3; Reay, 1970; Wright & Bailey, 1993). Around Shetland, mature sandeels spawn from December to late January (Gauld & Hutcheon, 1990). Sandeels generally mature at the age of 2 years, although larger fish may mature earlier and a few smaller fish may mature later (Macer, 1966; Gauld & Hutcheon, 1990). Generally, the reproductive parameters for sandeels in the north western North Sea are considered similar to those in other areas of the North Sea with reproductive potential being mainly dependent on fish aged two and older (Gauld & Hutcheon, 1990; Macer, 1966).

Sandeels lay demersal eggs attached to sand grains on the sea bed (Reay, 1970; Warburton, 1982). Adults are not thought undertake spawning migrations but the eggs are laid, and hatch, on the sandeel grounds (Reay, 1970). Early in spring, vast numbers of sandeel larvae appear suddenly in the water column, over short periods of time, suggestive of synchronised spawning (Ryland, 1964). Measurements of egg size and gonad maturity of adult sandeels indicate *A. marinus* does have a very short spawning period compared to related species (Macer, 1966).

Eggs hatch as larvae, generally during March at Shetland, when North Sea circulation is largely wind-driven thus larval transport by currents is likely to be variable between years (Wright & Bailey, 1996; Proctor *et al.*, 1998). At first, larvae drift passively with the currents but as the larvae grow they are able to make vertical migrations in the water column (Ryland, 1964). In the water column currents may flow in different directions at different depths, so the dispersal distance will be determined by the time spent in these layers of water flow. Larvae metamorphose into juvenile fish when they are 40 – 55 mm total length and this happens during late May to early June at Shetland (Wright & Bailey, 1996). The young sandeels settle on sandeel grounds during June and July at Shetland, when they recruit to the fish stock and to the fishery simultaneously.

1.2.3 Life-Cycle – post-settlement

After recruiting to the stock, sandeels show a diurnal cycle of emergence in the summer –forming dense shoals in the water column during the day (Winslade, 1974b,c; Wright & Bailey, 1993). Very few sandeels are caught at the night during this time (Macer, 1966). Towards the end of the summer, sandeels disappear from the water column as they enter the sediment for overwintering, emerging briefly to spawn mid-winter (Winslade, 1974b,c). Burying in the sediment appears to serve the dual purpose of conserving energy and avoiding predation (Reay, 1970). Emergence from the sediment during the summer is probably influenced by food availability and ambient environmental conditions (Winslade, 1974a,b,c).

Swimming activity is associated with light and feeding, as sandeels are visual feeders on zooplankton (Winslade, 1974a,c). Field studies around Shetland revealed sandeel shoals were recorded in the top 10m of the water column only during early and mid morning, coinciding with the peak in stomach fullness which occurred mid-morning (Wright & Bailey, 1993). As swimming activity is directly related to feeding, it is supposed that once a sandeel is satiated it will stop swimming and rebury (Winslade, 1974c). It appears sandeels have a light intensity threshold for feeding – below this they are unable to detect and capture prey. This can explain the seasonal variation in sandeel catches as the largest landings usually occur in June when light intensity is strong and daylength is long (Winslade, 1974b). Outside of the normal fishing season (April – September) it is probable that the threshold light intensity is not reached, so this may be one factor limiting sandeel activity. Buried sandeels may be able to detect light intensity (Winslade, 1974b), hence the penetration of light through sand and through water could restrict the depth of burial in the sand and also the maximum depth at which sandeels are found. As mentioned earlier, the aeration of the sediment influences the distribution of sandeels (Reay, 1970) and will also affect the depth to which sandeels can bury (depending on the depth of sediment aeration).

During the winter sandeels remain below the sand surface in a state thought to be similar to hibernation. In the Pacific sand lance, *A. hexapterus*, very little growth occurs during this period (Blackburn & Anderson, 1997). The disappearance into the sand may be linked to fat content (as well as light intensity). Fish may have to achieve a certain level of energy reserves in order to survive overwintering and spawning (Winslade, 1974c; Ciannelli, 1997). There is generally a relative increase in fat content with age hence older fish may reach the condition for overwintering before younger fish. There is evidence from fishery catches that the larger sandeels vanish first, weight-at-age and mean length-at-age of sandeels in certain areas of the North Sea were found to decrease after July (Macer, 1966; Pedersen *et al.*, 1999). It is thought this apparent decrease in weight is due to the larger sandeels entering the overwintering phase early, thus leaving only the smaller fish available to the fishery (Winslade, 1974c; Pedersen *et al.*, 1999).

Observations *in situ* of the Pacific sand lance, *A. hexapterus*, revealed that the fish were particularly vulnerable to predators during the transition between day and night when they were moving from the water column to bury in the sediment for the night and *vice versa* (Hobson, 1986). Therefore, entering the overwintering stage as soon as the required body condition is attained will reduce exposure to this crepuscular predation. The overwintering stage may be viewed as an adaptation for survival during a period when conditions are unfavourable for feeding and predation risk is high (Winslade, 1974c).

The growth rates of sandeels around Shetland are generally slower than elsewhere in the North Sea (Wright & Bailey, 1993; ICES, 1999). This could be indicative of a latitude trend (Shetland is north-west North Sea). Analysis of length and age data of the northern sand lance (*A. dubius*) in the north-west Atlantic suggested a decrease in maximum size, age, length-at-maturity and growth rate with declining latitude (Nelson & Ross, 1991). This variation with latitude could be due to a number of factors such as temperature, prey availability, temperature effects or competition which affect growth and/or survival - Nelson & Ross (1991) suggested a combination of factors are acting synergistically and the influence of these factors changes from year to year thus producing the fluctuations in the abundance of northern sand lance. Similarly, studies of the larvae of the Pacific sand lance (*A. hexapterus*) from the Northwest Pacific found that northern larvae tended to grow slower so larvae of the same level of development were smaller in the north although these larvae developed faster (Grigorev & Sedova, 1997).

Adult sandeels are considered to be site-faithful, once settled, adults tend to remain on grounds – Reay (1970) discusses evidence for this and cites a study conducted by Popp Madsen (1963) in the southern North Sea. Tagged adult sandeels were released and recaptured during the summer of 1958 and 13% (of 858) were recovered. A later sandeel tagging project carried out on sandeel grounds at Shetland showed high recoveries of tagged fish (19%-63% from releases at each ground in the study in 1985; Kunzlik *et al.*, 1986). A number of distinct sandeel grounds are fished in Shetland coastal waters (Wright, 1996), so the settled sandeel stock could be considered as a number of sub-units with little movement between them. Thus, the Shetland sandeel stock (with appropriate data) is highly suitable for a spatial model of population dynamics.

1.3 North Sea Sandeel Fishery

The North Sea sandeel fishery commenced in 1953 with landings of 4,500 tonnes, although some small catches had been landed before this (Macer, 1966). The fishery increased rapidly and 1,039,000 tonnes were landed in 1989, since then landings fluctuated below 1,000,000 tonnes (Figure 1.4; ICES 1999). The industrial fishery for sandeels initially developed to provide fishmeal factories with supplies during the slack period between winter and late summer industrial herring fisheries (Macer,1966). North Sea sandeel fisheries are seasonal, operating during daylight between April-October to coincide with the summer diurnal emergence behaviour of sandeels, as sandeels are caught by trawling above the seabed (Macer & Burd,1970).

At present, the sandeel fishery in the North Sea accounts for approximately two-thirds of total landings of fish from the North Sea (Kirkegaard,1999) and forms the largest single-species North Sea fishery. In 1998, the EU set a precautionary total allowable catch (TAC; maximum catch to be landed *per annum*) of 1,000,000 tonnes for North Sea sandeels to halt further expansion of the fishery (Scottish Office Press Release). Sandeel fisheries throughout the North Sea are based mainly on the lower age classes, that is sandeels less then 2 years old (Warburton,1982). As sandeels generally mature at age 2 (Reay,1970), this means fish are being removed from the stock before they spawn to produce new recruits.

1.4 Shetland Sandeel Fishery

During the late 1980s considerable public attention was paid to the industrial sandeel *Ammodytes sp.* fishery around Shetland. The fish stock was declining as was seabird breeding success around Shetland (Monaghan, 1992). Controversy arose due to a perceived conflict between fishermen and seabirds (Hildén, 1997). Environmental and conservation groups, such as Greenpeace and the Royal Society for the Protection of Birds (RSPB), were campaigning (and still are) for tighter regulation in sandeel fishing (Avery & Green, 1989; Aikman, 1997). The Shetland sandeel fishery was the subject of much public debate.

In contrast to the attention paid to it, the sandeel fishery around Shetland is extremely small. This is not an international fishery as the stock occurs within 6 mile fishery limits (within UK territorial waters), so it is managed solely by the UK and in addition, is fished only by local vessels (Reeves, 1999). Landings from the Shetland fishery are very low, in comparison with the North Sea sandeel fishery, averaging 20,360 tonnes per annum before 1991 with a maximum of 52,000 tonnes landed in 1982 (Figure 1.5; ICES, 1999). The North Sea fishery landed on average 677,120 tonnes per annum for the same period, and a peak of 1,039,100 tonnes was landed in 1989 (Figure 1.4; ICES, 1999). The value of industrial fish catches (per tonne) are often considerably less then that of whitefish for human consumption. Fisheries statistics published by the Shetland Islands Council (1999), valued sandeel landings in Shetland at approximately £359,000 (£30 per tonne) in 1986 when whitefish landings, such as cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*), were worth approximately £9,980,000 (estimated at £828 and £565 per tonne respectively). So why was so much controversy caused by a small, low-value fishery?

The sandeel fishery around Shetland commenced in 1974 and landings rose to a peak of 52,000 tonnes in 1982 (Figure 1.5; ICES, 1999). Landings and recruitment then declined and the fishery was closed completely at end of season in 1990 after several years of extremely low recruitment when it was estimated that the spawning stock was at such a low level that the probability of a strong recruitment was unlikely (Reeves, 1999). During the 1980s, the marked decline in sandeel landings at Shetland concurred with a decline in the breeding success of several seabird species in the area (Monaghan, 1992).

The decline in seabird breeding success was of particular concern as Shetland is considered an internationally important breeding site for many seabird species (Avery & Green, 1989; Furness, 1990). Very little alternative prey of a suitable size and energy content are considered available for seabird chicks around

Shetland (Kunzlik, 1989). In particular, very few Arctic terns (*Sterna paradisaea*) were fledged over the seven years from 1984-1990 when the availability of young sandeels was extremely low (Monaghan & Uttley, 1989; Monaghan, 1992). It was argued that competition between fishermen and seabirds for the same sandeel resource accounted for the decline in seabird breeding success (Avery & Green, 1989). Fisheries can have adverse affects on seabird populations through a number of processes for example, by direct competition for prey (Furness & Tasker, 2000).

In addition, sandeels may form an important prey source for other marine predator populations (Furness, 1990; Sparholt, 1990; McConnell *et al.*, 1999), such as pinnipeds and also whitefish like cod (*G. morhua*) and whiting (*Merlangius merlangus*). Sandeels can form a major food source in certain areas or at certain times of the year for these larger fish (Greenstreet, 1996). Concerns were raised, as early as the 1970s, that the availability of sandeels may have important implications on catches for the more valuable whitefish fisheries (Langham, 1971b; Doyle & Greenstreet, 1999). Therefore, reducing sandeel availability may have adverse effects on the survival and growth of predatory fish populations.

Initially, environmental groups blamed the sandeel fishery at Shetland for the decline in the local sandeel stock (Avery & Green, 1989). However, the decline in recruitment commenced before the spawning stock biomass (SSB) reduced (Figure 1.6), as would be expected if the fishery were the cause (Kuzlink, 1989). In other words, if overfishing were the cause of decline, it is expected that firstly a reduction in SSB would occur then, as SSB decreases, the number of recruits would start to decline.

After several years of low recruitment at Shetland, the production of an extremely large year-class in 1991 (144 billion) signalled the start of the recovery of the stock. It is now accepted that environmentally-induced fluctuations in recruitment to the sandeel population may be responsible (Wright, 1996). The fishery was reopened in 1995 following some recovery of the stock.

In 1992 changes in legislation, due to the introduction of the Sea Fisheries (Wildlife Conservation) Act, requires wildlife conservation considerations to be taken into account when discharging functions under the Sea Fisheries Act. Due to the high uncertainty in sandeel assessments at Shetland, a precautionary approach to the management of this fishery management was adopted (ICES, 1999). This approach can be considered as "preventative anticipation", that is action is taken before stocks are over-exploited and a wide margin for error is allowed (Internet Guide to International Fisheries Law). The precautionary approach taken for Shetland sandeels, considers the importance of sandeels for local predators.

A management plan for Shetland was determined after consultation with the Shetland Fishermens' Association, Scottish Natural Heritage and the RSPB (Reeves, 1999). Initially, A TAC of only 3,000 tonnes was set (compared to the 52,000 tonnes landed by the fishery in 1982), with a closed season during June and July (the main seabird breeding season) and a fishery restriction to vessels less than 20m length. Due to the recent low level of exploitation, management is reviewed every three years (ICES, 1999). For 1998-2000 management period, the TAC was increased to 7000 tonnes, with the closed season in June and July still in place (Scottish Office Press Release). The 20m length restriction on vessels was still in force but this may be raised if it appears the TAC is unlikely to be taken (as has occurred in the preceding years).

Around Shetland, the sandeel fishery is also based on the lower age classes but this fishery relies heavily on 0-group fish – fish less then 1 year old – as opposed to 1-group fish in the North Sea fisheries. The fishery is seasonal, operating between April and September, with 0-groups appearing in catches from June onwards (Reeves, 1999). The number and area of sandeel fishing grounds around Shetland are limited as the sea bed contains rocky outcrops – rendering areas unsuitable for trawling (Warburton, 1982). Very little bycatch is landed in the sandeel fishery – analysis of commercial catches at Shetland in 1996 indicated that less than 0.25% of catches (by weight) were non-sandeel species (Goodlad & Napier, 1997).

The Shetland sandeel fishery may be small but the importance of sandeels as a trophic link in the ecosystem has been recognised for many years. As observed by Langham in 1971b, "even if the sandeel fishery in Scottish waters is small, the importance of sandeels in the marine food chain, on which the wider fishing industry depends, is sufficient justification for a detailed examination". The sandeel fishery at Shetland is important as public concern was first raised about potential adverse impacts of sandeel fisheries on marine predators in relation to this fishery (Reeves, 1999). Compared to other systems, the Shetland marine ecosystem is relatively well studied - coupled with the history of the fishery this makes the Shetland fishery a useful case study (Reeves, 1999).

Fisheries management covers a wide and complex range of objectives, such as optimising profits, employment or government revenues; or conserving rare species or ecosystem status; or reducing overexploitation of the stock or managing discarding (Jennings *et al.*, 2001). Generally, fisheries management can be considered as ensuring fisheries are exploited on an ecologically sustainable basis while also maximising economic returns and conserving the environment (King, 1995). In order to achieve these aims, it is necessary to have some understanding of the biology and ecology of the exploited sandeel stock and of the surrounding ecosystem.

1.5 Fluctuations in Sandeel Populations

Some small, prolific fish, such as sardines and herrings, show large variations in abundance over a short number of years. The ability to produce large population increases over short time scales can be thought of a life history adaptation to environmental perturbations (Kawasaki, 1980; Sharp, 1987). This ability may allow exploited fish populations to recover after collapses (Schwartzlose *et al.*, 1999, Hutchings, 2000). Despite this capacity, other aspects of population change need to be considered in the management of industrial fish stocks. For example, how will exploitation affect the ability of a population to recover, how will predator populations respond and will population collapse cause a change in ecosystem structure (Gulland, 1987)? One example of an apparent ecosystem shift is the replacement of anchovy by sardines (and *vice versa*) which has been recorded in several systems around the world (Schwartzlose *et al*, 1999).

Populations of sardine and anchovies tend to fluctuate out of phase and so these are considered as a "species pair", that is one species is thought to "replace" the other after a population decline (Daan, 1980; Schwartzlose *et al.*, 1999). The exact mechanism is still in doubt but functional replacement, competitive release and/or adverse interaction may all be acting (Daan, 1980; FAO, 1997; Klyashtorin, 1997; Bakun & Cury, 1999; Hall, 1999; Schwartzlose *et al.*, 1999). Functional replacement implies the two stocks concerned are functionally related by a comparable response to a common base so as one stock goes down, the other increases (Daan, 1980). An element of competition is present in functional response. Competitive release occurs when one species limits, for example the range or numbers of another species by "out-competing" the other species (for space or food for example). When the competitor is removed, the limited species expands its range or numbers (see Begon & Mortimer, 1981). The mechanism of adverse interaction, in the absence of substantial competition between two schooling fish species, proposed by Bakun & Cury (1999) is based on the compulsion of these fish to become members of schools of similarly sized fish of a similar body form. The less abundant species in the schools may be adversely impacted, through differences in food requirements, swimming speeds and spatial use, determined by the dominant species in the school.

Evidence suggests cycles of population growth in sardine/anchovy pairs may be triggered by the formation of one or a few powerful age classes and decline occurs at high population levels due to a decrease in production and in survivorship of eggs (Schwartzlose *et al.*, 1999). Cannibalism may be an important source of egg mortality at high stock levels (Bax, 1998). The life history strategy of anchovies (and of sandeels) is such that large, irregular variations in recruitment can occur over short periods of time (Kawasaki, 1980). Heavy exploitation (fishing) may influence natural population fluctuations, for example by preventing a species becoming dominant, and so may change ecosystem functioning (Schwartzlose *et al.*, 1999).

Sandeel populations also show large fluctuations in abundance over short-time scales. During the 1970s and early 1980s, sandeel (*Ammodytes sp.*) populations increased in the north-west Atlantic (Winters, 1983; Nelson & Ross, 1991), North Sea (ICES, 1999) and around Shetland (ICES, 1999). The populations in the north-west Atlantic and around Shetland then declined (Nelson & Ross, 1991; ICES, 1999). There is a diversity of possible causes of fluctuations in sandeel populations, such as environmental factors affecting mortality rates and prey availability, competitive release, changes in survival due to fluctuations in predator populations, and exploitation.

Sherman *et al.* (1981) and Jones (1983) present evidence that the increase in abundance of sandeel species in the north-west Atlantic and North Sea during the late seventies was probably due to changes in the tropic levels of the ecosystem as opposed to environmental factors. The collapse of the mackerel (*Scomber scombrus*) and herring (*C. harengus*) stocks in these areas due to overfishing coincided with a population explosion of sandeels. The decrease in the herring and mackerel stocks probably resulted in an increase in food supply for sandeels, as there is some diet overlap, and also increased survival of sandeels, as herring and mackerel are also piscivorous. Predation is an important influence on marine ecosystems and fish are a major predator on smaller size fish and fish larvae and eggs (Bax, 1998). Sherman *et al.* (1981) suggest the increases in sandeel and other small fast-growing fish concurrent with the decreases in herring and mackerels exclude the hypothesis that the changes are due to environmental factors.

Subsequently, similar hypotheses have been made for population change in the north-west Atlantic sandeel populations. In the late seventies the American sand lance (*A. americanus*) populations in the north-west Atlantic increased dramatically while the Atlantic mackerel (*S. scombrus*) stock was rapidly declining (Bowman *et al.*, 1984). This led Bowman *et al.* to suggest food supply was more abundant and predation reduced at this time, in part due to the mackerel decline, while spawning conditions were more favourable. Also, no fishery existed for sandeels so fishing mortality was very low. Therefore, interspecific interactions between mackerel and sandeels appear to be important for sandeel population growth and survival. Further, Bowman *et al.* predict that, if the hypothesis is correct, the abundance of north Atlantic sandeels would decrease in later years (after 1983) in part as the Atlantic mackerel population appeared to be recovering. Later studies, by Nelson & Ross (1991) and Fogarty *et al.* (1991), appear to support this prediction.

Nelson & Ross (1991) also suggest interspecific interaction between mackerel and the northern sandeel *A. dubius* (which co-occurs with *A. americanus* in the north-west Atlantic) is important in regulating sandeel numbers. Relative abundance indices of A. *dubius* increased in the late seventies then declined from 1982 – 1987 concurrent with an increase in mackerel biomass during the eighties. Fogarty *et al.* (1991) evaluated empirical evidence for the regulation of north-west Atlantic sandeel populations by Atlantic herring and mackerel. A significant negative interaction between sand lance recruitment and an index of herring and mackerel biomass was found. It was concluded that, considered together with the fact that sandeels appear to be an important prey species for herring and mackerel, this supports the hypothesis of interspecific interactions affecting sandeel abundance although alternative hypotheses cannot be dismissed.

Decline of other predator populations may also influence sandeel population dynamics. For example, Winters (1983) analysed population data of northern sand lance on the Newfoundland Grand Banks for the period 1968-79 and found a substantial increase in abundance since the 1960s. Winters suggested the decline in the Grand Bank Atlantic cod (*Gadus morhua*) population, for which sand lance are the dominant prey species, due to over-exploitation led to reduced natural mortality and increased recruitment in sandeels. Seabirds often target small fish, the maximum size of which depends on the gape of the seabird bill, especially during the breeding season when small fish are needed to feed chicks (small gapes) and so are considered major predators in some marine systems (Bax, 1998). It has been proposed that seabirds may deplete fish prey during the breeding season in waters around their colonies (Birt *et al.*, 1987). However, the effect on the fish population may be very localised, depending on the spread of seabird colonies and foraging ranges, but may be important when considering small-scale systems.

The sandeel population around Shetland has shown considerable variation in abundance since the fishery commenced. During the late eighties, recruitment declined drastically, even though SSB was high during the initial decline. Analysis of 10 years of the continuous plankton recorder (1933-39 & 1947-49) found the annual abundance of sandeel larvae in the North sea tends to fluctuate considerably between years (Ryland, 1964). Proctor *et al.* (1998) adapted a two-dimensional sea circulation model to model the transport of sandeel larvae on the north-west European shelf, this indicated larval advection into Shetland from Orkney may be an important addition to recruitment at Shetland. The model demonstrated that passive particle transport into Shetland was high in years of high recruitment and low in poor recruitment years. There was also a loss of particles from the Shetland system but the correlations with recruitment were much higher for particles entering the system.

The recovery shown by the Shetland stock in the early 1990s was triggered by the appearance of a very large year class in 1991. The question here is where did this large year class originate from? Was it internally produced or was there an influx of recruits from elsewhere?

1.6 Sandeels and Seabirds

As the sandeel stock and fishery landings around Shetland declined in the late eighties, a concurrent decline in seabird breeding success occurred (Monaghan, 1992). Theoretically, competition between seabirds and fishermen can take two main forms, they can compete for sandeel recruits in any year or the fishery can reduce SSB thereby causing a reduction in recruitment (Tasker & Becker 1992, Hildén, 1997). At Shetland, both the fishery and breeding seabirds mainly take 0-group sandeels (recruits; Monaghan, 1992). Due to the dependence of seabirds on certain fish species in their diet, it has been suggested that seabirds be used as monitors of fish abundance (Cairns, 1992; Litzow *et al.*, 2000). However, this is most likely to be on a small scale (foraging area for colonies). At certain times of the year, there are areas of overlap in the exploitation of sandeels between fisheries and seabirds (Wright & Begg, 1997), and this has been recognised in the present management of the Shetland sandeel fishery. Since reopening in 1995, the fishery now closes during June and July to avoid competition with breeding seabirds.

Shetland is not the only area where concerns regarding the adverse effects of sandeel fishing for seabirds have been recognised and acted on. The sandeel fishery moved into the Wee Bankie area, off the Firth of Forth in East Scotland, in 1990 and a concurrent decline in seabird breeding, as the fishery expanded, occurred at nearby colonies (Aikman, 1997; Rindorf *et al.*, 2000). This area forms an important feeding ground for breeding seabirds in the estuary and on the Isle of May so there is strong potential for competition between seabirds and the fishery (Wanless *et al*, 1999). Evidence suggests the fishery could exacerbate the foraging success of breeding seabirds when sandeel biomass is low (Rindorf *et al.*, 2000). A study of diet composition of kittiwakes by Lewis *et al.* (2001) indicates environmental factors appear to be the dominant influence on the sandeel population hence kittiwake breeding success. In 1999, it was agreed this area will be closed to sandeel fishing from April to August (Scottish Executive Press Release 1999). This is a more radical decision then the Shetland closure as the Wee Bankie is fished by vessels a number of countries, mainly Denmark, hence an international agreement was reached between the countries concerned (European Commission Fisheries Web Site).

1.7 Assessment & Management of Sandeel Fisheries

One of the most basic questions in stock assessment is "How many fish are there?". It is not possible to simply go out and count all the fish in the sea, instead data collected from commercial landings and research cruises (which are costly and time-consuming) are used to assess stock size and composition. The size of commercial fish stocks are generally estimated using Virtual Population Analysis (VPA). This is a technique that uses fishery landings to estimate historic fishing mortality and the numbers of fish in each cohort (age-class, see Hilborn & Walters, 1992 for further details). Reasonable estimates of fishing mortality on recent cohorts can be obtained if the population is heavily fished.

At present, an annual VPA model is used to assess the stock (ICES, 1999). However, due to the low exploitation in recent years and high natural mortality rates, the model is very sensitive to the input data and thus the results can only be taken as an indication of trends in the stock. The recent low catch rates and low effort of the Shetland fishery will affect input parameters as landed fish may not be representative of the entire age-class. Catch data for assessments are supplemented with data from bottom trawl research surveys which have been conducted at the fished grounds since 1984 (except for 1987 and 1995). It was considered inappropriate, for a number of reasons, to define safe biological limits for the stock in terms of defined reference points (ICES, 1999). Therefore a precautionary approach has been taken which considers the importance of sandeels for local predators - as a result the TAC is set at low levels.

Stock-recruit data for Shetland sandeels are highly variable and there is no obvious relationship so does a relationship exist (Figure 1.7)? Myers & Barrowman (1996) demonstrated, by analysing stock-recruit data for 364 fish stocks, that strong year classes are more likely when SSB is large therefore providing proof of the stock-recruit relationship (see Chapters 3 & 4 for further discussion). Zheng (1997) examined stock-recruitment data for 28 anchovy, herring, mackerel and sardine stocks world-wide and found that, though recruitment was highly variable, it was significantly related to SSB and was generally compensatory density-dependent. It was concluded that the status of spawning stocks is central to the management of these fisheries thus overfishing should be avoided. Defining the stock-recruit relationship for the Shetland sandeel stock is therefore important for fishery management. However if, as suspected, a large proportion of the recruits originate from outside Shetland (Wright, 1996) then this relationship will be obscured.

1.8 Thesis Aims and Structure

The aims of this project are to produce age-structured population models of the sandeel stock at Shetland. Understanding recruitment dynamics is a vital part of the project, therefore much of the thesis concentrates on recruitment. Time series analysis is applied to the Shetland and North Sea data and stock-recruit models parameterised. A model for external recruitment is also developed. A suite of baseline models are thus identified, accounting for a number of possible recruitment scenarios. Fishing mortality rates are altered and the resulting model output is compared to the baseline models.

The thesis has been split into seven chapters (including this introductory chapter). The next chapter (2) reviews available data and analyses synchrony in recruit time series on fishing grounds around Shetland. Due to the importance of recruitment, Chapters 3, 4 and 5 are devoted to stock and recruitment issues. In Chapter 3, the basic population model is introduced and methods of simulating recruitment using time-series forecasting methods are tested. This uncouples recruitment from stock size but increases our knowledge of the underlying patterns and these models can be incorporated into the traditional stock-recruit models used in Chapter 4.

Ricker (1954; 1975) and Shepherd (1982) stock-recruitment models are fitted to the Shetland data in Chapter 4 and autocorrelated stochasticity around the stock-recruit curve added. The models are fitted to the complete data set and to a reduced data set, removing four years which may be considered outliers, so two sets of curves are parameterised for each stock-recruit model. These are incorporated into the population model and simulations carried out.

Chapter 5 develops models to simulate local and external recruitment. This is problematic due a lack of data, as the size and frequency of external recruitment is unquantified. It is assumed that the stock-recruit relationship for sandeels around Shetland is similar to that in other areas of the North Sea. Ricker stock-recruit models are fitted to the North Sea sandeel data and these are scaled for use with the Shetland data. By determining the difference in the lognormal variance around the curves between the complete Shetland data set and the scaled North Sea data, it is possible to estimate external recruitment. These models were incorporated and tested into the population model.

Chapter 6 discusses the potential effect of sandeel availability on seabird breeding success and explores the consequences of varying fishing exploitation rate. Species considered particularly vulnerable to sandeel availability are identified and functions of breeding success against total sandeel biomass are devised. Finally, population dynamics under varying rates of fishing mortality are analysed. Chapter 7 is the discussion chapter.

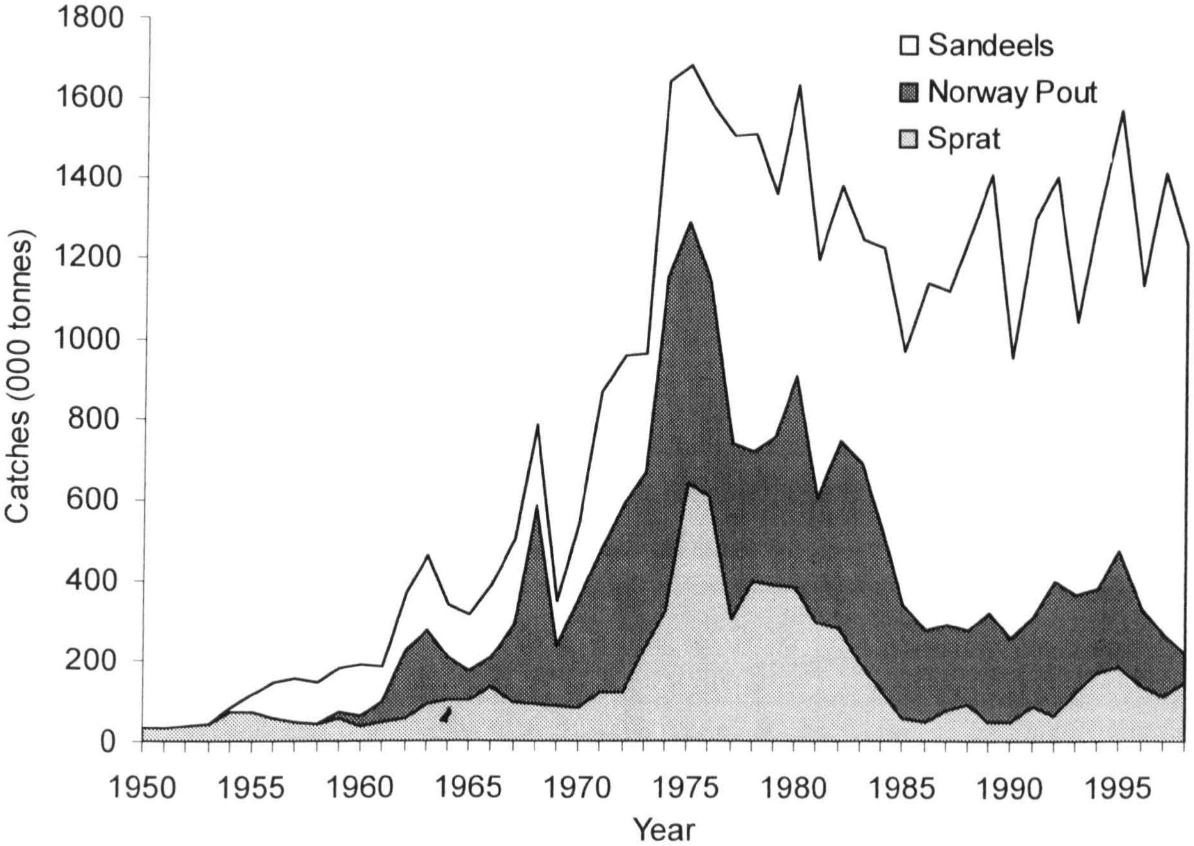


Figure 1.1 Landings of sandeels, Norway pout and sprat from the North Sea and north-east Atlantic over 1950-1997 inclusive (from FAO Yearbook Statistics).

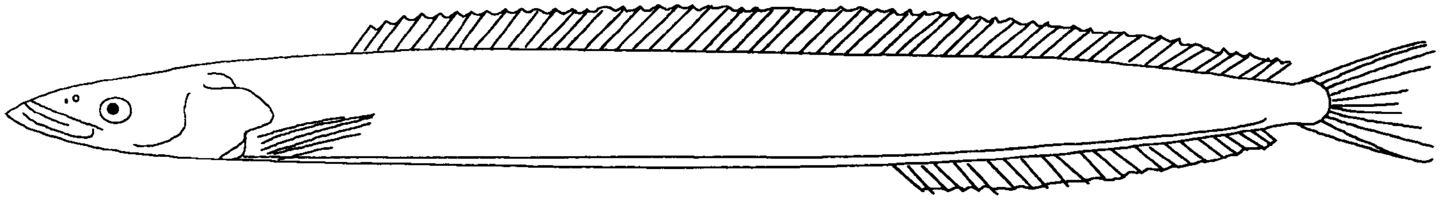


Figure 1.2 Line drawing of *Ammodytes marinus* (not to scale)

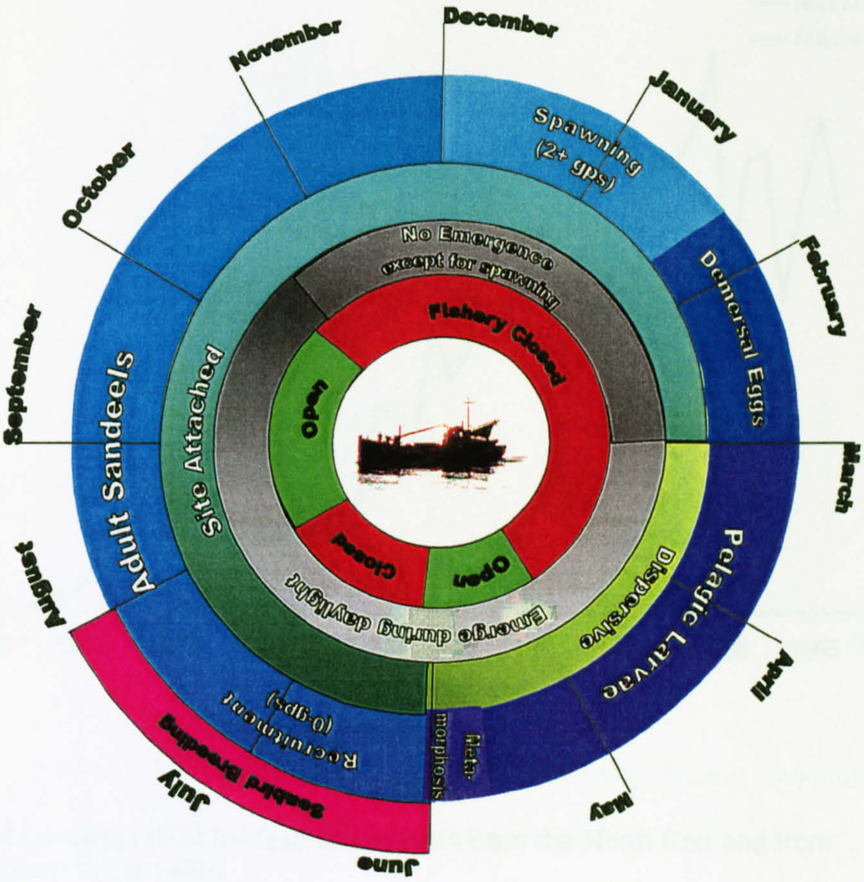


Figure 1.3 Diagram of annual cycles of Shetland sandeels and the associated fishery. Outer blue circle represents life stage, green circle represents dispersive/site attached stages of fish in first year of life, grey circle represents emergence behaviour of settled fish (0-groups and older) and inner red/green circle represents the status of the fishery. Main seabird breeding season is also indicated (pink outer).

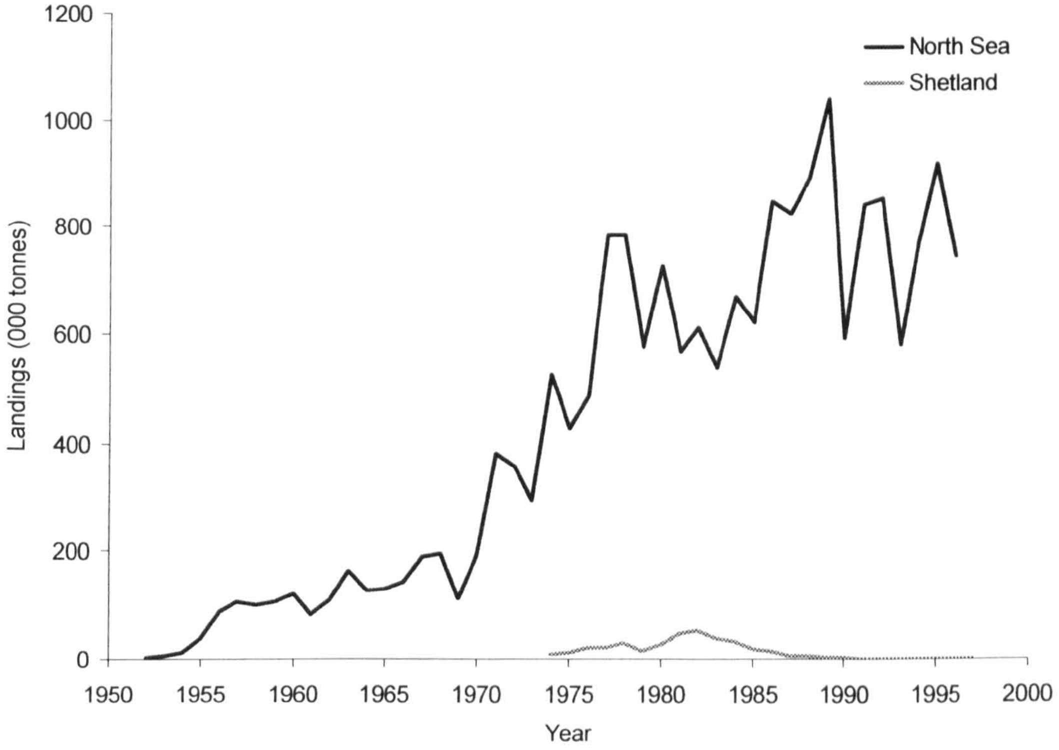


Figure 1.4 Landings (000 tonnes) of sandeels from the North Sea and from Shetland (from ICES 1999).

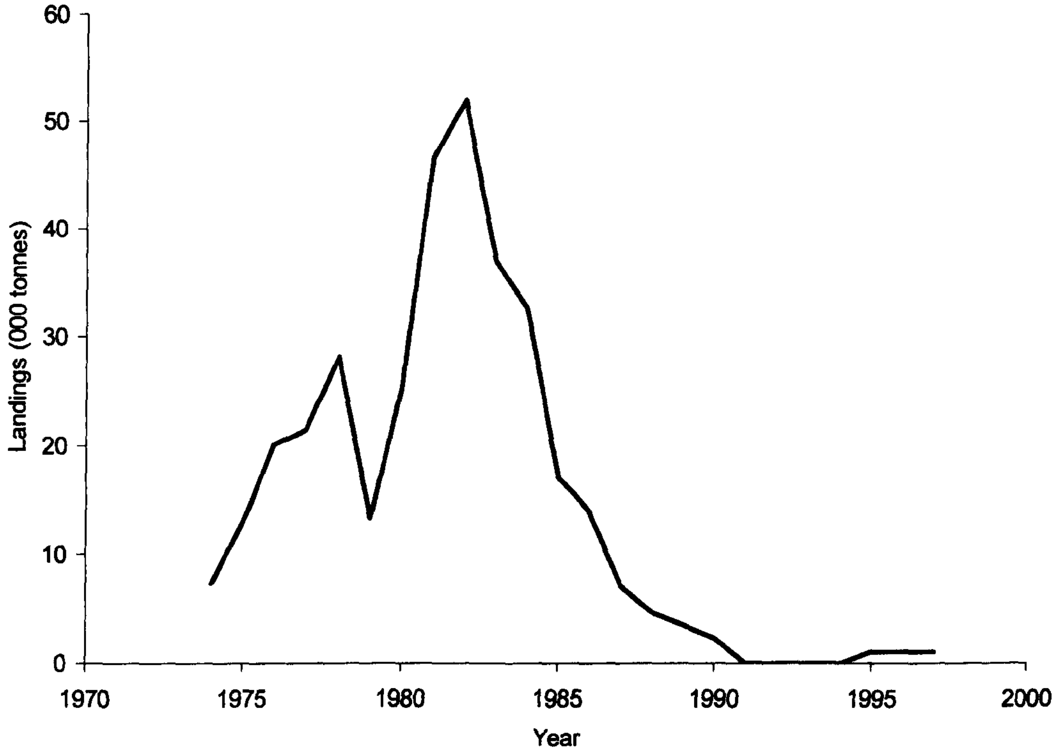


Figure 1.5 Landings (000 tonnes) from the Shetland sandeel fishery over 1974-1996 (from ICES 1999).

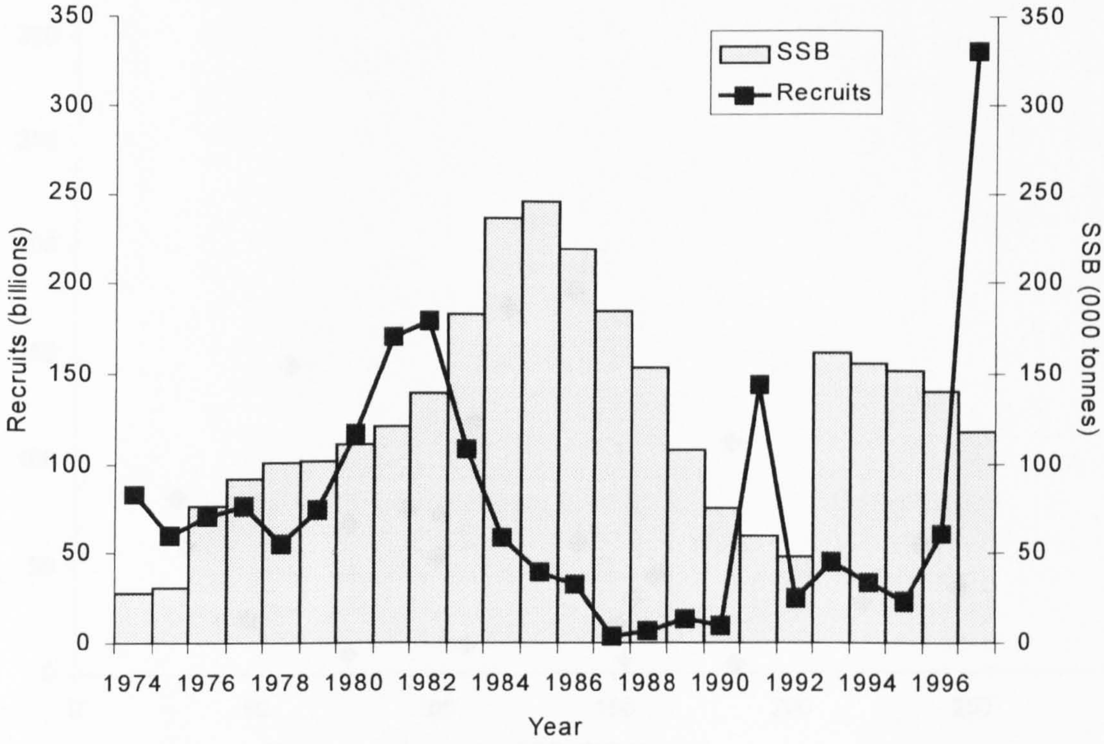


Figure 1.6 Stock trends for sandeels at Shetland (from ICES 1999).

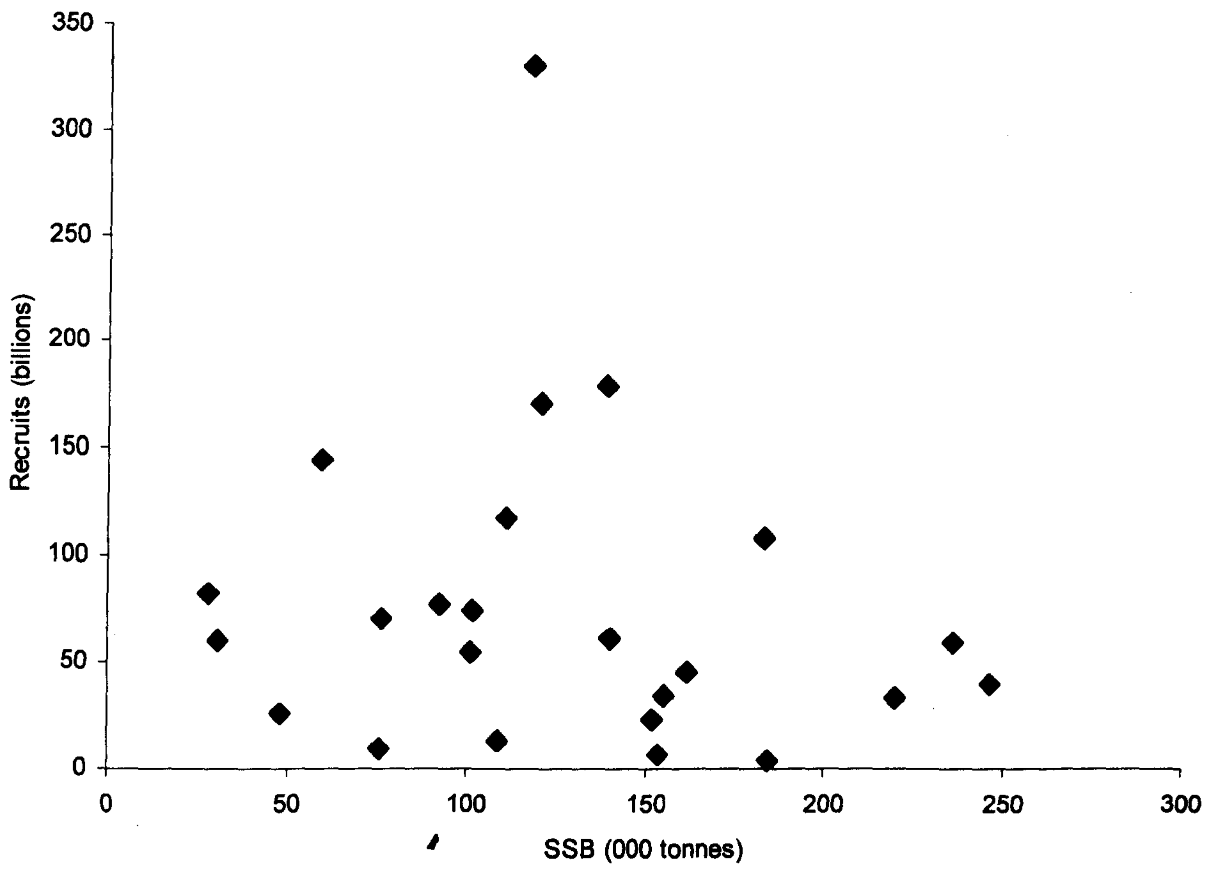


Figure 1.7 Stock-recruit data for sandeels at Shetland over 1974-1997 inclusive (from ICES 1999).

CHAPTER 2

POPULATION CHARACTERISTICS AND SYNCHRONY

2.1 Introduction

This Chapter is written in two parts, the first part considers the available data for sandeels at Shetland and how these are generated while the second part is concerned with synchrony between fishing grounds in recruit time series. Bootstrap analysis is carried out to determine confidence intervals on mean estimates of synchrony and the correlation statistics (for recruitment between sandeel grounds) are plotted against distance. Cluster analysis was conducted to determine the linkage between sandeel grounds. Finally, conclusions of synchrony in the spatial recruit time series are discussed.

2.2 Population Data PART 1

Before constructing a model of the Shetland sandeel stock, it is necessary to have some understanding of influences on population dynamics and how population estimates are generated. The biology and ecology of sandeels at Shetland were discussed in Chapter 1. Population increases occur due to the addition of juvenile sandeels, which are recruited to the exploited population (fished stock) in the summer following hatching (that is, as 0-group fish). The population decreases occur through natural mortality, *M*, and fishing mortality, *F*. Natural mortality refers to fish that die due to predation, disease or other natural causes, while fishing mortality is death caused by the fishery. The balance between all of these (assuming for now no immigration or emigration) will influence changes in population size. For example, if recruitment is low and mortality high then the population size will decline over time. A population model of the Shetland sandeel stock will need to incorporate functions for *F*, *M* and recruitment but the model represents the exploited (settled) population, pre-recruit mortality is not considered. Population estimates for Shetland sandeels are derived from catch-at-age estimates and survey data by an annual separable virtual population analysis (VPA) model assuming constant natural mortality (see below).

2.3 Virtual Population Analysis (VPA)

VPA is a technique that analyses catches from each year class over a number of years to estimate historic fishing mortality and stock numbers and involves a computationally intensive iterative procedure (see Megrey, 1989; Hilborn & Walters, 1992; King, 1995; Jennings *et al.*, 2001 for details). In other words, VPA calculates how many fish must have been in the sea to account for the number caught (Sparre, 1991). Each cohort (year class: fish in a stock born in the same year) is assessed individually in this model which makes no underlying statistical assumptions (Hilborn & Walters, 1992).

VPA involves working backwards from the most recent year using catch-at-age (or length) data from commercial landings. The inputs required for the model are the annual natural mortality coefficient *M* (which is assumed to be constant between years), the fishing mortality coefficient *F* in the most recent year (referred to as terminal *F*) and the catch, *C*, for each year. *M* and terminal *F* are estimated prior to running the model (see below). VPA uses the calculated numbers of fish in the cohort in year *t*, together with *C* and *M* in year *t-1*, in an iterative process to calculate *F* and so cohort numbers in year *t-1*. The results are used to estimate *F* and cohort numbers in year *t-2* and so on.

Age-specific natural mortality rates (*M*) must be estimated (or guessed) for VPA and it is assumed *M* is constant between years. Using an incorrect natural mortality rate may have a major impact on the estimated stock sizes in VPA. If *M* is too large then estimates of cohort size will be too large and if *M* is too small then cohort size will be underestimated (Hilborn & Walters, 1992). However, if exploitation is high (so $F > M$) then an incorrect *M* will have little impact on estimates as fishing mortality dominates (Hilborn & Walters, 1992). An incorrect terminal *F* estimate will have little effect on estimated parameters of younger age-classes as estimates of fishing mortality converge asymptotically with their true values when working backwards in the sequential procedure (Megrey, 1989). VPA does not supply a clear picture in the most recent fishing year as estimates of population size in this year depend on the estimate of terminal *F* (Megrey, 1989). The use of data supplied by 'tuning fleets', for example research vessels, allows predictions with greater confidence for recent population numbers and these data are used routinely with some VPA software such as extended survivors analysis (XSA; see Jennings *et al.*, 2001).

Fishing mortality rates for the stock at Shetland (mean *F* (0gp) = 0.074) are considerably less than natural mortality rates (mean *M* (0gp) = 0.800). VPA can produce reasonable estimates of fishing mortality on recent cohorts if the stock is heavily fished. Jennings *et al.* (2001) suggest, that as a rule of thumb, VPA works best when F/Z is between 0.5 and 1.0, where *Z* is the total mortality rate ($Z=F+M$). For 0-group Shetland sandeels the mean F/Z is only 0.08. Additionally, there are missing data years for the Shetland stock. Due to the scarcity or absence of catch data in the Shetland data set, an annual separable VPA model was developed by Cook & Reeves (1993) to produce population estimates.

2.4 Annual Separable VPA

The closure of the fishery over 1991-1994 and the subsequent low landings have led to a lack of suitable data for Shetland sandeel assessment models. As VPA works backwards sequentially a complete time series of data are required, missing data will stop historic population estimations. Sandeel assessments at Shetland are now carried out using an annual separable VPA, which allows estimation of all parameters, even if observations are missing in some years (Cook & Reeves, 1993; ICES, 1999). However, no recent population estimates for Shetland sandeels have been produced due to the poor quality of the input data (ICES, 2001).

In VPA, estimates of historic population numbers are produced simultaneously with historic fishing mortality estimates. There are eight age classes in the annual sandeel population estimates for which 24 years of fishery assessment data are available. These range from 0-group (fish which hatched that year) to the oldest age class, 7+, which contains all fish aged 7 and older. In any particular year, large number of the population are less then 3 years old (Figure 2.1). Due to the high natural mortality rates (Table 2.1), the probability of an individual fish surviving beyond a year is very small.

The annual separable VPA model used in recent years for stock assessment at Shetland was found to be highly sensitive to input options (Cook & Reeves, 1993; ICES, 1999). ICES (1999) warned that stock estimates resulting from the latest assessment can only be regarded as an indication of the overall trends in the stock and not of absolute levels. For VPA to be effective, it is normally required that exploitation rates are high (if most of the population are caught by fishermen than eventually most of the fish in each age class will have been landed and counted. This is more accurate than trying to estimate how many were eaten by predators). For Shetland sandeels, age-specific natural mortality rates are considerably larger than fishing mortality rates, so will have a proportionally greater influence on fish numbers, thus introducing high uncertainty.

Evidence suggests that some sandeels recruiting to the Shetland stock may originate from outside the system (Wright, 1996; see below). If this is the case, then the estimates produced by VPA will be affected. VPA assumes no net emigration or immigration. If net immigration occurs, then this will cause cohort sizes to be overestimated (Hilborn & Walters, 1992). This is particularly a problem if immigration occurs at older ages, as this will be magnified in the backwards sequential calculations. However, tagging studies (Popp Madsen, 1963 cited by Reay, 1970; Kunzlik *et al.*, 1986) have indicated that it is unlikely that settled (recruited) sandeels move between grounds so there will be no magnification of numbers backwards through the cohort.

2.4.1 Fishing Mortality Rates F

Fishing mortality refers to death due to capture by the fishery and is estimated from commercial catch data. Catch-at-age data are generated from biological information collected by sampling a small portion of the overall catch together with a measure of the total commercial catch (Megrey, 1989; Hilborn & Walters, 1992). The rate of decrease of a population due to a fishery can be expressed as:

$$\frac{dN}{dt} = -FN_t \qquad 2.1$$

where N is the number of fish at time t and F is the instantaneous fishing mortality coefficient (Beverton, 1994).

F varies between years depending on factors such as the size of the fishing fleet, the biomass of fish available to the fishery and the effort with which the stock is fished. Fishing mortality rates for Shetland sandeels declined in the 1980s as the stock declined and economics forced fishermen to turn to other species. There is no fishing mortality over 1991-1994 as the fishery was closed and, since reopening, fishing mortality has been extremely low. Fishing mortality rates for sandeels at Shetland over 1974-1983 were calculated by VPA (Table 2.2), whereas after 1983 an annual separable VPA model was used (Table 2.3).

2.4.2 Natural Mortality Rates M

Natural mortality rates refer to death by predation (excluding fishing), disease and other natural causes. Death due to predation is a major component of natural mortality (Sissenwine, 1984), particularly for young fish (Bax, 1998). Natural mortality generally decreases with age, as larger fish have fewer predators than smaller fish. The maximum size of prey taken by a marine predator is determined by the "gape" of the predator (for example, bill gape for seabirds, mouth gape for fish). As the predator increases with size, so the size range of available prey increases, although predators may actively select a particular size range (Bax, 1998). Thus predation pressure is highest on small fish, as these are available to a greater range of predators than large fish.

As discussed above, using an incorrect natural mortality rate may have a major impact on the estimated stock sizes in VPA. Producing estimates of natural mortality is problematic as it is difficult to observe and quantify fish dying from natural causes, therefore an 'educated guess' is usually taken. Available data, such as information on predator biomass and diet composition, may be used in estimating natural mortality. The instantaneous rate of decrease of a population due to natural causes can be expressed as:

$$\frac{dN}{dt} = -MN_t \qquad 2.2$$

where N is the total number of fish at time t and M is the instantaneous natural mortality coefficient (Beverton, 1994).

Natural mortality rates for the stock assessment of sandeels at Shetland are assumed to be the same as those used in the main North Sea assessments (Table 2.1; ICES 1999). In other words, it is assumed that predation pressure on sandeels around Shetland is generally similar to the average predation pressure encountered by sandeels across the North Sea. Semi-annual estimates of natural mortality for North Sea sandeels are derived from multispecies virtual population analysis (MSVPA). MSVPA, which is a direct extension of VPA, was developed for exploited fish populations in the North Sea (see Pope, 1991; Sparre, 1991; Stokes, 1992; Magnússon, 1995 for further details). MSVPA incorporates predator-prey interactions between certain fish species. Basically, MSVPA calculates how many fish must have been in the sea to account for the number caught by fisheries and found in the stomach contents of predators (Sparre, 1991). The model includes four prey fish species (sprat *Sprattus sprattus*, herring *Clupea harengus*, Norway pout *Trisopterus esmarkii* and sandeel *Ammodytes* sp.), two predator species (saithe *Pollachius virens* and mackerel *Scomber scombrus*) and three species which are incorporated both as predators and as prey (cod *Gadus morhua*, whiting *Merlangius merlangus* and haddock *Melanogrammus aeglefinus*; Stokes, 1992; Magnússon, 1995). Predation interactions between fish species were determined by extensive stomach sampling programs carried out in 1981 and 1991.

MSVPA does not require the natural mortality rate to be estimated independently as an input into the model, as is required for VPA. Instead natural mortality is split into two parts: *M1* and *M2*, where *M2* is the predation mortality due to predators included in the model and *M1* is residual natural mortality (Stokes, 1992; Magnússon, 1995). *M1* is the natural mortality caused by predators other then the MSVPA predators and by disease and other natural causes. *M1* is estimated externally (that is, it is required as model input), as in VPA, but *M2* is calculated within the model. The model has provided insight into the magnitude of predator-prey relationships and led to revised natural mortality rates, which for the prey species were generally higher then previously assumed and were variable from year to year (Pope, 1991; Stephenson, 1997).

MSVPA has produced annual estimates of age-specific natural mortality rates for sandeels in the North Sea. For stock assessment of North Sea sandeels, natural mortality rates are taken as an average of the rates calculated by MSVPA (ICES, 1999). The Shetland sandeel stock is assessed on an annual basis, rather than semi-annual as in North Sea assessments. Therefore, the half-year *M* values used in North Sea assessments are combined to produce annual values of *M* for Shetland assessments (Table 2.1).

It was assumed that the average natural mortality for sandeels at Shetland is similar to that in others areas of the North Sea. However, very large concentrations of seabirds are found around Shetland during the main breeding season (June-July), many of which are dependent on young sandeels to feed their chicks (Monaghan, 1992). Coupled with the fact that sandeel fishing grounds occur very close inshore around Shetland (within breeding seabird foraging ranges), localised natural mortality rates for Shetland may vary from those for the North Sea as a whole (Bailey *et al.*, 1991).

Consumption of sandeels by seabirds can be high around Shetland, a bioenergetics model produced by Furness (1978) indicated that seabirds at Foula (Shetland) may consume 20-40% of small fish (predominantly sandeels) within 45km of the colony. In contrast, considering the whole North Sea, seabird consumption averages only about 4% of the sandeel stock (Furness & Tasker, 1997). In the whole North Sea, predatory fish probably consume a far greater biomass of sandeels than seabirds (Furness & Tasker, 1997) and so mortality due to consumption by seabirds probably has less effect on stock numbers. This may also be the case around Shetland, however calculations conducted by Furness (1990) for consumption of sandeels at Shetland over 1981-1983 indicated that predation by seabirds may be comparable, or greater, than consumption by predatory fish. Furness (1990) also suggests that, as the Shetland sea area is considered more productive than many other parts of the North Sea, predation by fish may also be higher here. However, it would be reasonable to expect sandeel production to be higher also, which does not appear to be the case.

Due to the high density of seabirds at Shetland, it may be reasonable to conclude that natural mortality rates for sandeels are higher around Shetland than in the whole North Sea. But, it is not possible to simply alter the value for *M* used in the basic population models. VPA requires *M* as an input to estimate population size, therefore changing *M* would alter the population estimates produced for Shetland sandeels. As the models are using population estimates produced by VPA, it was necessary to include *M* at the rates used in assessments.

2.5 External Recruitment

The Shetland sandeel population is assessed as a separate stock from North Sea sandeel fisheries, as Shetland sandeels show a relatively slow growth rate compared to the main North Sea stocks and the grounds are considered isolated from those in the North Sea (Bailey *et al.*, 1991). There is increasing evidence that the Shetland population is not a separate stock but forms part of a much larger population of North Sea sandeels (Nævdal *et al.*, 1996; Wright, 1996), this will have implications for stock assessment.

The widespread abundance of sandeel larvae in offshore waters in some years (Langham, 1971a; Wright & Bailey, 1993) suggests the sandeel population at Shetland is not isolated from neighbouring populations. Larval surveys in Scottish waters have indicated the presence of several spawning areas around the Shetland Isles and the Orkney region (Wright & Bailey, 1993) and larvae have been found all around the Scottish coasts (Langham, 1971a). Analysis of aggregated data from routine plankton surveys over 1961-1974 indicated that the waters to the north and west of Orkney can be considered a major spawning area for sandeels as larval production here far exceeds that near Shetland (Wright & Bailey, 1993). Unfortunately, the sandeel population around Orkney is unfished, as the grounds are not suitable for trawling, therefore there are few data for the Orkney population.

In certain years, there may be an influx of external recruits into the Shetland system (Wright, 1996) but the frequency and size of this input is unquantified. Similarly, advection of larvae and pre-settled recruits away from Shetland may occur. As this is a loss to the population, assuming the numbers lost by advection are related proportionally to sandeel density, it can be considered as part of natural mortality *M*. But if there is a high loss of recruits from Shetland, compared to the North Sea, then *M* may be underestimated for Shetland. However, if immigration at Shetland is equal to emigration, there will be little effect on population estimates. Proctor *et al.* (1998) adapted a 2-dimensional sea circulation model to simulate the transport of sandeel larvae on the north-west European shelf. This indicated that the loss of pre-recruits from the Shetland area is probably less then the input from other areas. As immigration occurs before recruitment to the Shetland stock and fishery, this will have little influence on the VPA model but will affect the stock-recruitment relationship at Shetland (see Chapter 5 for further discussion).

2.6 Characteristics of Population Data

It is intended to produce stochastic models that reproduce the characteristics of the historical population time series. Therefore, it was necessary to choose population characteristics to compare model output with population assessments around Shetland. The two distributions chosen were recruitment numbers and SSB. As these are short-lived fish (up to eight years) with high natural mortality rates, 0-group fish (recruits) make up a considerable portion of the total stock biomass and usually account for a large proportion of annual landings by the fishery (Kunzlik, 1989). Recruitment is a crucial component of the models, as large fluctuations in the number of recruits are thought to be a major factor driving the high variation in year class strength. The second set of characteristics selected were those of the SSB distribution, which will enable comparison of the population structure. Before constructing a model of the population dynamics of the Shetland sandeel stock, it was necessary to investigate the underlying distributions and characteristics of the SSB and recruitment time series.

2.6.1 Recruitment

The highest recruitment on record occurred in 1997, when it was estimated 330 $\times 10^9$ fish recruited to the stock around Shetland (Figure 2.2b). In 1987, the lowest recorded recruitment of 3.7×10^9 recruits occurred, producing a ratio of 89:1 for largest to smallest recruitment. This represents a large range in variation but was within ranges found by Hennemuth *et al.* (1980) in eighteen selected fish stocks (ranges of 92:1 and 100:1 were found in recruit time series of George's Bank haddock and North Sea haddock respectively).

A Kolmogorov-Smirnov 1-sample goodness-of-fit test (hereafter K-S test) indicted the recruitment distribution could be considered normal ($P=0.229$, $Z=1.041$) with a mean of 76 ± 73 $\times 10^9$ (Figure 2.3a). However, the shape of the recruitment histogram suggested this distribution could be more appropriately described as lognormal (Figure 2.4b). The recruit data were natural log-transformed and retested for normality with a 1-sample K-S test. This indicated the distribution could be considered lognormal ($P=0.813$, $Z=0.636$) and confirmed our suspicion that a lognormal distribution was more appropriate (P(lognormal) > P(normal)). Back-transforming the mean produced a median recruitment of 48.4 x10^9 fish.

An extremely large recruitment occurred in 1997 (330 x10^9 fish) and this was skewing the data distribution to the right (Figure 2.3a). The 1997 estimate, being recent, has a high amount of uncertainty (see VPA section) but high numbers of 0-group fish were caught during research surveys. A mean of 3,129,222 0-groups per 30 minute tow was caught in 1997 compared to the average catch of 648,961 0-groups per 30 minute tow over 1974-1997 inclusive (excluding 1987 and 1995 for which no data exists; ICES 1999). One question that needs to be addressed is: was the occurrence of the extremely large recruitment in 1997 a freak event? If 1997 is considered a freak event then a normal distribution would be more suitable then a lognormal distribution to describe the data.

The data point representing 1997 in each distribution was standardized to find the normal deviate using Equation 2.3 (Zar 1999):

$$Z = \frac{X_i - \mu}{\sigma} \qquad 2.3$$

where Z is the normal deviate, X_i is the value for 1997, and μ and σ are the mean and standard deviation of the distribution respectively.

The proportion of the distribution which was greater than X_i was determined from an appropriate statistical table (Zar, 1999). For the normal distribution, the probability of obtaining a value of 330 x 10^9 (1997 value) or greater was 0.03%. For the lognormally distributed data, the probability of obtaining the corresponding value or greater was 3.75%. Thus in a series of 24 years of recruit data, it would be expected that 0.9 years would have a value of 330 x10^9 or above in the lognormal distribution and 0.01 years in the normal distribution. In the historical data, 1 year of 24 had a value of 330 x10^9 or greater which corresponds to the expected value from the lognormal distribution. Thus, in the absence of further information, it was decided to assume the recruit distribution was lognormal.

Hennemuth *et al.* (1980) used K-S tests to analyse the recruitment distributions of eighteen fish stocks for fits to normality and lognormality. It was found that, in most cases, the log transformed data gave a considerably better to normality than the untransformed data and the null hypothesis (that the data are normally distributed) was rejected for only one stock. Therefore, assuming lognormality for the Shetland sandeel recruit data may not be a bad idea. It should be remembered that the sample size in the tests was only 24, so the likelihood of a departure from normality being identified is reduced compared to larger data sets. Also, only two distributions were considered (normal and log-normal) - there are other probability functions, such as a gamma distribution, which may be suitable to describe the data.

2.6.2 Spawning Stock Biomass (SSB)

Spawning stock biomass (SSB) is defined as the total biomass of all reproductively mature fish. Sandeels generally mature as 2-group fish (Gauld & Hutcheon, 1990) so it is assumed, for assessment purposes, that 100% of fish aged 2 and above spawn and 0% of 0-group and 1-group fish (ICES, 1999). However, larger fish may mature earlier and a few smaller fish may mature later (Macer, 1966; Gauld & Hutcheon, 1990). Values for maturity were determined from biological sampling at Shetland by FRS (Gauld & Hutcheon, 1990). Over 1974-1997 inclusive, SSB varied between 28,000 – 246,000 tonnes with a mean of 126,800 tonnes (Figure 2.2a).

A K-S 1-sample test was used to determine if the SSB distribution could be considered normally or lognormally distributed (Figure 2.4; Zar 1999). The K-S test indicated that the distribution could be considered normally distributed (P=0.997, Z=0.404). The SSB data were then natural log-transformed and the K-S test repeated. This indicated that the distribution could also be considered lognormally distributed (P=0.692, Z=0.712) with a median corresponding to 111,100 tonnes. SSB showed a higher probability of a normal distribution than lognormal (P(lognormal) > P(normal)), therefore it was assumed the actual distribution was normal.

SSB is calculated as:

$$S = \sum_{i=2}^{7} N_i W_i \qquad 2.4$$

where S is spawning stock biomass, i is the age class of sandeel, N_i is the number of sandeels in age-class i and W_i is the average weight of a sandeel in age class i.

Weight-at-age, W (average weight of a fish in an age class), was taken from the sandeel assessments at Shetland (ICES, 1999; Table 2.4). These represent the long-term mean weight-at-age from the first half-year catches - it was assumed that weight-at-age was constant between years. This is highly unlikely as weight-at-age will be influenced by environmental factors such as food availability. Evidence for differing growth rates over 1990-1992 was shown by Wright (1996). Wright analysed the length-frequency distributions, and also the age composition from daily otolith increments, of 0-group sandeels present around Shetland in June and found that 0-groups tended to be larger in 1991.

It is assumed for the Shetland sandeel assessments that age at maturity and fecundity are constant and independent of density and all fish aged two and above reproduce. This is probably not the case so may contribute to the apparent lack of relationship between spawning stock biomass and recruitment (Figure 1.7; Sissenwine, 1984). There is evidence that some sandeels may mature early, as 1-group fish, while others may delay maturation (Macer, 1966; Gauld & Hutcheon, 1990). This may alter the perceived stock recruit relationship based on the assumption that all fish aged two and above are reproductively mature. For example, if 20% of 1-group fish spawn each year then the spawning stock biomass may be greatly underestimated in some years (Figure 2.5). Alternatively if, for example, 20% of 2-group sandeels delay spawning then the SSB will be overestimated (Figure 2.5). Figure 2.5 assumes that the percentage of sandeels maturing early or delaying maturity is constant between years. This assumption is unlikely as these percentages will vary between years depending on factors such as environmental conditions, food availability and/or density of adult sandeels. As the models will be compared to the historical data set it was assumed, for this thesis, that 100% of fish aged two and above spawn. Furthermore, without estimates of the percentages maturing at age, it is not possible to explore the effects on the stock-recruit relationship.

2.7 Spatial synchrony PART 2

A seminal work on synchronous fluctuations of populations over large areas was that of Moran (1953). Moran found that when captures of lynx (*Lynx canadensis*) in Canada were split into regions, strong synchronisation between even widely separated areas became clear. Moran hypothesised the synchrony was the effect of large scale climatic perturbations and showed captures of lynx were related to weather conditions. The hypothesis has become known as the *Moran effect*. Subsequent evaluations (and documentation) of synchrony in animal populations include mammalian species (such as ermine, *Mustela* erminea; muskrat, *Ondatra zibethica* and red fox, *Vulpes vulpes*) in Canada (Swanson & Johnson, 1999), species of mammals, birds & fish in Finland (Ranta *et al.*, 1995; Ranta *et al.*, 1997), bird populations in Britain (Paradis *et al.*, 2000), butterfly populations in Britain

(Pollard, 1991; Sutcliffe *et al.*, 1996) and soay sheep, *Ovis aries*, in the St Kilda archipelago (Grenfell *et al.*, 1998).

Synchrony in population dynamics is hypothesised to arise through two main factors (see Ranta *et al.*, 1995; Swanson & Johnson, 1999). Firstly, dispersal of individuals from regions of high density will increase population size in adjacent areas thus synchronising regional dynamics. Secondly, large scale climatic perturbations can synchronise density changes in populations over large areas (Moran effect). Plotting a measure of synchrony of population pairs against the distance between them will show the synchrony-distance relationship. Model simulations produced by Ranta *et al.* (1995) revealed that dispersal produces a negative relationship between distance and degree of synchrony, and local variation in density dependant structure. Whereas, although the Moran effect alone can cause synchrony, there is no trend with distance. Dispersal and the Moran effect acting together tended to produce a negative correlation between the degree of synchrony and distance apart, which is indistinguishable from the results produced by dispersal alone.

Grenfell *et al.* (1998) analysed time series from sheep populations on two islands in the St Kilda archipelago. There is no migration between these populations but population fluctuations were highly synchronised. Model simulations indicated large-scale weather variations account for part of the high degree of environmental correlation needed to produce the population synchrony. However, climatic factors may not necessarily act with the same force everywhere. Later model simulations by Ranta *et al.* (1999) indicated that a spatially autocorrelated disturbance (such as many climatic factors) can produce a negative relationship between synchrony and distance.

Studies of synchrony in marine populations are inherently more problematic due to the difficulty of collecting comparable data. Recently, analysis has been conducted on a number of species. Ranta *et al.* (1995) included Baltic whitefish in their studies and found a correlation of –0.43 between synchrony and distance with a mean synchrony of 0.44. Zheng (1997) calculated correlation coefficients for recruitment time series of herring stocks world-wide. Generally, significant correlations were found between stocks in the same region that could not be explained by spawning biomass, so environmental forcing on a regional scale may be important.

Fox *et al.* (2000) analysed recruitment time series for plaice (*Pleuronectes platessa*) stocks around the United Kingdom. Tests for synchrony between pairs of stocks all showed positive correlation and synchrony was strongest between neighbouring stocks. Tests for correlation between plaice recruitment and local sea surface temperature from different months of the year revealed negative relationships with the strongest correlations occurring between February and June (recruits in egg and larval stages). It seemed likely that key processes affecting recruitment are operating during the egg and larval stages through changes in predation pressure.

2.8 Analysis of Synchrony at Shetland

There are a number of discrete exploited sandeel grounds around Shetland and these can be considered to be sub-populations as, once-settled, tagging studies have indicated sandeels do not move very far (Kunzlik *et al.*, 1986). Catch data are derived from landings at the local fishmeal plant and no account is taken of the fishing grounds from which catches originate (Wright, 1996), therefore it is not possible to use these data for analysis of synchrony. However, research surveys have been conducted during June and July on many of the grounds since 1984 and from these the average number of fish per timed tow has been determined (ICES, 1999). Unfortunately, there were no similar data available for sandeel populations neighbouring Shetland, such as around Orkney, or for sub-populations on unexploited grounds around Shetland.

Time-series of recruitment on 18 sandeel grounds around Shetland were available, ranging from East and West Fair Isle in the south, up to Balta and Fethaland in the North and from the east mainland, out to Foula (Isle of) in the west (Figure 2.6). For three of the grounds (Colsay, South Fethaland and South Foula) there were six or less data points available, therefore these grounds were excluded from analysis. For the rest, data were generally available from 1984 to 1997 inclusive excluding 1987 and 1995 when no research surveys were conducted (thus giving 12 data points). A few grounds also had further missing years. Plotting the time series indicated some grounds may be synchronised (Figure 2.7). Generally, Mousa (heavy line Figure 2.7) always appeared to contain high numbers of 0-groups compared to the other grounds but this was not the case when considering the 1+-groups series.

For each possible pair of grounds, the degree of synchrony and geographical distance between them was determined to evaluate the synchrony-distance. Kendall's rank-order correlation (Zar, 1999) was used with ln-transformed data for each of the two data sets (0-group and 1+-groups). The distance between grounds was estimated and calculated synchronies plotted against this to give the spatial extent of synchrony.

Bootstrapping (Efron & Gong, 1983, also see Hilborn & Mangel, 1997) was used to determine if observed mean synchrony was significantly different from zero and to set confidence limits (Ranta *et al.*, 1995; Paradis *et al.*, 2000). Bootstrap analyses samples, with replacement, from the data set to be analysed to generate a number of new "replicate" data sets. The parameters of interest are estimated for each bootstrap data set to obtain probability distributions for each parameter. From these, confidence intervals can be calculated.

Firstly, it was necessary to determine the geographical distance between the sandeel grounds. An outline map of the Shetland area was retrieved from JEBCO Atlas of the World Oceans CD ROM and imported to ArcInfo GIS 3.2. The latitude and longitude of some sandeel grounds were supplied by P. Wright (Table 2.5) and these were pasted directly onto the Shetland map using the appropriate tool in ArcInfo. For the remaining grounds, the position of the ground was determined by eye from ordinance survey maps and from a map of sandeel grounds shown by Wright (1996). These were also added to the map in ArcInfo.

There were two possible ways to calculate the distance between grounds. Firstly, linear distance between fishing grounds can be calculated directly by taking the ordinates of each ground (supplied by ArcInfo) and using Pythagorus theorem. Secondly, the shortest sea route could be determined between grounds. As fish cannot disperse across a landmass, the shortest sea route is a more realistic measure of distance. For example, the shortest linear distance between Trink (TRI) and Mousa Sound (MOU) is only 11km across land but the shortest distance by sea is 42km. It is possible in ArcInfo to place routes along the coastline on the map but the coastline for Shetland is extremely convoluted and this may overestimate some distances. Instead, the network analyst function was used to draw shortest sea routes along the coast between pairs of sites and this returned estimates of distances in km. Where two sites were separated by sea only (for example, Trink and Ham'o Foula), a straight line was used to connect them. Where a bay encroached on the coastline between two sites, the line crossed the mouth of the bay. Distances between each pair of sites were determined (Table 2.6).

To determine synchrony, both data sets were natural log transformed. Due to missing data points, it was not possible to determine trends in the data. The total recruitment time series for Shetland showed no trend (see Chapter 3), so it was assumed the series for the individual grounds also contained no trends. Where value in the raw data was a zero (not a missing data point), it was assumed that fish were present but at extremely low levels. To allow analysis (as it is not possible to ln-transform a zero), zeros were replaced with a value equal to half the lowest number recorded over all the grounds. Correlations between pairs of data series were determined in SPSS. Kendall's rank-order correlation (Zar, 1999) was selected as this made no assumptions about normality in the underlying data sets. The correlation statistic, T, and level of significance for each of pair of time series (91 possible pairs) was determined for each data set (Tables 2.7 & 2.8).

For 1+ group data, positive correlations of 10 of the series pairs (11%) were significantly different from zero at P=0.05. T varied between –0.500 (Fethaland vs. Boddam Voe) and +0.636 (West Fair Isle and Breakon, significant at P(0.01)). Nineteen of the correlations for 0-group series (21% of total correlations) were significantly different from zero at P=0.05. T statistics varied between –0.289 (Braeside vs. East Fair Isle) and +0.837 (Boddam Voe vs. West Fair Isle, significant at P(0.01)).

Bootstrapping (Efron & Gong, 1983) was used to determine confidence limits and test for significant difference from zero (Paradis *et al.*, 2000). For each bootstrap simulation, 15 grounds were selected at random with replacement from the original 15 grounds. The correlation statistic for each possible set of grounds was determined and the mean calculated and stored. For each set of data, 5000 bootstrap simulations were performed. The resulting histograms of mean synchrony with fitted normal curves are shown in Figure 2.8. Interestingly, the mean of the historical data was lower than the bootstrap mean in both cases but was within the 95% confidence limits (Table 2.9). This is probably due to the occasional presence of negative correlations in the paired time series (none of these were significant). Large negative correlations will reduce the mean (as, for example, the distance between 2 and 5 is much smaller than that between –2 and 5). Sampling at random with replacement, may result in the selection of no or only a few cases for which correlations are negative, therefore the estimates of the mean will be much higher.

For each set of data, correlation statistics T were plotted against distance between sites (Figure 2.9). A trendline was fitted to each graph and the R^2 statistic calculated. The fitted trendlines showed no variation with distance for either of the data sets (0gp:-0.001; 1+gp:+0.001) and the R^2 values were also extremely low (0gp: 0.007; 1+gp: 0.011). Regression analysis indicated none of the fitted trendlines were significantly different from a slope of zero therefore it was concluded none of the data sets show any decline in synchrony with distance.

_ As synchrony exists and there is no trend with distance, we can conclude that fluctuations in the sandeel population are probably due to large scale environmental perturbations (Moran effect) and/or to high dispersal rates between grounds. Without further data, it cannot be determined which of these effects, if either, is dominant. It is highly likely that large scale environmental perturbations are influencing recruitment at Shetland. Arnott (unpublished) showed that, after accounting for density-dependent population effects, a significant negative correlation exists between recruitment in North Sea sandeels and the North Atlantic Oscillation winter index - an important atmospheric pressure gradient associated with climatic fluctuations in the North Atlantic. However, high dispersal rates of recruits between Shetland grounds may also occur. Repeated acoustic transects carried out by FRS in June 1991 indicated a net northward shift of around 8km in 5 hours in the peak density of 0-group sandeels between Sumburgh and Fair Isle (Wright & Bailey, 1993). Further, a drifting drogue deployed in the vicinity of south-east Shetland during June 1991 moved rapidly south and north along the east coast depending on the position of the tidal cycle when released (Wright & Bailey, 1993).

The numbers of recruits (0-groups) sampled at Mousa Sound always appear to be high compared to those on other grounds (Figure 2.7). It has been hypothesised that recruits immigrating from Orkney spawning grounds colonise Mousa Sound first and, in years of high recruitment, 'excess' recruits spread out around Shetland from here (Wright & Bailey, 1993). Effectively, Mousa may be acting as a "catchment" for external recruits. If this were the case, it is expected that recruits on Mousa and neighbouring grounds would be relatively highly synchronised.

Of the five grounds on the south-east mainland – Braeside (BRA), Mousa sound (MOU), Baas (BAS), Boddam Voe (BOD) and Grutness (GRU) – only two pair combinations showed significant correlation between 0-group time series. Mousa sound and Braeside could be considered synchronised at a probability level of 0.05 and Baas and Grutness at a probability level of 0.01. Could this be indicative of external recruits moving north along the coastline?

2.9 Cluster Analysis

Hierarchical cluster analysis in SPSS with Pearson's correlation was used to determine the linkage between grounds of 0-group abundance. The resulting dendogram revealed four groups at a distance of 9 (Figure 2.10). Baas (BAS) off the south-east mainland formed 1 group, Grutness (GRU), Mousa sound (MOU) and Braeside (BRA) formed a second group. These three grounds are also off the south-east mainland, but Grutness is separated from the other two by Boddam Voe and Baas. Boddam Voe and Baas appear to be a little further inshore then the grounds in the second group so local current flow could be influencing dispersal here.

The two Fair Isle grounds (EFI and WFI) form a third group with Boddam Voe (BOD) in the south-east mainland while the grounds at Foula (SFO and HAM), off the west and east mainland (TRI and SSA) and in the north (SVO, FET, BRE and BAL) form the remaining group.

2.10 Conclusions from Synchrony & Cluster Analyses

The conclusions that can be drawn from studies of synchrony are that population processes in different areas are rarely independent of each other (Ranta *et al*,. 1995). Populations with synchronous fluctuations over large areas have a high risk of population extinction (as all areas decline simultaneously; Ripa & Lundberg, 1996; Heino *et al.*, 1997). Could this have been seen around Shetland in late 1980s when sandeel recruitment on many grounds was extremely low? The effects of fluctuations in population size may be exaggerated in sandeels compared to other studies (like birds and mammals which live longer) as a large proportion of the stock consists of recruits.

Like sandeels, marine benthic invertebrates are relatively sedentary when settled so dispersal of pre-settlement stages are important for population migration and expansion. Dispersal of larvae and juvenile stages of marine invertebrates, like the dungeness crab *Cancer magister* and the red sea urchin *Strongylocentrotus franciscanus*, have been shown to have a critical influence on population dynamics and the effectiveness of spatial management policies (Botsford *et al.*, 1998).

Estimated recruitment at Mousa Sound showed little variation over 1984-1997 inclusive varying between 33 – 2250 million fish. Even during the late 1980s recruitment was still high here (estimated 1800 million recruits in 1989, second largest density over the years considered). Cluster analysis revealed the group of grounds off the south-east mainland, which include Mousa Sound are linked and the synchrony analysis revealed that Mousa Sound and Braeside and Grutness and Boddam Voe could be considered significantly synchronised. These regions also had high densities of 0-groups in 1989, when the density at Mousa was extremely high, although densities were extremely low, or virtually nil, in 1988 and 1990. The drifting drogue, deployed by FRS in the vicinity of south-east Shetland during June 1991 indicated that, on reaching Mousa, the drogue remained in this area (Wright & Bailey, 1993). A further deployment, releasing the drogue near Mousa lasted for 30 hours, during which time the drogue remained in this area. This suggests that local circulation features around Mousa will lead to the accumulation of passively drifting particles in this area and could account for the high levels of recruits found in Mousa over the study years. When recruitment is extremely high in this area, as in 1989, recruits may migrate (actively) to neighbouring areas.

Wright (1996) proposes that the sandeel grounds around Orkney produce recruits that enter the Shetland system and stock changes around Shetland, in part, reflect this pre-recruit immigration. A similar occurrence of a lesser harvested population acting as a sink (Gunderson *et al.*, 2001) thus ensuring the persistence of a heavily fished population has been proposed by Fogarty (1998) for the American lobster *Homarus americanus.*

Without further information, such as weekly abundance estimates of recruits on grounds or local measures of climatic factors, it is impossible to determine the underlying causes of population fluctuations in sandeels. If the immigration of external recruits is crucial for the persistence of the Shetland sandeel population, and is leading to synchrony in population abundance, then research needs to concentrate on the external recruit spawning grounds and the larval dispersal paths.

Fluctuations may also be the result of wide-scale environmental forcing and correlating recruitment with measures of environmental parameters, for example sea surface temperature or salinity, may indicate possible influences. Drawing conclusions from significant results when correlating fish stock recruitment and environmental parameters, especially when only considering one population, is risky. This subject is considered in detail by Myers (1998) who also suggests approaches to improve research in this area. Myers re-examined the success of previously published environment-recruitment correlations with new data and found very few were verified on retesting. As Myers notes, in an exploratory analysis it is difficult not to find environmental variables that are nominally statistically significant. Myers suggests the most reliable data for estimating recruitment are from research surveys independent of the fishery (as otherwise trends in abundance may be an artefact of fishing).

While population estimates for Shetland sandeel may have high uncertainty, additional evidence of fluctuations in sandeel populations may be drawn from predator species, namely seabirds. Shetland is important for large numbers of breeding seabirds, many of which rely on the young age-classes of sandeel during the breeding season (Furness, 1990). Seabirds are considered useful as indicators of marine food supplies (Cairns, 1987). Studies at kittiwake colonies in Scotland indicate that sandeels are an important part of the kittiwake diet (Harris & Wanless, 1990; Harris & Wanless, 1997). Kittiwakes in the North Sea are considered to be relatively sensitive to changes in sandeel availability (Harris & Wanless, 1997; Furness & Tasker, 2000).

The reduced pattern of breeding success of kittiwakes around Shetland in 1988 was repeated elsewhere – at colonies on the east and west coasts of Scotland and on the Isle of Man (Harris, 1989; Harris & Wanless, 1990). Evidence suggests chicks died mainly due to starvation or exposure after being left unprotected (while parents were away on long foraging trips). Harris & Wanless (1990) suggest (in some areas) that the breeding success of kittiwakes may be a reasonable indicator of sandeel abundance in the water column. Harris & Wanless conclude, the failure of kittiwakes in Scotland over a large area in the late 1980s appears to be due to a shortage of prey (sandeels) and this was likely to have been caused by some widespread environmental or oceanographic factor.

2.11 Chapter Summary

- Fishery assessments of Shetland sandeels can only be regarded as an indication of the overall trends in the stock and not of absolute numbers (ICES, 1999).
- Cluster analysis of recruitment time series indicated generally the grounds on the south-east mainland could be considered more similar to each other than to the other grounds.
- Recruitment on sandeel grounds around Shetland appear to be synchronised suggestive of either high dispersal and/or large-scale climatic perturbations.

Table 2.1. Semi-annual natural mortality rates (*M*) for sandeels in the North Sea and annual rates for sandeels at Shetland (from ICES 1999).

Age	North Sea *M* Jan-Jun	 Jul-Dec	Shetland (annual) *M*
0		0.8	0.8
1	1.0	0.2	1.2
2	0.4	0.2	0.6
3	0.4	0.2	0.6
4	0.4	0.2	0.6
5+	0.4	0.2	0.6

Table 2.2. Estimates of annual mean *F* over age classes 1 and 2 produced by VPA for Shetland sandeels and seasonal XSA (SXSA) for North Sea sandeels (from ICES 1999).

Year	Shetland Mean F (1-2)	North Sea Mean F (1-2)
1974	0.073	
1975	0.134	
1976	0.189	0.550
1977	0.214	0.540
1978	0.222	0.680
1979	0.094	0.640
1980	0.160	0.680
1981	0.287	0.680
1982	0.307	0.620
1983	0.224	0.450

Table 2.3. Estimates of annual mean *F* over age classes 1 and 2 produced by annual separable VPA (Cook & Reeves 1993) for Shetland sandeels and seasonal XSA (SXSA) for North Sea sandeels (from ICES 1999).

Year	**Shetland Mean F (1-2)**	**North Sea Mean F (1-2)**
1984	0.186	0.350
1985	0.088	0.920
1986	0.099	0.530
1987	0.046	0.440
1988	0.061	0.660
1989	0.042	0.540
1990	0.044	0.780
1991	0.000	0.700
1992	0.000	0.450
1993	0.000	0.340
1994	0.000	0.520
1995	0.012	0.430
1996	0.009	0.530
1997	0.023	

Table 2.4: Stock weights at age for sandeels at Shetland (ICES 1999)

Age	Weight (g)
0	0.746
1	3.095
2	5.409
3	8.585
4	11.143
5	13.705
6	15.605
7+	21.254

Table 2.5. Longitude and latitude of sandeel grounds around Shetland (supplied by P. Wright). Three letter code for each ground is shown.

Ground	Code	Latitude	Longitude
Mousa Sound	MOU	59.97	-1.17
Braeside	BRA	60.00	-1.16
Baas	BAS	59.94	-1.24
Boddam Voe	BOD	59.91	-1.25
Gruting Ness	GRU	59.89	-1.25
Sands Voe	SVO	60.60	-1.33
Balta	BAL	60.72	-0.74
Colsay	COL	59.96	-1.38
Trink	TRI	60.03	-1.33

Table 2.8 Kendall's rank-order correlation statistic calculated between 1+-group time series for sandeel grounds around Shetland (see Figure 2.6 for key to ground codes). Values above the diagonal are Kendall's T statistic. Data below the diagonal refers to the significance of the tests. NS=not significant, 0.050=significant at P(0.05), 0.010=significant at P(0.01).

	BAL	BAS	BOD	BRA	BRE	EFI	FET	GRU	HAM	MOU	NFO	SSA	SVO	TRI	WFI
BAL	1.000	0.370	-0.145	0.194	0.249	0.083	0.304	0.398	0.369	0.132	0.381	0.200	0.066	0.261	0.181
BAS	NS	1.000	0.197	0.222	0.219	-0.188	0.170	0.359	0.267	0.326	0.344	0.362	0.233	0.224	0.449
BOD	NS	NS	1.000	0.071	-0.028	-0.366	-0.500	-0.167	0.000	0.000	-0.254	0.278	-0.167	-0.071	0.357
BRA	NS	NS	NS	1.000	-0.167	-0.130	-0.386	0.147	0.368	0.477	0.073	0.000	-0.183	0.270	-0.270
BRE	NS	NS	NS	NS	1.000	0.400	0.352	0.185	0.278	0.168	0.400	0.388	0.107	0.164	**0.636**
EFI	NS	NS	NS	NS	NS	1.000	0.426	0.431	0.037	0.015	0.462	-0.016	0.107	-0.073	0.257
FET	NS	NS	NS	NS	NS	NS	1.000	0.463	-0.092	-0.257	0.315	-0.093	0.037	-0.045	0.315
GRU	NS	NS	NS	NS	NS	NS	NS	1.000	0.112	0.076	0.523	0.016	0.107	0.110	0.367
HAM	NS	NS	NS	NS	NS	NS	NS	NS	1.000	0.500	0.204	0.396	0.204	0.574	0.278
MOU	NS	NS	NS	0.050	NS	NS	NS	NS	0.050	1.000	0.290	0.154	0.182	0.564	0.164
NFO	NS	NS	NS	NS	NS	0.050	NS	0.050	NS	NS	1.000	0.264	0.382	0.273	0.527
SSA	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	1.000	0.492	0.352	0.389
SVO	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	0.050	1.000	0.236	0.491
TRI	NS	NS	NS	NS	NS	NS	NS	NS	0.050	0.050	NS	NS	NS	1.000	0.164
WFI	NS	NS	NS	NS	**0.010**	NS	NS	NS	NS	NS	0.050	NS	0.050	NS	1.000

Table 2.6. Shortest sea distances between pairs of sandeel grounds around Shetland (see Figure 2.6 for key to labels)

	BAL	BAS	BOD	BRA	BRE	EFI	FET	GRU	HAM	MOU	NFO	SSA	SVO	TRI
BAL														
BAS	94													
BOD	97	3												
BRA	85	9	12											
BRE	39	106	109	97										
EFI	146	52	49	61	158									
FET	63	86	89	77	24	166								
GRU	99	5	2	14	111	47	91							
HAM	136	65	62	74	97	74	85	60						
MOU	88	6	9	3	100	58	80	11	71					
NFO	133	70	67	79	94	79	82	65	5	76				
SSA	68	26	29	17	80	78	60	31	91	20	96			
SVO	64	99	102	90	25	153	13	104	72	93	69	73		
TRI	157	36	33	45	118	59	106	31	40	42	43	62	93	
WFI	146	52	49	61	158	10	138	47	68	58	73	78	151	58

Table 2.7 Kendall's rank-order correlation statistic calculated between 0-group time series for sandeel grounds around Shetland (see Figure 2.6 for key to ground codes). Values above the diagonal are Kendall's T statistic. Data below the diagonal refers to the significance of the tests. NS=not significant, 0.050=significant at P(0.05), 0.010=significant at P(0.01).

	BAL	BAS	BOD	BRA	BRE	EFI	FET	GRU	HAM	MOU	NFO	SSA	SVO	TRI	WFI
BAL	1.000	0.186	0.609	0.065	0.382	0.231	0.187	0.346	0.467	0.407	0.573	0.569	0.202	0.303	0.070
BAS	NS	1.000	0.333	0.056	-0.152	-0.037	0.262	**0.597**	0.299	0.171	-0.016	0.400	0.123	0.187	0.150
BOD	0.050	NS	1.000	-0.255	0.183	0.429	0.327	0.203	**0.786**	0.310	0.535	0.556	0.111	0.618	**0.837**
BRA	NS	NS	NS	1.000	-0.103	-0.289	0.090	0.226	-0.068	0.574	-0.110	0.183	0.294	0.045	0.068
BRE	NS	NS	NS	NS	1.000	0.342	0.137	-0.087	0.390	-0.067	0.368	0.083	0.216	-0.144	0.185
EFI	NS	NS	NS	NS	NS	1.000	0.315	-0.037	0.315	-0.236	0.440	0.164	0.091	0.333	0.511
FET	NS	NS	NS	NS	NS	NS	1.000	0.467	0.386	0.110	0.333	0.257	0.477	0.568	0.568
GRU	NS	**0.010**	NS	NS	NS	NS	NS	1.000	0.156	0.304	0.144	0.413	0.350	0.369	0.156
HAM	NS	NS	**0.010**	NS	NS	NS	NS	NS	1.000	0.056	0.389	0.440	0.330	0.537	**0.611**
MOU	NS	NS	NS	0.050	NS	NS	NS	NS	NS	1.000	-0.031	0.534	0.168	0.204	0.019
NFO	0.050	NS	0.050	NS	NS	NS	NS	NS	NS	NS	1.000	0.290	0.351	0.278	0.426
SSA	0.050	NS	0.050	NS	NS	NS	NS	NS	NS	0.050	NS	1.000	0.273	0.550	0.147
SVO	NS	NS	NS	NS	NS	NS	0.050	NS	NS	NS	NS	NS	1.000	0.330	0.404
TRI	NS	NS	0.050	NS	NS	NS	0.050	NS	0.050	NS	NS	0.050	NS	1.000	0.500
WFI	NS	NS	**0.010**	NS	NS	0.050	0.050	NS	**0.010**	NS	NS	NS	NS	0.050	1.000

Table 2.9 Mean synchrony and 95% confidence intervals determined by bootstrap analysis in 0- and 1-group recruit time series of sandeels on grounds around Shetland.

Data Set	Data Mean	Bootstrap Mean	Upper 95%	Lower 95%
0-group	0.264	0.314	0.407	0.235
1-group	0.184	0.239	0.330	0.154

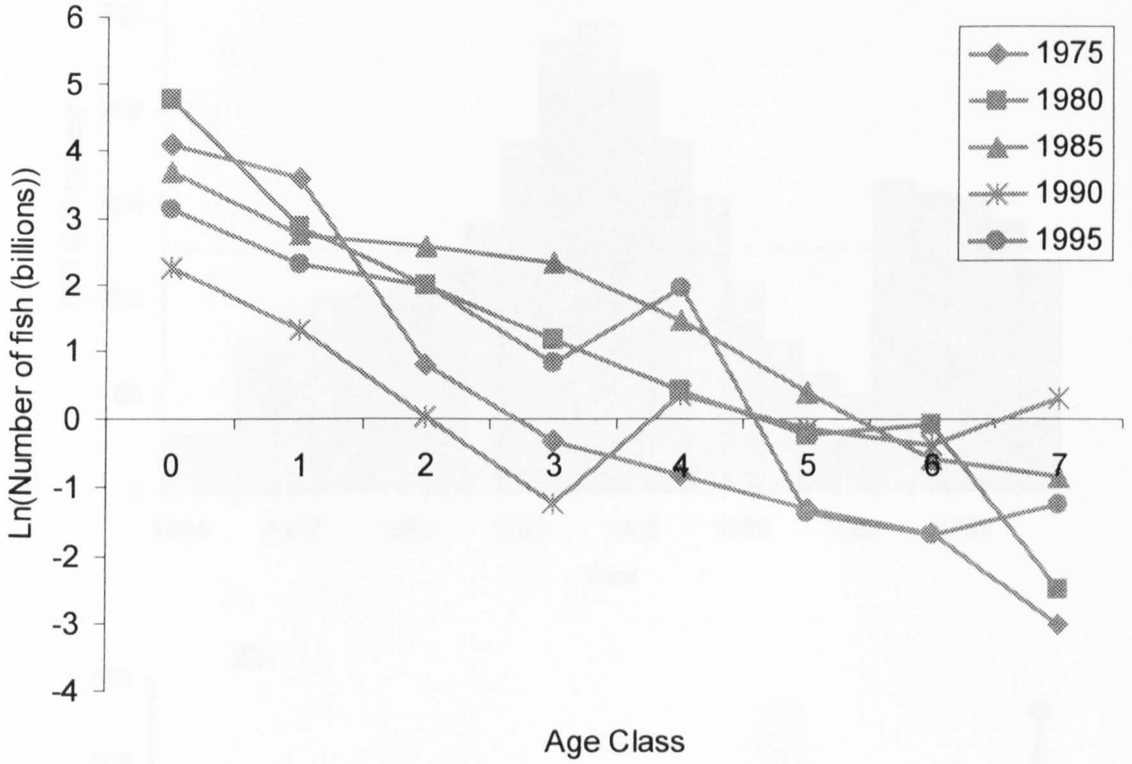
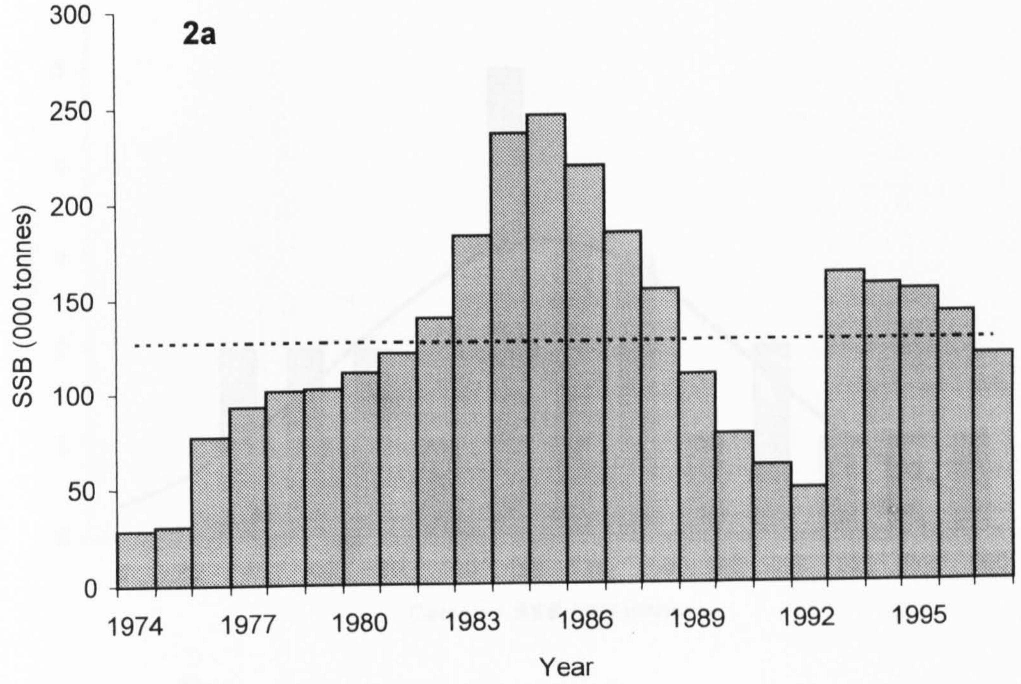


Figure 2.1 Estimated population structure (from ICES 1999) for sandeels at Shetland in five selected years.



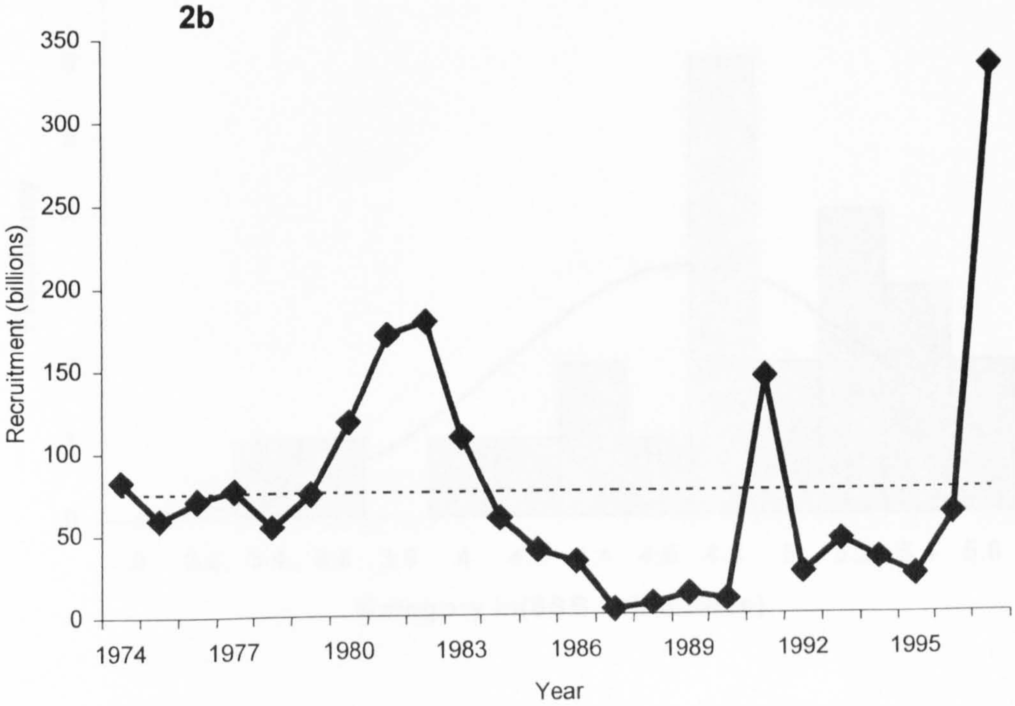


Figure 2.2 a) Trends in spawning stock biomass (SSB) and **b)** trends in recruitment for sandeels at Shetland (from ICES 1999). Dotted lines indicate mean values.

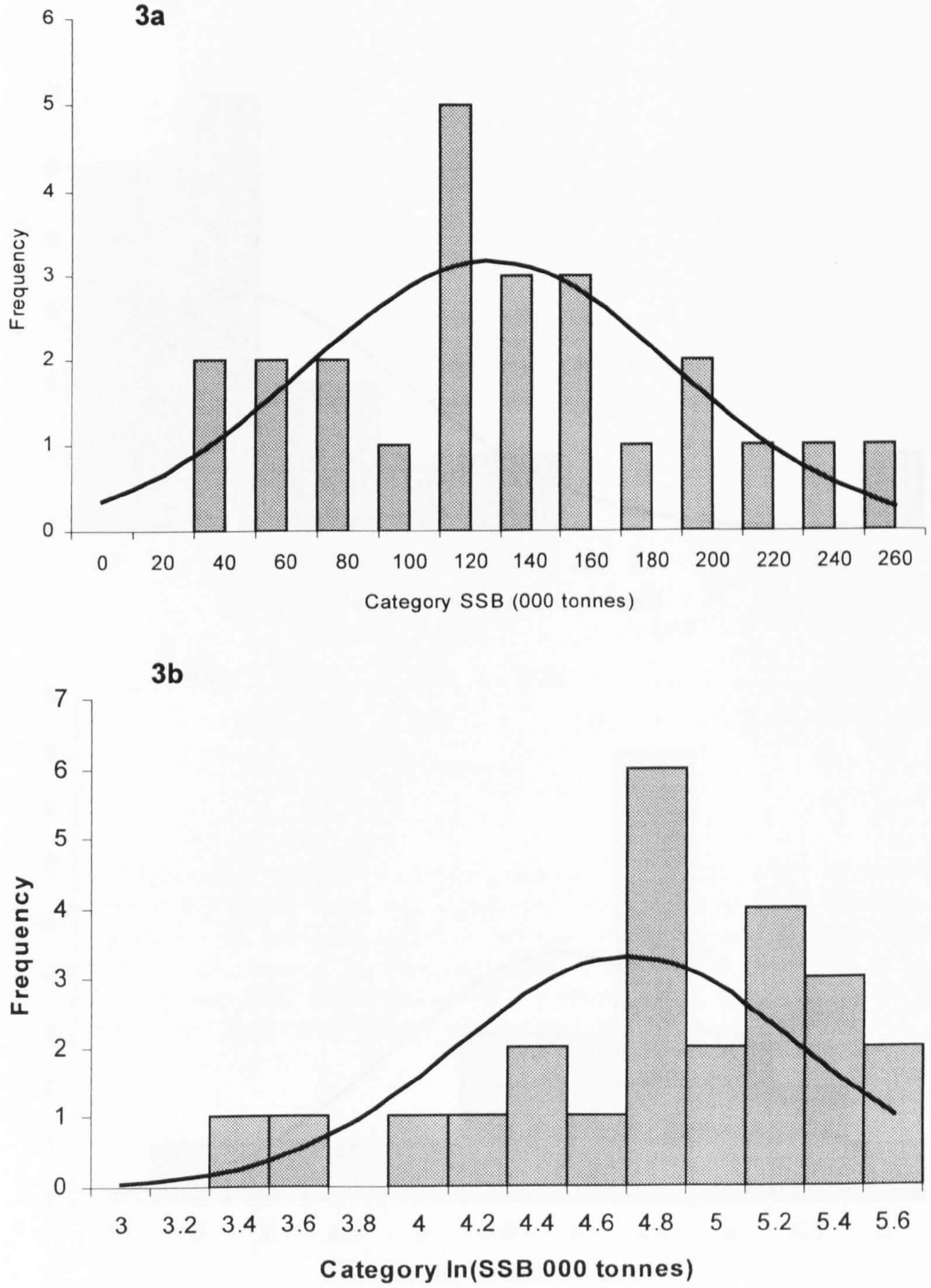


Figure 2.3 Sandeels at Shetland. **a)** Spawning stock biomass (SSB) distribution and **b)** distribution of ln-transformed SSB (ICES 1999). Solid lines show the fitted normal curves.

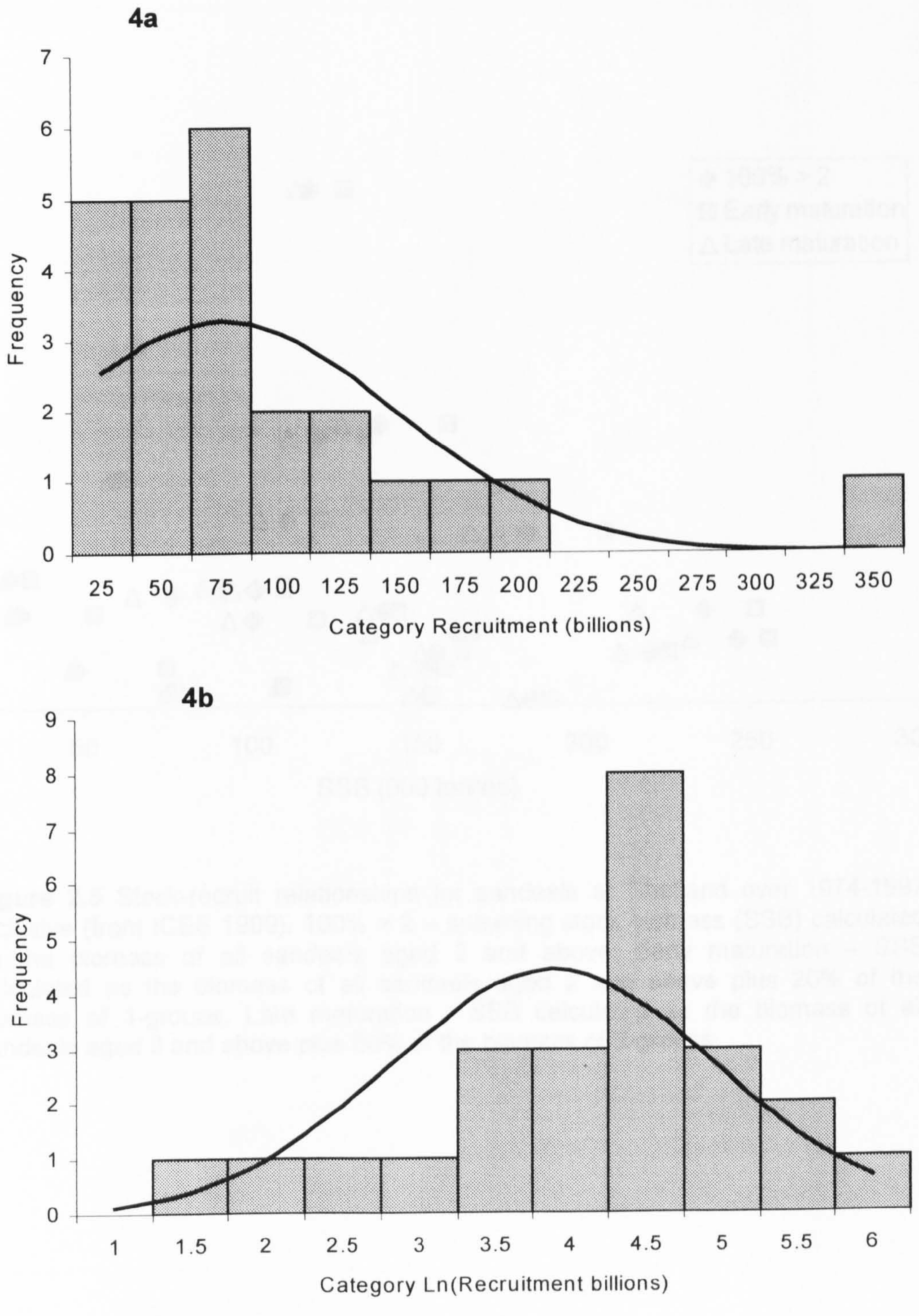


Figure 2.4 Sandeels at Shetland. **a)** Recruitment distribution and **b)** distribution of ln-transformed recruitment (ICES 1999). Solid lines show the fitted normal curves.

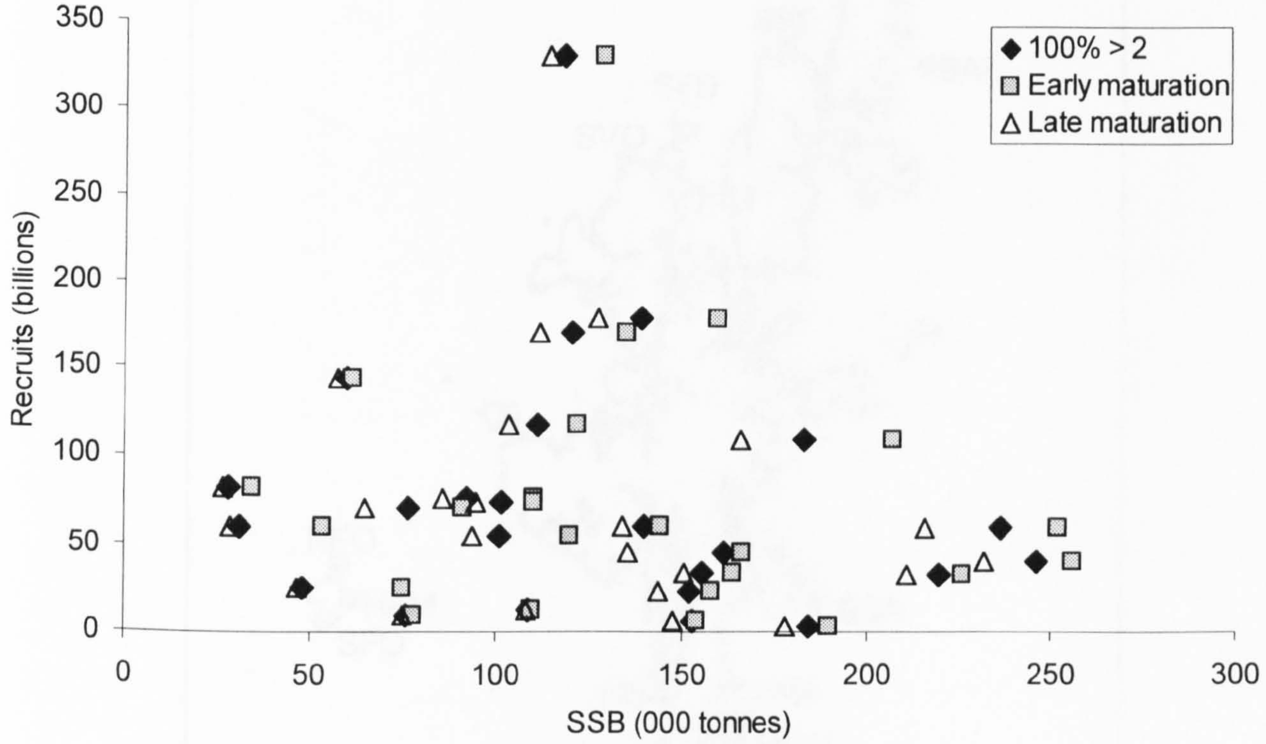


Figure 2.5 Stock-recruit relationships for sandeels at Shetland over 1974-1997 inclusive (from ICES 1999). 100% > 2 – spawning stock biomass (SSB) calculated as the biomass of all sandeels aged 2 and above. Early maturation – SSB calculated as the biomass of all sandeels aged 2 and above plus 20% of the biomass of 1-groups. Late maturation - SSB calculated as the biomass of all sandeels aged 3 and above plus 80% of the biomass of 2-groups

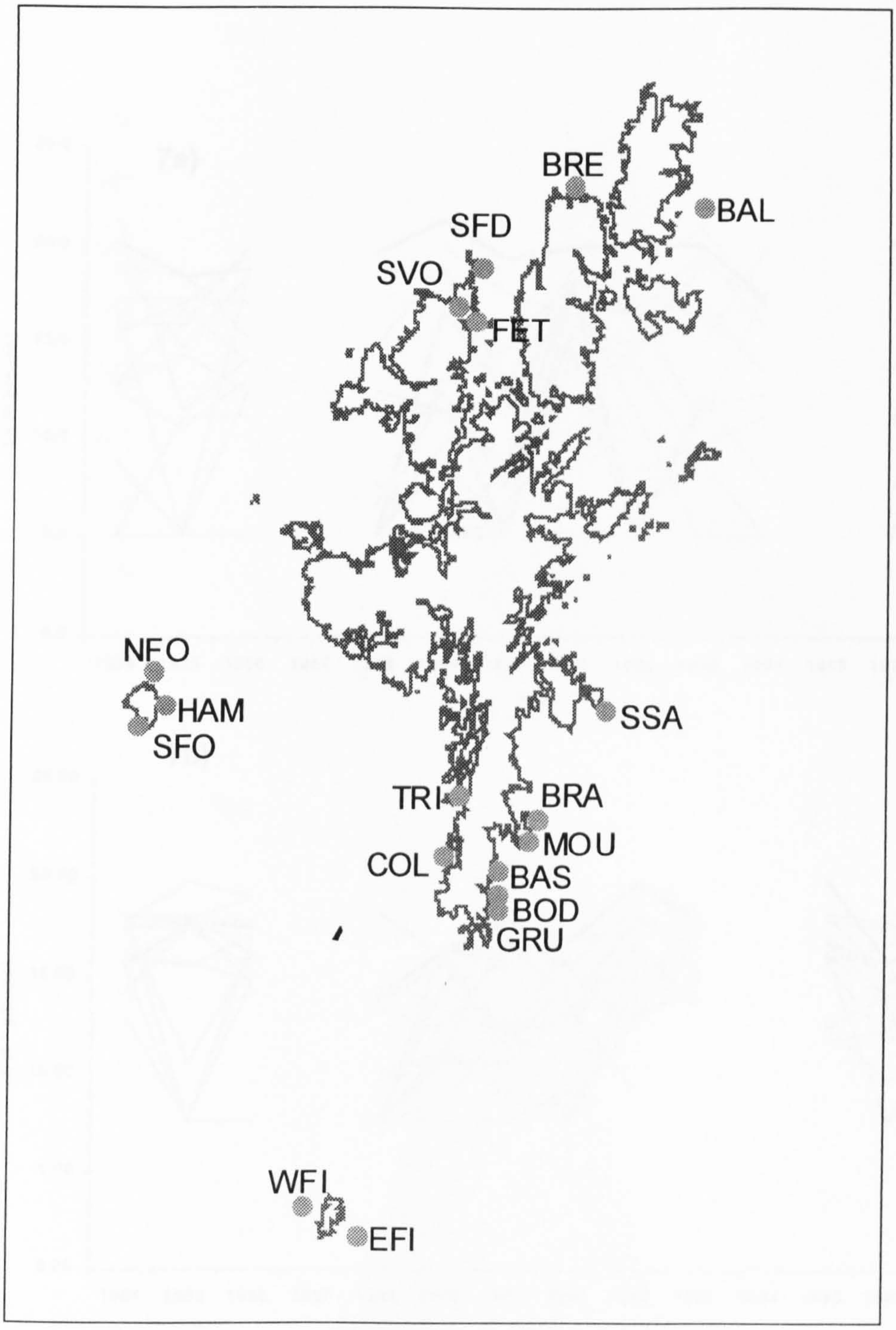
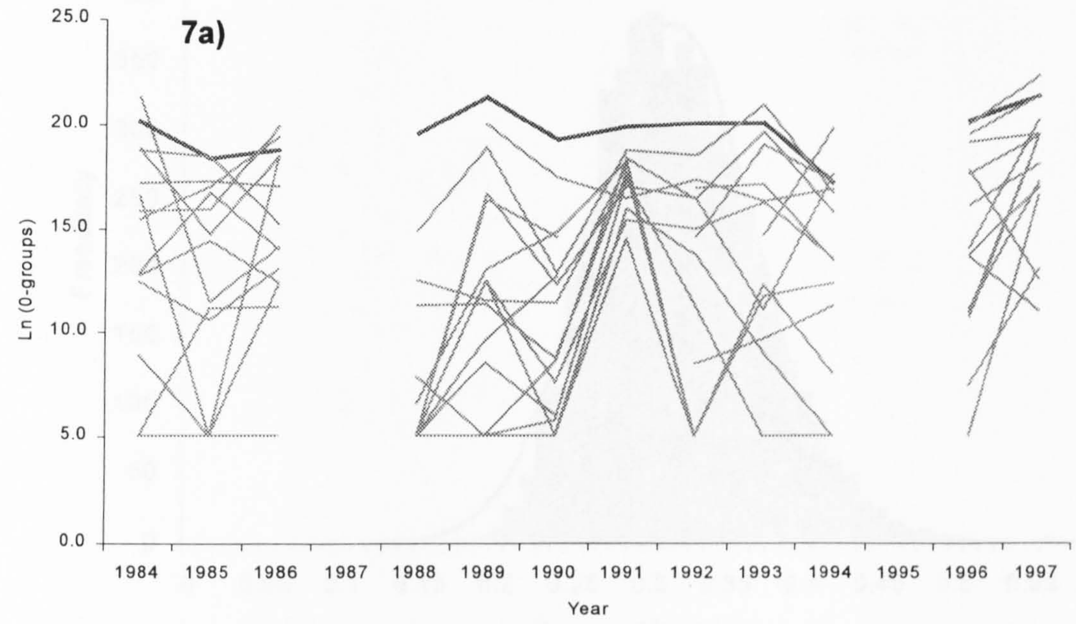


Figure 2.6 Map of showing sandeel fishing grounds at Shetland. SF0=South Foula, HAM=Ham o'Foula, NFO=North Foula, SV0=Sands voe, FET=Fethaland, BRE=Brekkin, BAL=Balta, SSA=South sands, BRA=Braeside, MOU=Mousa sound, BAS=Baas, BOD=Boddam voe, GRU=Grutness, EFI=East Fair Isle, WFI=West Fair Isle, COL=Colsay and TRI=Trink



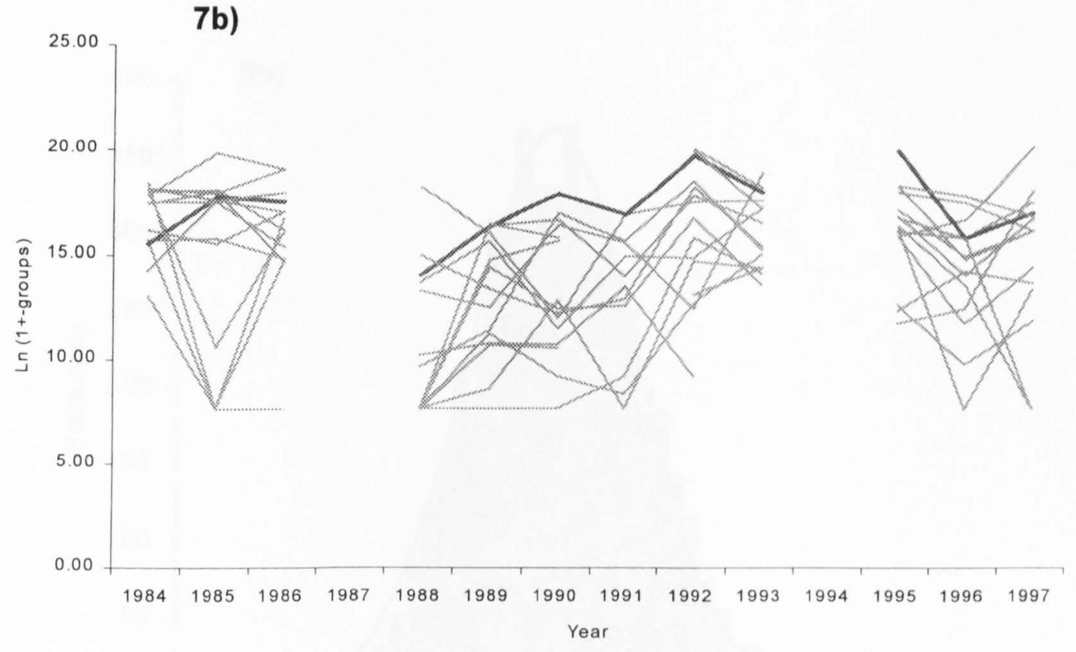


Figure 2.7 Time series for sandeel grounds around Shetland from research surveys. **a)** ln(0-group) series and **b)** ln(1+-groups) series. Heavy line indicates the series for the Mousa ground. No data available for 1987 and 1994.

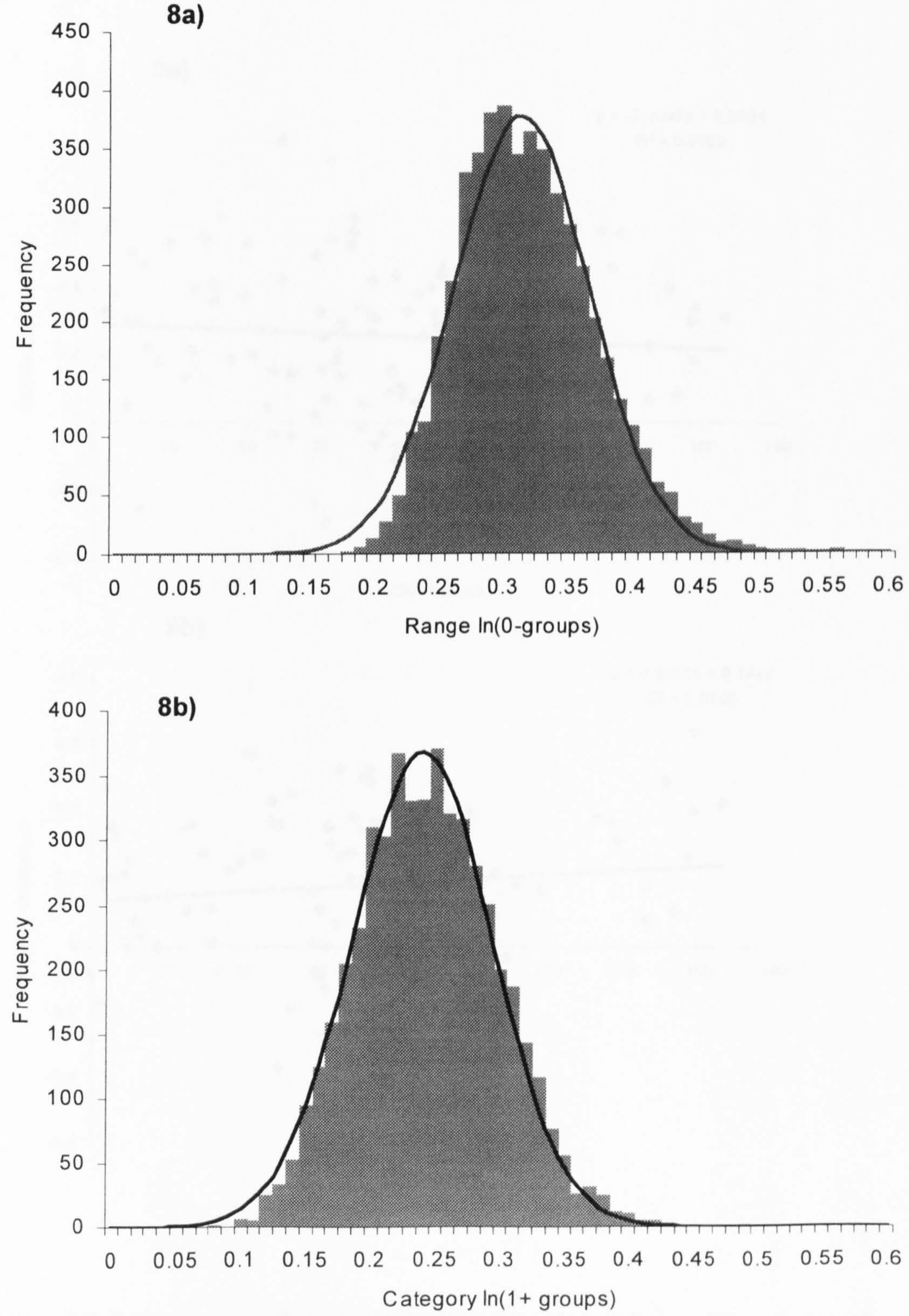


Figure 2.8 Probability distributions of mean synchrony between data series on sandeel grounds around Shetland returned by 5000 bootstrap simulations: **a)** 0-group fish **b)** 1+ group fish. Expected normal curves shown.

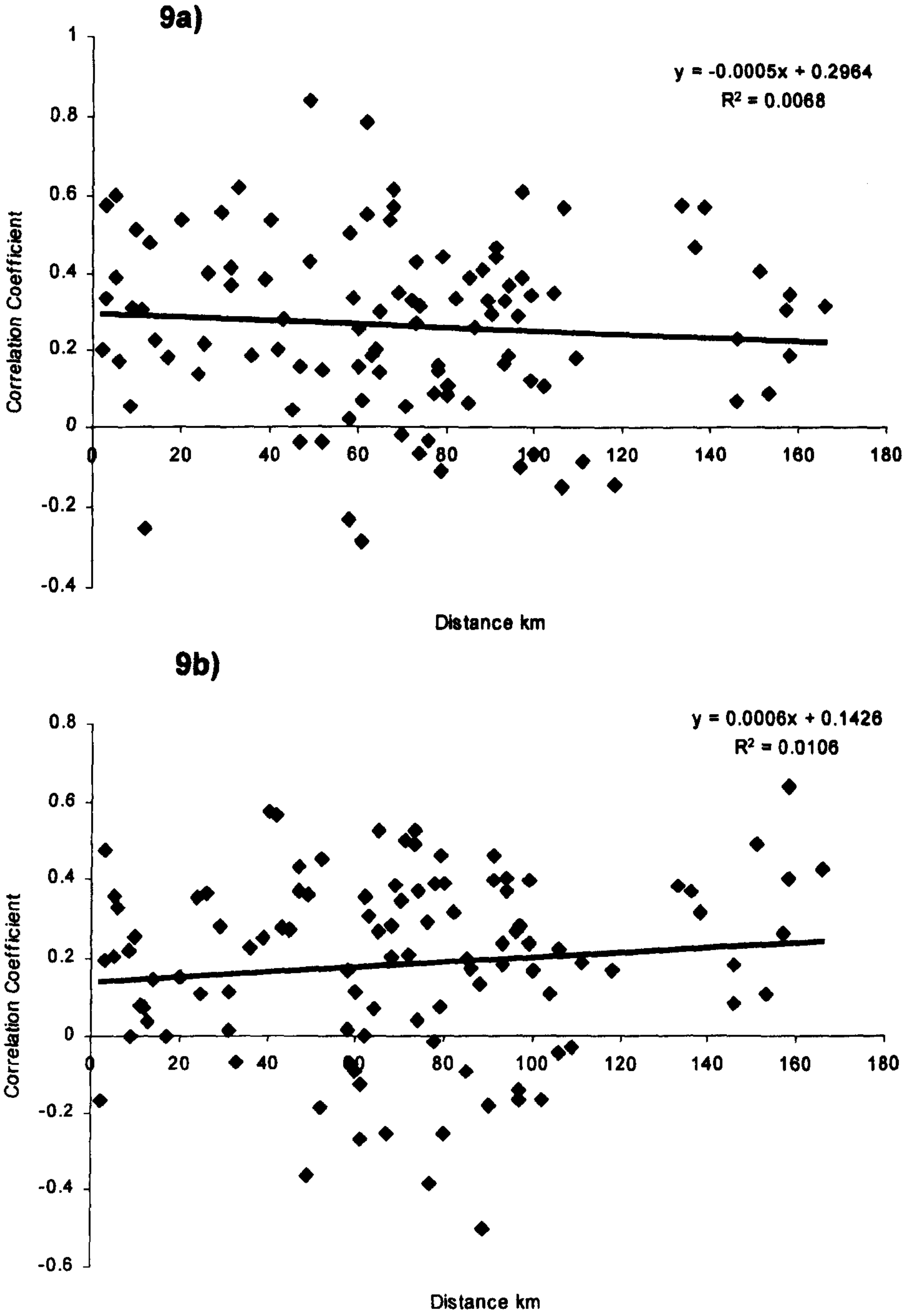


Figure 2.9 Correlation coefficient (Kendall's rank-order) between times series of sandeels abundance on pairs of exploited grounds against distance (by sea) between grounds. a) 0-groups b) 1+ groups. Trendlines fitted and equations and R^2 shown.

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CHAPTER 3

TIME SERIES MODELLING

3.1 Introduction

In this Chapter, a baseline population model of the Shetland sandeel stock is developed together with components to simulate recruitment using time series models. The population dynamics produced by these models will simulate the key recorded features of the historical data. The models were tested for robustness and the underlying biological assumptions considered to select suitable models to describe recruitment and population dynamics.

Traditional stock-recruit models express recruitment as a function of spawning stock biomass (hereafter SSB) however there is little evidence of a relationship between stock and recruit for the Shetland sandeel data (Figure 3.1a). In time series modelling, recruitment is determined as a function of previous recruitments so there is no relationship with SSB. While these models cannot be used to fully explore potential effects of fishery management practices, analysing patterns in the recruit time series will improve our understanding of recruitment dynamics. Additionally, these models can be incorporated in traditional stock-recruit models to produce recruitment time series that are a function of SSB and also of previous recruitments.

In the first section of this Chapter, the concept of the stock-recruit relationship is discussed in more detail together with evidence both for and against the relationship. Time series forecasting is analysed as a potential method to simulate recruitment. Two models are developed: autoregressive and moving average. A basic age-structured population model is then developed and the input required for the model and the output produced by the model discussed. The time series models parameterised to simulate recruitment are tested in the population model and suitable models identified.

3.2 Is recruitment related to SSB? PART 1

Recruitment is a crucial part of the population models as large fluctuations in the number of recruits are thought to be a major factor driving the interannual variation in class strength in some exploited fish populations (Spencer & Collie, 1997). Improving our knowledge of the underlying dynamics of recruitment is critical for selecting appropriate harvest strategies. In fisheries modelling, recruitment is traditionally described as a function of SSB using stock-recruit curves such as the Ricker (1954;1975) or Beverton-Holt (1957) models. However, stock-recruit data for Shetland sandeels is highly variable and there is no obvious relationship (Figure 3.1a). Strong environmental forcing may be obscuring the stock-recruit relationship however, the lack of a relationship could also equally be due to measurement errors or the limited data range (Hilborn & Walters, 1992).

The concept of stock and recruitment is a fundamental one in fishery management. This assumes there is a relationship between the size of the spawning stock (spawning stock biomass; hereafter SSB) in any particular year and the average number of recruits produced by that spawning that enter the exploited stock. This relationship is probably among one of the most dubious used in biology. Hilborn & Walters (1992) describe stock-recruit curves as dangerous, primarily because they give the impression of a predictable relationship between stock and recruitment rather then the stochastic phenomenon it really is.

Recruitment to exploited fish stocks is usually extremely variable between years. It can be considered as a series of processes: from spawning, survival and hatching success of eggs to the growth and survival rate of larvae and pre-recruit juveniles (via metamorphosis) to entry of young fish into the exploited stock (Hennemuth *et al.,* 1980). The pre-recruit stages generally incorporate a pelagic dispersive stage – some fish spawn pelagic eggs that float in the water column and most fish have pelagic larvae that drift with currents. Thus the number of recruits reaching a stock will be affected by hydrographic regimes – which can alter from year to year. Early life-stages are exposed to high mortality rates that are determined by factors such as predation, food availability and environmental conditions. Houde (1994) calculated that for a 'typical' cohort of marine fish only 0.12% of the eggs hatched, on average, are alive at metamorphosis. Considering all the factors, one can see why the relationship between stock and recruitment is usually poor, even when we disregard measurement errors.

Interpreting the relationship between recruitment and SSB can be misled by the effects of environmental factors, as SSB in one year is not independent of the stock size in previous years. For example, an exceptionally strong recruitment will result in a large year class which may be evident in the stock for several years, as illustrated by Sparholt (1996) for Baltic cod. Model simulations, with recruitment varying independently of SSB, showed that favourable conditions for recruitment persisting over a number of years will lead to an increase in SSB and so a positive correlation between the two. In other words, autocorrelation (correlation in the time series with lagged values of itself) in recruitment (dependant variable) is reflected by dependence, with a time lag, in SSB (independent variable). This may be evident in time series where trends in recruitment occur before trends in SSB –as seen in the Shetland sandeel data during the 1980s (Figure 3.1b).

Often the variance in recruitment is extremely large, so it has been disputed that a relevant relationship actually exists between SSB and recruitment. Koslow (1992) argued that for organisms with high fecundities (such as most marine fish), the concept of a deterministic stock-recruit relationship does not appear to be applicable, and therefore casts doubt on fishery population models dependant on such functions. Conversely, Myers & Barrowman (1996) reasoned that stock-recruit relationships are relevant. To provide conclusive evidence that strong year classes are more likely when SSB is large and so provide proof that there is a relationship between SSB and the size of recruitment produced (as more spawners should produce more recruits), Myers & Barrowman (1996) analyzed stock-recruitment time series for 364 fish stocks. They asked three simple questions: Does the largest recruitment occur when spawner abundance is high? Does the smallest recruitment occur when spawner abundance is low? and Is the mean recruitment higher if spawner abundance is above rather then below the median? Non-parametric methods were devised to answer these questions. In general, the answer to the questions was "yes", leading Myers & Barrowman to conclude fish populations should be managed so spawner abundance is sufficient to yield high recruitment. In other words, the stock-recruitment relationship should not be ignored in fishery management.

Subsequent to Myers & Barrowman (1996), Gilbert (1997) argued against stock-recruit functions. Gilbert took an alternative approach to analyse the same stock and recruitment data sets used by Myers & Barrowman. Gilbert tested two alternative hypothesises: that recruitment is positively related to SSB at low SSB (generally accepted stock-recruit paradigm) and that a "recruit-states" mechanism exists. The recruit-states mechanism proposed is that the stock switches between different levels of mean recruitment from time to time. Gilbert found the stock-recruit paradigm was not rejected for salmonids but generally, was rejected for marine spawning bony fish stocks (which include sandeels). For the marine spawning bony fish, the recruitment-states hypothesis was supported. This implies that the positive relationship between stock and recruitment found at low stock levels, may be the result of the dependence of SSB, with a time lag, on recruitment (as was shown in Baltic cod by Sparholt, 1996). Periods of low recruitment, which were not the result of low SSB (as was seen in the Shetland sandeel stock in the late 1980s), will result in a spurious relationship between stock and recruitment.

The stock-recruit paradigm is still being debated but in the absence of robust alternative methods, traditional stock-recruit models continue to be widely used today. Alternative methods are being developed to predict recruitment than as a deterministic function of SSB. For example, Evans & Rice (1988) consider recruitment as a probability distribution and developed algorithms that use the raw stock and recruitment data. Cook (2000) further explores this probabilistic approach to population change in exploited fish stocks, which avoids making strong assumptions about the functional relationship between stock and recruitment. Chen *et al.* (2000) apply a fuzzy logic model with genetic algorithm to analyse fish stock-recruit relationships. This model incorporates sea surface temperature as an environmental intervention.

3.3 Recruitment Models Using Forecasting Methods

The stock recruit relationships for sandeels in the North Sea and at Shetland (Figure 3.1) show considerable variability so it is difficult to identify models to predict recruitment as a function of SSB. Furthermore, the low exploitation rate of the Shetland stock reduces certainty in the assessment data used as the basis for stock-recruit models. Our understanding of recruitment processes around Shetland is complicated by the fact that the Shetland sandeel stock may not be a closed population but probably forms part of a much larger population (Wright & Bailey, 1993; Wright, 1996). Wright (1996) presents evidence that in some years, a portion of the recruits originated from outside the Shetland system (external recruits). If a net immigration of recruits occurs, this will obscure the stock-recruit relationship at Shetland but the frequency and size of external recruitment is unquantified.

Due to these problems, two approaches are being taken to model recruitment in this thesis: the first uses time series models to simulate recruitment as an extrapolation of the pattern in the historical series (this Chapter) and the second assumes that recruitment can be expressed as a function of SSB (Chapter 4). Modelling recruitment using time series models assumes recruitment in any year can be predicted as a function of previous recruitments. It was assumed that environmental forcing was such that any stock-recruit relationship was obscured. However, this method uncouples recruitment from SSB so one must be cautious if using these models to assess fishery management practices. In reality, increasing exploitation may eventually reduce SSB to such low levels that recruitment may be seriously reduced and the stock is no longer self-sustaining. Time series models do not account for declines in recruitment due to a decline in SSB. But, exposing patterns in recruitment is an important step to understanding recruitment dynamics (Zheng, 1997).

Modelling recruitment as independent (from SSB) time series will improve our understanding of recruitment dynamics and the techniques developed here can be combined with the stock-recruit models developed in the next Chapter.

Statistical forecasting techniques generate forecasts by extrapolating patterns in the historical data (Farnum & Stanton, 1989), these methods were applied to the recruit time series for Shetland sandeels. Time series analysis and forecasting is used extensively in business science to forecast trends in areas such as sales, economics and in the stock market (Farnum & Stanton, 1989; for examples see Bhawnani & Kadiyala, 1997; Saab *et al.*, 2001; Zucchini & Neumann, 2001). The techniques are also common in meteorological and oceanographic science where they are applied to time series such as sea surface temperature or air temperature (for examples see Kite, 1989; Woodward & Gray, 1993; Sfetsos, 2000; Franses *et al.*, 2001). Time series analysis is used widely in biology for analyzing population dynamics (for examples see Vickery & Nudds, 1984; Tomte *et al.*, 1998; Erb *et al.*, 2001; Fromentin *et al.*, 2001).

In fisheries science, time series analysis has generally been used to forecast fishery catches (Kirkley *et al.,* 1982; Stergiou, 1991; Park & Yoon, 1996; Stergiou & Christou, 1996; Farley & Murphy, 1997) or to identify possible environmental effects on fish growth (Calderon-Aguilera, 1991) or recruitment (Henderson & Corps, 1997). The techniques could be useful for short-term forecasting where it is impractical to fit stock-recruit models (when stock-recruit relationship is very weak) or to supplement stock-recruit modelling information.

There are some considerations to be aware of when using time series to predict recruitment. Firstly, estimates of recruitment may not be independent – they are usually the result of assessment models. Secondly, while these techniques may be useful in predicting future recruitment over a very short time scale, they take no account of changes in SSB. Therefore, declines in SSB which lead to a decline in recruitment will be missed - this would be disastrous for fishery management as it could result in stock collapse. If SSB is allowed to drop to low levels so recruitments are small, the stock may no longer be self renewing.

Traditional stock-recruit models provide insight into the response of the fish population to high exploitation which time-series models do not. So why use time series models? If the relationship between stock and recruitment is weak, fitting stock-recruit models may be difficult but time series models may be useful to predict recruitment over the short term (as fluctuations in SSB are slower then fluctuations in recruitment). The intention here is not to predict future recruitment but to produce models for recruitment that simulate the historical recruitment series. Additionally, quantitative forecasting of recruit time series may reveal underlying patterns of fluctuations in recruitment which are important for understanding recruitment dynamics. If any trends or autocorrelation is revealed in the recruit time series, then these models could be incorporated into the stock-recruit models.

Before fitting any models, the historical recruit time series are analyzed to determine if there is any underlying trend in the data and if the fluctuations are random or autocorrelated. The categories of time series models are then discussed and a method to compare goodness-of-fit between models. Two models are then considered: autoregressive and moving average.

3.4 Patterns in the recruit time series

Before forecasting, it is necessary to determine if a particular time series is stationary (that is, is the mean constant over time) or if there is a trend in the data, and also if fluctuations are random. Randomness in a series may be determined by a simple non-parametric test such as the Runs test (Farnum & Stanton, 1989; Zar, 1999). This test makes no assumptions that the series is drawn from a normal distribution. The null hypothesis for the Runs test is that the pattern of distribution of points in the series with respect to the median (whether data points are above or below the median) is random. Each observation is recorded as being either above (+) or below (-) the median and the number of 'runs' (sequences of +'s or –'s) is determined. The recruit time series for both Shetland and North Sea stocks were natural log-transformed and were analysed using the Runs Test function in SPSS.

The null hypothesis was rejected for both time series at P=0.05 (Table 3.1) therefore it can be concluded, with 95% confidence, that fluctuations are not random. The corresponding Z statistic was positive for North Sea sandeels and negative for Shetland sandeels (Table 3.1), so it can be assumed that the null hypothesis was rejected for different reasons in the two stocks. For the North Sea series, the Z statistic was positive thus indicating possible negative autocorrelation in the series, while for the Shetland series the Z statistic was negative thus indicating either positive autocorrelation or a trend. A Daniel's test was used to determine if there was an underlying trend in either series, this test is also nonparametric and is based on Spearman's coefficient (Farnum & Stanton 1989). The null hypothesis, that the series has no trend, could not be rejected for either series (P>0.05, Table 3.1).

Plotting the Shetland recruit time series indicated possible serial dependence in the observations, as observations close together in time fall on the same side of the mean (Brown & Rothery, 1993; Figure 3.2). The serial dependence of observations in a time series is referred to as *autocorrelation* (Brown & Rothery, 1993). There appeared to be a positive correlation between observations at a lag of one year in the recruit time series, as was demonstrated by plotting recruitment in year *t* against recruitment in year *t+1* (Figure 3.2b). In general, this implies that a 'good' recruitment year is likely to be followed by another 'good' year and 'bad' by 'bad'. In contrast, the North Sea recruit time series (Figure 3.2c) appeared to have a negative correlation at a lag of one year (Figure 3.2d).

The *autocorrelation function*, ACF, (Brown & Rothery, 1993; Farnum & Stanton, 1989) was plotted for lagged intervals up to ten years for the recruit time series using the time series graph function for autocorrelation in SPSS (Figure 3.3). ACF is a graph of the autocorrelation coefficients, r_k (correlation coefficient between observations at lag k), plotted against lag k (Farnum & Stanton, 1989). In Figure 2.6a, the autocorrelation coefficients are large and positive for short lags and the ACF appears to have a downward trend. This pattern may indicate a trend in the recruit time series however the Daniel's test for trend, carried out above, indicated this is unlikely.

The critical value for r_k , above which the null hypothesis, that there is no trend in data at lag k, is rejected (P=0.05), was calculated for each lag in the time series. This was equal to 2 x standard error (Farnum & Stanton, 1989). These values are shown in Figure 3.3 as black solid lines. For Shetland sandeels, only the autocorrelation coefficient at lag 1, r_1, is significant (greater than the critical value) hence the series can be considered to have a positive autocorrelation at a lag of 1 year. The autocorrelation coefficient, r_1, calculated at lag 1 was +0.54.

The positive autocorrelation in the Shetland recruit time series suggests strong environmental forcing on recruitment processes. The effects of environmental stochasticity, that is random temporal variation in the environment, on a population often last longer then one year. Positive serial correlations in recruitment time series were found in six of eighteen fish stocks analyzed by Hennemuth *et al.* (1980). All six species (Georges Bank cod, *Gadus morhua* and silver hake *Merluccius bilinearis*; South African pilchards, *Sardinops ocellata* and round herring, *Eutremus teres*; Norwegian herring, *Clupea harengus* and NW Atlantic mackerel, *Scomber scombrus*) had significant (P>0.05) positive correlations at a lag of 1 year. Hennemuth *et al.* speculate that these short term correlations would be expected when environmental conditions influencing egg and larval survival were similar in adjacent years. Therefore, positive correlations may indicate long term environmental regimes.

The ACF of the log-transformed recruit time series for North Sea was also plotted in SPSS (Figure 3.3b). Again, a significant correlation was found at a lag of 1 year but in this case the autocorrelation was negative (-0.628) not positive. This suggests that total stock biomass may be having an adverse affect on recruitment. There is evidence for this in North Sea haddock and whiting where high total stock biomass appears to cause a lowered recruitment (Cook & Armstrong, 1986).

3.5 Forecasting Models

All of the forecasting models and diagnostics described below were determined following techniques described by Farnum & Stanton (1989) in *Quantitative Forecasting Methods*. A full account of the methods can be found in this book. Where additional information was used, this is referenced in the text as normal.

There are a number of categories of forecasting models depending whether the time series is considered stationary, cyclic, seasonal or with a trend and whether error terms are random or autocorrelated. The tests conducted above have indicated that the recruitment time series for both Shetland and North Sea sandeels are stationary. The simplest no-trend model expresses the value in any year as the mean of the series plus a random error term:

$$y_t = \bar{y} + \varepsilon_t \qquad 3.1$$

where y_t is the series value at time t, $\bar{y}$ is the mean level of the series and ε_t is the error term.

As shown by inspection of the autocorrelation function, error terms are autocorrelated in both sandeel recruit series (positive in the Shetland data and negative in the North Sea data set) therefore this model (Equation 3.1) is not suitable. Alternative models to simulate recruitment, which can produce autocorrelated time series, include autoregressive and moving average. These may also be merged to produce autoregressive-moving average models. All of these models can be considered as subsets of models that form part of the methodology for time-series modelling commonly referred to as Box-Jenkins forecasting. Box-Jenkins time series models are called ARIMA (autoregressive-integrated-moving average) models (models with underlying trends need to be integrated (undifferenced) to achieve stationarity - hence the I in ARIMA). The number of autoregressive parameters (*p*), the degree of differencing (*d*) and the number of moving average parameters (*q*) are identified in Box-Jenkins models which are described as ARIMA(*p,d,q*). For example, ARIMA(1,0,0) refers to an autoregressive model of order 1 (as the degree of differencing and number of moving average parameters are set to zero) while ARIMA(0,1,2) refers to a second order moving average model with 1st degree differencing.

Autoregressive and moving average models are described and fitted to the Shetland recruit time series below. Only the AR model was fitted to North Sea sandeels as this model produced a suitable time series. To achieve a full understanding for the techniques for each model, the basic techniques of each model are discussed then the corresponding Box-Jenkins model is considered and fitted.

To compare between models, the root mean square errors, RMSE, were calculated for each time series:

$$RMSE = \sqrt{\sum_{i=1}^{n}\left(\ln(R_t) - \ln(\hat{R}_t)\right)^2} \qquad 3.2$$

where R_t is ln(R) from the historical time series in year *t*, $\hat{R}_t$ is ln(R) in the model time series and *n* is the length of the series.

An advantage of Box-Jenkins modelling is ARIMA models can easily be parameterised using the ARIMA function in SPSS. A disadvantage of Box-Jenkins modelling is, ideally, large data sets are needed (>50). It is difficult to identify suitable ARIMA models with smaller data sets as the statistical significance of autocorrelation or partial autocorrelation coefficients is compromised. Both sandeel recruit time series are short (24 years for Shetland and 22 year for North Sea sandeels) so this must be remembered when considering the model output.

3.5.1 Autoregressive Models

Autoregressive models are models for stationary time series that have serial dependence (autocorrelation), the models use only lagged values of the time series itself as predictor variables. These models are used when the current level of a series is thought to depend on the recent history of the series, so they are useful in situations such as sales forecasting as the amount spent in one period may affect the amount spent in successive times. In ecological modelling, autoregressive series are used when the effects of the random errors, ε, are thought to be felt over a number of periods (as often occurs with the effects of climatic perturbations). This may give rise to positive autocorrelation as is seen the Shetland recruit time series.

The basic autoregressive model is:

$$y_t = f(y_{t-1}) + \varepsilon_t \qquad 3.3$$

where f is some function, ε_t is a random normally distributed error term and y_{t-1} is such that:

$$y_{t-1} = f(y_{t-2}) + \varepsilon_{t-1} \qquad 3.4$$

The autoregressive equation is stochastic and y is regressed on lagged values of itself (y_{t-1}, y_{t-2}...) hence *autoregression*. Regression makes several assumptions: the mean of the series of the random variable ε is zero, ε follows a normal distribution, the variance of σ^2_ε is constant and the error terms (ε_t, ε_{t-1}...) are statistically independent. A problem arising with autoregressive models is that the independent values are actually previous values of the dependant variable so the error terms are not statistically independent.

Before fitting autoregression models is it necessary to determine the appropriate number of time lags. This can be achieved by analyzing the partial autocorrelation function (PACF) of the time series, as this is a measure of the correlation at time lag k after removing the effect of all shorter lags. The autocorrelation coefficients, r_k, for both the North Sea sandeel and Shetland sandeel recruit time series determined above indicated that correlations at time lag 1 may be significant (r_1=-0.6 and r_1=+0.5 respectively). The partial autocorrelation functions were determined using the Time Series Graph Function in SPSS.

The significance of PACF can be tested very simply by using a "rule of thumb" procedure to set confidence intervals, c.i.:

$$c.i. = \pm\frac{2}{\sqrt{n}} \qquad 3.5$$

where n is the size of the data set.

Only the lag at time 1 was still significant for either series (Figure 3.4) so the order of the autoregressive models will be 1 and take the form of:

$$\hat{y}_t = \beta_0 + \beta_1 y_{t-1} + \varepsilon_t \qquad 3.6$$

where β_0 and β_1 are regression parameters and ε_t is a normally distributed random variable with a mean of zero and standard deviation σ_ε.

To determine values for β_0 and β_1, a regression of y_t on y_{t-1} is carried out:

$$\hat{y}_t = \beta_0 - \beta_1 y_{t-1} \qquad 3.7$$

For the sandeel data, the time series being considered are those of the natural log transformed recruits thus y is substituted with $ln(R)$ in Equations 3.6 and 3.7. Linear regression was carried out using the Regression Function in SPSS. The values for β_0 and β_1 for Shetland and North sea sandeels determined by linear regression are shown in Table 3.2. The Durbin-Watson statistic for testing autocorrelation in the residuals returned by linear regression in SPSS was 2.123 for North Sea sandeels and 1.983 for Shetland sandeels. As these values are close to 2, this indicates independent error terms in both cases.

It was expected the forecast series will fluctuate around the mean of the historical series. β_0 does not correspond to the expected mean of the forecast series, $E(y_t)$, this was calculated as:

$$E(y_t) = \frac{\beta_0}{1 - \beta_1} \qquad 3.8$$

For both series, the mean of the historical series was similar to the mean of the forecast series (Table 3.2). For a first order autoregressive model, the autocorrelation coefficient, r_k, at lag k is given by (Brown & Rothery, 1993):

$$\hat{r}_k = \beta_1^k \qquad 3.9$$

Thus, for a first-order autoregressive model β_1 corresponds to r_1 at lag 1 and these values are close to the autocorrelation coefficients at lag 1 in the historical series (Table 3.2).

The autoregressive models were applied to the historical series and the results are shown in Figures 3.5 (North Sea) and 3.6 (Shetland). The RMSE were calculated for each model. Observations of the residual plots are used as a diagnostic test for deviations from regression assumptions and mis-specification of the functional form of the model. The residuals were plotted against the predictor variables, $\ln(R_{t-1})$, against the predicted variables, $\hat{\ln}(R_t)$, and against time, t.

For North Sea sandeels, the autoregressive model produced a time series that was similar to the historical series. The RMSE was 0.472 which was much lower then the value for the Shetland model of 0.871. The residual plots against the predictor and predicted variables revealed random, no-trend series however the residual plot against time appeared to have an upward trend (Figure 3.5). This may indicate a possible upward trend in historical $\ln(R)$ time series but the time series plot itself revealed no trend and this was verified by the Daniel's test for trend conducted earlier. Regression analysis indicated the trend in residuals with time was not significant (P=0.168). The pattern in this residual plot occurs because in the first half of the series the autoregressive model tends to overestimate low recruitment values while in the second half it underestimates high values. In part, this is the result of a change in the pattern of the historical time series from alternating high and low recruitments (1981-1986) to a 3-year cycle of 2 high then 1 low recruitment (1989-1995).

Although, the time series produced by the autoregressive model for Shetland sandeels lagged behind the historical time series, it did closely track any changes (Figure 3.6). This model is simply tracking the noise in the series which suggests, to forecast recruitment at Shetland, the most parsimonious model is to simply predict recruitment in year t as the recruitment in the previous year, $t-1$ (naïve forecasting, Equation 3.10).

$$\hat{y}_{t+1} = y_t \qquad 3.10$$

The naïve forecast model is also shown in Figure 3.6a (red line). The RMSE produced by the naïve forecast model was 0.963, larger then the value for the autoregressive model, 0.871 suggesting the autoregressive model is a better fit.

For the autoregressive model, the residual plots for Shetland sandeels against the predictor and predicted variables appeared to be a random no-trend series. However, the residual plot against time reveals possible heteroscedasticity. An assumption of regression is that variance of the error terms is constant (homoscedasticity), for this plot the variance appears to increase with time. This is probably a result of changes in the actual time series, in the first half of the plot the series shows strong positive autocorrelation while in the second half, this does not always hold true (a good year may be followed by a bad year instead of another good year). This produces a few large error terms, so the variance in the residual plot is caused by this rather then heteroscedasticity.

3.5.2 Box-Jenkins Autoregressive Models

Another form of the autoregressive model is the Box-Jenkins ARIMA(p,0,0) model. The model parameterised above expresses y_t as a function of y_{t-1}. Positive autocorrelation can lead to a situation termed autocorrelative drift. If y_{t-1} is very large or small, it is highly likely that y_t will also be very large or small. This can cause the series to drift away from the mean. The Box-Jenkins autoregressive model expresses y_t as a function of the residual at $t-1$, therefore the series is less likely to drift from the mean.

An ARIMA(1,0,0) model is similar to the autoregressive model described above (Equation 3.6) except by convention the parameters are denoted as Φ instead of β:

$$\hat{y}_t = \phi_0 + \phi_1 (y_{t-1} - \phi_0) + \varepsilon_t \qquad 3.11$$

where Φ_1 is the autoregressive parameter for $t-1$, Φ_0 is the constant term which is approximately equal to the average level of the series and ε_t is the error term at time t.

ARIMA(1,0,0) models were fitted for both sandeel recruit time series using the ARIMA function in SPSS. The values returned for the constant value Φ_0, the first autoregressive parameter Φ_1, and the resulting RMSE's are shown in Table 3.2. These were similar to the parameters for the basic autoregressive model. The time series forecast based on the actual time series are shown in Figure 3.7 which also include forecasts for a further three years in each case. As expected, the model series are very similar to the models fitted using the basic autoregressive model.

The North Sea sandeel recruit time series has negative autocorrelation so a good year (ln(R) above the mean) is generally followed by a poor year (ln(R) below the mean). An negative autoregressive model can be thought of as 'self-correcting', in that a very high or low value in one year will cause an opposing low or high value in the next year. This will have the effect over a number of years of high swings above and below the mean which gradually dampen out until the next high or low value is generated (through random errors). The opposite situation occurs in the

Shetland model as this has positive autocorrelation. A high (or low value) in one year will generally lead to a series of years above (or below) the mean, so the series tends to drift above or below mean until a random error is generated to counteract this.

3.5.3 Moving Average Models

Moving average models were also considered for simulating recruitment at Shetland as these give most weight to recent observations in a data set. The models should reduce the tracking of noise in the series by computing an average mean over the most recent observations (referred to as smoothing). The greater the smoothing, that is the more terms averaged over, the less the forecasts track noise. In moving average models only *k* number of the most recent observations are used to calculated the moving average mean (referred to as the moving average of length *k*). As the most recent set of observations are used in each forecast, the average changes over time (moves one step forward each time a new observation is obtained). For a moving average of length *k*, the forecast is calculated as:

$$\hat{y}_{t+1} = \frac{\sum_{n=1}^{k} y_{t-n+1}}{k} \qquad 3.12$$

where y is the observed value is year t and y_{t+1} is the forecast value in year $t + 1$.

Moving average models for three different lengths of *k* (2, 3 and 4) were fitted to the Shetland sandeel data using the Moving Average Function in the Data Analysis Toolpak of Excel. The model for k=1 was also determined but this model is simply the naïve forecasting model discussed above ($\hat{y}_{t+1} = y_t$, Equation 3.6).

The forecasts, calculated from the historical time series, are plotted together with the original time series in Figure 3.8. For Shetland sandeels, the moving average models track the actual series but with a lag and the lag increases as *k* increases. The amount of smoothing also increases with *k*. The root mean square errors, RMSE (Equation 3.2), were calculated for each forecast series and the results are shown in Table 3.3. *k* of 1 or of 2 is the optimal moving average length for Shetland sandeels but the autoregressive models fitted above had lower RMSEs (0.871 & 0.876) so were therefore better fits.

The RMSE's were high as the predicted series was tracking the actual series with a lag. But will this model produce feasible time series if used to simulate recruitment? Recruitment in any year is taken as the mean recruitment in the previous years. As these models are using the previous values in the series there is little constraint to ensure the simulated time series fluctuates around the historical series mean. A positive (or negative) value will generally produce another positive (or negative) value and so on, so series will drift away from the historical mean value. To stop drift in the mean, Box-Jenkins moving average models, ARIMA(0,0,q), were considered as these use a weighted average of the error terms from the previous years as opposed to the actual previous values.

In ARIMA(0,0,*q*) model, the most recent term is influenced by the most recent error terms not the actual values. Hence an ARIMA(0,0,2) model is expressed as:

$$\hat{y}_t = \theta_0 + \varepsilon_t - \theta_1 \varepsilon_{t-1} - \theta_2 \varepsilon_{t-2} \qquad 3.13$$

where θ_1 is the moving average parameter at $t-1$, θ_0 is the constant term (which is similar to the average level of the series) and ε_{t-1} is such that:

$$\varepsilon_{t-1} = y_{t-1} - \hat{y}_{t-1} \qquad 3.31$$

Box-Jenkins moving average models of order 1, 2 and 3 were fitted to the Shetland recruit time series using the ARIMA function in SPSS. The fitted parameters and resulting RMSEs are shown in Table 3.4 and the time series predicted using the historical time series are shown in Figure 3.9 (including forecasts for a further three years). The moving average models lagged behind the historical series but the smoothing effect seen in the previous moving average models was reduced. This is due to the different procedures for calculating forecasts. In the previous models the moving average was the average of the previous observations, in the Box-Jenkins model the error terms are used. Box-Jenkins MA models of orders 2 and 3 (RMSE=0.788 and 0.787) were an improvement on the previous MA models (RMSE(*k*=2) = 0.890) and the autoregressive models (AR1 = 0.871) as these had the lowest RMSEs.. As there is little difference in the RMSE for a Box-Jenkins model of order 2 and 3, model 2 was selected for simulations as this is the more parsimonious model.

3.6 Stochastic Age-Structured Population Model PART 2

A basic stochastic age-structured model of the Shetland sandeel stock was constructed using ICES stock assessment data (ICES, 1999) discussed in the previous Chapter. The model was used to test the time series models parameterised above to simulate recruitment. Models considered plausible were selected by comparing model output with the historical data as well as considering underlying biological assumptions. Due to the limited data available for the Shetland sandeel stock and uncertainty in our understanding of biological processes, it was envisaged that more than one feasible model would be identified. The baseline population models were written in Microsoft® Visual Basic 6.0. The models are stochastic so many simulations are run and the distributions of the output analyzed to assess model dynamics.

3.7 Model Structure

The models consist of an age-structured sandeel population with components for recruitment, mortality due to a fishery and natural mortality. Natural mortality is defined as death due to predators (excluding the fishery), disease or other natural causes. Sandeels are recruited to the population and simultaneously to the fishery as 0-group fish (fish less then a year old). Sandeels are removed from the population by the fishery and through death by natural causes.

There are eight age-classes of sandeel in the models. These range from 0-group fish (recruits; fish hatched that year),1-group fish (fish which hatched and recruited to the stock in the previous year) to 7+ group fish (fish seven years old and older). The models move in yearly time steps. The change in fish numbers in the total population, all age classes summed, over each year can be represented by:

$$N_t = N_{t-1} + R_t - (C_t + m_t) \qquad 3.14$$

where N_t is the total number of fish in the population in year t, R is the number of recruits, C is the number of fish caught by the fishery and m is the number of fish dying through natural causes.

The programme runs for a set number of years, each set is referred to as one simulation, and for a set number of simulations. At the end of each simulation, the output statistics are calculated and these are read into an Excel spreadsheet or SPSS data file.

A flow diagram of the basic model is shown in Figure 3.10. At the start of the programme, the maximum number of simulations and maximum number of years in a simulation are required as input. The programme also requires an initial population and population parameters at the start of each simulation. These can be stored within the programme and read in directly during operation. The population parameters required are weight-at-age, age-specific natural and fishing mortality rates and the parameters of the stock-recruit model. Each of these is discussed in detail below. The SSB (biomass of all fish aged two and above) is calculated using weight-at-age and the recruitment component applied to determine the numbers of recruits that join the population. The number of fish removed from each age class is calculated using the fishing and natural mortality rates, also discussed below.

At the start of each year, except the first year, fish are 'aged' by increasing the age class number. In other words, fish in age class 1 are moved to age class 2 and so on. The last class, 7+, is additive, so sandeels being aged remain in this class and the 6-group fish are added to them. At the end of each simulation, the output statistics are calculated to compare model population with the historical population. These are discussed in detail below together with the programme details.

3.8 Model Input

3.8.1 Initial population

An initial age-structured sandeel population (0-7+ groups; Table 3.5) was taken from the virtual population analysis (VPA) estimates produced by ICES (1999). For age classes 1 to 7+, the average (arithmetic mean) over the years 1974 to 1997 inclusive was calculated for each age class as input as the starting population. The number of 0-groups (recruits) was calculated stochastically within the programme.

3.8.2 Weight-at-age

Weight-at-age, the average weight of a fish in an age class, was also taken from the ICES working group report (1999; Table 3.5). It was assumed weight-at-age was constant between years. In reality, this will vary as weight-at-age is influenced by factors such as food availability and ambient temperature. Evidence for differing growth rates of 0-groups sampled from Shetland in June in 1990-1992 was presented by Wright 1996. By analyzing length-frequency distributions, and also the age composition from daily otolith increments, Wright showed that 0-groups tended to be larger in 1991 and there were significant differences in mean specific growth rates between years. For the purposes of model parameterisation, weight-at-age was kept constant between years.

SSB in each year is calculated from weight-at-age as the cumulative biomass of all fish aged 2 and above (Equation 3.15). Estimates of maturity for Shetland sandeels, originating from biological sampling, indicate 100% of fish aged two and above are considered reproductively mature and 0% of 0- and 1-group fish (ICES, 1999).

$$S = \sum_{i=2}^{7} N_i W_i \qquad 3.15$$

where S is spawning stock biomass, i is the age class of sandeel, N_i is the number of sandeels in age-class i and W_i is the average weight of a sandeel in age class i.

The SSB calculated in the first year of each simulation, calculated in the programme from the starting population and weight-at-age (Table 3.5), was 126,800 tonnes. This is the same as the average of the annual estimates of SSB calculated by ICES (1999) over the years 1974-1997 inclusive (126,800 tonnes).

3.8.3 Natural mortality rates

Age-specific natural mortality rates (M) were also taken from the ICES report (1999) for use in the Shetland population models (Table 3.5). The natural mortality rate is highest for 1-group fish (1.2) and 0-group fish (0.8). For stock assessment, it was assumed that the mortality rates of sandeels around Shetland are similar to other areas of the North Sea, thus the mortality rates from the North Sea assessments were used (ICES, 1999). The North Sea stock is assessed on a semi-annual basis as opposed to the Shetland stock which is assessed annually so the North Sea mortality rates were summed to find the annual rate. It was assumed that mortality rates, M, were constant between years although, in reality, these will vary depending on factors such as the relative availability of predator and prey biomasses.

The number of fish dying due to natural causes for each age class was calculated as:

$$m_t = [M/Z] N_t (1 - \exp[-Z]) \qquad 3.16$$

where m_t is the number of fish in the age class dying due to natural mortality in year t, M is the age-specific natural mortality rate, N is the number of fish in the age class and Z is the total mortality rate and is such that:

$$Z = M + F \tag{3.17}$$

where F is the fishing mortality rate.

3.8.4 Fishing mortality rates

As there are no population estimates for the unexploited stock, a fishery is included in the basic population model to allow comparison with the historical data. Age specific fishing mortality rates varied greatly over the years in the historical data (ICES, 1999). The highest rates occurred in 1982 when the largest recorded landing occurred (52,000 tonnes). Fishing mortality rates then declined and were zero over 1991-1994 inclusive (as the fishery was closed). Since the fishery reopened in 1995 the fishing mortality rates have been extremely low.

Mean and standard deviation of age-specific fishing mortality rates were calculated by averaging the values from the 1999 ICES report over the years 1974-1986 inclusive. Catch numbers and fishing mortality rates of 0-group sandeels over these years were high (ICES, 1999) with, on average, 5,800 million 0-groups being landed each year. During this period, the highest landings occurred in 1982 when 16,851 million 0-groups were caught, and the lowest landing was recorded in 1974 (929 million). After 1986, landings for all age classes were extremely low. The age-specific fishing mortality rates for each year were selected at random from the normal distribution parameterised from the mean and standard deviation fishing mortality rates (Table 3.5). Preliminary simulations of the population model with recruitment expressed as a Ricker function of SSB (various parameter combinations were tested), indicated these values of fishing mortality were suitable.

The number of fish dying due to capture by the fishery for each age class was calculated by:

$$C_t = [F/Z]N_t(1 - \exp[-Z]) \tag{3.18}$$

where C_t is the number of fish dying due to the fishery in year t, F is the fishing mortality rate, N_t is the number of fish in the age-class in year t and Z is the total mortality rate (Equation 3.17).

3.9 Model Statistical Output

The base-line models should reproduce the population dynamics observed for sandeels at Shetland. Therefore, the assessment data produced by ICES (1999) for the population size and structure of Shetland sandeels was considered to be the 'target' data. Parameters producing model output that gave the best fit to the target data were considered to best simulate population dynamics. Various criteria were used to assess the fit of model output to target data: the arithmetic mean and standard deviation of the recruitment and SSB distributions and the autocorrelation coefficient, r_1, of the recruit time series. Kolmogorov-Smirnov 2-sample tests were used to calculate the probability that the model distributions were the same as the target distributions, as while the means of the distributions may be identical, differences may lie elsewhere (Dytham, 1999; Zar, 1999).

3.9.1 Location of Distributions

The mean and standard deviation of the SSB and recruitment distributions are measures of the 'location' of the distribution so these were compared to the values from the historical distributions. In Chapter 2, the distributions of SSB and of recruitment in the historical data were analysed. It was shown that SSB could be considered normally distributed while recruitment was log-normally distributed. Therefore, to assess model output, the recruitments produced are natural log-transformed and will be referred to as ln(R). For each model simulation, the mean and standard deviation of the SSB and ln(R) distributions were calculated and the overall mean and standard deviation was taken as the average of these of a number of simulations.

For recruitment, the mean ln(R) was calculated for each run of t years (1 simulation). The average of these over j simulations was ascertained as:

$$\overline{\ln}(R)=\frac{1}{j\max}\sum_{j=1}^{j\max}\left[\frac{1}{t\max}\sum_{t=1}^{t\max}\ln(R_{t,j})\right] \tag{3.19}$$

where $\overline{\ln}(R)$ is overall mean of the mean ln(R) produced by each simulation, $R_{t,j}$ is the recruitment produced by the model in year t of simulation j, $t$max is the number of years in a simulation and $j$max is the total number of simulations.

To calculate the overall mean standard deviation, $\overline{\sigma}_{\ln R}$, of the ln(R) distributions produced by each simulation of the model, the standard, σ_{lnR} of each run of *t* years was calculated. The mean of these, $\overline{\sigma}_{\ln R}$, over *j* simulations was then ascertained:

$$\overline{\sigma}_{\ln R} = \frac{1}{j\max}\sum_{j=1}^{j\max}\left[\sqrt{\frac{\sum_{t=1}^{t\max}\left(\ln R_{t,j} - \overline{\ln} R_j\right)^2}{t-1}}\right] \quad 3.20$$

where $\overline{\sigma}_{\ln R}$ is the mean standard deviations of log-transformed recruit distribution produced by the model, $\ln R_{t,j}$ is the ln(R) produced by the model in year *t* of simulation *j*, $\overline{\ln} R_j$ is the mean ln(R) produced by the model in simulation *j*, *t*max is the number of years in a simulation and *j*max is the number of simulations.

The overall mean SSB, $\overline{S}$, was calculated using Equation 3.19 by substituting ln($R_{t,j}$) with $S_{t,j}$ (SSB in year *t* of simulation *j*) and the overall mean standard deviation of the SSB was also calculated by substituting $S_{t,j}$ and $\overline{S}_j$ for the recruitment variables in Equation 3.20.

3.9.2 Comparing distributions

It is possible for two distributions to have identical means but have differences elsewhere. The Kolmogorov-Smirnov (K-S) goodness of fit test for continuous data delivers a probability that two distributions are the same (Sokal & Rholf, 1981; Zar, 1999). This was used to identify recruitment models that produced ln(R) and SSB distributions that were similar to the distributions in the historical data (target distributions). In this test the cumulative relative frequency in the test distribution is compared to the cumulative relative frequency of the historical distribution.

Annual estimates of SSB in the historical data were ranked in ascending order of size and the cumulative relative frequencies, $relF_i$, ascertained. The ranked values of the historical data were used as the classes to determine the cumulative relative frequencies of the test distributions. In the model, at the end of each simulation *j*, the SSB distribution was ranked into the classes determined by the target distribution. The test cumulative relative frequencies, $rel\hat{F}_i$, were calculated. The test statistic, *D*, was ascertained for each distribution as (Zar, 1999):

$$D = \max[(\max D_i),(\max D'_i)] \qquad 3.21$$

where

$$D_i = \left| relF_i - rel\hat{F}_i \right| \qquad 3.22$$

and

$$D'_i = \left| relF_{i-1} - rel\hat{F}_i \right| \qquad 3.23$$

where i is size class, $relF_i$ is the cumulative relative frequency of the historical data in size class i and $rel\hat{F}_i$ is the cumulative relative frequency of the model data in size class i.

This produced a K-S D statistic for each simulation j of t years. The overall mean D statistic, $\overline{D}$, produced over j simulations was then calculated:

$$\overline{D} = \frac{1}{j\max} \sum_{j=1}^{j\max} D_j \qquad 3.24$$

where D_j is the K-S D statistic produced in simulation j and $j$max is the total number of simulations.

An approximate critical value for D, above which the distributions being compared are considered significantly different, was calculated as described by Sokal & Rohlf (1981):

$$D_\alpha = K_\alpha \sqrt{\frac{n_1 + n_2}{n_1 n_2}} \qquad 3.25$$

where n_1 and n_2 are the sizes of the two samples (historical data and model data sets) and K_α is such that:

$$K_\alpha = \sqrt{\frac{1}{2} - \ln\left(\frac{\alpha}{2}\right)} \qquad 3.26$$

where α is the probability level. Thus for α=0.05 the value of K_α is 2.0466.

Zar (1999) suggested that for small sample sizes (say, $n \leq 25$) the power of K-S testing could be increased by employing a correction (δ-corrected K-S goodness of fit test). However, Zar refers to a report that shows if $n \geq 20$ the results of the corrected method are practically indistinguishable from the uncorrected method. The historical data series are for 24 years, so the models generally generated series of 24 years to compare with the historical series, therefore the correction to the K-S test was unnecessary.

3.9.3 Autocorrelation in Model Recruit Time Series

As discussed above, the historical ln(R) time series is positively autocorrelated at a lag of 1 year (r_1=0.51 as calculated by the method described below). To compare the autocorrelation in ln(R) time series produced by the models, the autocorrelation coefficient r_1 was calculated in the model as described below.

The autocorrelation coefficient r_1 in each simulation of t years was calculated as (Farnum & Stanton, 1989; Brown & Rothery, 1993):

$$r_1 = \frac{\sum_{t=1}^{t\max-1}\left(\ln R_t - \overline{\ln} R_j\right)\left(\ln R_{t-1} - \overline{\ln} R_j\right)}{\sum_{t=1}^{t\max}\left(\ln R_t - \overline{\ln} R_j\right)^2} \qquad 3.27$$

where lnR_t is ln(R) in year t, $\overline{\ln} R_j$ is the mean of ln(R) in simulation j of t years and $t$max is the total number of years in a simulation.

The overall mean autocorrelation coefficient, $\bar{r}_1$, over j simulations was ascertained by substituting $r_{1,j}$, the autocorrelation coefficient for simulation j, for D_j in Equation 3.24.

3.10 Model Simulations

Two time series models were parameterised above to simulate recruitment: autoregressive and moving average. These were both tested in the population model written in Visual Basic.

To simulate recruitment using the first order autoregressive model (Equation 3.11), y was replaced with ln(R) – log transformed recruitment – so recruitment (log-transformed) is expressed as:

$$\ln(\hat{R})_t = \phi_0 + \phi_1(\ln(\hat{R})_{t-1} - \phi_0) + \varepsilon_t \qquad 3.28$$

where Φ_1 is the autoregressive parameter for t-1, Φ_0 is the constant term which is approximately equal to the average level of the series, $\hat{R}_t$ is the recruitment predicted by the model in year t and ε_t is a normally distributed random number with a mean of zero and standard deviation, σ_ε, equal to:

$$\sigma_\varepsilon = \sigma_R\left(1 - \phi_1^2\right)^{0.5} \qquad 3.29$$

where σ_R is the standard deviation of the historical ln(R) distribution.

The moving average model (Equation 3.13) was also adapted to simulate recruitment in the population model as:

$$\ln(\hat{R})_t = \theta_0 + \varepsilon_t - \theta_1\varepsilon_{t-1} - \theta_2\varepsilon_{t-2} \qquad 3.30$$

where ε_t is the normally distributed random error term in year t. Error terms are independent and are normally distributed with a mean of zero and a standard deviation of:

$$\sigma_\varepsilon = \frac{\sigma_R}{(1 + \theta_1^2 + \theta_2^2)^{0.5}} \qquad 3.31$$

where σ_R is the standard deviation of the ln(R) distribution in the historical data.

These were incorporated into the population model written in Visual Basic and, for each model, 1000 simulations of 24 years were carried out. The results, as described above, were saved to an Excel spreadsheet.

3.10.1 Results

Histograms of the output distributions for mean and standard deviation of recruitment and the mean autocorrelation function of the recruit time series together with the mean K-S D statistic are shown in Figures 3.11 (autoregressive model) and 3.12 (moving average model). The results, together with the target values from the historical data series, are given in Table 3.6.

The distributions of mean and standard deviation of the model time series are normally distributed. The mean of the normal distribution of ln(R) was similar to both models tested (4.01 for autoregressive model and 4.00 for moving average model), corresponding to a mean recruitment of about 54.6 billion. This was slightly greater then the target value of 3.88, corresponding to a mean recruitment of 48.4 billion. The standard deviations of the model series (0.99 and 0.98 for the autoregressive model and moving average model respectively) were similar to the target value of 1.08.

The output histograms of mean r_1 (autocorrelation coefficient) produced by the models are shown in Figures 3.11c and 3.12c. The modal values produced by the autoregressive model was 0.45 which was slightly greater then the value produced by the moving average model (0.40). Both were close to the target value of 0.51 so overall, the model series could be considered similar to the target series.

The SSB histograms produced by the autoregressive model are shown in Figure 3.13. The results for both models are given in Table 3.6. The histograms of the SSB distributions were log-normally distributed. The modal value of the SSB distributions corresponded to a value of 125 x 10^3 tonnes for the autoregressive model and 135 x 10^3 tonnes for the moving average model, close to the target value of 127 x10^3 tonnes. The modal values of the standard deviation of SSB histograms (45 and 55 for autoregressive and moving average models respectively) were slightly less then the target value of 60.

Generally, both models tested (autoregressive and moving average) produced model distributions for recruitment and SSB that were similar to the target (historical) distributions. The histograms for mean and standard deviation of recruitment (and SSB) produced by both the autoregressive and moving average models were similar. This is due to a constraint called invertability imposed on Box-Jenkins moving average models. A factor of invertability is that every moving average model can be inverted and written as a infinite-order autoregressive model. The autoregressive model produced a greater range of models with positive autocorrelation, comparing the histograms of the r_1, autocorrelation coefficient, produced by both models (Figures 3.11c and 3.12c) indicates the moving average models produced more recruitment time series with small or negative r_1 coefficients. In view of the similarity between the models, the autoregressive model was selected to simulate recruitment in the population model of Shetland sandeels.

3.11 Final Autoregressive Models

The autoregressive model tested above, produced time series with a mean ln(recruitment) of 4.01 – higher then the target mean of 3.88. This model used values for ϕ_0 and ϕ_1 identified by fitting the model to the historical time series.

Time series modelling is data intensive, it is recommended that a long time series, of at least 50 data points, is used (Farnum & Stanton, 1989). The Shetland series is only 24 years long so confidence in the fitted autocorrelation function (0.51) and parameters of the autoregressive and moving average models is reduced. Therefore, parameters for the final autoregressive model were selected by considering the historical time series and the output from model simulations.

The mean ln(recruitment) of the historical series (3.88) was selected as parameter ϕ_0 as in the Box-Jenkins autoregressive model, ϕ_0 represents the mean of the series. ϕ_1 represents the degree of autocorrelation at time lag 1 in the series so it was assumed this would be close to the value from the historical data set (0.51). 1000 simulations of 24 years were carried out and the results are shown in Table 3.6 (AR test 2).

The parameters of the ln(recruitment) and SSB distributions produced by the model were very close to the parameters of the historical data distributions (Table 3.6). However, the autocorrelation coefficient r_1 of ln(recruit) time series returned by the model (0.40) was less then that in the historical time series (0.51). Increasing the input value of parameter ϕ_1 should increase the output mean r_1 value. r_1 was varied between 0.5 and 0.8 in steps of 0.1 and 1000 simulations of 24 years were carried out for each value. An input value of 0.68 was found to produce an output r_1 of 0.51. Increasing the input value of ϕ_1 slightly reduced the mean standard deviation of ln(recruit) and the median SSB (Table 3.6).

3.12 Conclusions

Time series models were fitted to the Shetland sandeel recruit data and simulations carried out in a population model. A first order Box-Jenkins autoregressive model was identified as the most suitable model to simulate recruitment. However, simulations indicated that the values for the parameters of the Box-Jenkins autoregressive model, fitted using the ARIMA function in SPSS, produced model output series which were slightly different to the historical series (Table 3.6). The mean of the output ln(recruit) distribution (4.01) was higher then the target value (3.88) while the median standard deviation of the SSB distribution (45) was lower then the target value (60). But, by reducing the constant term, ϕ_0, in the autoregressive model to the mean of the historical ln(recruit) series (3.88), model output series were produced which were closer to the historical series.

3.13 Summary

- Evidence for a relationship between recruitment and SSB in the Shetland sandeel stock is weak so recruitment was predicted using time series models. Uncoupling recruitment from SSB will not produce estimates of potential changes to the stock size bought about increased/decreased exploitation rate but increases our knowledge of recruitment dynamics.
- An age-structured population model was constructed in Visual Basic 6.0 to simulate the dynamics of the Shetland sandeel stock but the recruitment component needed to be further developed.
- Autoregressive and moving average models were tested to simulate recruitment.
- A 1st order autoregressive model was selected to simulate recruitment.

Table 3.1 Analysis of natural log-transformed recruit time series for North Sea sandeels and Shetland sandeels (from ICES 1999) using a Runs test for randomness (Farnum & Stanton 1989, Zar 1999) and a Daniel's test for trend (Farnum & Stanton 1989). n= length of time series, Sig. = significance at 95% level.

		North Sea	Shetland
Runs test	Median (billions)	587	60
	+ cases (above median)	11	12
	- cases (below median)	11	12
	n cases	22	24
	Number of runs	17	7
	Z	1.966	-2.296
	Sig. (2-tailed)	0.049	0.022
Daniel's test	Spearman's Rho	0.039	-0.323
	Sig. (2-tailed)	0.863	0.124

Table 3.2 Time series analysis of natural log-transformed recruit, ln(R), time series for North Sea sandeels and Shetland sandeels. Historical: analysis of ln(R) series from historical data (from ICES 1999), r_1=autocorrelation coefficient at lag 1. AR: model series from a first order autoregressive model (Equation 3.6) fitted to historical series, $E(y_t)$=expected mean level of series, β_0 and β_1=parameters of model, RMSE=root mean square errors (Equation 3.2). ARIMA(1,0,0): model series from a Box-Jenkins first order autoregressive model (Equation 3.11) fitted to historical series, ϕ_0 and ϕ_1=parameters of model.

Time Series		**North Sea**	**Shetland**
Historical	r_1	-0.628	0.540
	Mean ln(R)	6.265	3.880
AR	$E(y_t)$	6.258	3.946
	β_0	10.657	1.585
	β_1	-0.703	0.598
	RMSE	0.472	0.871
ARIMA(1,0,0)	ϕ_0	6.255	4.006
	ϕ_1	-0.669	0.579
	RMSE	0.472	0.876

Table 3.3 Root mean square errors (Equation 3.2) for moving average models (Equation 3.12) of length *k* fitted to natural log-transformed recruit time series of Shetland sandeels (from ICES 1999).

k	RMSE
1	0.963
2	0.950
3	1.002
4	1.081

Table 3.4 Parameters of Box-Jenkins moving average models, ARIMA(0,0,q), fitted to natural log-transformed recruit time series for sandeels at Shetland. RMSE=root mean square errors

	Shetland		
	ARIMA(0,0,1)	ARIMA(0,0,2)	ARIMA(0,0,3)
θ_0	3.92	4.00966	4.0241
θ_1	-0.453	-0.42089	-0.5565
θ_2	-	-0.98982	-0.6621
θ_3	-	-	-0.44834
RMSE	0.931	0.788	0.786

Table 3.5 Input parameters for Shetland sandeel population model (from ICES 1999). Weight-at-age = average weight of a fish in an age class, M = natural mortality rate, F = fishing mortality rate and σ_F = standard deviation fishing mortality rate

Age Class	Population (millions)	Weight-at-age (g)	M	F	σ_F
0		0.746	0.8	0.074	0.032
1	17769	3.095	1.2	0.254	0.110
2	7393	5.409	0.6	0.096	0.041
3	3796	8.585	0.6	0.056	0.024
4	1957	11.143	0.6	0.073	0.032
5	1005	13.705	0.6	0.069	0.030
6	523	15.605	0.6	0.056	0.024
7+	491	21.254	0.6	0.056	0.024

Table 3.6 Comparison of output from 1000 simulations of 24 years of time series models used to simulate recruitment of sandeels at Shetland with values from historical distributions. Historical: historical data from ICES (1999), MA: second order moving average model, AR: first order autoregressive model, ϕ_0=constant term in AR model, ϕ_1= first autoregressive parameter in AR model, ln(R)=natural log transformed recruitment (billions), SD=standard deviation, r_1=autocorrelation coefficient of ln(R) time series at lag 1, SSB=spawning stock biomass (000 tonnes).

	ϕ_0	ϕ_1	Mean ln(R)	SD ln(R)	r_1	Median SSB	Median SD SSB
Historical			3.88	1.08	0.51	127	60
MA			4.00	0.98	0.45	138	71
AR test 1	4.01	0.58	4.01	0.99	0.40	138	75
AR test 2	3.88	0.51	3.88	1.01	0.40	126	63
AR test 3	3.88	0.68	3.88	0.95	0.51	119	61

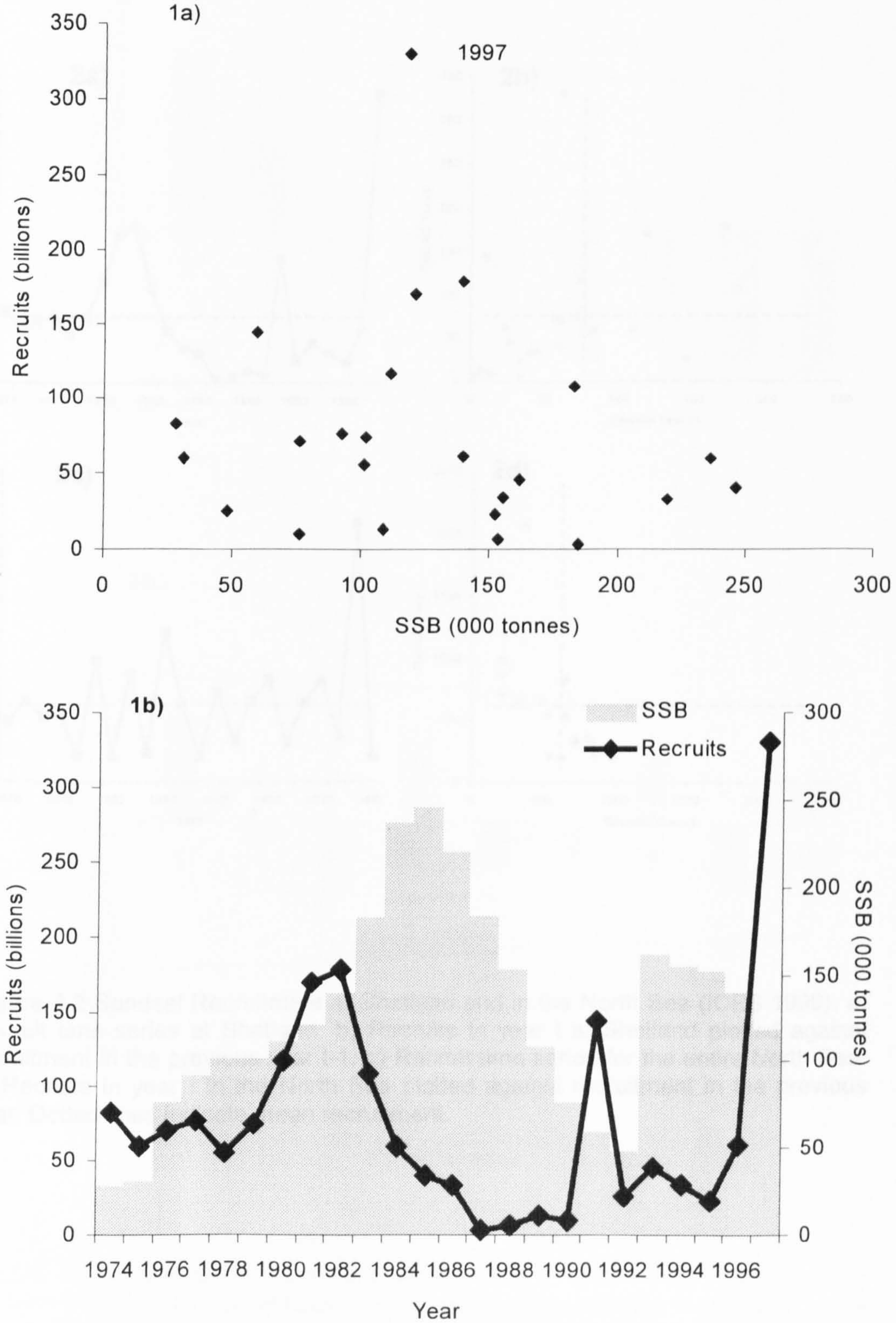


Figure 3.1 a) Stock-recruit data for sandeels at Shetland and **b)** trends in SSB and recruitment for sandeels at Shetland (from ICES 1999).

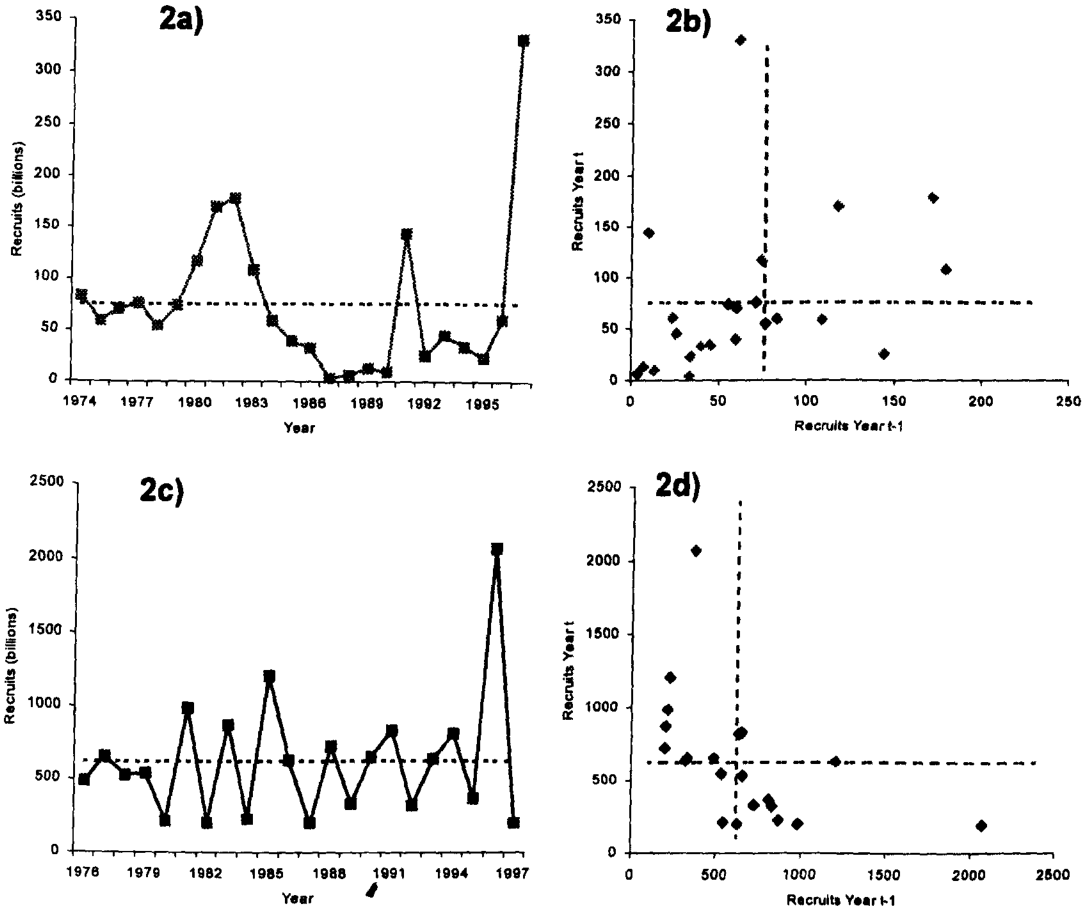


Figure 3.2 Sandeel Recruitment at Shetland and in the North Sea (ICES 1999). **a)** Recruit time series at Shetland. **b)** Recruits in year t at Shetland plotted against recruitment in the previous year t-1. **c)** Recruit time series for the entire North Sea. **d)** Recruits in year t in the North Sea plotted against recruitment in the previous year. Dotted lines indicate mean recruitment.

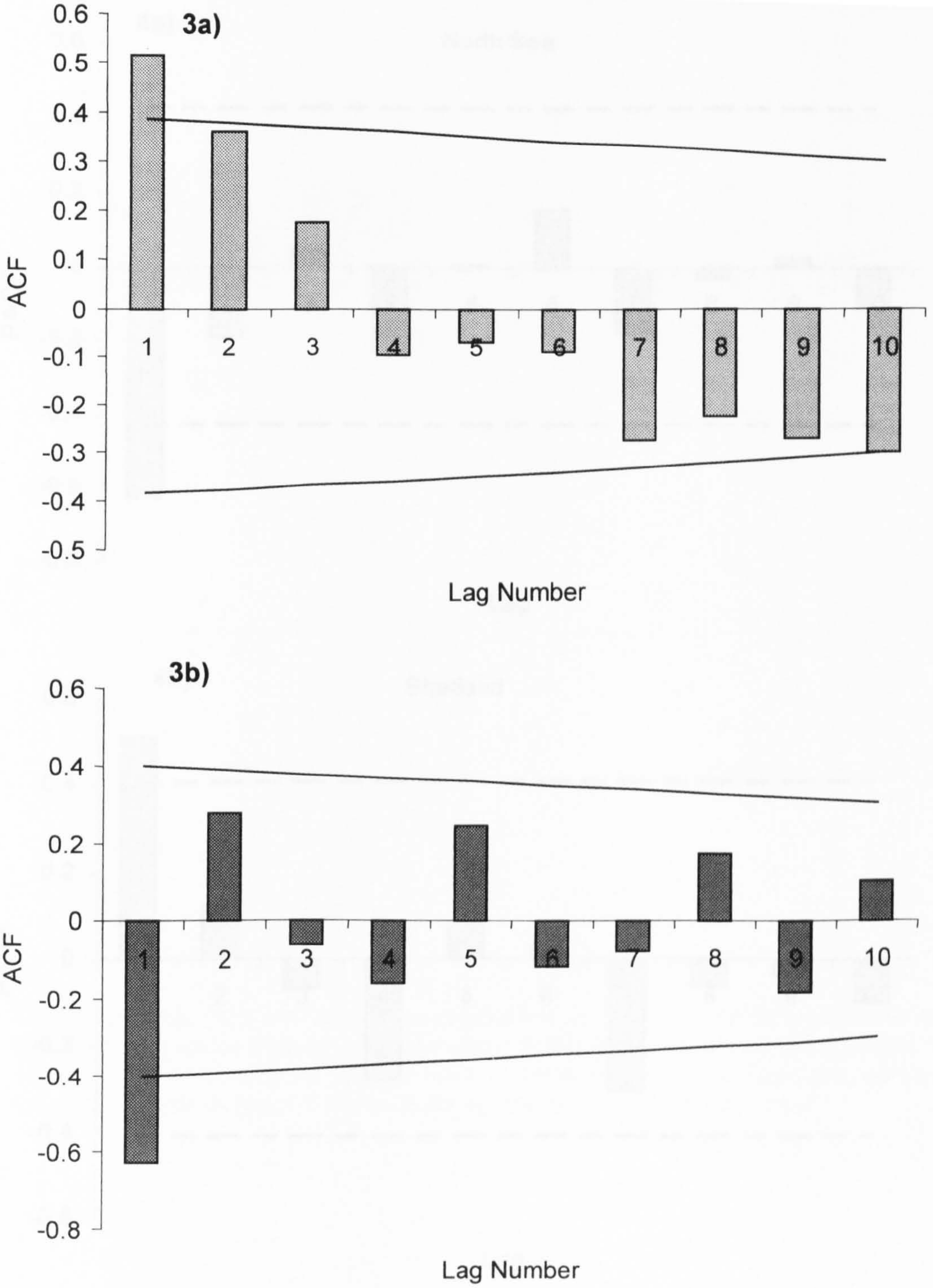


Figure 3.3 a) Sandeels at Shetland **b)** sandeels in North Sea. Autocorrelation function (ACF) for the natural-log transformed recruit time series at time lags 1 year to 10 years (data from ICES 1999). Solid black lines represent critical values outside of which the ACF is significant

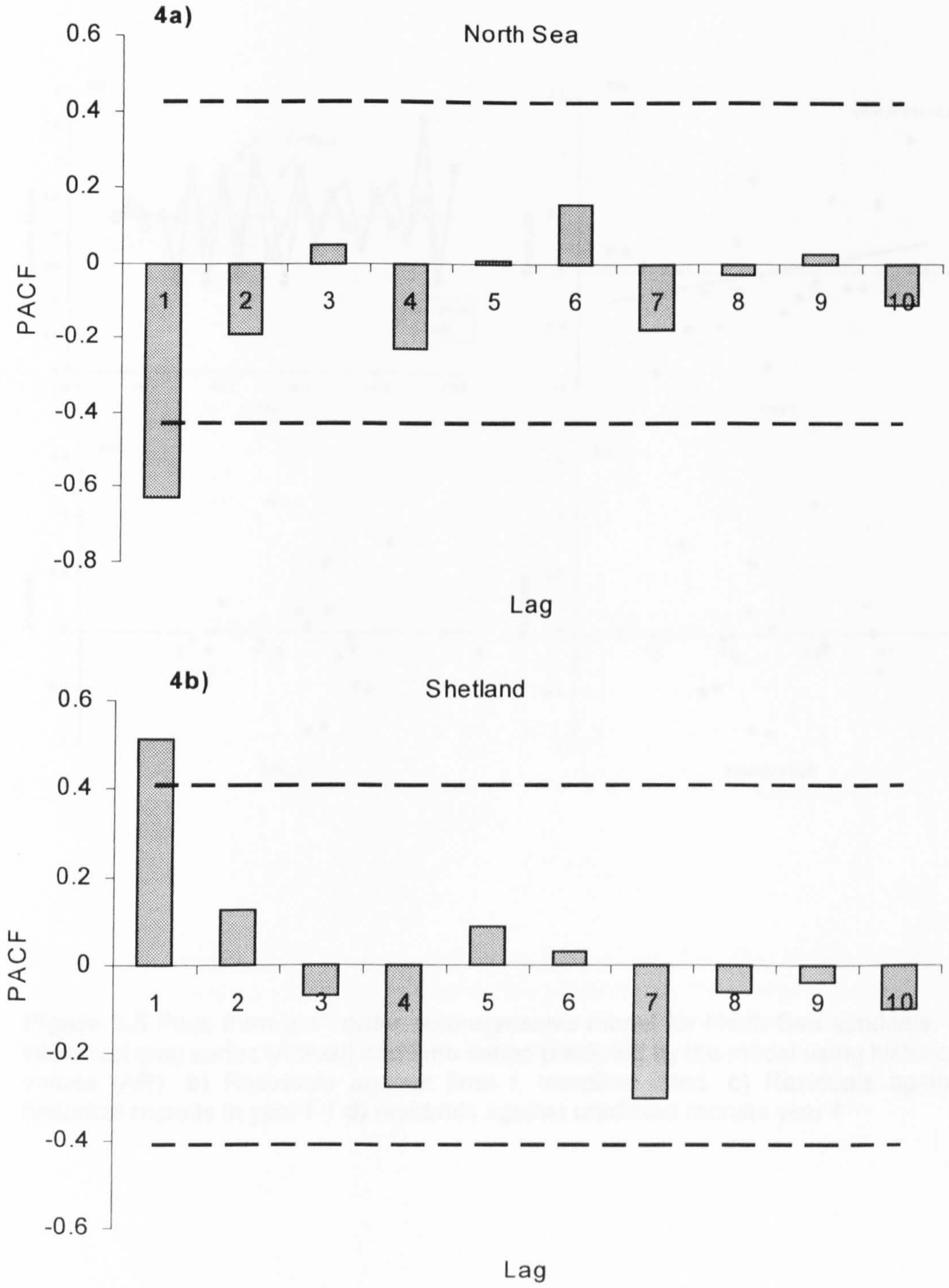


Figure 3.4 Partial autocorrelation function (PACF) for natural log-transformed recruit time series of **a)** North Sea sandeels and **b)** Shetland sandeels at lags of 1 year. Dotted lines indicate the confidence limits.

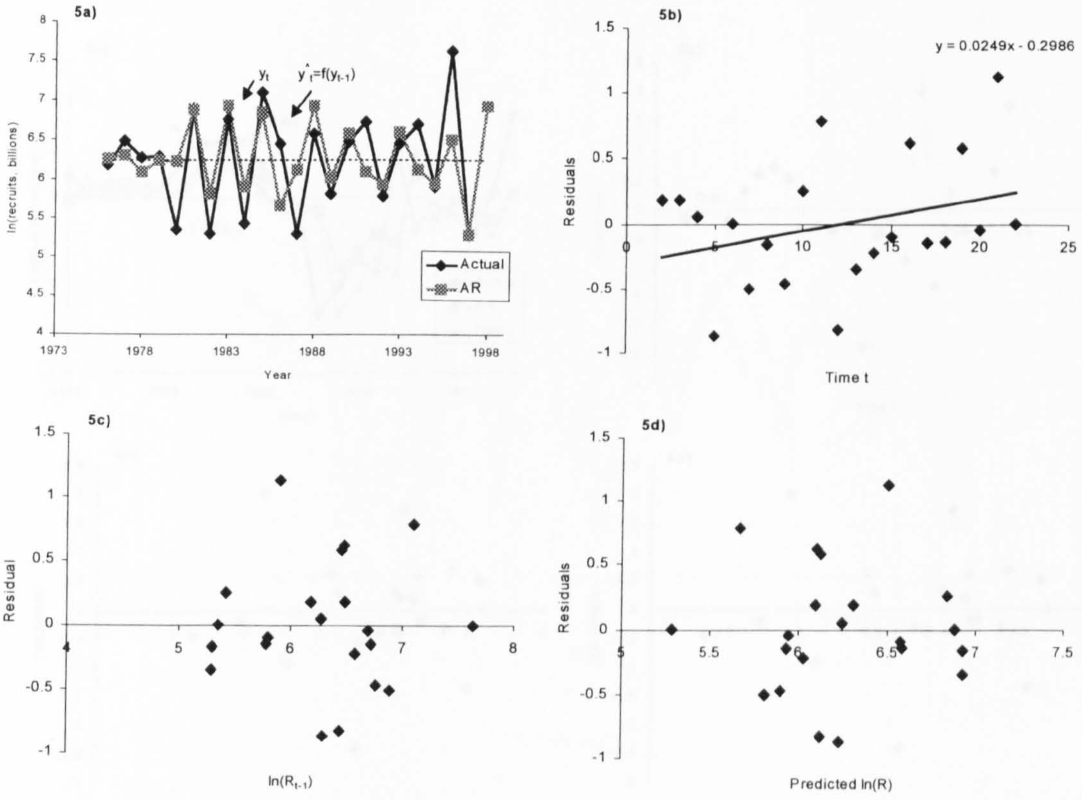


Figure 3.5 Plots from a 1st order autoregressive model for North Sea sandeels. **a)** Historical time series (Actual) and time series predicted by the model using historical values (AR). **b)** Residuals against time *t*, trendline fitted. **c)** Residuals against historical recruits in year *t-1* **d)** residuals against predicted recruits year *t*

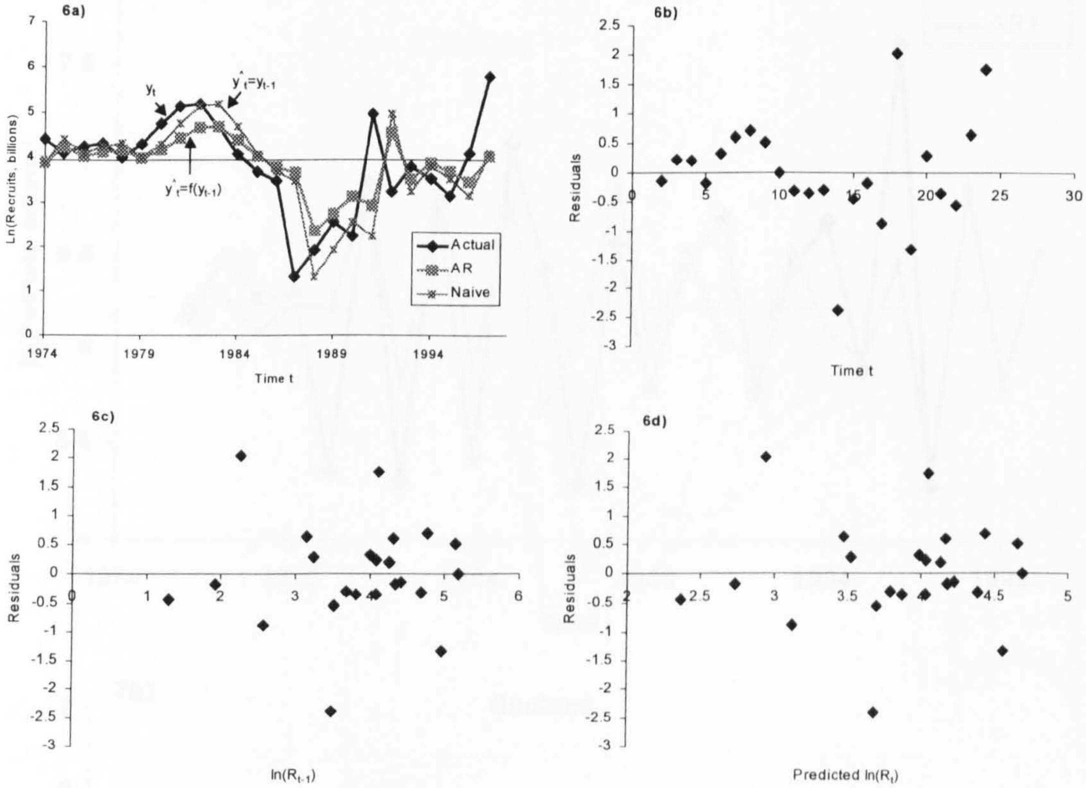


Figure 3.6 Plots from a 1st order autoregressive model for Shetland sandeels. **a)** Historical time series (actual) and time series predicted by the model using historical values (AR). **b)** Residuals against time t, trendline fitted. **c)** Residuals against historical recruits in year t-1 **d)** residuals against predicted recruits year t

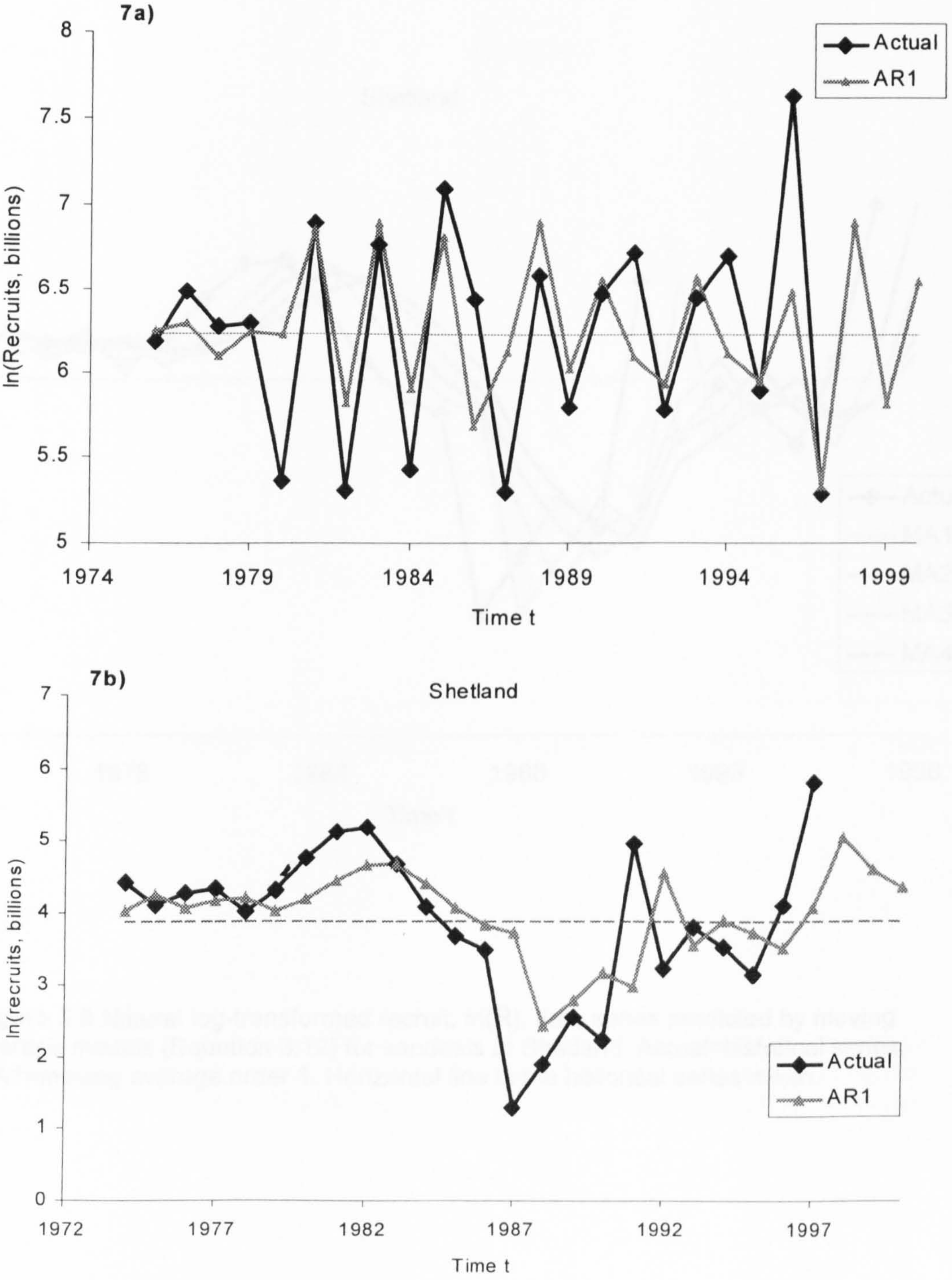


Figure 3.7 ARIMA(1,0,0) models fitted to **a)** North Sea sandeels and **b)** Shetland sandeel recruit time series. Actual=historical time series, AR1=ARIMA time series predicted using the historical data. Horizontal lines indicate mean ln(Recruitment)

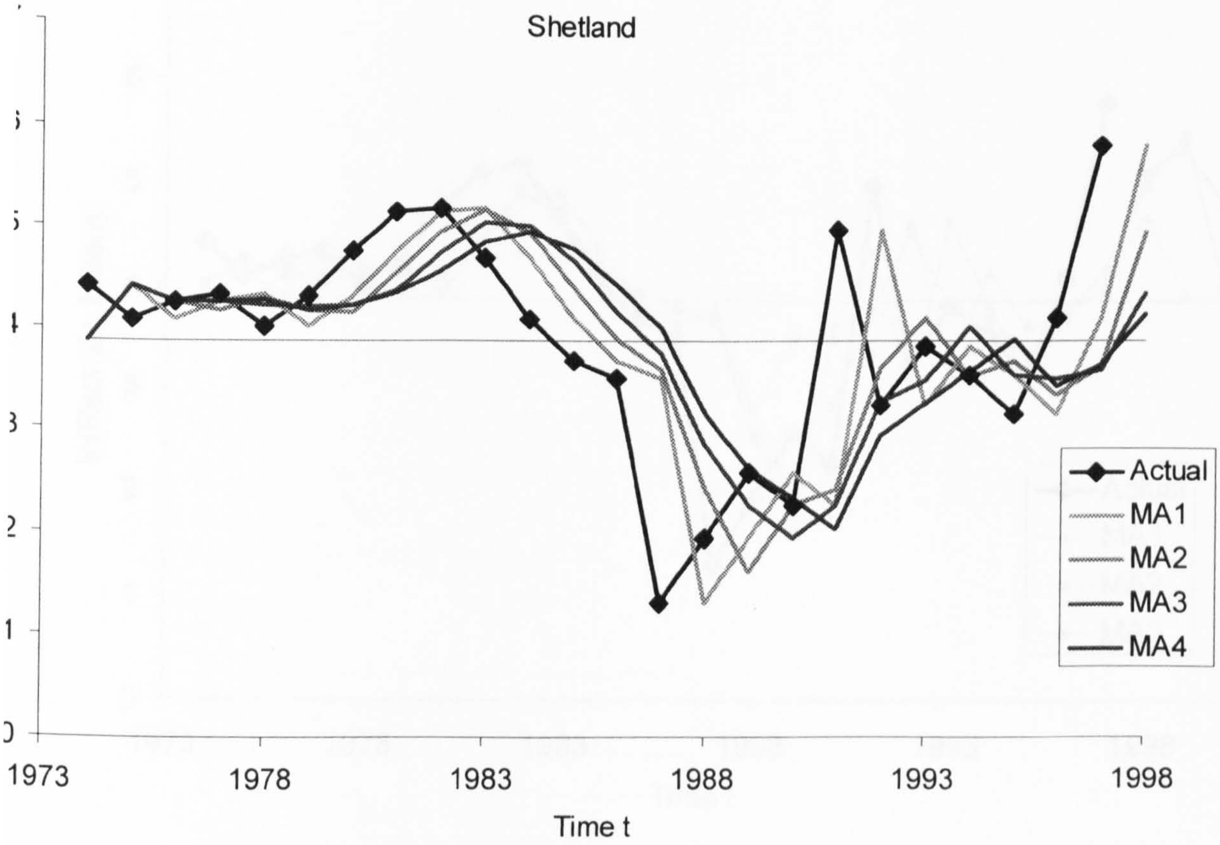


Figure 3.8 Natural log-transformed recruit, ln(R), time series predicted by moving average models (Equation 3.12) for sandeels at Shetland. Actual=historical series, MA1=moving average order 1. Horizontal line is the historical series mean.

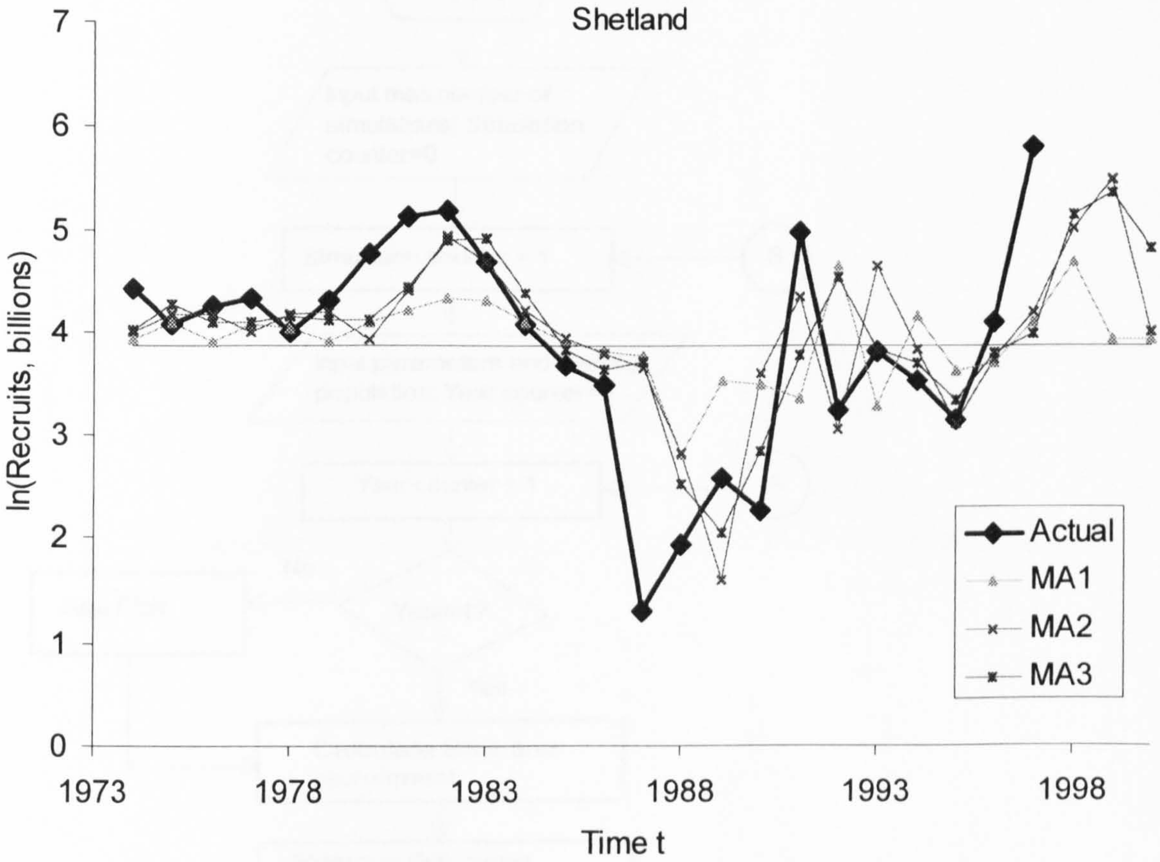


Figure 3.9 Natural log-transformed recruit, ln(R), time series predicted by ARIMA(0,0,q) moving average models (Equation 3.13) for sandeels at Shetland. Actual=historical series, MA1=ARIMA(0,0,1). Horizontal line is the historical series mean.

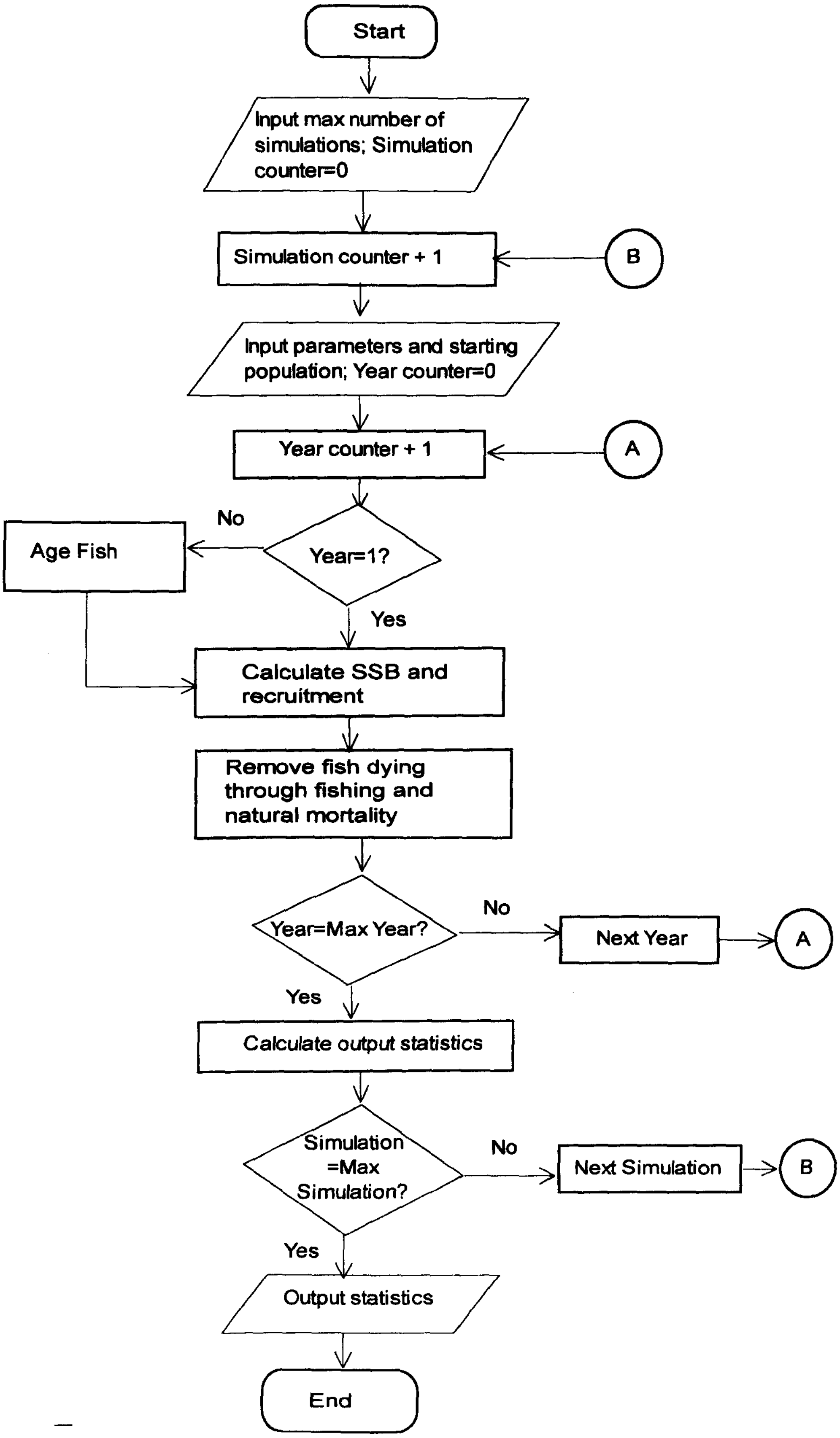


Figure 3.10 Flow diagram of baseline sandeel population model

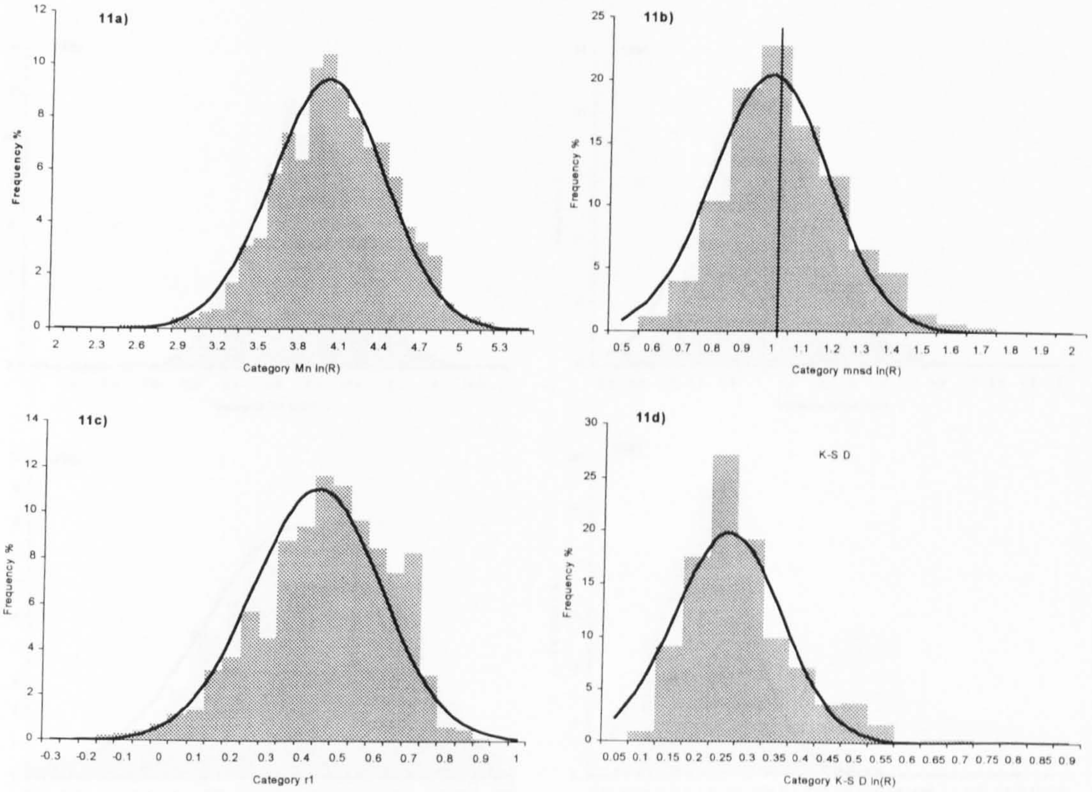


Figure 3.11 Recruitment ln(R) output distributions from 1000 simulations of 24 years of a stochastic population of sandeels at Shetland with recruitment simulated as a first order autoregressive model. Expected normal curves shown. **a)** Mean ln(R), **b)** standard deviation of ln(R), **c)** mean autocorrelation coefficient **d)** mean Kolmogorov-Smirnov D statistic.

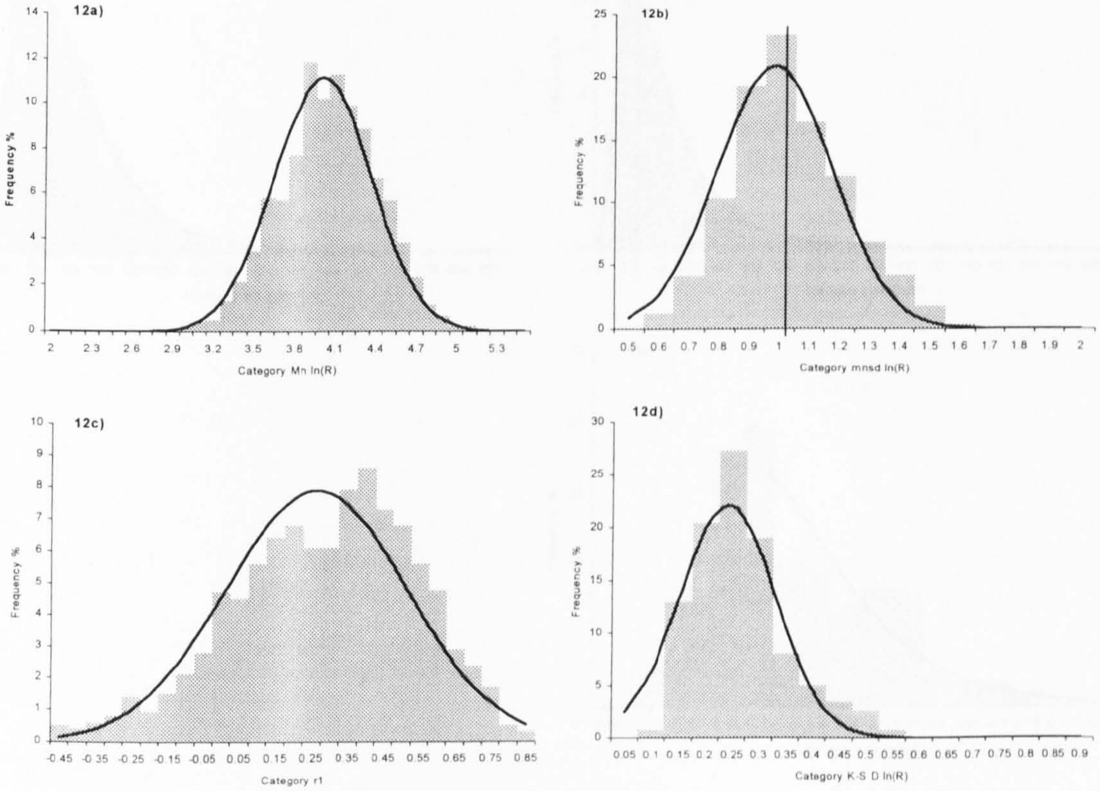


Figure 3.12 Recruitment ln(R) output distributions from 1000 simulations of 24 years of a stochastic population of sandeels at Shetland with recruitment simulated as a second order moving average model. Expected normal curves shown. **a)** Mean ln(R), **b)** standard deviation of ln(R), **c)** mean autocorrelation coefficient **d)** mean Kolmogorov-Smirnov D statistic.

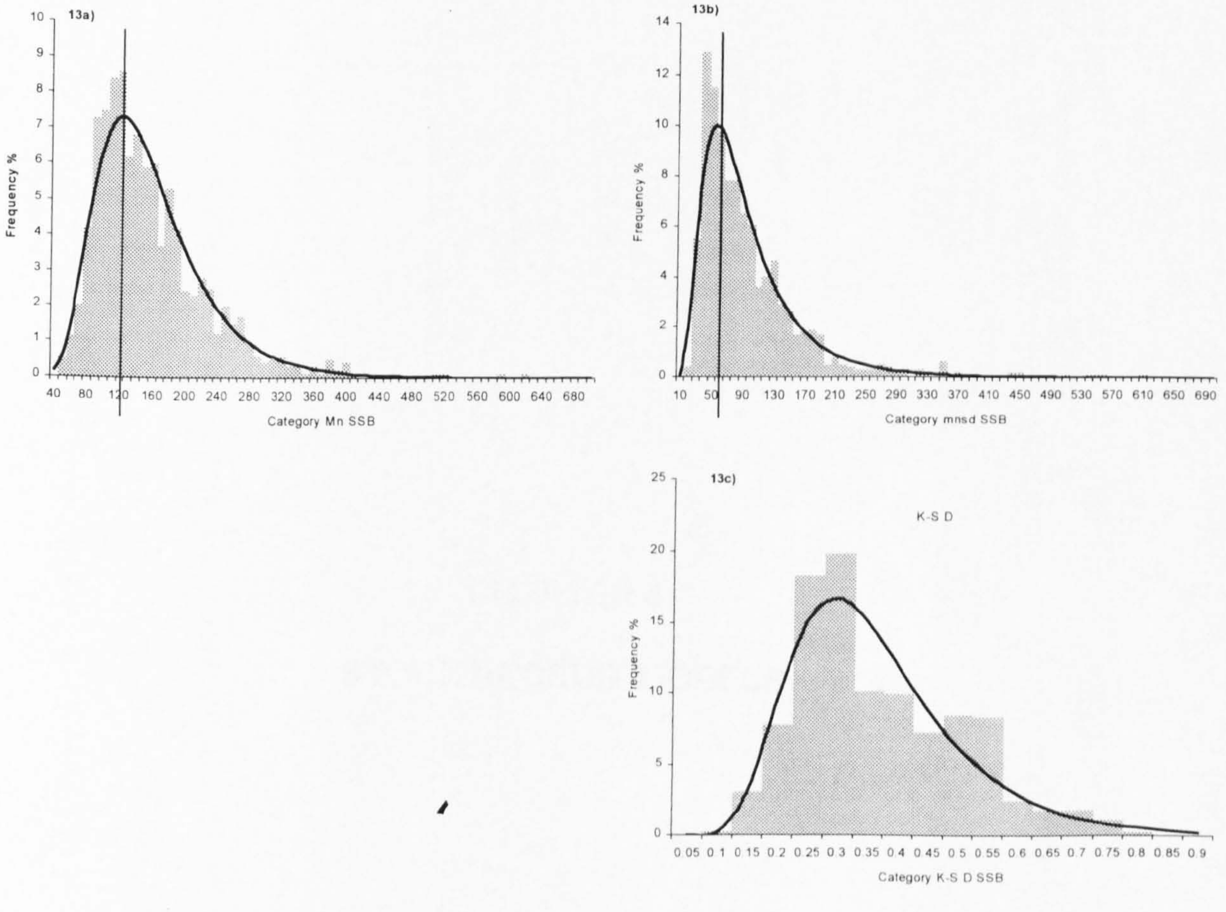


Figure 3.13 SSB output distributions from 1000 simulations of 24 years of a stochastic population of sandeels at Shetland with recruitment simulated as a first order autoregressive model. Expected log-normal curves shown. **a)** Mean SSB, **b)** standard deviation of SSB, **c)** mean Kolmogorov-Smirnov D statistic.

CHAPTER 4

STOCK RECRUIT MODELS

4.1 Introduction to Chapter

This Chapter introduces stock-recruit models and fits both Ricker (1954; 1975) and Shepherd (1982) models to the Shetland data. Although stock-recruit analysis using the Shepherd model is presented here with baseline model simulations, this was rejected in subsequent analyses due to high uncertainty in the data and problems with defining a stock-recruit relationship for this model.

It is assumed in this Chapter that no net immigration of recruits occurs, that is, no net "external" recruitment. After introducing the concept of stock-recruit models and discussing stock and recruitment issues at Shetland, the Chapter is then split into three parts. In the first part, the Ricker model is discussed and fitted to the Shetland sandeel stock using linear regression. In order to estimate confidence intervals, bootstrap analysis was applied and the results were compared with the output of a direct search method to identify optimal parameters. Ultimately three curves were identified, an optimal Ricker curve together with two curves representing 95% confidence intervals.

Shepherd stock-recruit models are parameterised in part 2, these cannot be fitted by simple linear regression as for the Ricker model. Initial estimates for the parameters of the Shepherd curve were found using the subjective methods described by Shepherd (1982). Final estimates were found by minimizing the "sums of squared differences" between observed recruits (historical) and predicted recruits. Bootstrap analysis was then applied. The histograms returned by bootstrap analysis for each parameter were multi-modal so there is more than one optimal stock-recruit curve. The reasons for this were considered and plausible curves identified.

In the third part, the population model written in Visual Basic 6.0 in the previous Chapter, was adapted so that recruitment was simulated using the Ricker curves parameterised. Autocorrelated stochasticity was added and the models were tested for robustness using the population model. Simulations for each recruitment model were run and the results analyzed and discussed.

4.2 Stock-Recruit Models

As discussed in the previous Chapter, the concept of recruitment as a deterministic function of spawning stock biomass (SSB) is fundamental to fishery management. However, in many species of exploited fish, the relationship is weak, and it has been disputed that it exists. So why use stock-recruitment relationships? Stock-recruit curves can provide understanding of the affects of changing harvest pressure on recruitment, thus ultimately on stock size. For example, if increasing fishing pressure reduces SSB, this could lead to either a reduction or an increase in recruitment. The response to exploitation will depend on the underlying shape of the stock-recruit model (see below). Recruitment is usually highly variable about the fitted stock-recruit model. Trying to understand and model causes of variation in recruitment should improve our ability to manage fish stocks sustainably. However, this is one of the most challenging problems in fisheries science.

Using an unrealistic stock-recruit curve in the population models may make the simulated population appear more or less resilient to high exploitation rates than the real population. If the model is then used to guide management decisions, the consequences could be potentially disastrous. To illustrate this, two different stock-recruit curves for a hypothetical fish population are shown in Figure 4.1. For the unexploited population, the spawning stock biomass (SSB) is 100% and recruitment is at 100%. With curve 1, as SSB is reduced, recruitment also reduces. The reduction in recruitment occurs immediately with the reduction in SSB, and the decline in both is slow, potentially giving enough warning of stock decrease to allow corrective measures to be taken. With curve 2, a decline in SSB initially produces an *increase* in recruitment. It is only when SSB is reduced to 33% of its original value that recruitment drops below 100%. Once SSB is below 33%, the decline in recruitment is rapid and this situation can quickly lead to stock collapse. It may often be difficult to determine if the stock is approaching critical SSB levels.

Traditional stock-recruit models include those of Ricker (1954; 1975) and Beverton-Holt (1957). In the Beverton-Holt model, recruitment increases with SSB towards an asymptote (Figure 4.1, curve 1). In the Ricker model, the curve is dome shaped so recruitment decreases at high levels of SSB (Figure 4.1, curve 2). These models are widely used in fisheries management.

A full discussion and analyses of stock-recruit models can be found in Hilborn and Walters (1992). Observing the stock-recruit scatterplots for sandeels at Shetland and in the North Sea (Figure 4.2) one can identify several features. For North Sea sandeels, recruitment generally increases with SSB, but is the very low recruitment (200 billion) at the highest SSB (1634 x10^3 tonnes) an outlier or indicative of a trend for recruitment to decrease at high SSBs? For Shetland sandeels, it appears that initially recruitment increases with SSB, then decreases at higher SSBs. The variability in recruitment appears highest at mid-sized SSBs. A common feature in both plots, is the occurrence of an extremely high recruitment at a mid-sized SSB – although this occurred in different years in the two stocks (1996 in the North Sea and 1997 at Shetland). Considering the temporal pattern in recruitment (by joining the data points), one can see the distinction between the two stocks. Recruitment to the Shetland stock generally shows slow changes in recruitment numbers, regardless of SSB, while the North sea stock is much more variable and recruitment appears to be more strongly linked with SSB. Both stocks show lower then expected recruitments in 1987 and 1988.

Hilborn & Walters (1992) discuss the simplest assumption regarding stock and recruitment, that is recruitment is directly proportional to SSB. This model is density independent: the average relationship is shown for Shetland and North Sea sandeels in Figure 4.2 (trendlines). This model is too simplistic, as it assumes recruitment will continue to rise with SSB indefinitely. This cannot be the case as eventually density-dependent factors will dominate, for example, through competition for food or space. However, stock-recruit relationships are usually density independent near the origin.

Two stock-recruit models were chosen for analysis: the Ricker model (1954; 1975; Figure 4.1 curve 2), which is widely used, and the Shepherd model (1982; Figure 4.10). The Ricker model having only two parameters (Shepherd model has three parameters) is the easier to fit to the data. However, the three parameters in the Shepherd curve makes this much more flexible. These models were chosen as both can be dome-shaped, so density dependence dominates at high stock levels. Ricker (1954) proposed several mechanisms that result in a compensatory stock-recruit relationship, such as competition for living space, competition for food resulting in starvation and cannibalism (Sissenwine, 1984). It is likely that competition for resources occurs on sandeel grounds. Sandeels overwinter buried in sediment of a suitable grain size and during the summer they emerge during the day to feed in the water column. Wright *et al.* (2000) showed that post-settled sandeels actively select well-flushed sediments of particular grain sizes for burying thus competition for space may arise on sandeel grounds. Additionally, adult sandeels are not thought to make spawning migrations but spawn, and the larvae hatch (in early spring), on the sandeel grounds so potential may exist for cannibalism. However, it is unknown if adults are feeding at this time. All of these factors suggest that the stock-recruit relationship for sandeels at Shetland is likely to be dome-shaped.

Recruitment is very variable in many populations of commercially exploited fish so a potential range of recruitments exists for each SSB. Stock-recruit curves return either the *average* or *median* recruitment for a given SSB. That is, for any given SSB the curve passes either through the mean of the potential recruitments or potential recruitments are lognormally distributed and the curve passes through the "center of gravity" of this distribution. An additional term is often used to incorporate random variation (Hilborn & Walters, 1992). Hilborn & Walters (1992) recommend that a log-normal distribution be the starting assumption for stock-recruitment work.

This assumption was justified by Hilborn & Walters (1992) by considering the following theory. The stock-recruitment process consists of a number of life history stages progressing from egg to recruit and total survival is the product of these stages. If both sides are log-transformed and it is assumed the survival rate in each life history stage is an independent random variable, then the sum of the (log-transformed) series will have a distribution that approaches the normal distribution as the number of summed values increases. Therefore, the overall survival rate should be lognormally distributed.

Hilborn & Walters (1992) summarized, in part, that the observed pattern for a number of different actual data sets conform to the lognormal pattern. Features of the lognormal distribution are that recruitment cannot be negative, occasionally a large recruitment will occur – due to the long tail of the distribution, and the amount of variation will be proportional to the recruitment predicted by the stock-recruit curve, so variability will be lower at small recruitments and much larger at higher recruitments (Hilborn & Walters 1992).

4.3 Stock & Recruitment at Shetland

Stock assessments at Shetland are prone to high levels of uncertainty due to high natural mortality rates, large variation in recruitment and low exploitation rates (Cook & Reeves, 1993) as well as the inherent inaccuracy of the assessment measurements. The closure of the fishery over 1991-1994 and the subsequent low landings have led to a lack of suitable data for fishery assessment models. Assessment models use the numbers and average weight of fish caught per age-class to estimate historic fishing mortality and stock numbers (see Hilborn & Walters, 1992; Jennings *et al.*, 2001). The recent low catch rates and low effort of the Shetland sandeel fishery will affect these input parameters as the landed fish may not be representative of the entire age-class, thereby reducing certainty in the assessments. In particular, in 1990 the level of sampling was considered too poor to provide satisfactory age compositions (Cook & Reeves, 1993). ICES (1999) noted that stock estimates resulting from the assessment can only be regarded as an indication of the overall trends in the stock, and not of absolute levels.

There are a number of difficulties in trying to determine a stock-recruit relationship for sandeels at Shetland. Firstly, there appears to be strong environmental forcing as was shown by the analysis of the time series for autocorrelation given in Chapter 3 and seen in the temporal pattern in recruitment in Figure 4.2. During the 1980s, recruitment declined and this was followed by a corresponding decline in SSB (see Figure 2.2). As discussed in Chapter 3, this may induce a spurious relationship between stock and recruitment as the low SSBs were probably the result of low recruitments, not the other way round.

Additionally, Wright (1996) presents evidence that some recruits to the Shetland system may originate from outside Shetland waters. Recruits originating from around Orkney may arrive at Shetland either by passive transport during the larval phase or active movements immediately prior to settlement (Proctor *et al.*, 1998). There is also evidence for advection of larvae away from Shetland, but a 2-dimensional sea-circulation model, adapted to model the transport of larvae on the north-west European shelf, indicated this loss may be less then the gain of recruits (Proctor *et al.*, 1998). If *net* immigration does occur, then this will obscure the stock-recruit relationship at Shetland.

The approach taken to these problems was to construct a number of stock-recruit models for recruitment at Shetland. Models which were considered biologically plausible were identified and simulations using these models are analyzed. Two approaches were taken to produce sets of recruitment models. Firstly, it was assumed that there is no net immigration to the Shetland stock and stock-recruit models were fitted (this Chapter). For the second approach (next Chapter), it was assumed that a proportion of recruitment each year originates from outside of Shetland waters, ('external' recruits).

4.4 Ricker Models PART 1

This part of the work is concerned only with the Ricker stock-recruit model – full details can be found in Hilborn & Walters (1992). The Ricker model (1954; 1975; Equation 4.1) was selected as this is one of the seminal stock-recruit models that, though developed in the 1950s, is still widely used today. The model produces dome-shaped stock-recruit curves, which for reasons outlined previously, were expected for sandeel populations. At low SSBs, recruitment increases with SSB and high SSBs density-dependence dominates, so recruitment decreases with further increases in SSB (Figure 4.3). The Ricker model is simple to fit, by using linear regression, and confidence limits for parameter estimates can by determined by bootstrap analysis.

The Ricker model is expressed as:

$$R = Se^{a(1-S/b)} \qquad 4.1$$

where R is recruitment, S is SSB and a and b are fitted constants.

The more common form of the Ricker model is:

$$R = aSe^{-bS} \qquad 4.2$$

where a represents the slope from the origin and b describes how quickly recruits-per-spawner drops at high SSB. If a is high then the maximum recruitment is high. b is the density-dependent parameter and if b is high then the maximum recruitment decreases and the level of SSB at which this occurs decreases (Figure 4.3; see Jennings *et al.*, 2001 for further details).

4.5 Ricker model fit by linear regression

Parameters of the Ricker model can be estimated using simple linear regression. Equation 4.2 is transformed so it can be expressed as a linear equation of the form:

$$Y_i = \alpha + \beta X_i + \varepsilon_i \qquad 4.3$$

where Y is the dependent variable, X is the independent variable, α and β are constants and ε is an error term (Zar, 1999). Linearising Equation 4.2 using natural logarithms gives:

$$\ln\left(\frac{R}{S}\right) = \ln(a) - bS + w \qquad 4.4$$

where R is the number of recruits, S is SSB, a and b are constants and w is the residual (error term).

Plotting *ln(R/S)* against S and fitting a regression line will give estimates for a and b (Figure 4.4a). The intercept of the line will equal *ln(a)* and the slope is equal to $-b$ (from the equation for a straight line Equation 4.3). Parameters a and b were estimated using the linear regression function in the Data Analysis Toolpak of Excel. This method produces estimates and variances for parameter b and for *ln(a)* and the variance, σ_w, around the stock-recruit curve (Table 4.1). The linearised plots, residual plots and the resulting stock-recruit curves (heavy curves) are shown in

Figure 4.4. There is no trend in the residuals (Figure 4.4b) so it can be assumed that the pattern in the stock-recruit data is reasonably well represented by the curve.

Equation 4.4 assumes lognormal errors therefore the stock-recruit model actually being fitted can be described as (see Hilborn & Walters, 1992):

$$R = aSe^{-bS}e^{w} \qquad 4.5$$

where w is normally distributed with a mean of zero, therefore e^{w} is lognormally distributed.

This means that, for any given stock size, the residuals are likely to be lognormally distributed about the curve. This is not the same as mean (average) recruitment. To find the stock-recruit curve which passes through the mean recruitment for any given SSB, it is necessary to transform parameter *a*. Hilborn (1985) demonstrated that, to define the average curve, the expected value of e^{w} is $e^{\sigma^2/2}$ (from the equation to transform the median of a normal distribution to the mean, see Evans *et al.*, 2000). Therefore, the average stock recruit curve will have parameter *a'* defined as:

$$a' = ae^{\sigma_w^2/2} \qquad 4.6$$

where σ_w is the standard deviation of the residuals (*w*).

The value of parameter *a'* (3.768) was greater then parameter *a* (2.134). This was the effect of the large variation about the stock-recruit curve. The Ricker curve which passes through the average recruitments is also shown in Figure 4.4c. As recruitment will be simulated in the models by using stock-recruit curves with lognormal variation, it was not necessary to correct parameter *a* to *a'*.

4.6 Ricker model fit by bootstrap analysis

Confidence intervals (c.i.) for parameter estimates can be determined using bootstrap analysis (see Efron & Gong, 1983) described in Chapter 2. Bootstrap analysis samples at random, with replacement, from the original data set to generate probability distributions for parameter estimates. A program to perform bootstrap analysis was written in Visual Basic 6 as a Macro behind an Excel spreadsheet. For each bootstrap simulation, *n* stock-recruit pairs were selected at random with replacement from the original *n* pairs (historical data). *ln(R/S)* was determined for every stock-recruit pair and the slope (-1*parameter *b*) was calculated using an equation for simple linear regression (Equation 4.7; Zar, 1999).

$$-b = \frac{\sum_{i=1}^{n}\left(S-\bar{S}\right)\left(\ln(R/S)-\overline{\ln}(R/S)\right)}{\sum_{i=1}^{n}\left(S-\bar{S}\right)^{2}} \tag{4.7}$$

where S is SSB, $\bar{S}$ is mean SSB in the selected series, R is number of recruits, $\overline{\ln}(R/S)$ is mean logged residual and n is the length of the stock-recruit series.

Parameter a was calculated as:

$$a = e^{\left(\overline{\ln}\left(R/S\right)-\left(-b*\bar{S}\right)\right)} \tag{4.8}$$

The standard deviation of the residuals σ_w from the parameterised Ricker curve were also determined. 1000 bootstrap simulations were performed and a, b, $\sigma_{w,}$ $\bar{R}$ and $\bar{S}$ were recorded for each simulation. From these recorded values, the overall mean was calculated for a, b and σ_w and also the standard error of a, σ_a, and of b, σ_b (Table 4.2).

The probability distributions of parameter estimates returned by bootstrapping are shown in Figure 4.5. The upper and lower 95% confidence intervals were determined as the 0.05 and 0.95 percentiles respectively. The value of parameter *a* estimated by bootstrapping (2.421)) was similar but not identical to the mean value estimated by linear regression (2.134). The histogram of parameter *a* returned by bootstrapping appears to be slightly skewed and so may be better represented by a lognormal distribution (Figure 4.5a & b). Parameter *a* was log-transformed in Equation 4.5 and therefore cannot be less then zero. A 1-sample Kolmogorov-Smirnov (K-S) test for normality (Zar 1999) indicated that the distribution was more likely to be lognormally distributed (P=0.188) then normal (P=0.000).

The histogram of *ln(a)* returned by bootstrap analysis is shown in Figure 4.5(b). The mean of the distribution corresponds to the log transformed optimal value of parameter *a*. This is slightly different to the value determined from parameter *a* histograms above so has been designated *a"*. Back-transforming the mean value of *ln(a)* will return *a"*. The value estimated for *a"* was 2.191, much closer to the value estimated by linear regression (2.134). The upper and lower 95% confidence limits for parameter *a* were 4.451 and 1.032 respectively.

For parameter *b*, the mean and standard deviation returned by bootstrapping (0.012763 ± 0.003338) were similar to the values returned by linear regression (0.012501 ± 0.003782; Table 4.2).

Bootstrapping estimated confidence intervals for the parameters of the Ricker curve. Using these values in the Ricker model should parameterise curves representing the upper and lower intervals. Parameters *a* and *b* are highly correlated as they are related by Equation 4.2. Equation 4.2 can be rearranged to express *a* as a function of *b*:

$$a = \frac{S \exp^{-bS}}{R} \qquad 4.9$$

Therefore, for a given SSB and recruitment, altering one parameter will necessitate a corresponding alteration in the other parameter. This high correlation is shown in Figure 4.6, the best fit estimate for the parameters (*a*", *b*) found by bootstrapping is indicated by the light square. The correlation between the parameters is very high (R^2=0.735).

Figure 4.6 shows there is a spread of closely correlated values for *a* and *b* that all produce 'good fit' stock recruit curves. This can be explained by considering the 'landscape' for fits to the historical data produced combinations of *a* and *b*. If the fit (sums of squares) is plotted on a 3-dimensional graph against parameter *a* and parameter *b*, the best fits will show as a 'valley' in this landscape. To demonstrate this, all fits were calculated for combinations of *a* and *b* within specified ranges using a direct search method described below.

4.6.1 Ricker model fit by direct search

As was shown above, the parameters of the Ricker curve are highly correlated. In order to visualise the Ricker function, and this correlation, a direct search method was applied. For a range of parameter combinations, the Ricker model was applied to the Shetland sandeel data and the least logged square differences (Equation 4.10) determined for each combination. The results were then compared to the optimal parameter combinations produced by bootstrapping and by linear regression.

For the stock-recruit model, the intention is to parameterise the curve with minimal log-normal variance, therefore the least squares of the logged residuals was selected for minimisation (Equation 4.10):

$$\sum_{i=1}^{n}\left(\ln\left(R/\hat{R}\right)\right)^{2} \tag{4.10}$$

where R is observed recruitment for a given SSB in historical data, $\hat{R}$ is recruitment predicted by the model from each historical SSB using the Ricker model and n is the length of the historical stock-recruit series.

A range of plausible parameter values, in appropriate steps, was selected for parameter a and parameter b of a Ricker model fitted to the Shetland sandeel data. a was varied between 0.3 and 6 in steps of 0.3, while b varied between 0.003 and 0.022 in steps of 0.001. A direct search program was written in Visual Basic 6 as a Macro to an Excel spreadsheet. For each possible combination of a and b, the predicted recruitment was determined from the historical values of SSB. The square-root of the least logged square differences (RLSD) of the log-transformed predicted recruitment and historical recruitment were determined and recorded. All possible combinations of a and b for the ranges and step sizes specified were tested.

The square root sums of the differences, RLSD, for the parameter ranges tested, varied between 5.12 (a=2.10, b=0.012) and 15.93 (a=3.00, b=0.021). The 'best fit' values returned when a=2.10 and b=0.012 corresponds closely to the optimal parameter values identified by linear regression (a=2.13, b=0.013) and by bootstrap analysis (a=2.19, b=0.013). Parameter a was tested in steps of 0.3 in the direct search method (so a=2.10, 2.40, 2.70,....), so reducing the step size should identify a best fit combination which is closer to the combinations returned by linear regression and bootstrap analysis.

The 3-dimensional 'landscape' of fits produced by combinations of parameters a and b is shown in Figure 4.7. This plot, takes the form of a landscape with a valley. The floor of the valley corresponds to the optimal parameter combinations shown in Figure 4.6, hence there are a number of closely correlated combinations which produce good fits to the historical data. The landscape is shown in a 2-dimensional form in Figure 4.8 as it is easier to identify optimal parameter combinations from this plot. The light area corresponds to best fits (RLSD between 5.00 and 5.25), the parameter combinations identified by both linear regression and bootstrap analysis fall within this area. The shape of the best fit areas corresponds to the shape of the spread of optimal parameter combinations found by bootstrap analysis in Figure 4.6.

4.6.2 Results of Bootstrap Analysis

As shown above, there is a close correlation between optimal values of parameter *a* and *b* of the Ricker model. The correlation is positive logarithmic so if *a* is low then *b* is low and if *a* is high then *b* is high. Each value of parameter *a* has a corresponding optimal value of parameter *b*. Selecting the values representing 95% confidence intervals for each parameter may not return a correlated pair, as these values were not selected simultaneously. The correlation equation shown in Figure 4.6 were used to calculate the optimal value of parameter *b* for mean and confidence interval values of *a* (Table 4.3). These values were similar to the values determined from the bootstrap parameter distributions.

The fitted Ricker curve and curves representing upper and lower confidence intervals are shown in Figure 4.9a. It was expected that the three curves would pass through a data point equal to mean SSB and median recruitment as the data only determines mean (or median) recruitment at mean SSB well. The data point where the three curves cross is equal to a SSB of 155 thousand tonnes and recruitment of 47 billion (Figure 4.9a, circle). This was different to the values for mean SSB (127 thousand tonnes) and median recruitment (60 billion) in the historical data. So why don't these curves cross at median recruitment and mean SSB?

Each set of parameters found by bootstrapping in Figure 4.6 represents a stock-recruit curves which passes through mean SSB and median recruitment. Hilborn & Walters (1992) suggest that the simplest way to explain these alternatives is that the data only determines mean recruitment at mean SSB very well, and the alternatives represent the family of curves that pass through this point but with different slopes. But in bootstrap analysis, for each simulation *n* pairs of stock-recruit values are selected at random, with replacement, from the original data set. Therefore, the mean SSB and median recruitment will be different for each simulation depending on the stock-recruit pairs selected. In other words, during each bootstrap simulation, a stock-recruit curve is fitted through median recruitment and mean SSB but these values will alter slightly between simulation depending on the stock-recruit pairs selected.

This method parameterised a Ricker curve with 95% confidence intervals for the sandeel stock, but it must be remembered that the decline in recruitment in the late 1980s preceded a decline in SSB. This may induce a spurious relationship between stock and recruitment as SSB is dependent, with a lag of 2 years, on recruitment (see above and Chapter 3 for further details). Additionally, the curves appear to be strongly influenced by the series of four low recruit years that occurred during the late 1980s. The effect of these four years is pulling the curves down towards the *x*-axis. The question to be considered is: are these years outliers (therefore rare occurrences) or typical of the range of recruit values for the SSB range? The curves fitted so far assume these values are not outliers but, in the face of uncertainty, these values were removed from the data and further Ricker models identified by bootstrap analysis. Although removing data points is not recommended practice, in this case the points were removed experimentally to determine if these years could be considered biologically different.

4.7 Ricker Models - Reduced Data Range

The four low recruitment years (1987-1990 inclusive) were removed from the historical stock-recruit data and bootstrap analysis was reapplied, as described above, to identify parameter probability distributions. 1000 simulations of 24 years were performed and the results saved in an Excel spreadsheet. Estimates for parameters *a* and *b* were recorded for each simulation together with estimates of mean recruitment, mean SSB and the standard deviation of the residuals around the Ricker curve, σ_w.

Estimates for parameters *a* and *b* are shown in Table 4.3 and the curves are displayed in Figure 4.9b. Compared to the Ricker curves estimated using all the historical data (Figure 4.9a), these curves have steeper slopes from the origin and the maximum recruitment estimated by each curve (maximum height of the curve) is greater. The mean SSBs of the bootstrap stock-recruit pairs were similar for both sets of data (126 x 10^3 tonnes for all the data, 127 x 10^3 excluding low years), but the median recruitment was higher for the data sets excluding the low years (89 x 10^9) then for the complete data set (59 x 10^9).

Removing the four low recruitment years, greatly increased the estimate of parameter *a* (from 2.191 to 2.851) but had little effect on parameter *b* (0.013 complete data set and 0.012 reduced data set). So, the four low recruit years are "pulling" the curve down towards the origin, in other words these years could be considered biologically different. But which of these models is the more suitable to describe recruitment dynamics at Shetland? The complete and reduced historical data sets only contain 24 and 20 points respectively, without many more data points or without further data points at low SSB levels (to provide information the slope of the curve from the origin) it is difficult to discriminate between them. Additionally, considering the 95% confidence intervals, these curves are not significantly different. Therefore, simulations will be carried out using both models.

4.8 Shepherd Models PART 2

This part of Chapter 4 is concerned with the Shepherd stock-recruit model. Shepherd (1982) proposed a stock-recruit model (Equation 4.11; Figure 4.10) which is more flexible then the Ricker model. The model has three parameters so the shape of the curve can be altered to be dome-shaped, to increase to an asymptote or to increase indefinitely. The greater flexibility of the Shepherd model is due to increased complexity but this makes producing parameter estimates inherently more difficult. Estimates cannot be found by simple linear regression, as was used for the Ricker model. Instead, optimal parameter combinations were identified by least sums of logged square differences and by bootstrap analysis.

The Shepherd stock-recruit model (1982) takes the form:

$$R = aS/[1+(S/K)^{\beta}] \qquad 4.11$$

where R is recruitment, S is SSB and a, K and β are constants.

Parameter a is the slope of the curve from the origin and is a measure of the maximum recruitment–per-unit-biomass, this is only attained at low stock sizes where density-dependent mortality of pre-recruits is least (Shepherd 1982). Parameter K is the *threshold biomass*, that is the biomass above which density-dependent effects dominate density-independent effects. Parameter β, is the *degree of compensation*, which is an aspect of density dependence in recruitment. If $\beta<1$ then density dependent effects are very small and the number of recruits will continue to rise indefinitely as the stock size increases (Shepherd 1982).

By changing the parameters (a, K and β), the shape of the Shepherd curve can be altered to copy the shape of other stock-recruit curves (Figure 4.10). If $\beta = 1$, then the Shepherd curve takes the shape of a Beverton-Holt curve (1957) which rises to an asymptote. As stock size increases the number of recruits also increases, and at high stock levels the number of recruits approaches (but does not meet) a maximum. Thus at high stock densities, the density-dependent effects compensate for any increase in spawning stock size and therefore any potential increase in recruitment. If $\beta > 1$, the stock-recruit curve is dome-shaped like the Ricker (1954, 1975) curve. Recruitment increases with spawning stock size to a maximum and, beyond this, declines with further increases in recruitment. At high stock biomasses, the density dependent effects are so strong that recruitment declines as stock size increases (Shepherd 1982). This may occur in cases where there is competition for limited resources, such as food or space. Shepherd (1982) suggests 'it may be permissible to expect β to lie in the range 0.5 to 2'. β should only be greater then 2 where strong evidence of density dependence exists.

4.9 Fitting Shepherd model by 'least squares'

Initial estimates for parameters *a*, *K* and β were obtained using the subjective methods described by Shepherd (1982). Parameter *a* is a measure of recruits-per-unit-biomass which occurs at low SSB so Shepherd suggests estimating *a* by drawing a straight line through the origin just to the left of the data points or so 10% of data points are to the left of the line – the slope of the line is an estimate of *a*. A straight line drawn to the left of all data points gives a value 3.20 (Figure 4.11 dotted line). However, the position of the line was influenced by a very high recruitment produced at a mid-sized SSB. As the models being fitted will pass through median recruitment and mean SSB with log-normal errors, the stock-recruit data was ranked by SSB and the average ln(R/SSB) for the bottom 25% of values was selected as an initial estimate for parameter *a*. This returned a value of 1.48, much less then the value estimated (Figure 4.11 solid line). This value was taken as an initial estimate of *a*.

Selecting a value less then 1 for an initial estimate of parameter β assumes that recruitment will continue to rise with SSB. This is unlikely in any exploited fish stock as eventually density dependent effects will dominate (for example, through competition for food). Selecting a value greater then 1 assumes that recruitment declines with SSB at high SSBs. While the stock-recruit scatter plot (Figure 4.11) suggests this may occur in the Shetland sandeel stock and high density dependence is biologically plausible (see Introduction), the degree of overcompensation is difficult to determine objectively. Therefore, as an initial estimate, β was taken to be 1 so recruitment increases to an asymptote with SSB.

Once initial estimates have been made for parameters *a* and β, it is possible to estimate *K* by rearranging Equation 4.11 and using values of SSB and R through which it is desirable the curve should pass (Equation 4.12).

$$K = S^* /(aS^* /(R^* - 1))^{1/\beta} \qquad 4.12$$

where S^* and R^* are the desired values of SSB and recruitment respectively through which the curve should pass.

Shepherd (1982) states that S^* and R^* need not be the mean values from the historical data. As the curve will be applied with lognormal variance in the population model simulations, R^* was taken to be the median recruitment from the historical data and S^* the mean SSB. The values for a, K and β estimated subjectively, were used as initial estimates for fitting the Shepherd stock-recruit model (Table 4.4). To assume log-normal error in the fitted curve, the parameters were fitted to minimize square root of Equation 4.10 (RLSD) using the Solver Function (Fylstra *et al.*, 1998) in the Data Analysis Toolpak of Excel.

A curve was parameterised with a low threshold SSB of 44,000 tonnes (above which density dependent effects dominate, Table 4.4). Minimizing RLSD, reduces the effect of extremely large recruitments but will increase the relative effect of small recruitments. The curve produced by these parameters (Figure 4.12, curve 1) was strongly influenced by the series of years of extremely low recruitment (<15 billion) which occurred in the late 1980s. Without a long data set (there are only 24 years of data), it is difficult to determine if these low recruitments for relatively mid-sized SSBs are rare. Therefore, this greatly reduces any confidence in the fitted stock-recruit models.

4.10 Fitting Shepherd Model by Bootstrap Analysis

Bootstrap analysis (see Efron & Gong 1983) was also applied to the Shepherd model to estimate parameters. The problem was more complex than solving the linear regression equations for the Ricker model. It is possible to find optimal parameter estimates for the Shepherd model by using non-linear regression but this is difficult to code in a computer programme. Therefore, the Solver function in Excel was used to minimize the RLSD. By writing a Macro to an Excel spreadsheet, it is possible to define a basic Solver model, to run Solver and return the results to an Excel spreadsheet for each set of randomly selected stock-recruit data. This means optimal parameters can be determined quickly and simply with a minimum of coding.

A program was written in Visual Basic 6 as a macro to an Excel spreadsheet to perform bootstrap simulations. For each bootstrap simulation, n stock-recruit pairs were selected at random, with replacement, from the historical data (series length n). For each set of n stock-recruit pairs the mean SSB, mean recruitment and root squared log differences (RLSD) were determined. The Solver function was then applied (within the program) to minimize the squared log differences. For each simulation, the initial Solver parameters were set to the initial parameters determined earlier (Table 4.4). 1000 simulations were run and the mean recruitment, mean SSB, squared log differences and Shepherd parameters estimated for each simulation, were read into an Excel spreadsheet.

Estimates, returned by 1000 bootstrap simulations, for parameter *a* varied between 0.35 and 194, parameter *K* between 0.02 and 249 and parameter β between 0.55 and 17.69. These represent large ranges and portions of each range (high values of parameter *a* and low values of parameter *K*) will be biological unreasonable. According to Shepherd (1982) the feasible range parameter β is 0.5 to 2, much smaller then the range identified by bootstrap analysis.

Histograms for all three parameter probability distributions are shown in Figure 4.13. There appears to be more then one optimal parameter combination. Histograms for parameters *a* and β could be considered unimodal. There is a strong mode for parameter *a* at category 1-2 and a strong mode for parameter β between 1 and 1.5. These are both feasible ranges, *a* describes the slope from the origin which was subjectively estimated to be approximately 1.48 (within modal histogram range). β represents the density dependence and, for fish species in general, Shepherd (1982) suggests this should lie between 0.5 and 2. The modal histogram range for β indicates this is probably between 1 and 1.5. Considering the biology and ecology of sandeels, it was assumed that β would be greater then 1 as there is potential for strong density dependence.

The histogram for parameter *K* is more complex and could be considered multimodal. There is a high frequency of values in category 0-10 but a relatively constant frequency of values between 10 and 130. The strong correlation between parameters *a*, *K* and β is shown in the 3d scatterplot in Figure 4.14 and the bubble plot in Figure 4.15. Using these relationships, it was possible to identify general stock-recruit curves relating to the modal parameter values.

Firstly the high frequency of values for parameter *K* in the category 0-10 was considered, so all combinations with parameter *K* in this range were selected. Generally, when *K* was low, parameter β was low (0.55 – 1.9) but parameter *a* ranged from 5.8 to 194 (Figures 4.14 and 4.15). Thus, the high frequency of *K* values below 10 accounts for part or all of the modal values for β (1-1.5) and all the high values for parameter *a*.

When *K* was < 10 (modal value = 5.6), the corresponding values for a and β were determined (18 and 1.4 respectively) and the curve parameterised by this combination shown in Figure 4.12 (curve 2). This curve is not considered plausible.

Basically, the best fit model in this case is a constant recruitment model which can account for the modal parameter ranges found by bootstrap analysis. If recruitment relatively constant, the best fit Shepherd model will have a very steep line from the origin to the constant recruitment value. Hence parameter *a* will be very high (steep line from origin), parameter *K* will be very low (low turning point) and parameter β will be close to 1 (so curve levels out). β is not exactly 1 due to the trade off between the three parameters. This is not a plausible model for simulating recruitment as it basically assumes no relationship between SSB and recruitment.

Part or all of the modal peak of parameter β at category 1-1.5 can be accounted for by the combinations with low values of parameter *K*. Parameter combinations where $K < 20$ were removed and the probability distribution of parameters *K*, β and *a* reassessed. The modal value for parameter *a* is still in the range 1-2, but the smaller categories in this histogram has narrowed the range down to 1-1.5 (Figure 4.16). This was expected as low values of *K* were correlated with high values of *a*. The modal value of parameter β was altered to the category 2 – 2.5. Although Shepherd (1982) suggests a maximum value of 2 for β, it was noted that with strong evidence for density dependence β may set to greater then 2. Due to the potential competition for resources such as space (as only certain areas of the seabed are suitable for sandeels to bury themselves), it is expected that density dependence will be strong in sandeel populations.

Taking the modal value for parameter *a* (1.25) from the reduced histogram, the corresponding values for β and *K* were estimated (3.2 and 120 respectively) and the stock-recruit curve parameterised plotted (Figure 4.12, curve 3). This produced a dome-shaped curve that could feasibly describe the stock recruit relationship for sandeels at Shetland although parameter β is fairly high (3.2). Although β is higher then the maximum value suggested by Shepherd (1982), Shepherd does note that β could be higher if evidence exists for strong density dependence. For reasons discussed earlier (through competition for resources) density dependence in sandeels may be very high. Taking the modal value for parameter β (2.23) and calculating the corresponding values for *a* and *K* produces estimates of 2.28 and 70 respectively (Figure 4.12, curve 4). At very low values of SSB, this curve was similar to the curve fitted by non-linear regression.

The series of four low recruit years in the late 1980s strongly influenced the statistical fit of the Shepherd model. When these years were included, it was not possible to fit feasible stock-recruit models. In this case, the best model identified was a constant recruitment model - therefore there was no influence of stock biomass on recruitment. These four years also influenced the fit of the Ricker models parameterised in part 1. Although there is no biological reasoning for excluding these data points, for exploration of the data set, the four low recruit years were removed from the historical data set and new estimates for the Shepherd curve parameters were identified by bootstrap analysis.

4.11 Shepherd Models – Reduced Data Range

The four low recruit years that occurred over 1987-1990 inclusive, were removed from the historical data. Initial subjective estimates for parameters *a*, *K* and β were adjusted accordingly. *a* was estimated to be 2.5 and parameter β was set to 1, for the reasons outlined before (unlikely to less then 1). An initial estimate for parameter *K* was found by using the estimates of *a* and β in Equation 4.12. S^* was taken to be mean SSB (126 x 10^3 tonnes) and R^* was median recruitment (66 x 10^9) in the reduced data set. This returned an initial estimate for parameter *K* of 26. Bootstrap analysis was then applied, using the methods described in detail above. 1000 simulations were carried out and the results saved to an Excel spreadsheet.

The resulting histograms are shown in Figure 4.17. The major difference between these histograms and the histograms determined earlier using the complete historical data set (Figure 4.13) is that these histograms are unimodal. This means there is just one 'best fit' value for each parameter, compared to the multiple values estimated previously and confidence intervals can be estimated. From the histograms, the mean value for parameter *a* was 2.00 and the median value of parameter β was 2.6. For parameter *K*, there is not a distinct modal value, but the mode occurs within the range 60 – 120. The mean value was 96, therefore this was assumed to be the best estimate for parameter *K* from the histogram. From the relationships between *a* and *K* and between β and *K*, estimates for parameter *K* returned from the values for *a* and β specified above were 91 and 94 respectively. These are very close to the median value of *K* (96) from bootstrap analysis.

As the histograms of parameter distributions were unimodal, it was possible to estimate confidence intervals from the appropriate percentiles. The 75% confidence intervals were determined and the resulting curves are shown in Figure 4.18. The parameter values are given in Table 4.4. The upper and lower 75% confidence intervals for parameter *K* were chosen for two reasons: firstly, these correspond with the modal range of *K* shown in the parameter distribution histogram (Figure 4.17) and secondly, the lower 95% limit returns negative value for parameter *a* so this model produces recruitment values between 0 and –2 (billion) over the historical data range (recruitment cannot be negative).

To conclude this section, analysis with the complete data set (all data points) indicated the best fit model shows no relationship between SSB and recruitment. Removing the four low recruitment years (1987-1990) enabled a Shepherd model to be parameterised with 75% confidence intervals. Therefore, the four low recruit years appear to be 'biologically different' and so can be considered atypical of the recruit data for the SSB range. In other words, some additional factor was affecting recruitment during this period.

4.12 Model Simulations PART 3

The intention is to produce recruitment models which reproduce the parameters of the historical data set. Only the Ricker models are considered here due to the difficulties in defining Shepherd stock-recruit models. A term for stochasticity was introduced into the Ricker models and the models were written into the population model constructed in Visual Basic in Chapter 3. Simulations were carried out and the results compared with the historical data set. The Ricker model was then further adapted to include a function to autocorrelate the residuals and simulations carried out. Finally, the conclusions drawn from all the model simulations are discussed.

4.13 Stochastic Ricker Models

Ricker models (Equation 4.2) were parameterised for Shetland sandeels in Part 1, however the models include no term for stochasticity. Recruitment, in any exploited fish population, is variable about the stock-recruit curve so an additional term was incorporated to induce stochasticity. As discussed in part 1, the residuals of the Ricker model fitted to the sandeel data where lognormally distributed about the curve:

$$R = aSe^{-bS}e^{w} \qquad 4.5$$

where a and b are constants, R is recruitment, S is SSB and w is normally distributed with a mean of zero (therefore e^{w} is lognormally distributed) and standard deviation σ_{w}.

Equation 4.5 can be rewritten as:

$$R = aSe^{w-bS} \qquad 4.13$$

w represents the lognormal distribution of the residuals about the Ricker model. For the 'best fit' Ricker model identified by bootstrap analysis for the complete data set, the mean of the residuals was equal to 0.00 and the standard deviation equal to 1.07. Therefore, it was assumed for simulations that σ_w equals 1.07.

4.13.1 Simulations

The Ricker model with stochasticity (Equation 4.13) was included in the population model developed using Visual Basic in Chapter 3. 1000 simulations of 24 years were carried out for the mean Ricker curve identified by bootstrap analysis for the complete historical data set. The mean and standard deviations of SSB and ln(recruitment) for each simulation were calculated in the programme and saved as output. In addition, for the first ten simulations, the parameter output values for each year were recorded.

The results are shown in Table 4.5. The observed mean values for mean ln(recruitment) produced by the model (3.79) were slightly less than the historical value (3.88). These correspond to median recruitments of 44 billion and 48 billion respectively. The median standard deviation of ln(recruitment) produced by the model was 1.15, higher then the target value of 1.08. However, inspecting the distribution histogram revealed the modal value lay between 1.05 and 1.1 therefore, the curve was generally producing ln(recruit) distributions with standard deviations similar to the standard deviation of the historical distribution. The mean SSB values, 138 x10^3 tonnes, was greater than the historical mean value (127 x10^3) but again the distribution histogram revealed the modal values lay between 125-130 x10^3 tonnes. The median standard deviation the SSB distribution (61) was close to the historical value (60). In conclusion, this model produced ln(recruit) and SSB distributions which were generally similar to the target (historical) distributions.

To visualize the population dynamics, the first six simulations carried out Ricker curve were selected and the ln(recruit) and SSB time series plotted together with the time series from the historical data (Figure 4.19). While the series for the mean Ricker curve could be considered to generally be within the maximum and minimum values observed in the historical data (heavy line), there were some extreme values for SSB and for ln(recruits). The large peaks in recruitment (produced due to stochasticity), such as that produced in year 15 of Figure 4.19a blue time series (573 x10^9 recruits) are followed, at a lag of 2 years, by a large peak in SSB (Figure 4.19b year 17, 410 x10^3 tonnes). This, in turn, produced an extremely small recruitment that year due to the shape of the stock-recruit model (year 17, 5 x 10^9 recruits).

The historical ln(recruit) time series showed positive autocorrelation (r_1=0.51) as determined by Equation 3.14 in the previous Chapter. Although the Ricker model did not include a term to autocorrelate the residuals, some inherent autocorrelation exists due to the shape of the stock-recruit curve. The mean r_1 values returned by the Ricker model is also shown in Table 4.5 – this was equal to 0.07.

To summarize, the mean Ricker model with log-normal stochasticity, parameterised by bootstrap analysis, could be considered to generally produce distributions of ln(recruit) and SSB which were similar to the historical series. However, the model sporadically produces very large recruitments which greatly increase SSB at a lag of two years (as the fish enter the spawning population at age 2). These large recruitments are the result of the long tail of the stochastic log-normal distribution about the stock-recruit model. The model did not show any significant autocorrelation in the ln(recruit) time series. Incorporating autocorrelation in the recruit model may reduce the frequency with which extremely large recruitments occur, as the residual of recruitment in any year will be a function of SSB and the recruitment residual in the previous year. In order to induce autocorrelation, an additional term needs to be incorporated into the stock-recruit model.

4.14 Autocorrelated Ricker Model

In the model constructed above, variation in recruitment about the stock recruit curve, was completely random. This type of variation in a time series about a mean, where the observations are distributed randomly and independently from the same normal distribution, is referred to as *white* noise (Brown & Rothery 1993). Population models often incorporate environmental stochasticity as random (white) noise, however in reality this is rarely the case. Environmental stochasticity can induce variation in population size and population growth rate but the effects usually persist longer than one season or even one year. These long-lasting effects will induce *positive* autocorrelation in the time series, which is referred to as *red* noise.

Environmental factors appear to be a major force driving variability in recruitment to the Shetland sandeel stock. There is strong evidence for autocorrelation in the Shetland recruit series, therefore introducing autocorrelation in recruitment should improve model fit to the historical data. It must be remembered that the historical series is short (24 years) so confidence in the autocorrelation estimate is reduced. Autocorrelation in recruitment may be an important aspect of Shetland data, particularly due to implications for marine predators. For example, seabird breeding success was greatly reduced during the late 1980s (Monaghan 1992) when a series of very low recruitment years occurred (even though SSB was high). To improve our understanding of recruitment dynamics, it is vital autocorrelation is incorporated in the stock-recruit model.

As analyzed in the previous Chapter, the ln(recruit) time series for Shetland sandeels is positively autocorrelated. The ln(recruit) time series can be reproduced using an autoregressive model and the order of this model was 1 (year):

$$\ln(R_t) = \phi_0 + \phi_1(\ln(R_{t-1}) - \phi_0) + \varepsilon_t \qquad 4.15$$

where R_t is the recruitment in year t, ϕ_1 is the autoregressive parameter for t-1, ϕ_0 is the constant term which is approximately equal to the average level of the series and ε_t is a normally distributed random number with a mean of zero and a standard deviation, σ_ε, equal to:

$$\sigma_\varepsilon = \sigma_R(1-\phi_1^2)^{0.5} \qquad 4.16$$

where σ_R is the standard deviation of the ln(recruit) distribution.

This model simulated a positively autocorrelated ln(recruit) time series. By combining this model with the Ricker model, it should be possible to autocorrelate the residuals around the stock-recruit model. To reiterate, variation around the Ricker model is lognormally distributed so the model takes the form:

$$R = aSe^{w-bS} \qquad 4.13$$

where a and b are constants, R is recruitment, S is SSB and w is normally distributed with a mean of zero. To incorporate autocorrelation, the residuals (as described by e^w in Equation 4.13) were autocorrelated by adapting a first order autoregressive model (Equation 4.15). As the residuals are distributed about the stock-recruit curve with a mean of zero, the series mean, ϕ_0, becomes zero. Substituting w for $ln(R)$ in Equation 4.15 and setting ϕ_0 to zero gives:

$$w_t = \phi_1 w_{t-1} + \varepsilon_t \qquad 4.17$$

To avoid confusion with the time series models analyzed in the previous Chapter, ϕ was expressed as α so:

$$W_t = \alpha W_{t-1} + \varepsilon_t \qquad 4.18$$

ε is normally distributed random number with a mean of zero and a standard deviation σ_ε, which is equal to:

$$\sigma_\varepsilon = \sigma_w \sqrt{\left(1-\alpha^2\right)} \qquad 4.19$$

where σ_w is the standard deviation of the log-transformed residuals about the stock-recruit curve.

The equation for a Ricker model with autocorrelated residuals is therefore:

$$R_t = aS_t e^{\alpha w_{t-1} - bS + \varepsilon_t} \qquad 4.20$$

where R_t is recruitment in year t, S is SSB, a, b and α are constants and α is the coefficient of autocorrelation.

4.14.1 Simulations

The autocorrelated Ricker (Equation 4.20) model was incorporated into the population model (see Chapter 3) and simulations run using the mean Ricker curve parameterised using the complete historical data set. It was assumed that the standard deviation of the residuals, σ_w, was 1.07 (as was returned by analysis of the historical recruitment around the Ricker curves). As the autocorrelation in historical ln(recruit) time series was 0.51 the input autocorrelation coefficient, α, was set to this value. 1000 simulations of 24 years were run for each Ricker model and the results saved to an Excel spreadsheet.

Introducing autocorrelation had little effect on the parameters of the ln(recruit) and SSB time series produced by the population models compared to the output from the stochastic (non-autocorrelated) model (Table 4.5), with the exception of the autocorrelation coefficient, r_1, of the ln(recruit) time series which was higher. The ln(recruit) and SSB time series produced by the first six simulations are shown in Figure 4.20. Compared to the stochastic, non-autocorrelated model output (Figure 4.19), the recruit time series shows autocorrelation, in that the series tends to wander one side of the mean or another for a number of years at a time.

α (input autocorrelation coefficient) was set to 0.51 for the models, but the mean output value was 0.37. Considering the output histogram for r_1 revealed the modal value lay between 0.40 and 0.45. Increasing the input value of α should increase the output autocorrelation in the ln(recruit) time series, r_1. To test this, simulations using the mean Ricker curve were run with α varying between 0.0 and 0.8 in steps of 0.1. 1000 simulations of 24 years were carried out for each value of α. The results are shown in Figure 4.21. As α increases so output r_1 increases but r_1 is always less then α. A mean output r_1 of 0.5 is produced when the input value of α is 0.73, this represents very strong forcing on the stock-recruit relationship.

Time series plots of the historical ln(recruit) at Shetland indicate that forcing on the stock-recruit relationship may be very high, even though there are only 24 years of data (Figure 4.2b). Simulations were repeated with the input autocorrelation parameter, α set to 0.73, the results are shown in Table 4.5. Increasing α to 0.73 did produce, on average, ln(recruit) time series with higher autocorrelation coefficients (r_1). The ln(recruit) and SSB time series produced by the first six simulations were plotted together with the time series from the historical data (Figure 4.22). An input autocorrelation coefficient, α, of 0.73 represents very high forcing on the stock-recruit relationship, as can be seen in Figure 4.22 compared to Figure 4.20 where α=0.51. Series are above or below the mean for longer periods of time, on average, then in Figure 4.20.

In conclusion, a Ricker model with autocorrelated residuals was developed for Shetland sandeels, assuming no net external recruitment. Due to the short time series in the historical data (24 years) confidence in the calculated autocorrelation coefficient (0.51) is reduced. Therefore, in the face of uncertainty, the mean Ricker model parameterised by bootstrap analysis will be used in future model simulations together with both a high (0.73) and moderate (0.51) input coefficient of autocorrelation.

4.15 Model Simulations – Reduced Data Set

The sporadic extreme recruitments produced by the models are, in part, due to the large variation in the residuals around the stock-recruit curves (standard deviation of ln(residuals), σ_w=1.07). The large variation is mostly the result of four low recruit years observed in the late 1980s (see above for discussion). Removing these will reduce the variation around the stock-recruit model, so reducing the frequency with which large recruitments occur - although it is not good practice to remove data points from analyses (without very good reasons). The intention is to explore various scenarios for recruitment so removing the four low recruit years accounts for the scenario that these were rare events.

Ricker models (mean plus 95% confidence intervals) were parameterised above using the reduced Shetland sandeel data set (minus four low years; Figure 4.9b). Removing the four low years increased the mean of the historical ln(recruit) distribution to 4.25 and reduced the standard deviation to 0.69 (Table 4.5) but had little effect on the mean and standard deviation of the SSB distribution. The standard deviation of the residuals around the mean Ricker curve was 0.642, much less then the standard deviation (1.07) around the Ricker model for the complete data set. The mean curve identified will be tested in model simulations.

The models were tested as described above using the population model written in Visual Basic 6.0. Autocorrelated log-normal stochasticity in recruitment about the Ricker curves was introduced using Equation 4.20. The standard deviation of the residuals, σ_w, was set at 0.642 (from the reduced historical series). An autocorrelation coefficient was not determined for the reduced historical data set as a continuous series is required for this. Instead, it was assumed coefficient would be similar to that seen in the complete data set (0.51). The input coefficient of autocorrelation, α, was set to 0.51 and 1000 simulations of 24 years were run. The time series for the first six simulations for each Ricker curve are shown in Figure 4.23.

While the mean and standard deviation of the ln(recruit) distribution was similar to the values of the reduced historical distribution, the mean of the SSB distributions were larger then the historical mean and the standard deviations less (Table 4.5). The ln(recruit) and SSB time series from the first six simulations show that while recruitment generally varies within the maximum and minimum values of the historical data set, the occurrence of low years is rare. However, due to autocorrelation, if a low year occurs it is likely this will be followed by more low years.

The mean output autocorrelation coefficient, r_1 (0.36), was less then the input autocorrelation parameter α (0.51), so increasing α should increase r_1. As before, simulations using the mean Ricker curve were carried out with α varying between 0.4 and 0.8 in steps of 0.1. 1000 simulations of 24 years were carried out for each value of α.The results are shown in Figure 4.19 (squares). An input value of α = 0.73, is required to produce an mean output autocorrelation coefficient of 0.5, this represents very strong forcing on the stock-recruit relationship. The relationship between the input autocorrelation parameter, α, and the output autocorrelation coefficient, r_1, was similar to the relationship for the Ricker curves parameterised using the complete data set.

The population simulations were rerun with α set to 0.73. Increasing the input autocorrelation coefficient from 0.51 to 0.73 had little affect on the mean ln(recruit) distribution but decreased the standard deviation from 0.64 to 0.55. The recruitment and SSB time series produced by the first six simulations are shown in Figure 4.24.

4.16 Summary of Ricker Model Simulations

Simulations of the population model were carried out using two Ricker stock-recruit curves to simulate recruitment. The first curve was parameterised by using the complete historical data set and the second using a reduced historical data set (minus four low years). The autocorrelation coefficient from the complete historical ln(recruit) data series was calculated as 0.51, so this value was used as the input autocorrelation coefficient in the recruitment models. The output recruit series generally had a lower autocorrelation coefficient (0.36-0.37) then the input value. Further simulations, varying the input autocorrelation coefficient, indicated an input value of 0.73 would produce average output values of 0.50.

The historical recruit time series is only 24 years long, so confidence in the calculated autocorrelation coefficient is reduced. In view of this both input autocorrelation coefficients were considered to produce recruit time series which were similar to the historical series.

4.17 Chapter Conclusions

Bootstrap analysis was used to parameterise a Ricker stock-recruit model for the Shetland data set with 95% confidence intervals. However, the series of four low recruit years in the late 1980s strongly influenced the statistical fit of these curves. Similarly, bootstrap analysis was also applied to the Shepherd stock-recruit model. In this case, the best fit model identified was similar to a constant recruitment model - therefore there was no influence of stock biomass on recruitment. Again, the four low recruit years in the late 1980s appeared to be influencing the model fit.

Although there is no biological reasoning for excluding these data points, for experimental exploration, the series of four low recruit years was removed from the data set and bootstrap analysis was reapplied to fit both Ricker and Shepherd models. A Ricker model was parameterised which, considering 95% confidence intervals, was not significantly different to the curve parameterised previously using the complete historical data set. Removing the data points also enabled a Shepherd curve, with confidence intervals, to be parameterised. Hence, these four low recruit years could be considered to be biologically different. There are three main hypotheses that could explain this.

Firstly, assuming recruitment can be expressed as a function of SSB, the four low recruit years are atypical of the expected range of recruitment for the SSB levels. Some extra factor was suppressing recruitment in these years. There could be any number of possibilities affecting pre-recruit stages, for example high sea temperature at crucial periods of the year may affect egg survival and hatching, ecological changes may reduce availability of suitable plankton for the feeding larvae and juveniles, or predation on the pre-recruit stages could have been extremely high during these years.

Some evidence of causes for ecological changes in the North Sea over this period (1987-1990 inclusive) can be found in time series of over 50 years from the Continuous Plankton Recorder (Lindley *et al.*, 1990; Edwards *et al*,. 1997; Holliday & Reid, 2001). The appearance of planktonic oceanic indicator species in the North Sea during this time suggests an exceptional inflow of Atlantic water resulting in, what can be considered as, an ecological regime shift. There may be evidence of large-scale changes in the recruitment patterns for North Sea sandeels. As discussed in Chapter 3, the North Sea recruit time series shows two periods of different patterns: during 1979-1985 recruitment alternates between high and low years (see Chapter 3, Figure 3.7a) this then changes to a three year cycle of two high recruits followed by one low recruitment (1988-1995).

The second hypothesis, discussed by Hildén (1997), is that SSB was only perceived to be high in the late 1980s. Hildén suggests this is unlikely for Shetland sandeels but could occur if the natural mortality rate is seriously overestimated, if the age of maturity is underestimated, if catches are overestimated or if the fishing mortality of the oldest age group is underestimated. There are no independent estimates for the natural mortality rates of sandeels at Shetland, for stock assessment these are assumed to be the same as that of sandeels in other areas of the North Sea. However, due to the large numbers of seabirds nesting at Shetland it is possible that natural mortality rates may even be underestimated here (Furness, 1990, Bailey *et al.*, 1991). It is also unlikely that the age of first spawning is underestimated, it is assumed that all sandeels aged 2 and above are mature, so this may even be overestimated as a proportion of the 1-group fish may be mature.

It is also unlikely that catches are overestimated as the stock is fished only by a small number of local vessels and all catches are landed at the fishing processing plant in Shetland. So was SSB overestimated in the Shetland stock during the late 1980s? Although possible, it must be concluded this is unlikely. Additional evidence exists in research survey indices conducted annually in August at Shetland during 1984-1997 inclusive (excluding 1987 and 1995). These indicate that SSB was not low during the late 1980s.

The third hypothesis, advanced by Wright (1996), is that an unspecified number of recruits originating from outside Shetland waters enter the Shetland system in certain years. This makes it difficult to define a stock-recruit relationship from locally produced recruits as this input is unquantified. The low recruitment seen during the late 1980s, could then be explained by a reduction in the transport of larvae and pre-recruits to Shetland (Proctor *et al*,. 1998). Only locally produced recruits are joining the stock during this period, so these four years may provide an indication of the underlying true stock-recruit relationship. This hypothesis will be considered further in the next Chapter (5) and models developed to simulate external recruitment. The addition of external recruits may be vital for the persistence of the stock at Shetland.

4.18 Summary

- A Ricker model with 95% confidence intervals was fitted to the complete historical data set (including low years) by bootstrap analysis.
- The Shepherd stock-recruit model was also fitted to the complete data set using bootstrap analysis. The model identified was constant recruitment, that is stock biomass has no influence on recruitment. Two curves were parameterised by removing combinations which showed no relationship between stock and recruitment, but the probability of these curves is low.
- The four low recruit years in the late 1980s could be considered to be atypical of the expected range of recruitment for the SSB levels – these years are biologically different. Some extra factor may have been affecting recruitment in these years.
- Removing the four low years enabled both a Ricker curve and a Shepherd curve to be fitted by bootstrap analysis, with confidence intervals.
- Simulations were carried out with the two Ricker models (parameterised using complete data set and reduced data set) with autocorrelated variability about the stock-recruit curve. Two levels of

autocorrelation were tested: α=0.51 and α=0.73. Both produced SSB and ln(recruit) series which were considered suitable when compared to the historical data set.

Table 4.1. Ricker model parameter estimates (*a* & *b*) and corresponding variances (σ_{lna} & σ_b) for Shetland sandeels (recruitment in billions, SSB in 000 tonnes). $\square_w$ is the resulting variance around the stock-recruit curve.

Parameter	Shetland
b	0.01250
σ_b	0.00378
ln(a)	0.75796
σ_{lna}	0.52855
a	2.134
σ_w	1.06641

Table 4.2 Sandeels at Shetland. Estimates for the parameters (*a*", *b*) of the Ricker stock-recruit model fitted to the complete historical data set (from ICES 1999) and the data set minus four low recruit years (1987-1990 inclusive). The mean parameters estimated by bootstrap analysis and upper and lower 95% confidence intervals (c.i.) shown. Bootstrap *b* is the value estimated from bootstrap analysis, Correlation *b* is the value estimated from the correlation between *a* and *b*

		Bootstrap a"	Bootstrap b	Correlation b
All data	mean	2.191	0.012763	0.012762
	lower 95% c. i.	1.032	0.007909	0.007930
	upper 95% c. i.	4.451	0.018696	0.017311
Minus Low Years	mean	2.851	0.011736	0.011735
	lower 95% c. i.	1.784	0.008718	0.009178
	upper 95% c. i.	4.538	0.014690	0.014270

Table 4.3. Parameters (a, b) of the Ricker (1954, 1975) stock-recruit model estimated by linear regression and by bootstrap analysis for the Shetland sandeel stock. a = mean value for parameter a, σ_a = standard error of parameter e, a'' = adjusted a (see text), b = mean value for parameter b, σ_b = standard error of parameter b, 95% c.i. = 95% confidence intervals, σ_w = standard deviation of the residuals.

	Parameter	Shetland sandeels
Linear Regression	$b \pm \sigma_b$	0.012501 ± 0.003782
	a	2.134
	σ_ω	1.066
	Mean R	76
	Median R	60
	Mean SSB	127
Bootstrap	$b \pm \sigma_b$	0.012763 ± 0.003338
	b lower 95% c. i.	0.007909
	b upper 95% c. i.	0.018696
	$a \pm \sigma_a$	2.4206 ± 1.1646
	a lower 95% c. i.	1.032
	a upper 95% c. i.	4.451
	$ln(a) \pm \sigma_{ln(a)}$	0.7845 ± 0.4458
	a''	2.191
	σ_w	1.010
	σ_w lower 95% c. i.	0.746
	σ_w upper 95% c. i.	1.244
	Mean R (billions)	59
	Mean SSB ($x10^3$ tonnes)	127

Table 4.4 Estimates of parameters, α, β & K, of the Shepherd (1982) stock-recruit model estimated subjectively, by non-linear regression and by bootstrap analysis using the complete historical data set (produced two curves shown in Figure 4.19) and using a reduced data set (minus four low recruit years). Parameter probability histograms produced using the reduced data set were unimodal allowing 75% confidence intervals (c.i.) to be estimated.

		Shetland	
Shepherd model parameter	**a**	***K***	***β***
Initial values estimated subjectively	1.48	54	1.0
Non-linear regression estimate	2.91	44	1.8
Bootstrap complete data set (curve 3)	1.25	120	3.2
Bootstrap complete data set (curve 4)	2.30	70	2.2
Bootstrap reduced data set mean	2.00	96	2.6
Bootstrap reduced data set lower 75% c.i.	1.51	69	2.2
Bootstrap reduced data set upper 75% c.i.	2.81	124	3.3

Table 4.5 Output from population models for sandeels at Shetland with recruitment expressed using Ricker models with stochastic and autocorrelated stochastic residuals. Two Ricker models tested: curve representing 'best fit' (mean) determined using the complete historical data set and curve representing 'best fit' determined using a reduced historical data set (minus four low years). σw =input standard deviation of residuals, σ=input autocorrelation parameter, ln(R)=mean of output ln(recruit) distribution, σR=standard deviation of output ln(recruit) distribution, r_1=output autocorrelation in ln(recruit) time series, SSB=mean output spawning stock biomass distribution and σS=standard deviation of output SSB distribution. Mean or median for each parameter distribution shown together with the modal category from plotted histograms.

Complete Data Set			ln(R)		σ_R		r_1		SSB		σ_S	
σ_w	α	**Model**	**mean**	**mode**	**median**	**mode**	**mean**	**mode**	**median**	**mode**	**median**	**mode**
		Historical	**3.88**		**1.08**		**0.51**		**127**		**60**	
1.07	0	Stochastic	3.80	3.85-3.90	1.15	1.05-1.10	0.08	0.01-0.02	138	125-130	61	55-60
1.07	0.51	Autocorrelated	3.78	3.80-3.85	1.05	0.95-1.00	0.37	0.40-0.45	132	120-125	66	55-60
1.07	0.73	Autocorrelated	3.79	3.85-3.90	0.90	0.85-0.90	0.50	0.50-0.55	118	115-120	56	55-60

Reduced Data Set			ln(R)		σ_R		r_1		SSB		σ_S	
σ_w	α	**Model**	**mean**	**mode**	**median**	**mode**	**mean**	**mode**	**median**	**mode**	**median**	**mode**
		Historical	**4.25**		**0.69**		**0.51**		**126**		**63**	
0.64	0.51	Autocorrelated	4.27	4.20-4.25	0.64	0.55-0.60	0.36	0.35-0.40	141	140-145	44	40-45
0.64	0.73	Autocorrelated	4.28	4.30-4.35	0.55	0.50-0.55	0.49	0.50-0.55	137	130-135	41	35-40

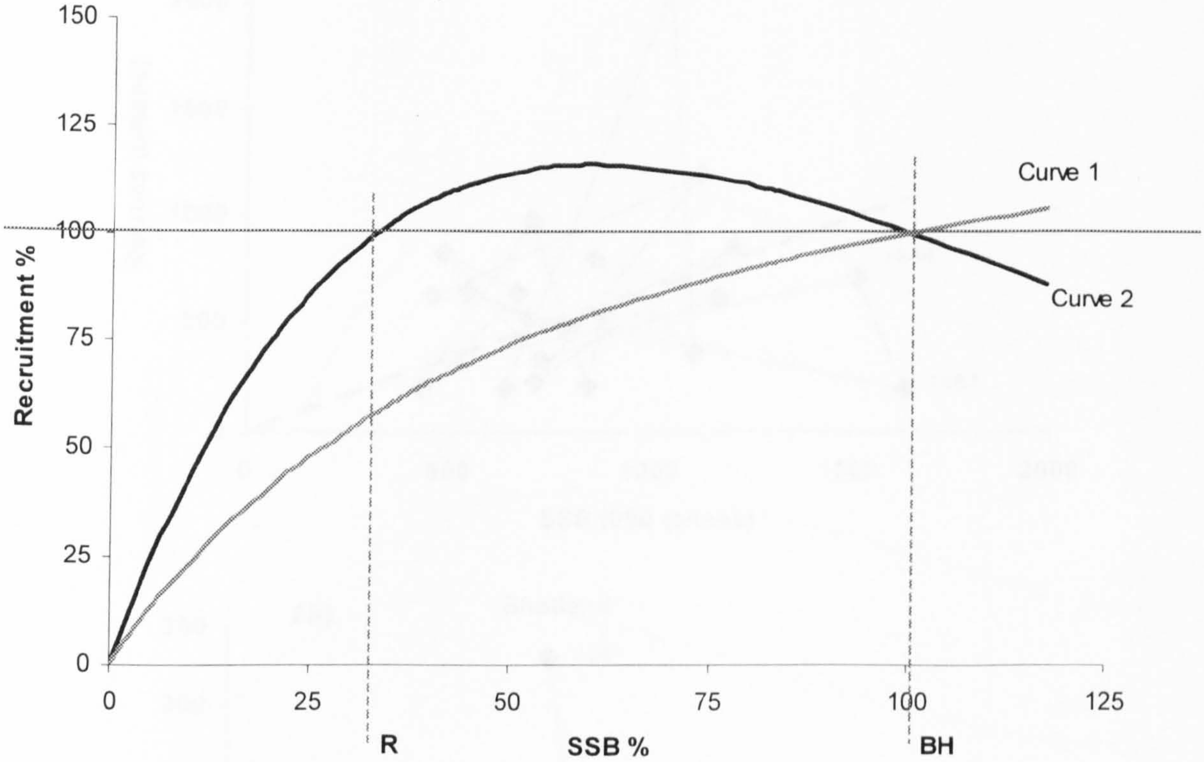


Figure 4.1 Stock-recruit curves for a hypothetical fish stock. SSB=spawning stock biomass. R & BH = threshold SSB biomasses for curves 1 (R) and 2 (BH), below which recruitment drops below 100% of starting level (when SSB=100%)

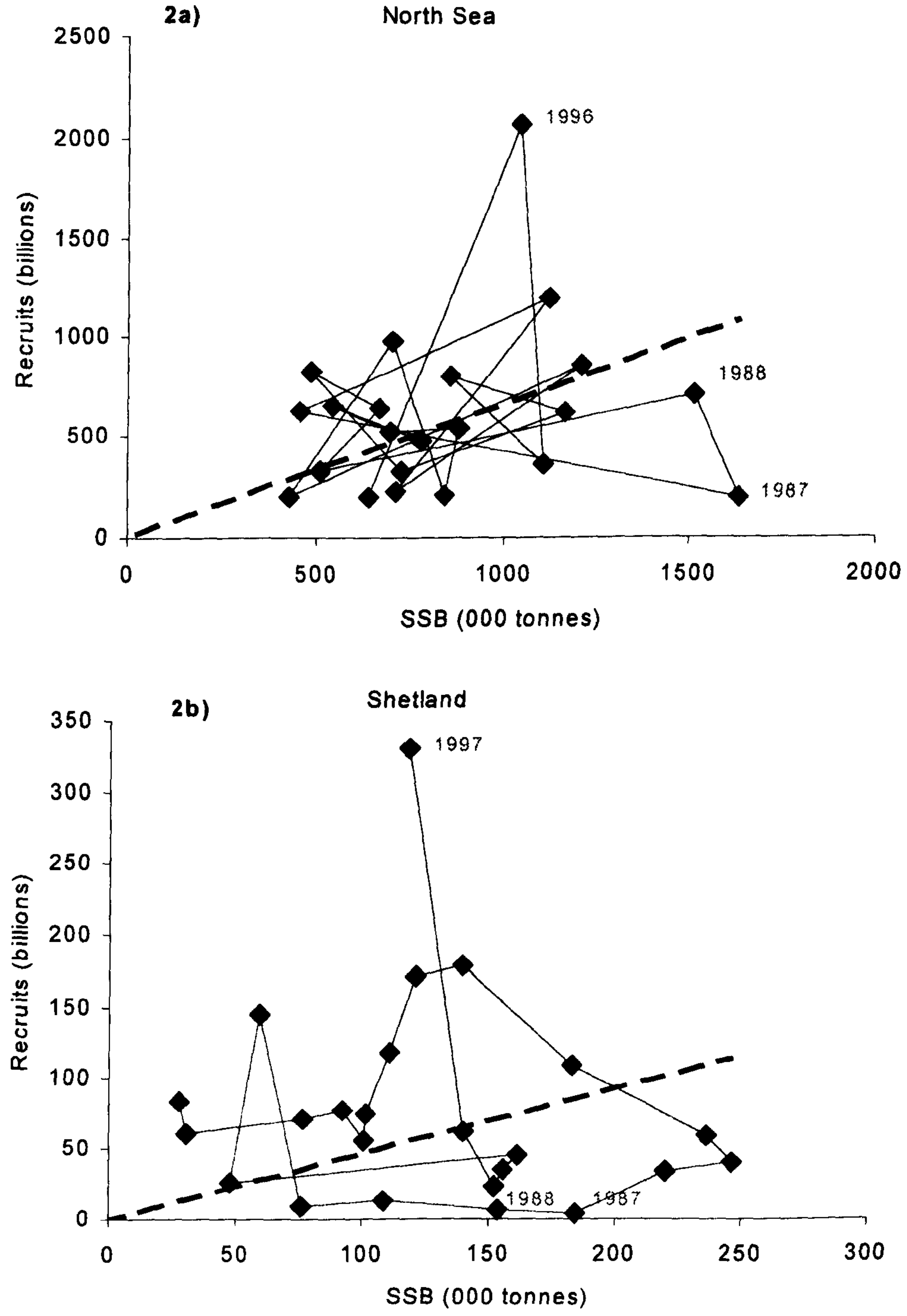


Figure 4.2 Stock-recruit scatterplot and trajectory of recruitment for sandeels in **a)** North Sea and **b)** Shetland (ICES 1999). dotted lines represent models expressing recruitment as a linear function of SSB.

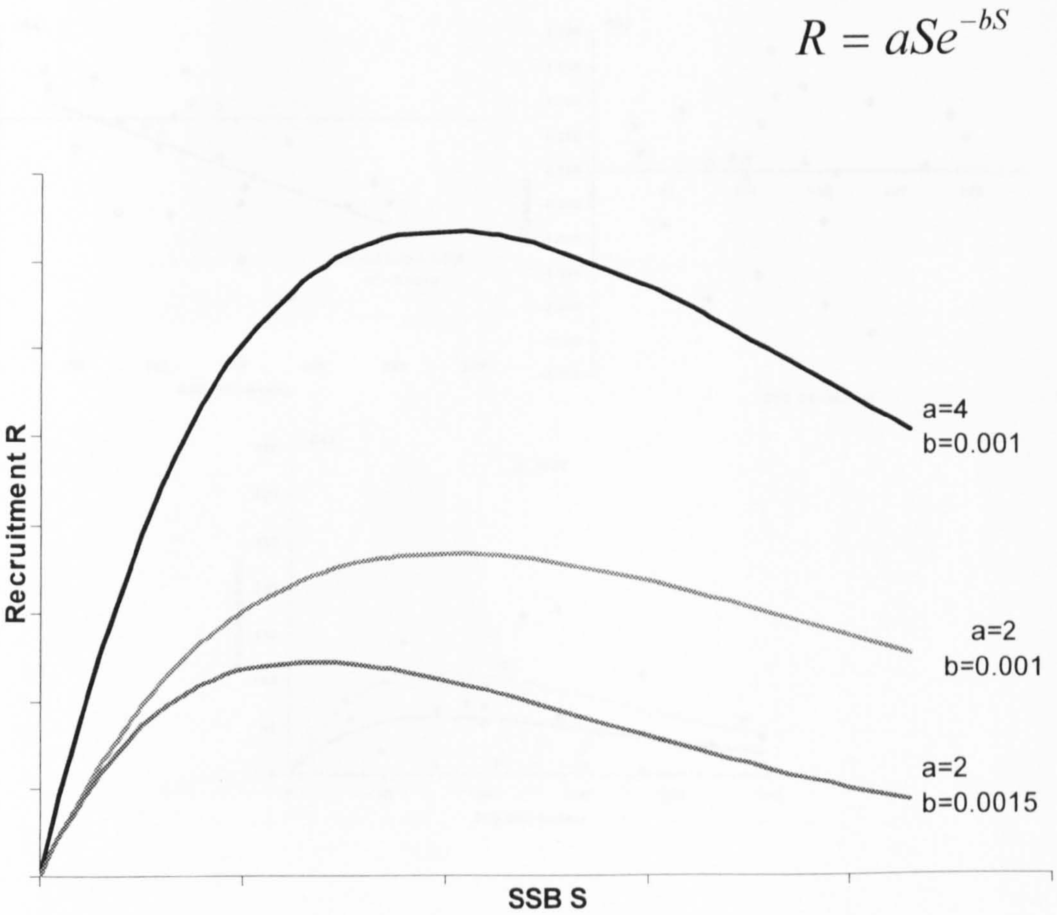


Figure 4.3. Ricker (1954, 1975) stock-recruit curves with different values of parameter *a* and parameter *b*.

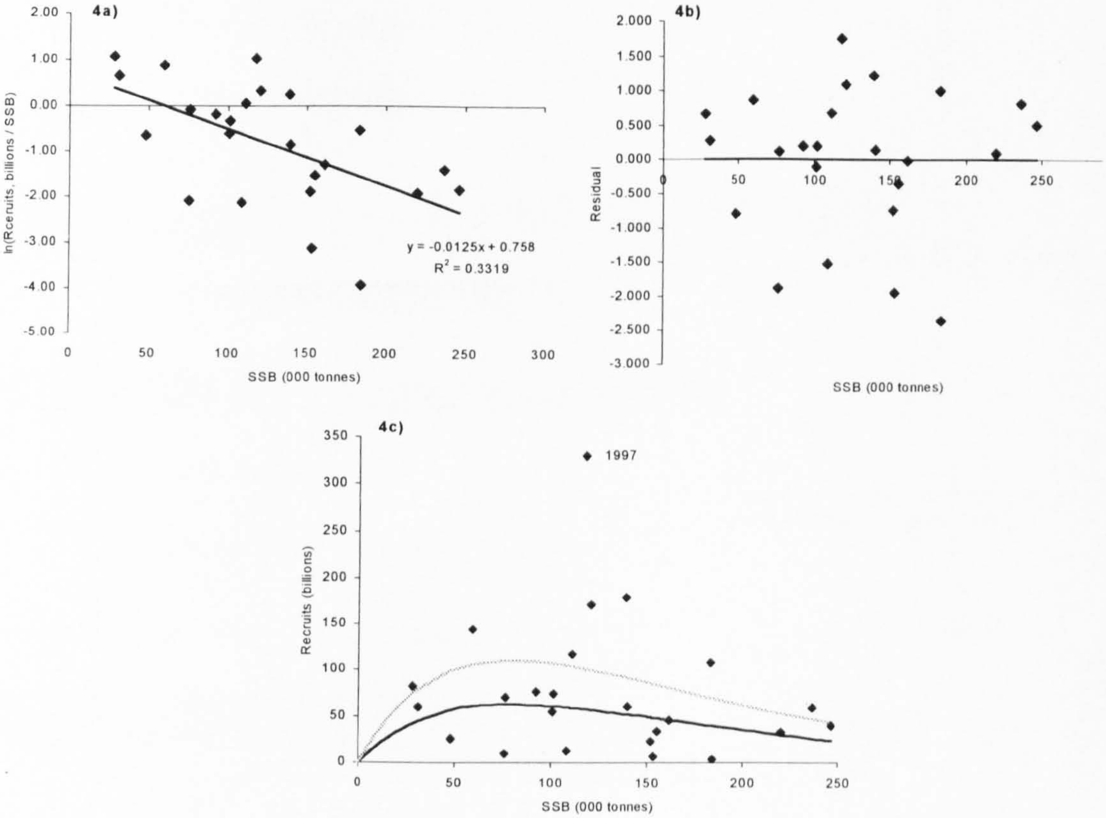


Figure 4.4 Sandeels at Shetland **a)** ln(recruits/SSB) against SSB, trendlines fitted and equations and R^2 shown. **b)** residuals from Ricker curve (black curve graph c) against SSB. **c)** stock-recruit data with Ricker curve (black line) parameterised by linear regression - light curve is the corresponding Ricker curve passing through average recruitment.

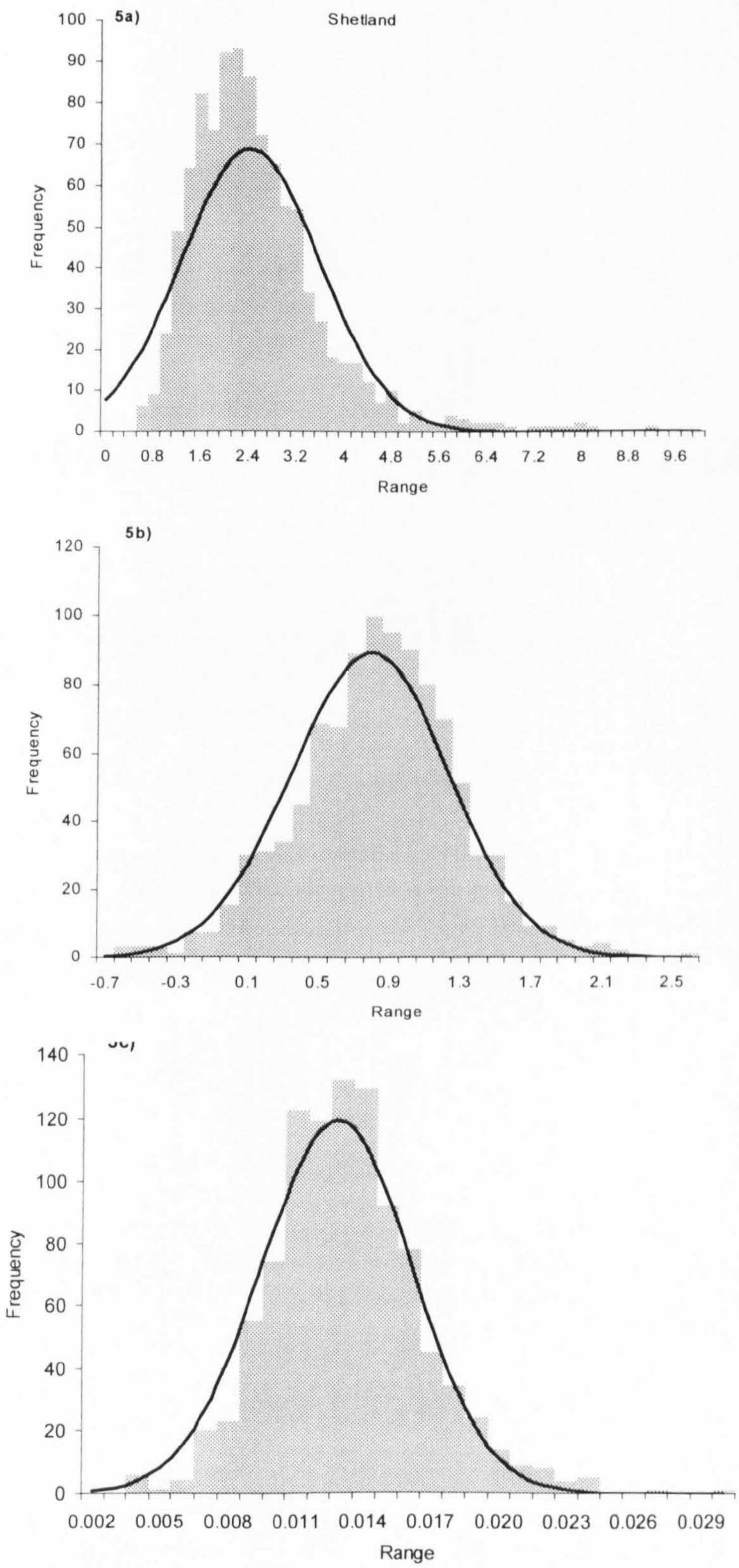


Figure 4.5.Histograms of values for parameters (*a*, *b*) of the Ricker stock-recruit model returned from 1000 bootstrap simulations (see text for details) for sandeels at Shetland **a)** – parameter *a*, **b)** – ln(parameter *a*), **c)** – parameter *b*. Expected normal curves shown.

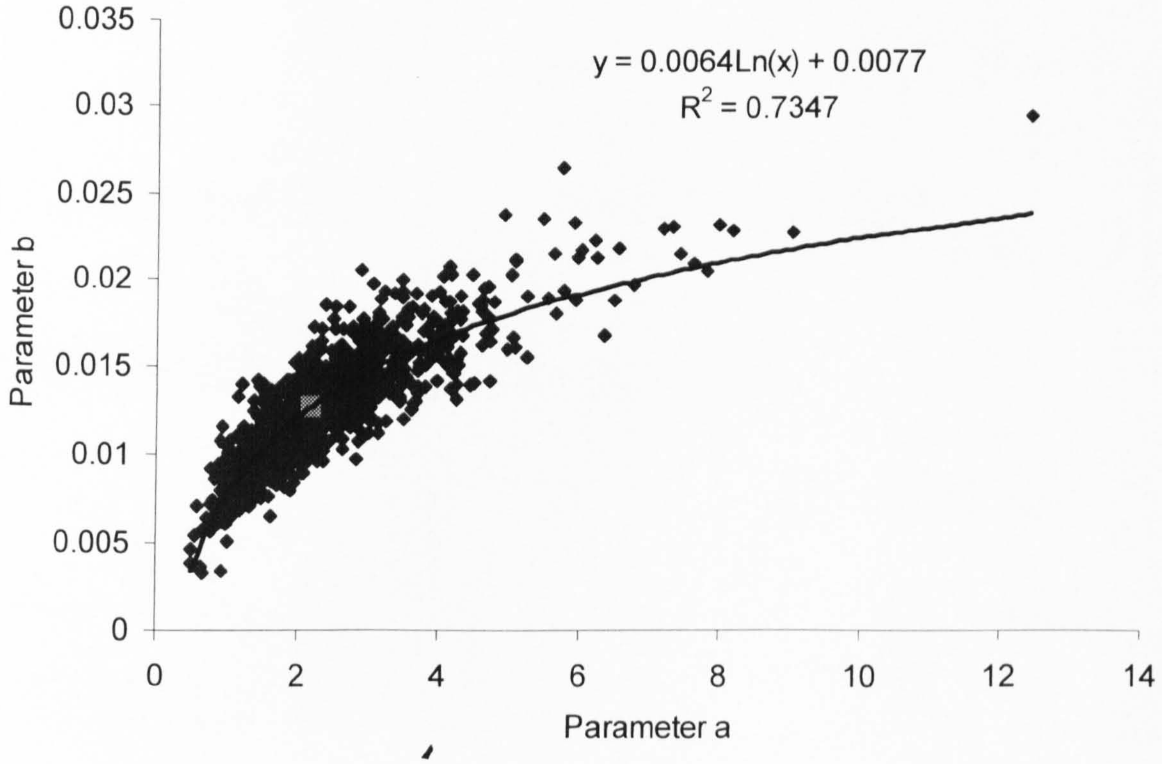


Figure 4.6. Correlation between estimates of parameters *a* and *b* of the Ricker stock-recruit model returned by 1000 bootstrap simulations (see text) for sandeels at Shetland. Trendlines with corresponding equation and R^2 are shown.

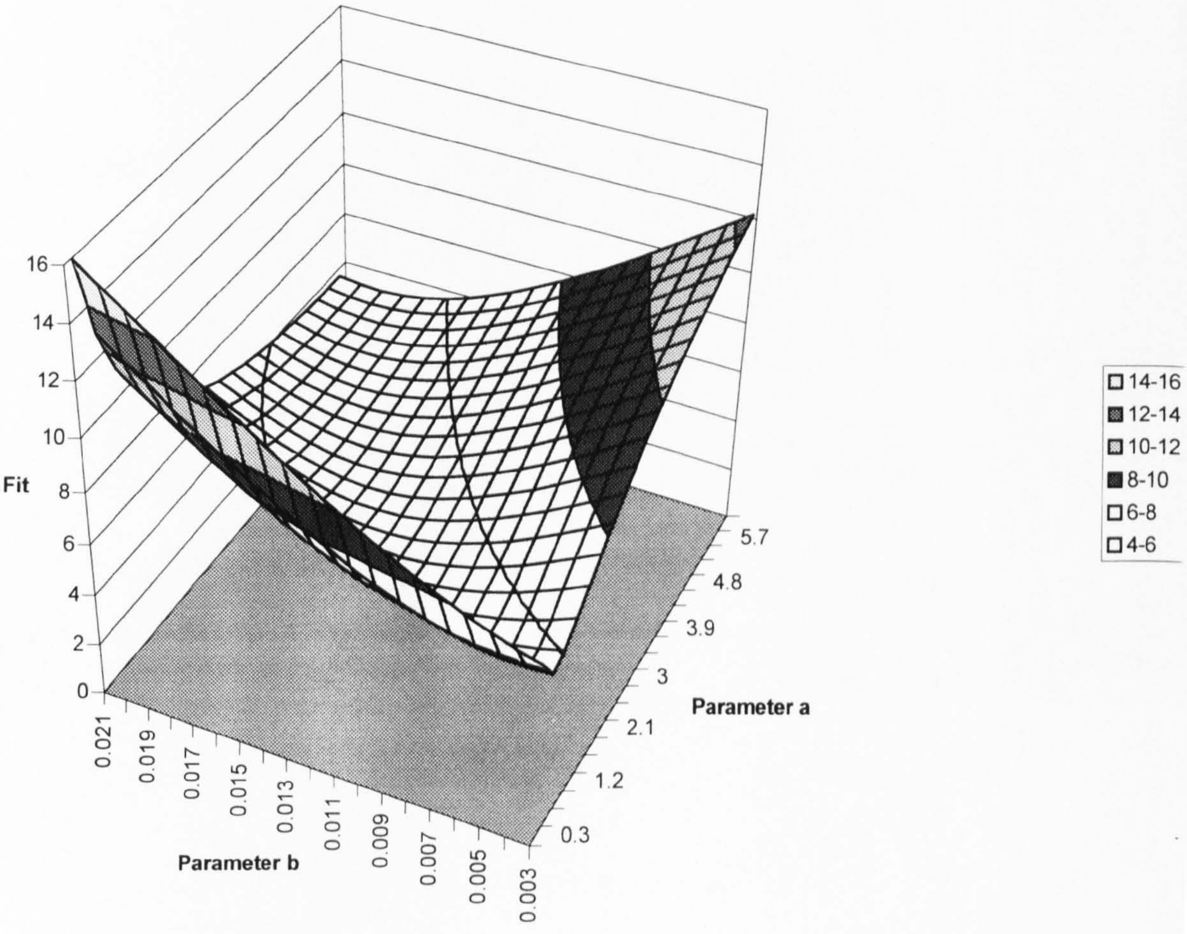


Figure 4.7 Results of direct search method to find optimal combinations of parameters *(a,b)* of the Ricker stock-recruit model for sandeels at Shetland. Fit refers to sums of squares of the differences of the logged recruit series (see text).

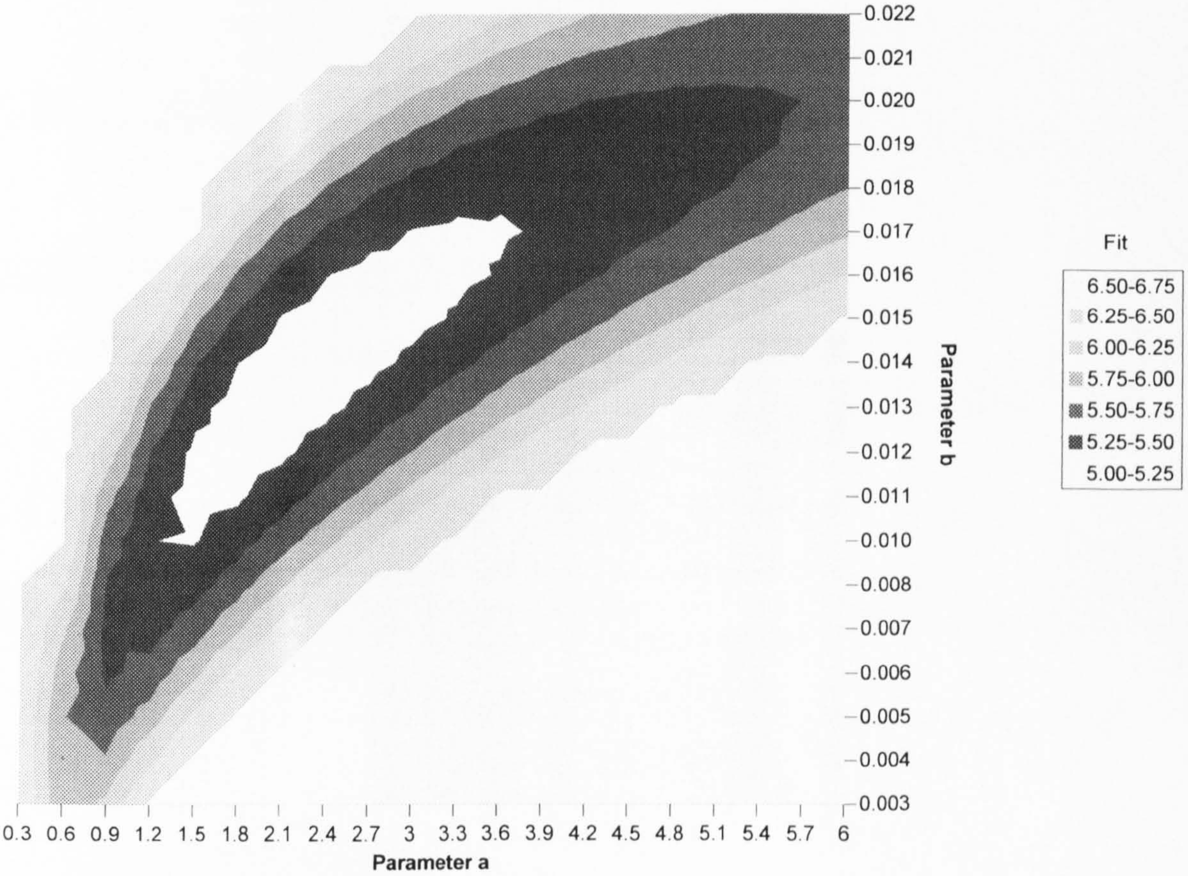


Figure 4.8 Results of direct search method to find optimal combinations of parameters (*a,b*) of the Ricker stock-recruit model for sandeels at Shetland. Fit refers to sums of squares of the differences of the logged recruit series (see text).

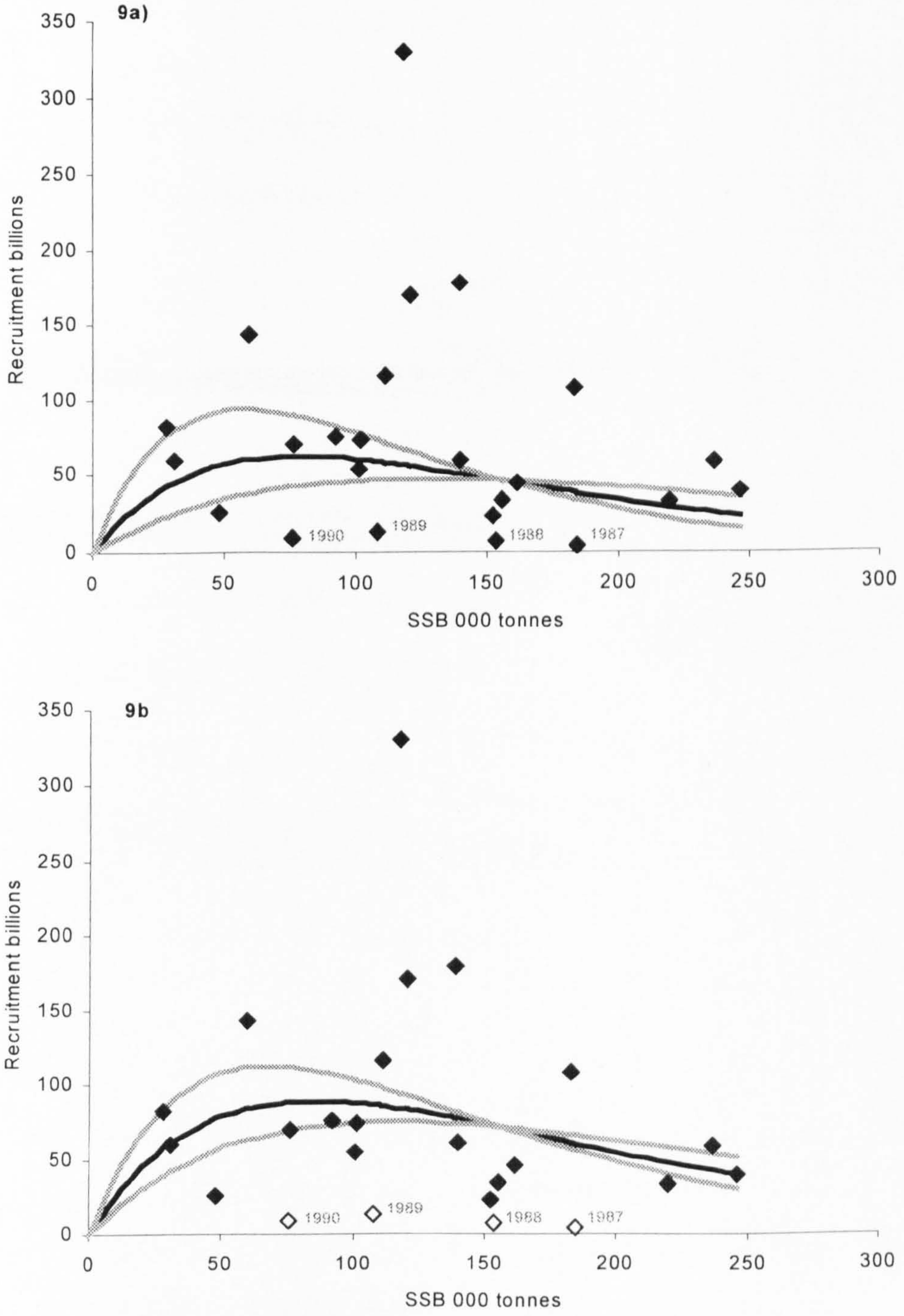


Figure 4.9 Ricker stock-recruit curves with 95% confidence intervals estimated by bootstrap analysis for sandeels at Shetland using **a)** the complete historical data set (from ICES 1999) and **b)** the data set minus four low recruit years (1987-1990 inclusive).

$$R = \frac{aS}{1 + \left(S/K\right)^{\beta}}$$

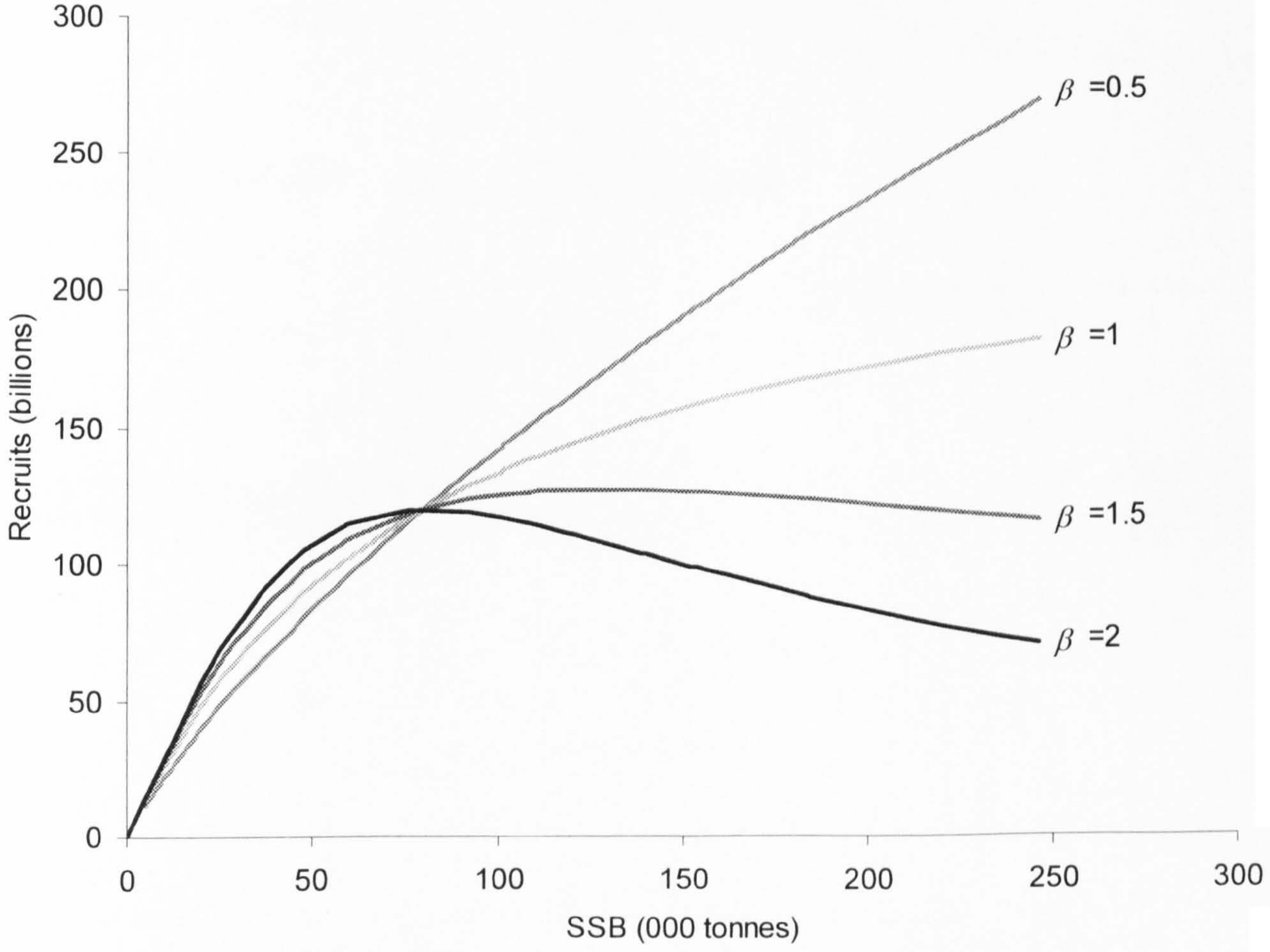


Figure 4.10 Shepherd (1982) stock-recruit curves with varying values of parameter β

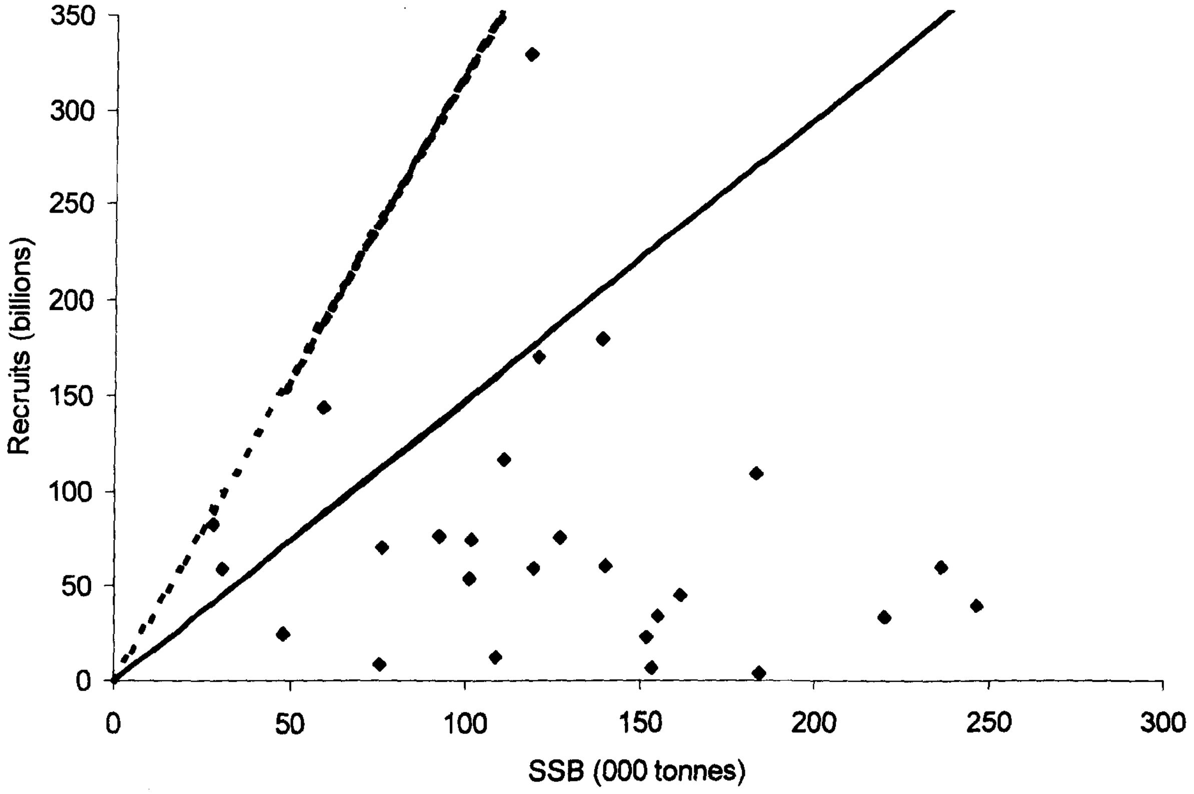


Figure 4.11 Stock-recruit data for sandeels at Shetland (from ICES 1999). Dotted lines represent estimates for parameter *a* of the Shepherd (1982) stock-recruit model estimated by drawing a line from the origin to the left of the data. The solid line represents the estimate from the average ln(R/SSB) for the bottom 25% data points ranked by SSB.

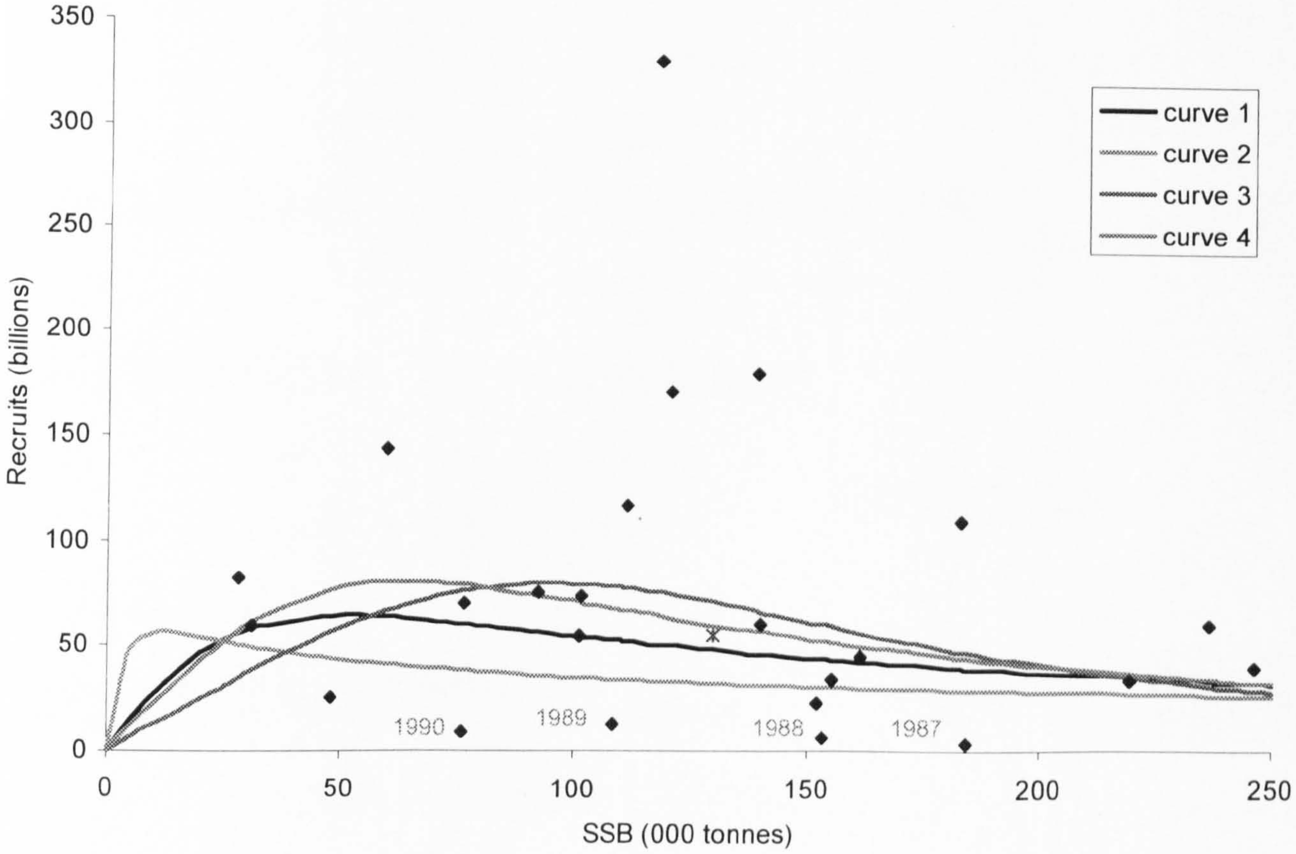


Figure 4.12 Stock-recruit data for sandeels at Shetland with fitted Shepherd (1982) stock-recruit models. Curve 1: subjectively estimated parameters, Curve 2: curve estimated be bootstrap analysis from modal value returned for *K* (5.6). Curve 3: curve estimated using modal value of parameter *a* from the reduced histograms returned by bootstrap analysis (K>20). Curve 4: curve estimated using modal value of parameter β from the reduced histograms returned by bootstrap analysis (K>20).

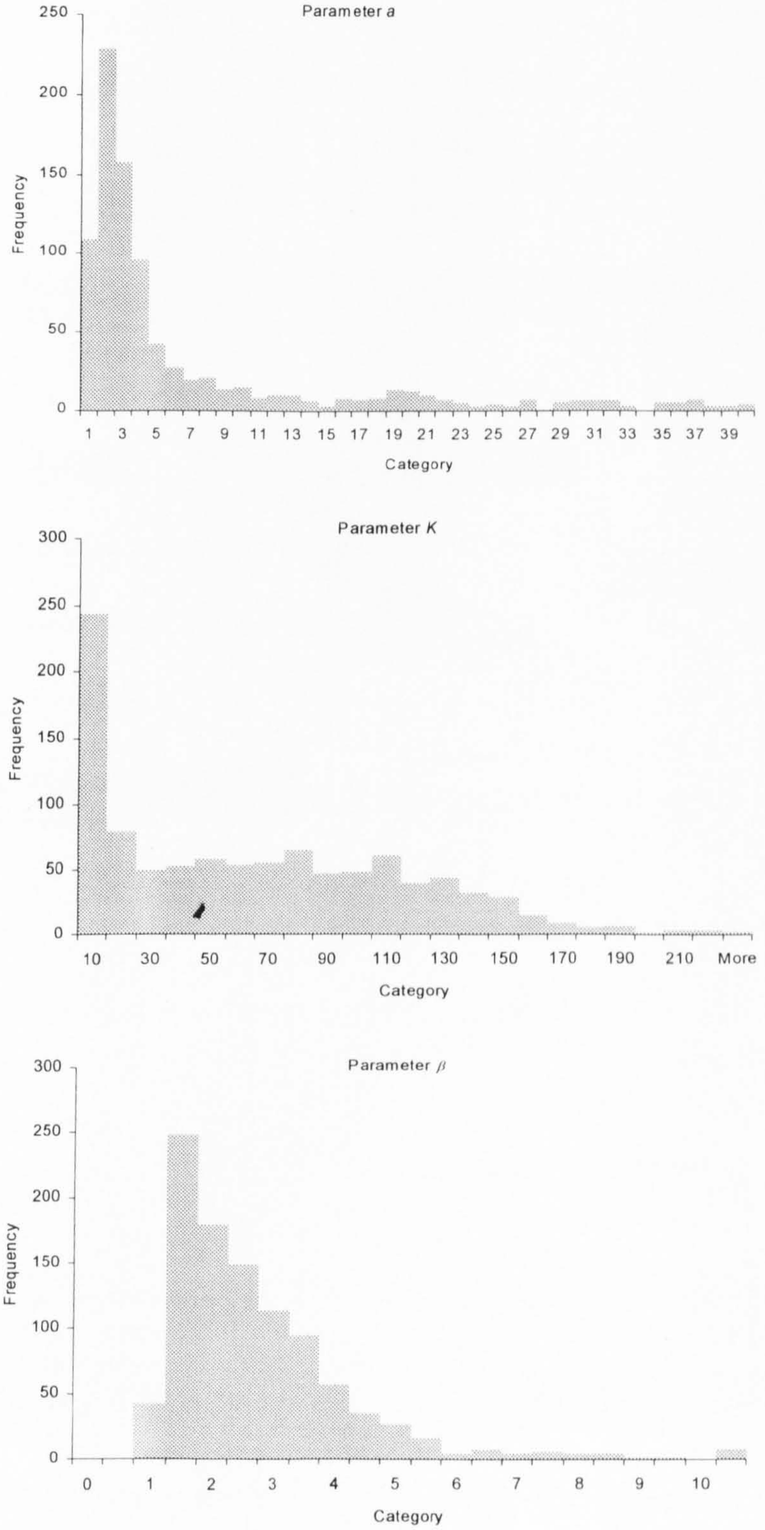


Figure 4.13 Sandeels at Shetland. Histograms of probability distributions for the three parameters of the Shepherd (1982) stock-recruit model determined by bootstrap analysis using complete historical data set.

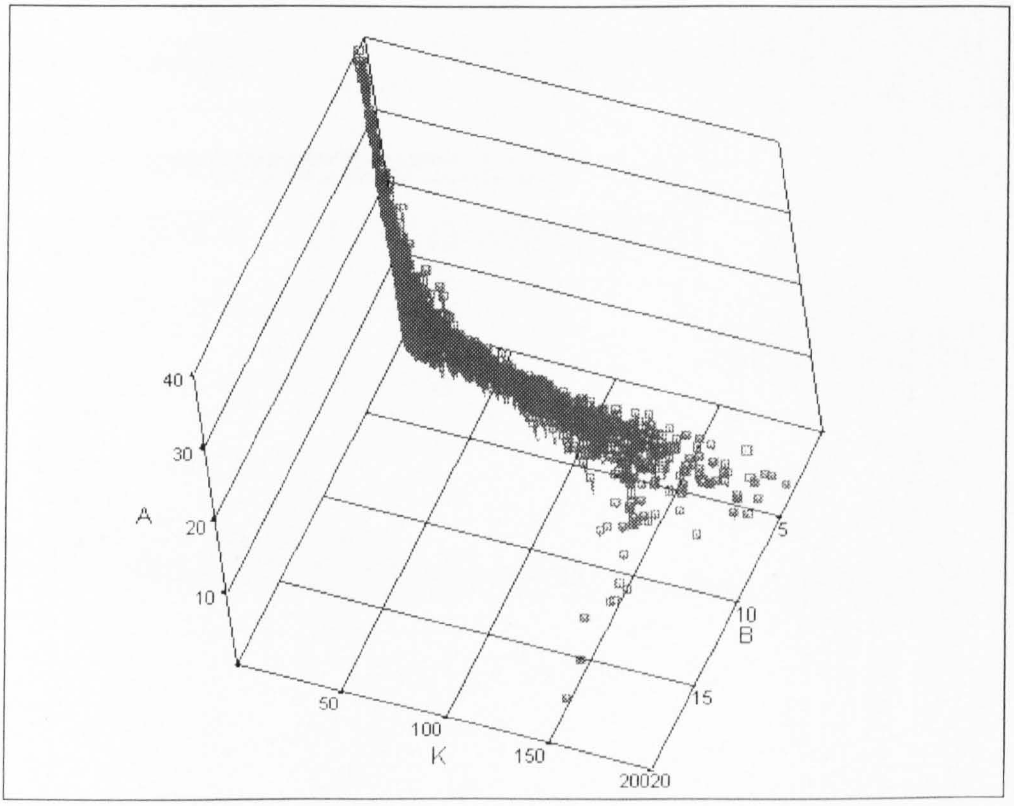


Figure 4.14 3d scatterplot of the three parameters (*a*, *K* & β - indicated by B) of the Shepherd (1982) stock-recruit model for sandeels at Shetland estimated by 1000 bootstrap analysis simulations using complete historical data set.

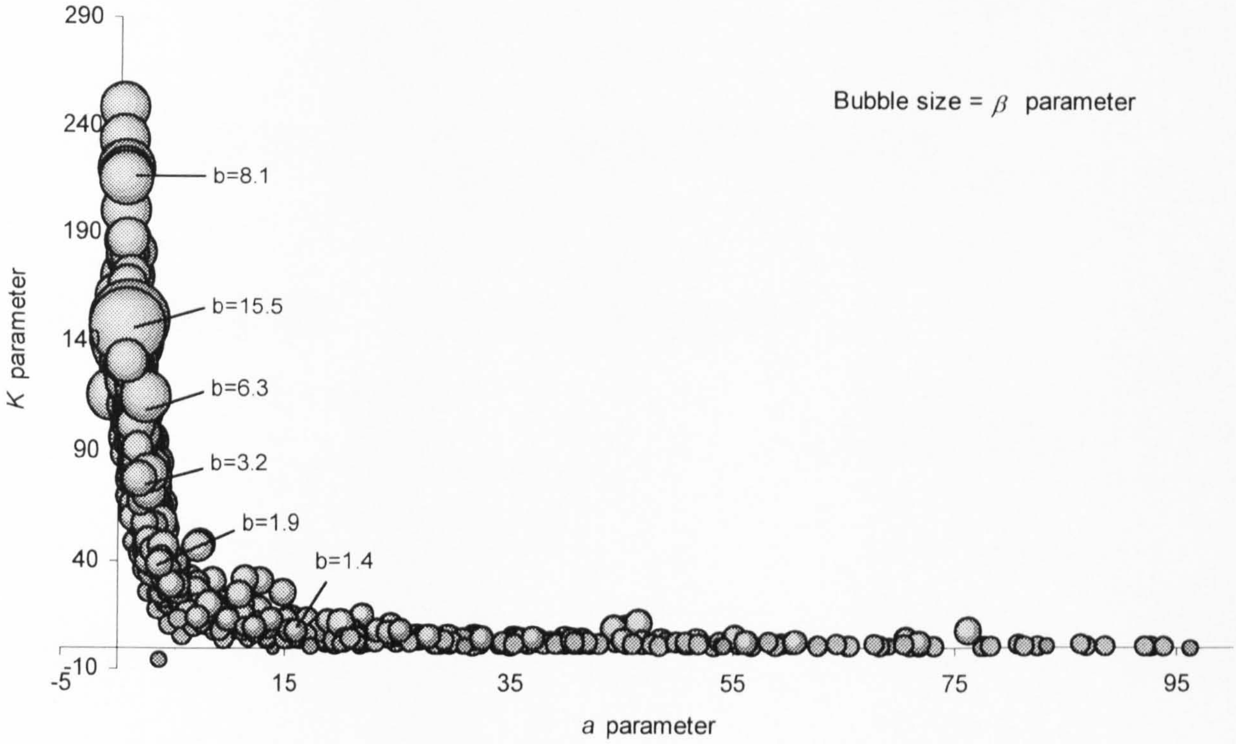


Figure 4.15 Sandeels at Shetland. Bubble plot of three parameters of the three parameters (*a*, *K* & *β*) of the Shepherd (1982) stock-recruit model estimated by 1000 bootstrap analysis simulations using complete historical data set.

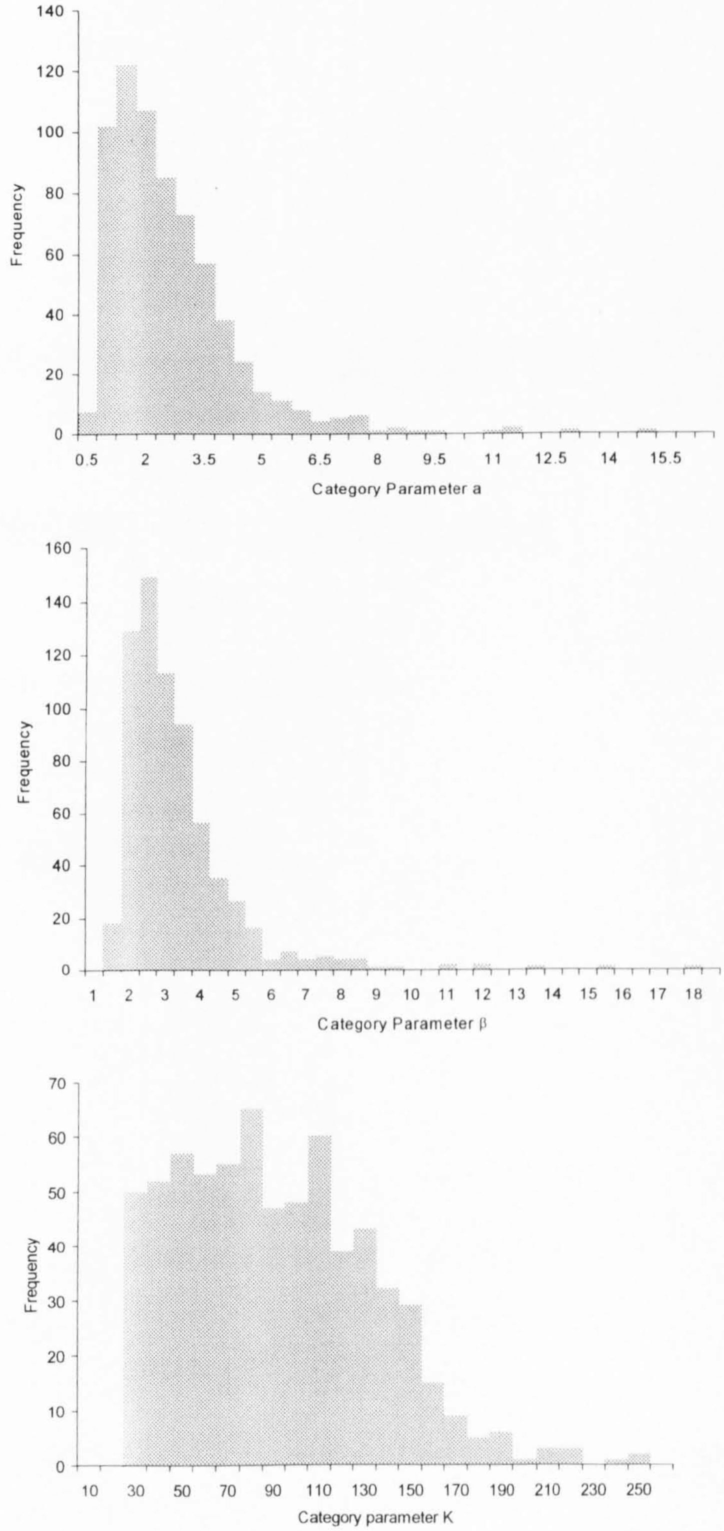


Figure 4.16 Sandeels at Shetland. Probability distributions for parameters of Shepherd model returned by bootstrap analysis after removing combinations with $K<20$.

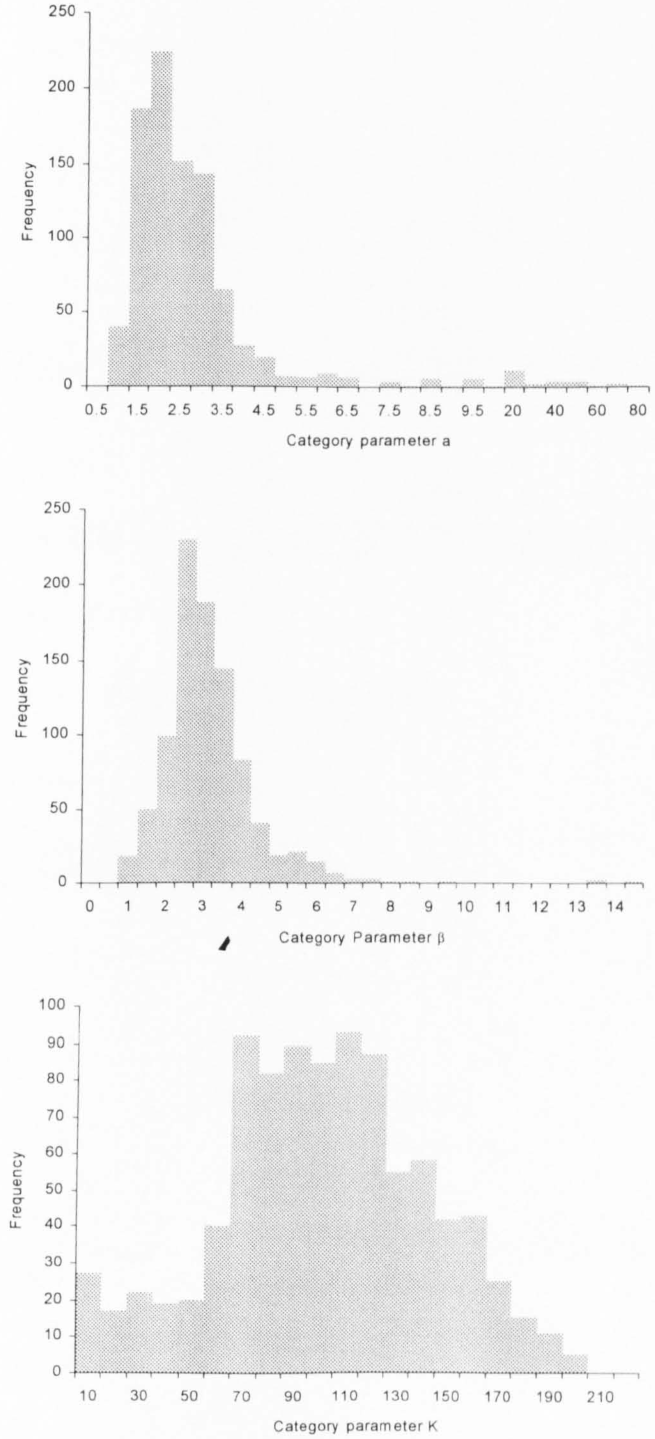


Figure 4.17 Sandeels at Shetland. Probability distributions for parameters of Shepherd model returned by bootstrap analysis using reduced data set (minus four low recruit years)

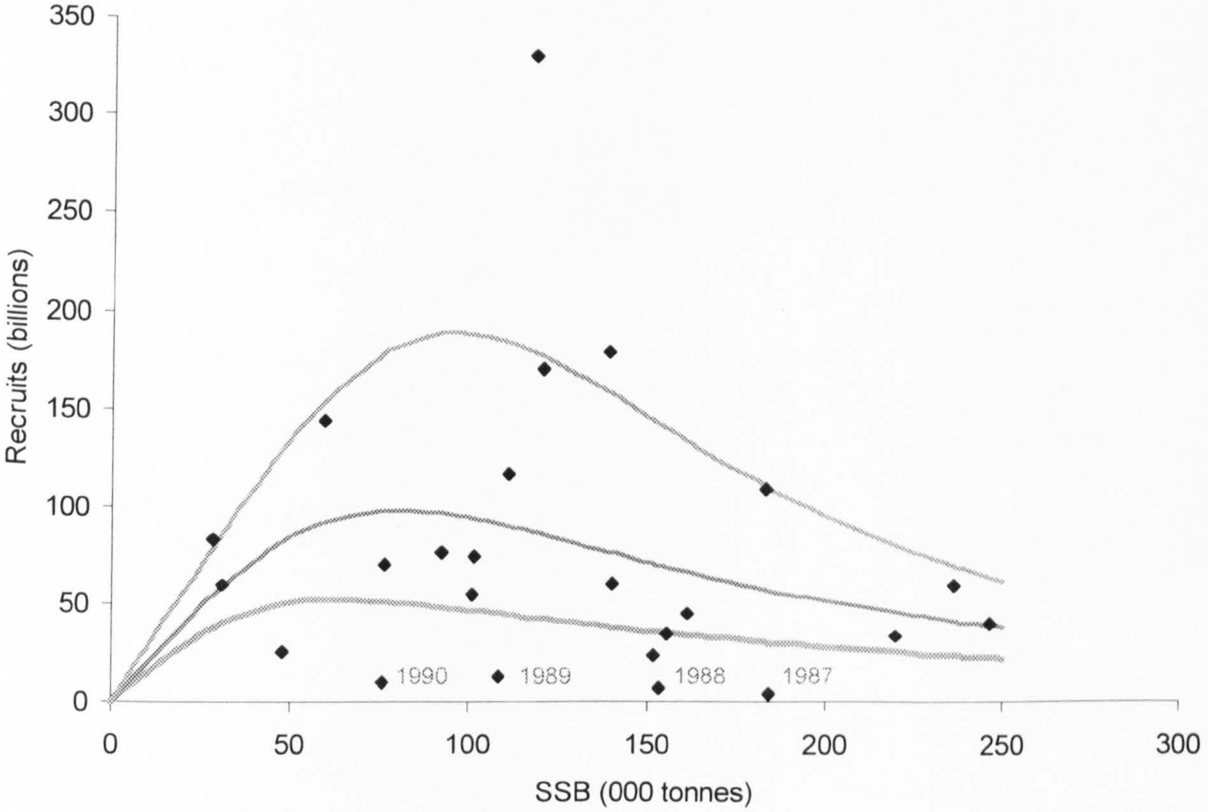
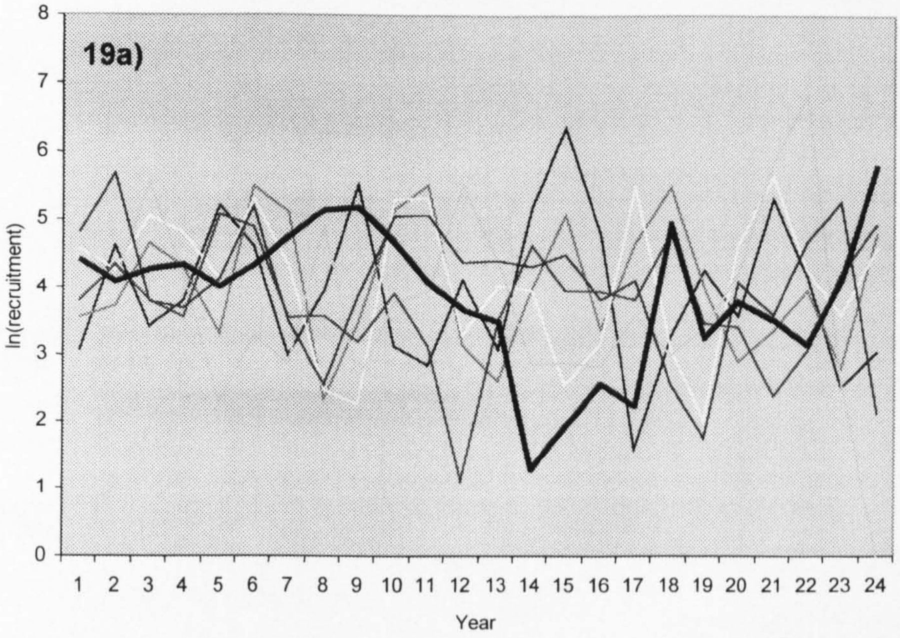


Figure 4.18 Sandeels at Shetland. Shepherd (1982) curve with 75% confidence intervals parameterised by 1000 bootstrap simulations using reduced data set (minus four low years 1987-1990 inclusive).



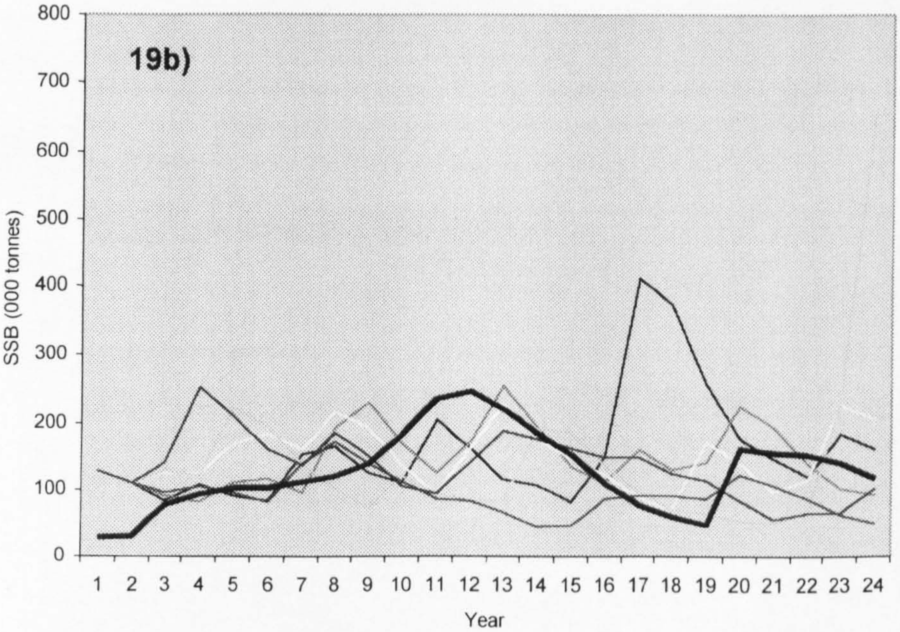
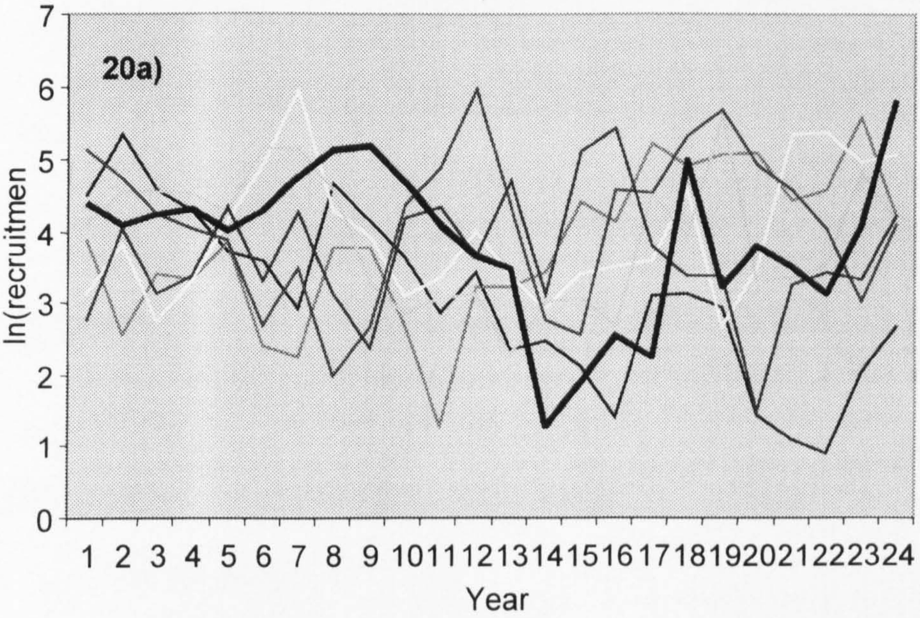


Figure 4.19 Sandeels at Shetland. Results of six simulations of 24 years of a population model with recruitment simulated by a Ricker model (parameterised by bootstrap analysis using complete historical data set) with stochasticity. **a)** ln(recruit) time series and **b)** SSB time series.



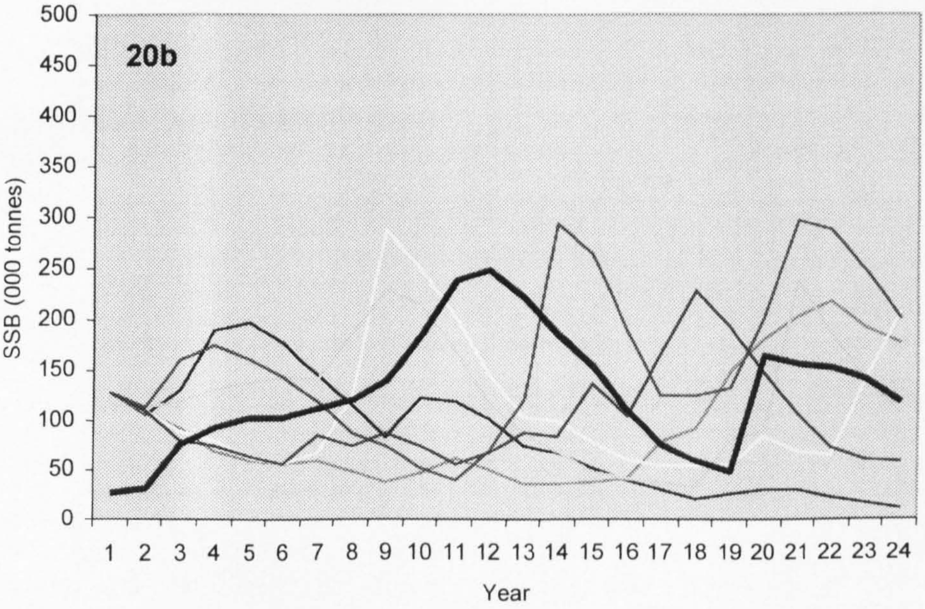


Figure 4.20 Sandeels at Shetland. Results of six simulations of 24 years of a population model with recruitment simulated by a Ricker model (parameterised using complete historical data set) with autocorrelated stochasticity. Input autocorrelation coefficient, α=0.51. **a)** ln(recruit) time series and **b)** SSB time series. Heavy line represents historical series (from ICES, 1999).

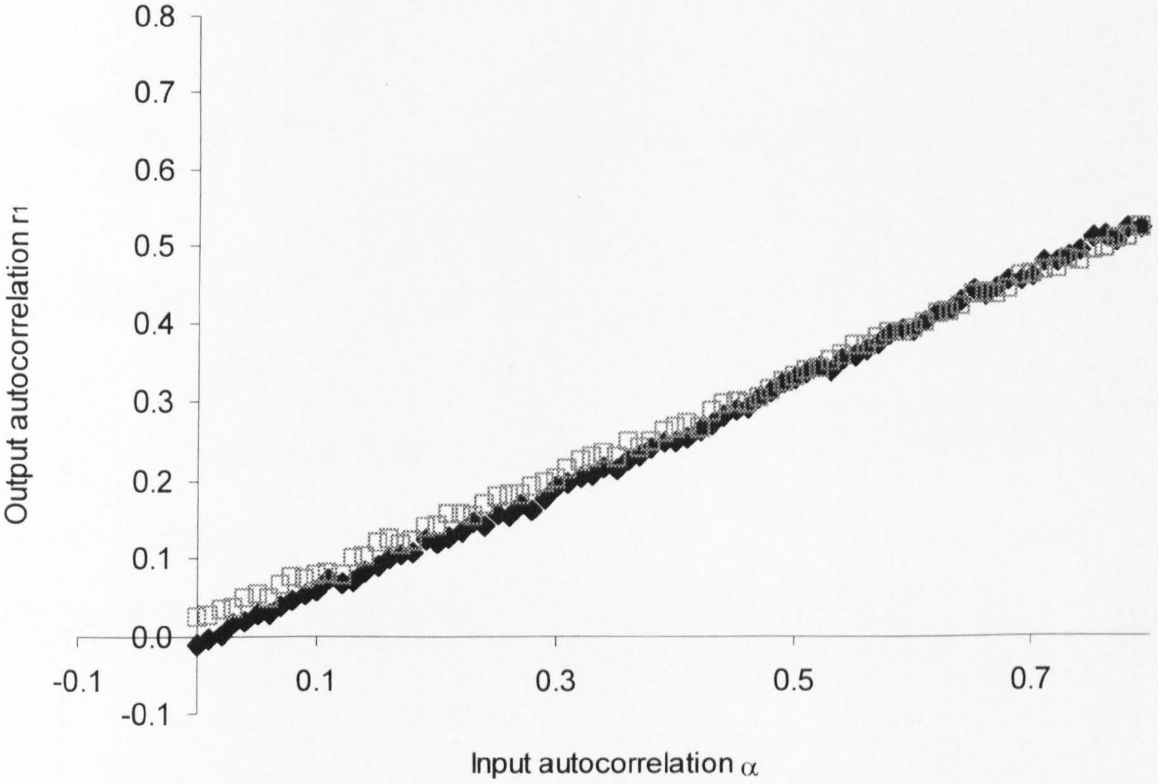
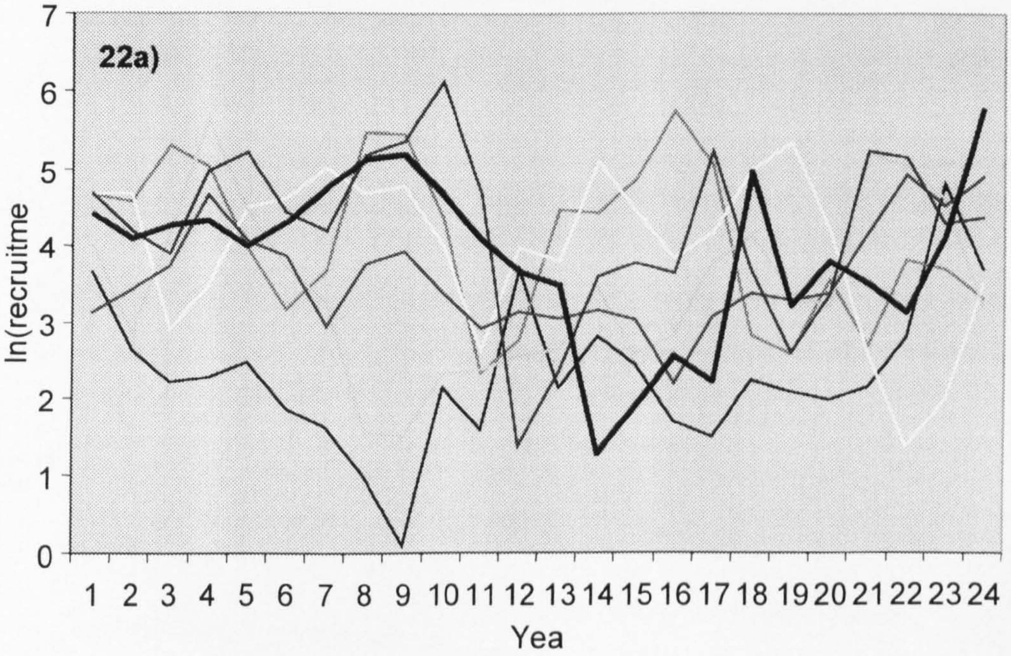


Figure 4.21. Relationship between input autocorrelation parameter, α, against the output autocorrelation, r_1, seen in the ln(recruit) time series for simulations of a population model of sandeels at Shetland. Recruitment is simulated by a stochastic Ricker model with autocorrelated log-normal residuals. Two series are shown, diamonds: 'best fit' Ricker curve parameterised by historical data set (from ICES 1999), standard deviation of residuals = 1.07. Squares: 'best fit' Ricker curve parameterised by reduced historical data set (minus four years), standard deviation of residuals = 0.65.



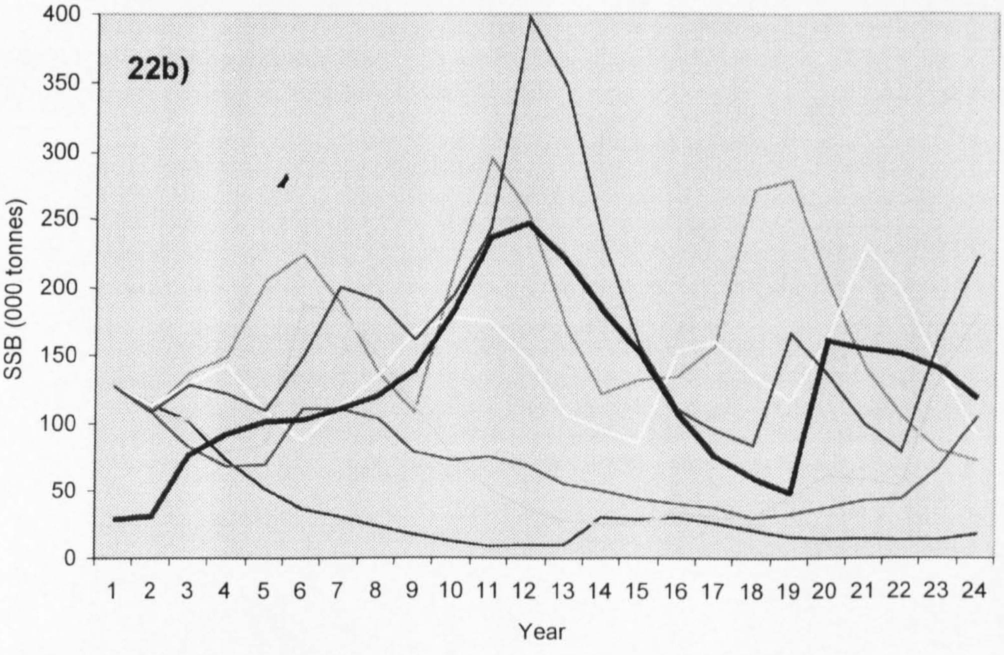


Figure 4.22 Sandeels at Shetland. Results of six simulations of 24 years of a population model with recruitment simulated by a Ricker model (parameterised using complete historical data set) with autocorrelated stochasticity. Input autocorrelation coefficient, α=0.73. **a)** ln(recruit) time series and **b)** SSB time series. Heavy lines represents historical time series.

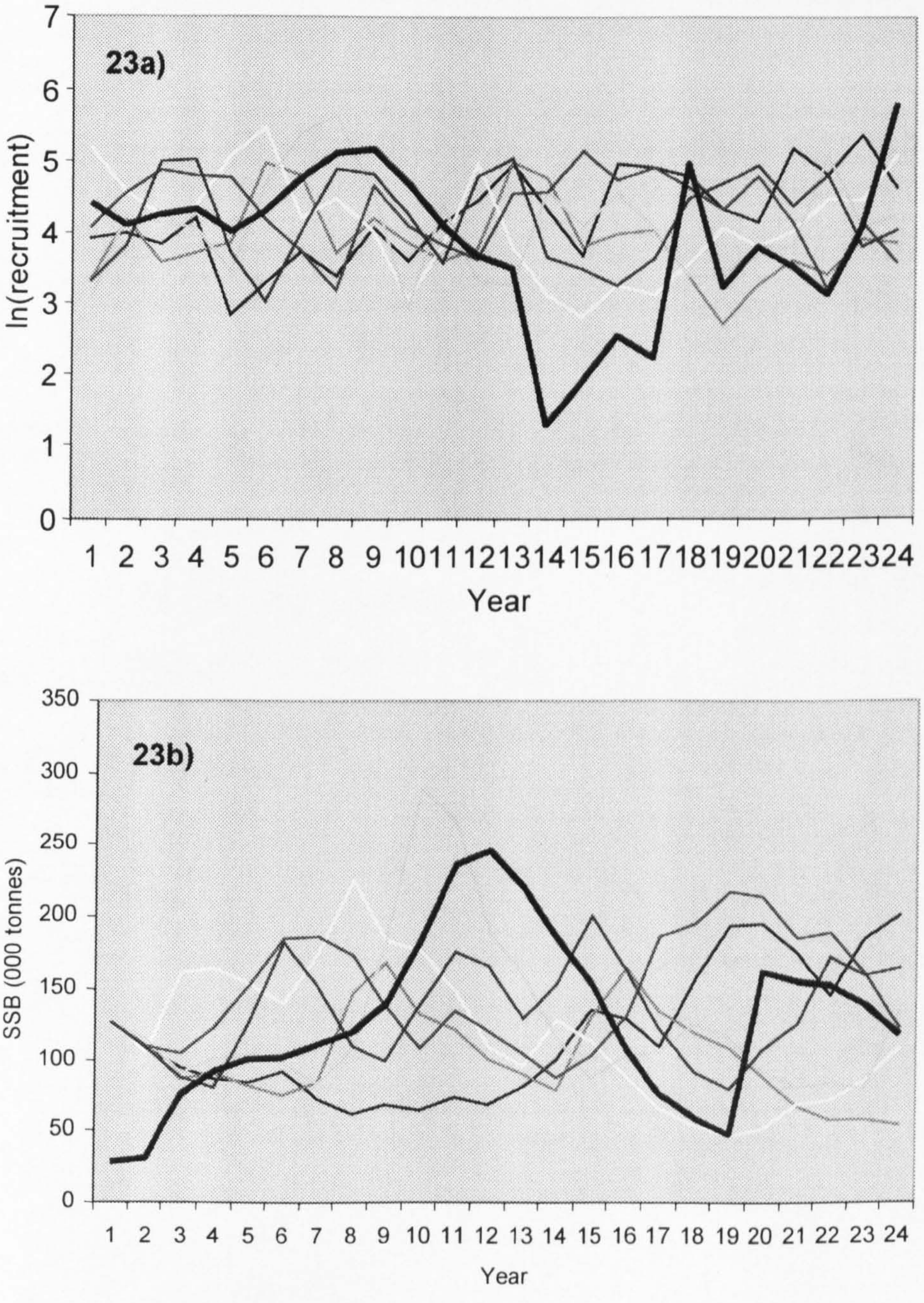
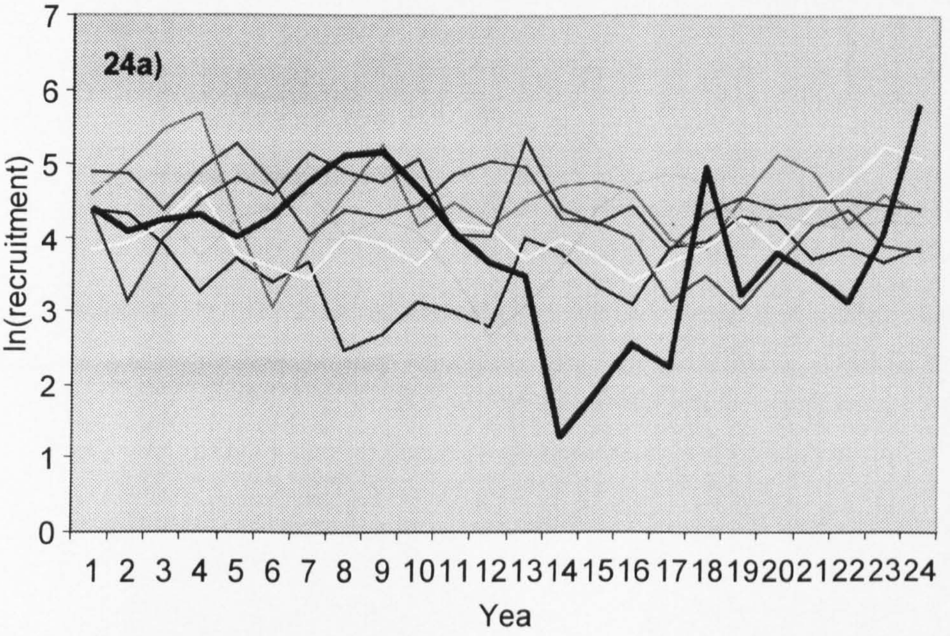


Figure 4.23 Sandeels at Shetland. Results of six simulations of 24 years of a population model with recruitment simulated by a Ricker model (parameterised using reduced historical data set) with autocorrelated stochasticity α=0.51. **a)** ln(recruit) time series and **b)** SSB time series. Heavy lines represent the historical series (from ICES, 1999).



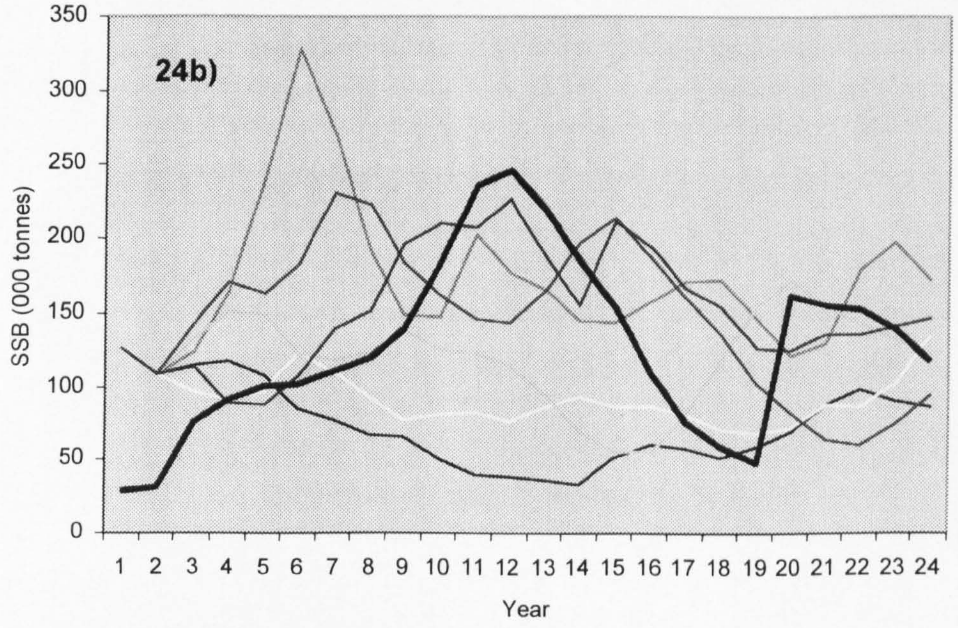


Figure 4.24 Sandeels at Shetland. Results of six simulations of 24 years of a population model with recruitment simulated by a Ricker model (parameterised using reduced historical data set) with autocorrelated stochasticity α=0.73. **a)** ln(recruit) time series and **b)** SSB time series. Heavy lines represent the historical series (from ICES, 1999).

CHAPTER 5

STOCK RECRUIT MODELS WITH EXTERNAL RECRUITMENT

5.1 Introduction

This Chapter develops models to simulate both local and external recruitment. As introduced in Chapter 2, our understanding of recruitment processes around Shetland is complicated by the likelihood that the Shetland sandeel stock is not a closed population but probably is part of a much larger population (Wright, 1996). The young sandeels recruiting to the exploited stock at Shetland appear to originate from two sources: 'local' recruits, which are spawned around Shetland and 'external' recruits which may originate from spawning grounds around Orkney (Wright & Bailey, 1993; Wright, 1996). External recruitment is considered to be sporadic, so in some years few or no external recruits reach Shetland, whereas in other years they may dominate in recruitment (Wright, 1996). It was determined, to attempt to increase our understanding to recruitment dynamics, to produce a model with external recruitment.

Firstly, evidence for external recruitment is discussed. To simulate local recruitment a scaled Ricker model fitted to the North Sea sandeel stock is applied to the Shetland data set - a method of scaling stock-recruit curves between the North Sea stock and the Shetland stock is determined. Ricker stock-recruit models are then fitted to the North Sea stock and confidence intervals on parameter estimates determined by bootstrap analysis. These curves are scaled and applied to the Shetland data. The variability around the curve in both the Shetland and the North Sea stock are analyzed to develop recruitment models that contain external recruitment. Two approaches are taken and simulations carried out. These indicate neither of these approaches produces recruit time series which are autocorrelated (the historical time series of recruitment at Shetland showed strong positive autocorrelation, see Chapter 3). The models were adapted to include autocorrelation in the local recruit and/or external recruit functions and tests carried out to determine the level of output autocorrelation in the total recruit time series. Two suitable models are identified to simulate local and external recruitment.

5.2 External Recruitment

External recruitment may be significant for the persistence of the exploited sandeel population at Shetland with external spawning stocks, probably around Orkney, acting as an important source of recruits. This phenomenon was proposed by Fogarty (1998) to explain the strong resilience of coastal American lobster (*Homarus americanus*) stocks to exploitation. Analysis indicated that larval dispersal from underexploited offshore populations to the fished inshore populations allows persistence of these heavily exploited stocks. Could this be happening with the sandeel population at Shetland? If so, this has implications for management – if external recruits form a significant addition to the Shetland stock then the size of the SSB of the Shetland population becomes less critical for fishery management. Recruitment is therefore more dependent on larval transport mechanisms and the SSB of the larval source populations. If larval transport mechanisms, thus external recruitment, cease then recruitment at Shetland could potentially be drastically reduced – did this happen in the late 1980s?

Proctor *et al.* (1998) adapted a two-dimensional sea circulation model for the passive transport of particles on the north-west European shelf to simulate the transport of sandeel larvae. Proctor *et al.* used data (1955-1993) on spawning location, age of larvae and time of hatching as input into the model. Particle drift was calculated for the larval life stage. The model produced an index, hereafter referred to as I, for the strength of the physical transport of passive particles between Orkney and Shetland. The index, I (solid line), is plotted with the recruitment (dashed line) to the Shetland sandeel stock over the years 1974-1993 inclusive (Figure 5.1). Assessment methodology for the Shetland sandeel stock has changed since this paper was published (ICES, 1999) with the result that estimates of the sandeel stock numbers have increased (Figure 5.1). However, according to ICES, the current assessment method is very sensitive to input parameters and so the results should be viewed only as an indication of stock trends. Therefore, although the estimates of the numbers of fish have increased, the conclusions drawn are unaffected as the overall stock trends are similar.

Proctor *et al.* (1998) concluded that in years of relatively low recruitment (1983-1990) particle transport from Orkney was generally low, while in 1981 and 1991, years of relatively high recruitment, particle transport was high. This is demonstrated in Figure 5.2, where total recruitment around Shetland (from ICES, 1999) was plotted against the transport index I. As I increases, so the total recruitment tends to increase, suggesting a positive relationship between recruitment and index I. 1982 was considered an anomaly as, although the particle drift model returned a low index ($I = 0.04$; Figures 5.1 and 5.2), a large external recruitment is thought to have occurred. Observations and trawl surveys carried out by the Marine Laboratory, Aberdeen, indicated it is likely a large number of external recruits entered Shetland waters during this year (Wright, 1996).

If *net* immigration to Shetland occurs this will obscure the stock-recruit relationship for Shetland sandeels and could account for the difficulty in fitting stock-recruit models in the previous chapter. In this case, the actual spawning stock for the Shetland population may be underestimated as SSB could be considered as the biomass of mature sandeels from a much larger area, which includes Shetland and probably Orkney. Rothlisberg *et al.* (1996), produced models of penaeid prawn larval advection to estuaries in Australia that included all the areas from which larvae originated – and found SSB could vary considerably annually. Rothlisberg *et al.* termed the SSB in these much larger areas as the *effective SSB*, that is the SSB over all areas from which the larvae originate. The spatial extent of the effective SSB, hence size, may change from year to year as larval transport mechanisms fluctuate. This probably occurs at Shetland as transport mechanisms for external recruitment fluctuate.

The frequency of external recruitment to Shetland is unknown – does this occur every year or sporadically? The transport index, returned by the 2-dimensional sea circulation model adapted by Proctor *et al.* (1998), indicates the passive transport rate of particles from Orkney to Shetland was generally high in years when recruitment at Shetland was high. The output of this model could be used as an indicator for the frequency and the size of external recruitment (assuming high transport indices are correlated with high external recruitment). However, there are no direct estimates of the size of external or local recruitment in any years so it is difficult to determine the nature of this relationship. Additionally, it must be remembered the transport index is itself the output of a model with many variables and unknown parameters.

How can a model of local and external recruitment be developed? The approach taken was to assume that the stock-recruit relationship for sandeels around Shetland is the same as that for populations in other areas of the North Sea. Stock-recruit curves can be fitted to the North Sea data and scaled for use with the Shetland data – this will give some indication of local recruitment. If the North Sea as a whole is considered then immigration and emigration will be negligible compared to the stock size (ICES, 1999).

5.3 Scaling Stock-Recruit Models

Sandeels in the North Sea can be thought of as a number of distinct spawning populations (including Shetland) with some transfer between them (Pedersen *et al.*, 1999). If the values for weight-at-age, maturity and natural mortality are similar between areas then it is reasonable to assume that the stock-recruit relationships are similar. For assessment purposes, the values of maturity (age at which sandeels first reproduce) and the natural mortality rates for sandeels at Shetland are taken to be identical to those used for the assessment of sandeels in the entire North Sea (ICES, 1999). However, sandeels at Shetland are considered to be slower growing the North Sea sandeels, which is one reason why these were considered as a separate stock. The mean weight-at-age (from ICES, 1999) from catches in the first half of the year for sandeels in the northern North Sea and in the southern North Sea over 1993-1997 are shown in Figure 5.3 together with the long-term mean weight-at-age from the first half-year catches of sandeels at Shetland (from ICES, 1999).

Generally, weight-at-age is more variable in the northern North Sea than in the southern North Sea (Figure 5.3). In 1996, mean weight-at-age of 4 and 5+ group sandeels in the northern North Sea was considerably greater then in the other years but this was not the case in the southern North Sea. 1996 was also the year with the highest recorded recruitment in the North Sea (2.069 x 10^9), almost double the previous record for recruitment (1.206 x 10^9 in 1985). Variation in weight may be due to difference in catchability with age – later in the summer older sandeels may not be available to the fishery (Pedersen *et al*,. 1999). The long-term mean weight-at-age for sandeels at Shetland is less then the mean weight-at-ages for sandeels in the northern and southern North Sea. Within the northern North Sea the data becomes biased after 1990 due to the inclusion of the small fish off the Firth of Forth (Wright, P. pers. com.). For the purpose of this modelling exercise, it was assumed that weight-at-age at Shetland was not significantly different from that in other areas of the North Sea. Therefore, it can be assumed that the stock-recruit relationship, that is the shape of the stock-recruit curve, at Shetland follows that of populations in other areas of the North Sea.

If the sandeel population of the North Sea as a whole is considered, the transfer of sandeels in and out of the system will be negligible. Using a stock-recruit curve which was fitted to data for the entire North Sea to predict local recruitment at Shetland will alleviate any problems of immigration or emigration. As the units involved are different (the North Sea is much larger than Shetland), the scale of the curves will vary. An appropriate scaling factor would have to be applied to use the North Sea stock-recruit curve with Shetland data.

Two methods of scaling by area were considered, these were: i) the ratio of ICES statistical rectangles for Shetland to that of the entire North Sea and ii) the ratio of estimated area of suitable sandeel habitat around Shetland to that in the North Sea. For ICES stock-assessment work, the North Sea is divided into rectangles of ½° latitude and 1° longitude. The ratio of ICES rectangles in Shetland to that in the entire North Sea was calculated and was found to be approximately 1:11. The latter method (ii) was based on surveys of area of sediment of suitable grain size around Shetland and in the North Sea. This was found to be approximately 1:11.3 (Wright pers. com.). As both methods produced similar ratios, a scaling factor of 1/11 was selected.

5.4 Ricker Models

The Ricker (1954; 1975) stock-recruit model (Equation 5.1) was parameterised for North Sea sandeels using the technique of bootstrap analysis (Efron & Gong, 1983) as described in Chapter 4 for Shetland sandeels.

$$R = aSe^{-bS} \qquad 5.1$$

where R is recruitment, S is SSB and a and b are constants.

Bootstrap analysis samples at random, with replacement, from the original data set to generate probability distributions for parameter estimates. For each data set selected from the original set, a Ricker model was fitted and values returned for parameters a and b recorded together with the standard deviation of the residuals, σ_W, about the Ricker curve. The mean SSB and mean recruitment of the selected data set were also recorded. 1000 bootstrap simulations were performed. The results are shown in Table 5.1 together with the corresponding results for the Shetland data set (from Chapter 4).

The North Sea Ricker model parameterised above was scaled down, using the scaling factor of 1:11 identified, and applied to the Shetland data. The resulting curve, together with the scaled down curves representing 95% confidence limits, are shown in Figure 5.4. Compared to the Ricker curve parameterised previously (in Chapter 4) using the entire Shetland data set (Figure 5.5), the slope from the origin (parameter a), which represents recruits per unit spawning stock biomass, is lower for North Sea sandeels (1.26) than for Shetland sandeels (2.19). 95% confidence intervals for parameter estimates are shown in Table 5.1. The estimate of parameter a for Shetland sandeels (2.19) falls within the 95% confidence intervals of the estimate for North Sea sandeels (0.60 – 2.31) so the curves are not significantly different. Although this means that there is no strong evidence that the mean estimates for parameter a of the Ricker model for Shetland sandeels and North Sea sandeels are different, it does not provide strong evidence that they are similar either.

Parameter b describes how quickly recruits-per-spawner drop at high SSBs (density-dependent parameter). Estimates of parameter b for the North Sea are scaled for comparison with the Shetland data (by multiplying by the scaling factor). The mean estimate for Shetland (0.0128) is much larger then the mean estimate for North Sea sandeels (0.0087) and is within the North Sea 95% confidence intervals (-0.0004 – 0.0160). Again, there is no strong evidence that the mean estimates for parameter *b* for Shetland and North Sea sandeels are different (or similar). Considering the potential for sampling error in the data sets and the large variability in recruitments, the stock-recruit relationships for Shetland sandeels and North Sea sandeels are surprisingly similar (Figure 5.5).

Why is variability in the Shetland data much higher than in the North Sea sandeel data? The North Sea stock is probably formed of a number of sub-populations (Pedersen *et al.,* 1999) each with SSB and recruitment time series. Annual estimates of SSB and recruitment for the North Sea stock can be considered as the summed values from all these sub-populations. As has been shown by Scheuring & Jánosi (1996), variability in a population consisting of a number of sub-units is less than the variability of the constituent sub-populations, and reduces as the number of sub-populations increases. In other words, the influence of an extreme value in recruitment in one sub-population may be reduced by taking the average over all sub-populations (as this may be counteracted by high recruitment in another sub-population) hence the total average variability is less then the individual variability. This could account for the reduced variability in the North Sea population compared to the Shetland population. However, if the sub-populations fluctuate in phase with each other, as may occur if large scale climatic perturbations affect all sub-populations (see Chapter 2 work on spatial synchrony), then total average variability may not be less then sub-population variability. Analysis of sub-population data sets for the North Sea could distinguish between these two hypotheses.

In the previous Chapter, it was found that the four low recruitments which occurred in the late 1980s strongly influenced the statistical fit of the stock-recruit models. Although there is no biological reasoning for removing these data points, they were removed and the stock-recruit models refitted in order to explain their effect here. This allowed a further curve to be parameterised (Figure 5.5) which returned much higher estimates of recruitment for a given SSB than the curves fitted using the complete Shetland data set and North Sea data set. Hence these four "unusual" years have a very strong influence on model fit.

Although Wright (1996) indicates net external recruitment to Shetland may occur, there are no estimates for the size and frequency. As it was determined to produce a model with external recruitment, for the purpose of this modelling exercise, the Ricker stock-recruit curve fitted to the reduced Shetland data set (minus four low years) was selected. By assuming the difference between this curve and the scaled North Sea curve is due to the addition of external recruits, then a model can be developed.

5.5 Modelling External Recruitment

Two methods were developed to simulate external recruitment, both using the reduced Shetland data set. The first calculates total recruitment as the product of local recruitment predicted from a Ricker curve with log-normal error distribution and a second lognormally distributed factor with a lower limit greater than zero. The latter factor represents ln(total recruitment) as a multiple of ln(local recruitment) and is termed *external error.* When local recruitment is subtracted from total recruitment using this method, actual values of external recruitment are produced. The method exploits the phenomenon of additive variances in the logs of predicted local recruits and external error factor to achieve a greater standard deviation of the log total recruit distribution for Shetland compared to the North Sea. The advantage of this method is external recruitment is indirectly related to SSB so will be affected by density dependence at high SSBs.

The second method is an adaptation of the first with external recruitment independent of recruitment predicted by the Ricker curve (local recruitment). Through simulations of the first method, actual values for external recruitment are generated. The distribution of external recruitment was analyzed and, in simulations, a value for external recruitment is selected at random from this distribution. By uncoupling external recruitment from local recruitment, this method does not incorporate the effects of density dependence on external recruitment at high SSB, but it does have the advantage that at low SSBs a large external recruitment may occur (in the first method this is rare as external recruitment is indirectly linked SSB).

5.5.1 Method 1

Both methods assume that the stock-recruit relationship at Shetland is similar to that in other areas of the North Sea. Therefore, the Ricker model fitted to the North Sea data, once scaled, can be used to simulate local recruitment at Shetland (recruits spawned around Shetland). To produce external recruit models, the scaled parameters of the North sea data set are taken to represent the *local* recruitment parameters while the reduced Shetland data set represents *total* recruitment (local plus external).

The "best-fit" Ricker model identified by bootstrap analysis above was applied to the North Sea sandeel data. Recruitment was found to be lognormally distributed about the curve and the log-transformed residual distribution had a mean, μ_L, of zero and a standard deviation, σ_L, of 0.625. The North Sea Ricker curve was scaled (as described above) and applied to the reduced Shetland data set (Figure 5.5). The distribution of Shetland recruits about the scaled Ricker curve was also lognormally distributed but with a mean, μ_T, of 0.429 and a standard deviation, σ_T, of 0.668. The median recruitment ("center of gravity" of the lognormal distribution) was above the Ricker curve, indicating that recruitment at Shetland was generally greater then that predicted by the scaled Ricker model.

If it is assumed that the difference between these two residual distributions is due to the addition of external recruits, then a third distribution can be parameterised to represent the variance introduced by external recruitment (termed *external error*, denoted by *v*). It was assumed that the ln(residual) distributions, for both the North Sea and reduced Shetland data sets, were normally distributed and the external error distribution was also normally distributed. Means and variances of normal distributions are additive (Evans *et al.*, 2000) therefore the mean of the external error distribution, μ_v, can be parameterised as:

$$\mu_v = \mu_T - \mu_L \qquad 5.2$$

where μ_T is the mean of the logged total recruit residual distribution (from the Shetland data set) and μ_L is mean logged local recruit residual distribution (from the North Sea data set).

The mean standard deviation of the external error distribution, σ_v, can be calculated as:

$$\sigma_v = \sqrt{\sigma_T^2 - \sigma_L^2} \qquad 5.3$$

where σ_T is the standard deviation of the logged total recruit residual distribution (from the Shetland data set) and σ_L is standard deviation of logged local recruit residual distribution (from the North Sea data set).

Substituting the appropriate values into Equations 5.2 and 5.3 produced estimates of 0.429 for μ_v and 0.236 for σ_v.

Local recruitment, in simulations, is estimated from the scaled Ricker model with lognormal error terms using the method described in Chapter 4. The equation for local recruitment with lognormal error terms is:

$$R_L = R_R \exp^{w} \qquad 5.4$$

where R_L is local recruitment, R_R is recruitment predicted by the scaled Ricker model and w is a normally distributed random number with a mean of zero and standard deviation σ_L.

In this case, w is the distribution of the residuals of local recruitment about the stock recruit curve so the distribution of w is equal to the logged-transformed error terms in the North sea data around the stock recruit curve (σ_L=0.625).

Total recruitment is also estimated from the scaled Ricker model with lognormal error terms. The distribution of the logged-transformed error terms around the stock-recruit curve is assumed to equal the sum of w plus the external error distribution, v, so:

$$R_T = R_R \exp^{w+v} \qquad 5.5$$

where R_T is total recruitment, R_R is recruitment predicted by the Ricker model and w is a normally distributed random number with a mean of zero and standard deviation σ_L and v is a normally distributed random number with a mean of μ_v and standard deviation σ_v. The distribution of v is truncated so v cannot be less then zero (otherwise external recruitment will be negative).

Equation 5.5 returns an estimate for total recruitment which is always greater than the estimate for local recruitment. External recruitment is simply calculated as the difference between total recruitment and local recruitment. The resulting lognormal error distribution returned by Equation 5.5 is equal to the lognormal distribution of the reduced Shetland data series about the scaled stock-recruit curve (total recruitment).

To illustrate the relationship between total and external recruitment with local recruitment, five hundred stock-recruit pairs were selected, at random, from the reduced Shetland data set. For each SSB, local and external recruitment were simulated using the method described above. The values of local and external recruitment calculated for the first fifty stock-recruit pairs selected are shown in

Figure 5.6. As can be seen in Figure 5.6a, a high recruitment year (>250 billion) can result from a large local recruitment (data point 19), or from a large external recruitment (data point 8) or from a mid-sized local recruitment with a mid-sized external recruitment (data point 24). Generally, as local recruitment increases so external and total recruitment increases (Figure 5.6b&c) although the relationships with local recruitment are stochastic. In high recruitment years, a large proportion of the recruits may be of external origin, as was indicated by the sea circulation model adapted by Proctor *et al.* (1998).

5.5.2 Method 2

This method uncouples external recruitment from recruitment predicted by the Ricker model using the results of the model developed above. In the previous model (*Method 1*), five hundred stock-recruit pairs were selected at random from the reduced Shetland data set and stochastic values for local recruitment and external recruitment calculated. Analysis of the distribution of the log-transformed external recruitments produced by *Method 1* indicated this was normal with a mean, μ_E, of 3.09 and a standard deviation, σ_E, of 1.02.

In *Method 2*, local recruitment is simulated using the scaled Ricker curve with lognormal errors (Equation 5.4) described in *Method 1* while external recruitment is simply selected at random from the distribution parameterised. External recruitment is uncoupled from local recruitment so a large external recruitment can be selected when local recruitment is small (in *Method 1* this was a rare occurrence).

Fifty stock-recruit pairs were selected, at random, from the reduced Shetland data set and local and external recruitment were simulated using *Method 2*. The values of local and external recruitment generated are shown in Figure 5.7. If local recruitment is low a high external recruitment may still occur, as seen in Figure 5.7a, data point 21. There is still a positive relationship between external recruitment and total recruitment (Figure 5.7c) so years of high recruitment tend to be years when external recruitment is high (though due to stochasticity, not necessarily so (see Figure 5.7a data point 49).

5.6 Introducing autocorrelation

Neither of the two methods discussed above include functions to autocorrelate the recruit time series. Analysis of the historical ln(total recruit) time series for the complete Shetland data set revealed a high positive autocorrelation function (+0.51, see Chapter 3). Incorporating a function for autocorrelation in either the local or external recruit equations or in both should induce some autocorrelation in the total recruit time series.

In both *Methods 1* and *2*, local recruitment is simulated using the Ricker model with lognormal errors (Equation 5.4). A function for autocorrelation was combined with the Ricker model as described in Chapter 4. The residuals around the stock-recruit curve were autocorrelated by applying a first order autoregressive model so w at time t (Equation 5.4) is expressed as a function of w at time t-1:

$$w_t = \alpha w_{t-1} + \varepsilon_t \qquad 5.6$$

where t is time, α is a constant (the coefficient of autocorrelation) and ε is a normally distributed random number with a mean of zero and a standard deviation σ_ε equal to:

$$\sigma_\varepsilon = \sigma_L \sqrt{\left(1-\alpha^2\right)} \qquad 5.7$$

where σ_L is the target standard deviation of the log-transformed residuals (local) about the stock-recruit curve.

As the local recruitment residuals about the stock-recruit curve are assumed to be similar to the residuals from the North Sea, $\sigma_L = 0.625$.

A similar approach was taken to autocorrelate external recruitment in both *Methods 1* and *2* although external recruitment is calculated differently in both Methods. A first order autoregressive model, as described in Chapter 3, was combined with the external recruitment functions. The autoregressive model takes the form:

$$y_t = \phi_0 + \phi_1(y_{t-1} - \phi_0) + \varepsilon_t \qquad 5.8$$

where y_t is the value of y at time t, ϕ_0 is a constant term, ϕ_1 is the autoregressive parameter at time t-1 and ε_t is a normally distributed random number with a mean of zero and a standard deviation σ_ε.

In *Method 1*, sequential dependence in external recruitment is incorporated by autocorrelating variable v (external error term) in Equation 5.5. y is substituted with v in Equation 5.8 and ϕ_0 with the mean of the external error distribution (μ_v) parameterised above, so v in year t is calculated as:

$$v_t = \mu_v + \phi_1(v_{t-1} - \mu_v) + \varepsilon_t \qquad 5.9$$

where ϕ_1 is the coefficient of autocorrelation (constant) and ε_t is a normally distributed random number with a mean of zero and a standard deviation σ_ε equal to:

$$\sigma_\varepsilon = \sigma_v\sqrt{(1-\phi_1^2)} \qquad 5.10$$

where σ_v is the standard deviation of the external error distribution parameterised above.

The autoregressive model (Equation 5.8) was also used to autocorrelate external recruitment in *Method 2*. In *Method 2*, ln(external recruitment) is selected at random from a parameterised distribution. To autocorrelate the ln(external recruit) time series, y is replaced with ln(R_E) in Equation 5.8 and ϕ_0 with the mean of the ln(external recruit) distribution, μ_E:

$$\ln(R_{Et}) = \mu_E + \phi_1(\ln(R_{Et-1}) - \mu_E) + \varepsilon_t \qquad 5.11$$

where R_{Et} is external recruitment in year t, μ_E is mean ln(external recruitment), ϕ_1 is the coefficient of autocorrelation and ε_t is a normally distributed random number with a mean of zero and a standard deviation:

$$\sigma_\varepsilon = \sigma_E\sqrt{(1-\phi_1^2)} \qquad 5.12$$

where σ_E is the standard deviation of ln(external recruit) distribution parameterised above.

5.7 Model Simulations

The basic population model written in Visual Basic (Chapter 3) was adapted to test the recruitment models described above. Combinations of local and external recruitment models were tested as shown in Table 5.2. For each Method (1 & 2), four models were tested: i) local and external recruitment stochastic, ii) local recruitment autocorrelated, iii) external recruitment autocorrelated and iv) both local and external recruitment autocorrelated.

Firstly, simulations of both methods with stochastic (non-autocorrelated) local and external recruitment were carried out. For each model, 1000 simulations of 24 years were conducted and the results of each simulation saved to an Excel spreadsheet. The results are shown in Table 5.3.

Considering the recruitment parameters, both methods produced parameters for local and external recruitment which were similar and the distribution of the lognormal errors of local recruitment about the stock-recruit model were similar to the target (historical) distribution. It was expected that both methods would produce similar local recruitment distributions as the same technique is used to generate local recruits. Similarly, the parameters of the external recruitment distribution were similar for both methods. This was also expected, as Method 2 randomly selected external recruits from the distribution parameterised by Method 1. Neither method produced local or external recruit series which were significantly autocorrelated ($-0.056<r_1<0.002$).

However, the parameters of the total recruitment distribution produced by both Methods differed. Those produced by Method 1 were similar to the target values. For Method 2, the mean of the ln(recruitment) distribution (4.41) was higher then the target value (4.25) while the standard deviation (0.58) was less then the target value (0.69). Correspondingly, the mean and standard deviation of the lognormal error distribution around the Ricker curve was greater and less then the target values respectively. These differences were due to the technique used to simulate local and external recruitment in Method 2.

In Method 1, the parameters of the North Sea (local) and reduced Shetland (total) data sets are used to generate local and total recruitment, hence external recruitment. In Method 2, total recruitment is expressed as the sum of local and external recruitment. While local recruitment is generated as in Method 1, external recruitment is selected at random from the distribution parameterised by Method 1. Hence in Method 1, local and external recruitment are correlated (see Figure 5.6b) while for Method 2 there is no correlation between the two (see Figure 5.7b).

Neither method produced significant autocorrelation in the ln(total) recruit time series ($-0.01<r_1<0.01$). The values for the mean SSB produced by the models (150 Method 1, 154 Method 2) were greater then the target value (126) while the standard deviations (45 Method 1, 42 Method 2) were less then the historical value (63). The first four years in the historical time series have extremely low values of

SSB (<93) and these reduce the mean value. The simulated population starts from a SSB of 127, considerably higher hence the mean values produced by the models were larger then the target value.

The remaining combination of models shown in Table 5.2 were tested varying the input coefficient of autocorrelation. Local recruitment was autocorrelated by the same technique in Methods 1 and 2 (see Equation 5.6) with an input coefficient of autocorrelation α. α was varied between 0 and 0.95 in steps of 0.01 in simulations. External recruitment was autocorrelated in both Methods by adapting a first order autoregressive model which had an input coefficient of autocorrelation ϕ_1. ϕ_1 was also varied between 0 and 0.95 in steps of 0.01 in simulations. 1000 simulations of 24 years were carried out for each value of α and ϕ_1 so all combinations were tested.

The results from autocorrelating local recruitment only are shown in Figure 5.8. For Method 1, inducing sequential dependence in local recruitment produces ln(local recruit) time series with an output autocorrelation coefficients, r_{1L}, which are less then the input coefficient of autocorrelation α. Autocorrelation induced in the ln(total recruit) time series is slightly less then that induced in ln(local recruit) time series. Some autocorrelation is also induced in the ln(external recruit) time series. In Method 1, total recruitment is expressed as the ln(local recruitment) plus a random number so autocorrelating local recruitment directly autocorrelates total recruitment hence external recruitment.

Autocorrelating local recruitment in Method 2, induces autocorrelation in the ln(total recruit) time series but to a much lesser degree than Method 1. For this method, external recruitment is unrelated to local recruitment hence autocorrelating local recruitment has no effect on external recruitment and a lesser effect on total recruitment than in Method 1. The maximum r_1 of only 0.22 is produced by Method 2 when α>0.69.

The results of autocorrelating external recruitment are shown in Figure 5.9. As expected, autocorrelating external recruitment has a smaller effect on the output autocorrelation in the ln(total recruit) time series then autocorrelating local recruitment. The median external recruitment produced by the models is 22 billion, less then half the median number of local recruits produced (49 billion, Table 5.3). Autocorrelation the external error time series in Method 1 has little effect on the sequential dependence in the ln(external recruit) time series. Neither model produced an output autocorrelation of greater than 0.18 in ln(total recruit) time series.

The final pair of models incorporated autocorrelation in both functions for local and external recruitment. The results using Method 1 are shown in Figure 5.10. As indicated by the models above, autocorrelating the external error time series has little effect on the output autocorrelation, r_1, of the ln(total recruit) time series compared to autocorrelating the ln(local recruit) series. Output values of r_1>=0.5 are produced when the input autocorrelation coefficient in the local recruitment function is greater then 0.73.

For Method 2, autocorrelating the ln(external recruitment) series has a greater effect on the output autocorrelation r_1 of the ln(total recruit) series as shown in Figure 5.11. Values of $r_1 > 0.5$ are produced when the input autocorrelation coefficient for local recruitment is 0.62 or greater and when external recruitment is 0.60 or greater. As the input autocorrelation coefficient for local recruitment decreases so the minimum values required to autocorrelate external recruitment increase.

In conclusion, only three models produced high (0.5+) output autocorrelation in the ln(total recruit) time series. These were two models using Method 1: local recruitment autocorrelated and both local and external recruitment autocorrelated and one model from Method 2: both local and external recruitment autocorrelated. As autocorrelating external recruitment in the latter model of Method 1 had little affect on the total autocorrelation, this model was, in effect, similar to the local recruitment only autocorrelated model.

To induce the high autocorrelation (0.51) seen in the complete historical ln(recruit) time series required extremely high input coefficients of autocorrelation. The historical series contained only 24 data points, less then half the recommended minimum number (50) by Farnum & Stanton (1989) for Box-Jenkins forecasting models, therefore confidence in the calculated value is reduced. The autocorrelation coefficient is strongly influenced by the series of four low recruit years which were excluded for the external recruitment models developed above. It was therefore decided that 0.5 was an unreasonably high target value (as extremely high input values were required) and a reduced value of 0.4 was selected as the target value.

Of the two suitable models identified, Method 1 (local recruitment autocorrelated) produced output r_1 of 0.4 or greater when the input autocorrelation coefficient was 0.64 or greater. Method 2 (both local and external recruitment autocorrelated) produced an output r_1 of 0.4 when the input autocorrelation coefficient α for local recruitment was 0.42 or greater and for external recruitment ϕ_1 was 0.40 or greater. Considering the extreme values along the 0.4 (output r_1) boundary in Figure 5.12, when α=0.42, ϕ_1=0.82 and when α=0.80, ϕ_1=0.40. A data point from the middle of the boundary line was selected (α=0.54, ϕ_1=0.6) for the population model.

1000 simulations of 24 years were carried out for each of the two recruitment models selected with the input autocorrelation coefficients identified. The results are shown in Table 5.3. Incorporating autocorrelation had little affect on the recruitment parameters produced by each model when compared to the non-autocorrelated models except for the output autocorrelation coefficients, r_1.

For comparison with the stochastic population models shown earlier (Figures 5.7 and 5.8), a simulation of 50 years was carried out for both models and the results are shown in Figures 5.13 and 5.14. Method1 can produce series of very low recruitment years even when SSB is high (see years 11-14 Figure 5.12b), as seen in the Shetland stock in the late 1980s. Also, a high recruitment can be produced when SSB is low (see year 29, Figure 5.12b). High recruitment years tend to be years when external recruitment is large. For method 2 (external recruitment independent of SSB), large external recruitments can be generated even when local recruitment is low (Figure 5.13a).

As external recruitment to Shetland is unquantified, producing models to simulate external recruitment is a very challenging problem and there are many limitations and sources of bias in the models produced in this chapter. The models used differences between stock-recruit models fitted to the Shetland stock and to the North Sea stock to determine external recruitment. This assumes the reproductive parameters are similar in different areas of the North Sea, which may not be the case. Sandeels at Shetland are considered slower growing than sandeels elsewhere in the North Sea (ICES, 1999). Further, assessments assumed that 100% of fish aged 2 and above spawn (ICES, 1999) although evidence suggests some fish may mature earlier or later (Macer, 1966; Gauld & Hutcheon, 1990) – these may alter proposed stock-recruit relationships (see Chapter 2). It was assumed that net external recruitment occurred in the majority of years but strong evidence for external recruitment only exists for one of the historical data years (1991; Wright, 1996). It was assumed that the four low recruit years which occurred around Shetland 1987-1990 were biologically different so these were removed from the historical data set. This is not recommended practice but it was not possible to parameterise models for external recruitment if these four years were included.

5.9 Summary

- Evidence (see Wright, 1996) indicates external recruitment may dominate recruitment in some years. It was determined to produce a model including net external recruitment for the Shetland sandeel population.
- In order to make progress, it had to be assumed the reproductive parameters for sandeels at Shetland were similar to those in the North Sea. This allowed a stock-recruit model, parameterised using the North Sea sandeel data set, to be scaled to represent local recruitment at Shetland.
- Comparison of the scaled North Sea Ricker model with the model fitted to the Shetland data set revealed the stock-recruit relationships are surprisingly similar, so estimates of external recruitment could not be determined in the way originally proposed.
- The stock-recruit model fitted to the reduced Shetland data set (minus four low recruitment years) always returned higher estimates for recruitment so, even though there is no biological reasoning to remove data points, this curve was selected in order to develop an external recruitment models.
- Using the Ricker models fitted to the North Sea sandeel data and reduced Shetland data, two methods were developed to simulate local and external recruitment.
- Functions for autocorrelation were included in both the local and in the external recruitment models and simulations carried out for analysis.
- Comparison of model output with the historical Shetland recruit time series identified Model 1 (additive variances) and autocorrelated local recruitment, as the best fit model.

Table 5.1 Parameters of the Ricker (1954, 1975) stock-recruit model estimated by bootstrap analysis for the Shetland sandeel stock and the North Sea sandeel stock. *a*, *b* = mean estimates for parameters of the Ricker curve, σ_b = standard error of parameter *b*, 75% c.i. = 75% confidence intervals for estimates returned by bootstrap analysis, correlation *b* = estimates of parameter *b* returned from parameter *a* using the correlation function between *a* and *b*, a'' = adjusted *a* (see text), Mean R = mean recruitment (billions), Mean SSB = mean SSB (000 tonnes)

Parameter	North Sea sandeels	Shetland sandeels
$b \pm \sigma_b$	0.0007890 ± 0.0004802	0.012763 ± 0.003338
b lower 75% c. i.	0.000499	0.010557
b upper 75% c. i.	0.001140	0.014573
correlation b	0.000789	0.012762
correlation *b* lower 75% c. i.	0.000504	0.010958
correlation *b* upper 75% c. i.	0.001100	0.014586
$a \pm \sigma_a$	1.3664 ± 0.5304	2.4206 ± 1.1646
a lower 75% c. i.	0.977	1.654
a upper 75% c. i.	1.671	2.911
$ln(a) \pm \sigma_{ln(a)}$	0.2334 ± 0.4090	0.7845 ± 0.4458
a''	1.263	2.191
σ_w	0.587	1.010
σ_w lower 75% c. i.	0.533	0.896
σ_w upper 75% c. i.	0.640	1.118
Mean *R*	620	59
Mean SSB	856	127

Table 5.2 Combinations of local and external recruitment models incorporating autocorrelation. Numbers (1 & 2) refer to Method of modelling recruitment (see text).

		Local Recruitment			
		Stochastic		**Autocorrelated**	
External Recruitment	**Stochastic**	1	2	1	2
	Autocorrelated External Error	1		1	
	Autocorrelated External R	2		2	

Table 5.3. Results of 1000 simulations of 24 years of stochastic population models of sandeels at Shetland (Historical = values from historical data set ICES 1999). Local and external recruitment modelled by two methods (Method 1 and 2 see text), Local AC = local recruitment autocorrelated, Ext AC = external recruitment autocorrelated. R= recruitment, SD = standard deviation, r_1 = output autocorrelation coefficient, μ_T and σ_T = mean and standard deviation of lognormal errors from total recruitment about the Ricker curve. μ_L and σ_L = mean and standard deviation of lognormal errors from local recruitment about the Ricker curve. SSB = spawning stock biomass.

	Historical	Method 1	Method 2	Method 1 Local AC	Method 2 Local AC, Ext AC
Mean ln(Recruitment)	4.25	4.32	4.41	4.30	4.40
SD ln(Recruitment)	0.69	0.68	0.58	0.60	0.54
Median Recruitment (billions)	70	75	82	74	81
r_1 Recruitment	*0.51*	0.01	-0.01	0.40	0.39
μ_T	0.429	0.433	0.518	0.434	0.531
σ_T	0.668	0.654	0.566	0.594	0.545
Mean ln(Local R)		3.89	3.90	3.87	3.87
SD ln(Local R)		0.64	0.64	0.56	0.60
Median Local R (billions)		49	49	48	48
r_1 Local R		0.00	0.00	0.46	0.41
μ_L	0.000	0.002	0.005	0.004	0.000
σ_L	0.625	0.621	0.621	0.557	0.584
Mean ln(External R)		3.10	3.10	3.08	3.11
SD ln(External R)		1.03	1.01	0.98	0.93
Median External R (billions)		22	22	22	22
r_1 External R		-0.015	-0.056	0.138	0.443
Mean SSB (000 tonnes)	126	150	154	144	152
SD SSB	63	45	42	50	50

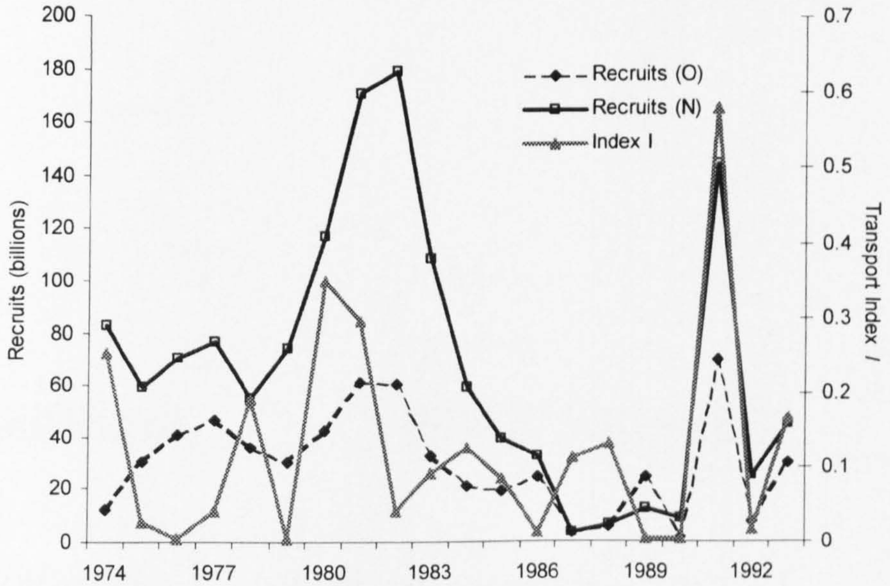


Figure 5.1 Sandeels at Shetland 1974-1993. Recruit time series (Recruits O) and index *I* for passive transport of particles into Shetland, from Proctor *et al* (1998). Recruit time series (Recruits N) from ICES 1999. Assessment methods have changed recently for Shetland sandeels and the recruit time series (Recruits N) is from recent assessments.

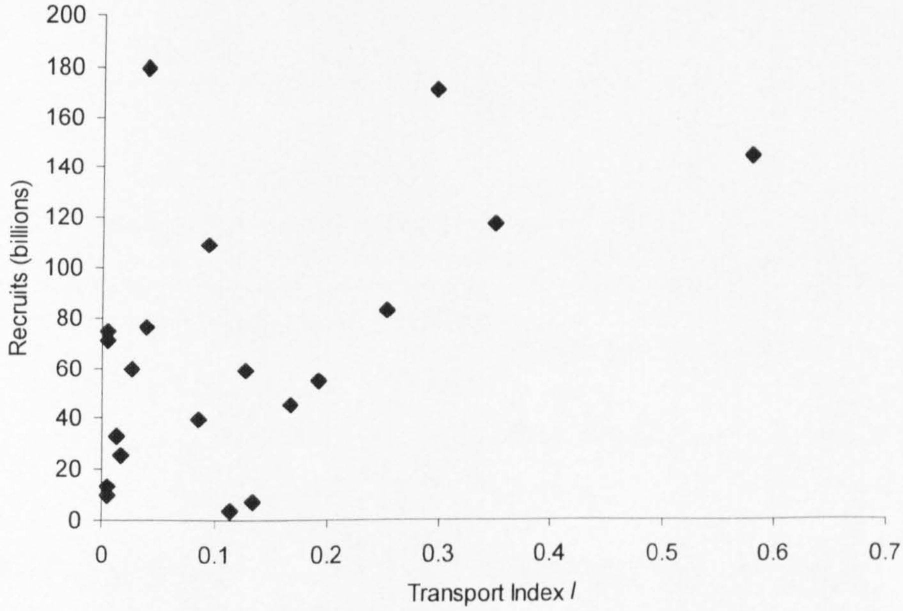


Figure 5.2 Sandeels at Shetland 1974-1993. Transport index *I* indicating the strength of passive particle transport from Orkney to Shetland (from Proctor *et al* 1998) against total recruitment (from ICES 1999).

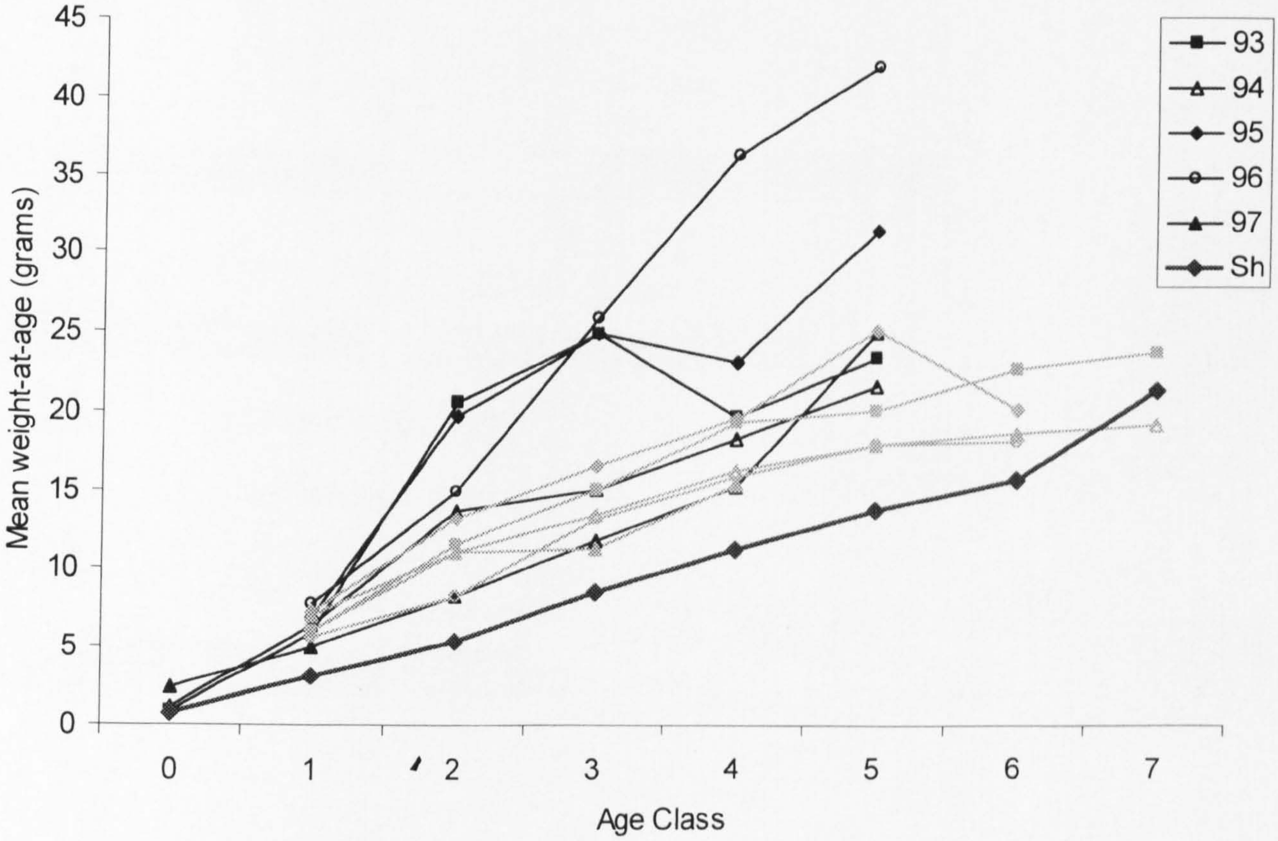


Figure 5.3 Mean weight-at-age (grams) of sandeels from 1st half year catches in the northern North Sea (dark lines) and southern North Sea (light lines) in 1993-1997 inclusive (ICES 1999) and for long-term mean weight-at-age from 1st half year catches of sandeels at Shetland (Sh; ICES, 1999).

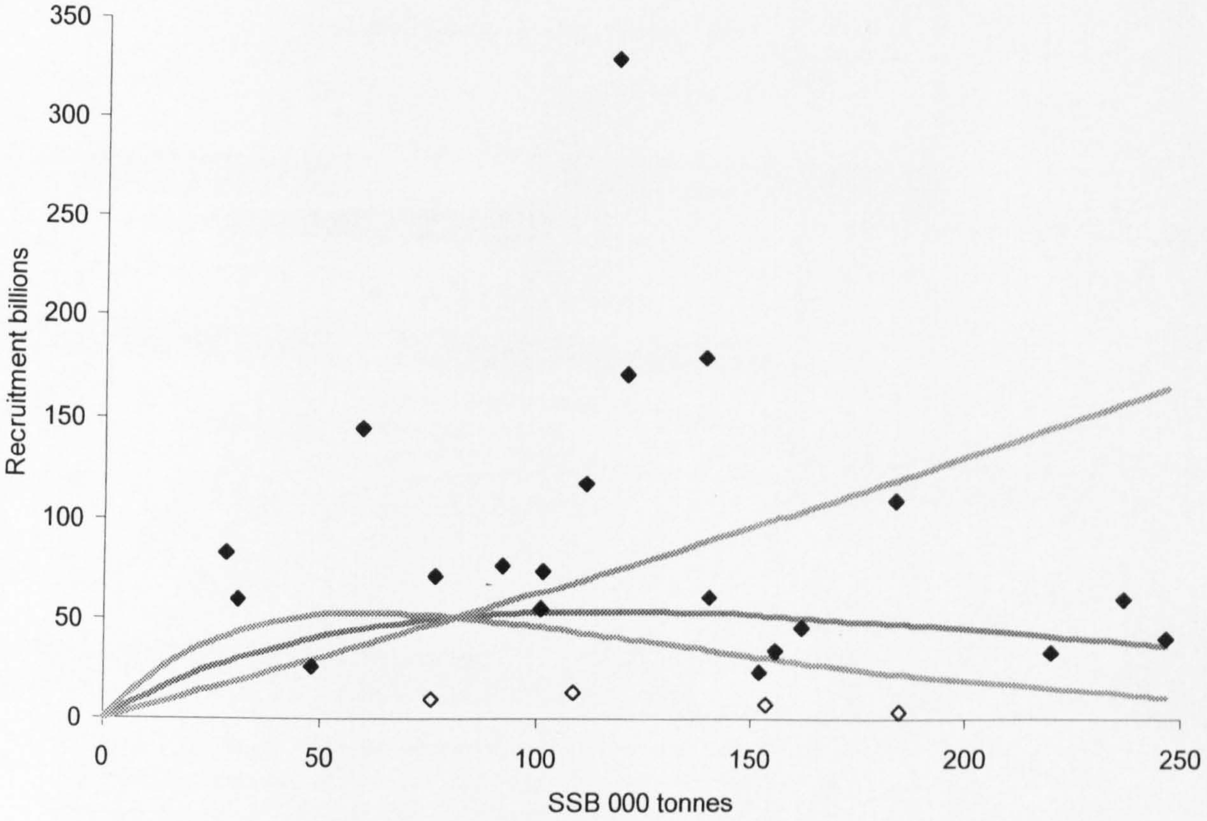


Figure 5.4 Mean Ricker stock-recruit curve with 95% confidence intervals estimated by bootstrap analysis for North Sea sandeels scaled and applied to Shetland stock-recruit data (diamonds). Four low recruit years indicated by white diamonds.

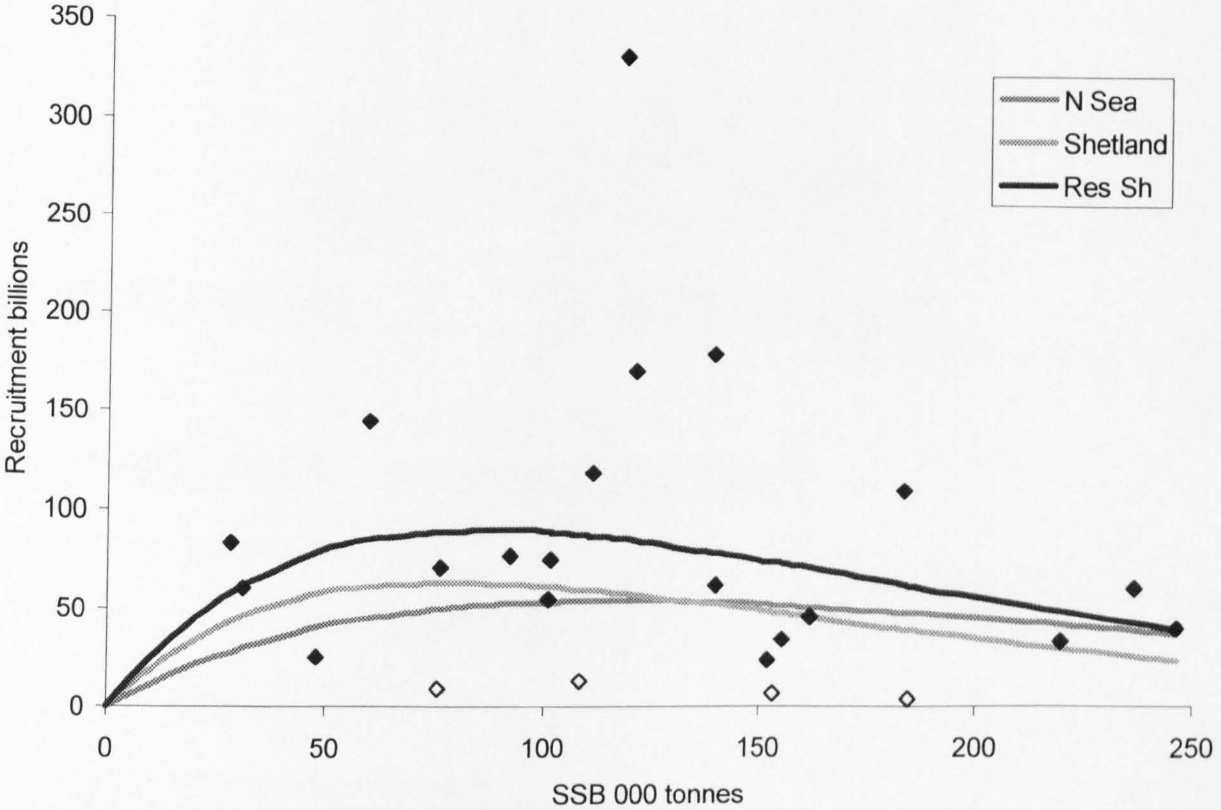


Figure 5.5 Mean Ricker stock-recruit curve estimated by bootstrap analysis for North Sea sandeels (N Sea) scaled and applied to Shetland stock-recruit data. Ricker curve estimated by bootstrap analysis for Shetland sandeels using the complete historical data set (Shetland) and using a reduced (minus four low years shown as white diamonds) data set (Res Shet).

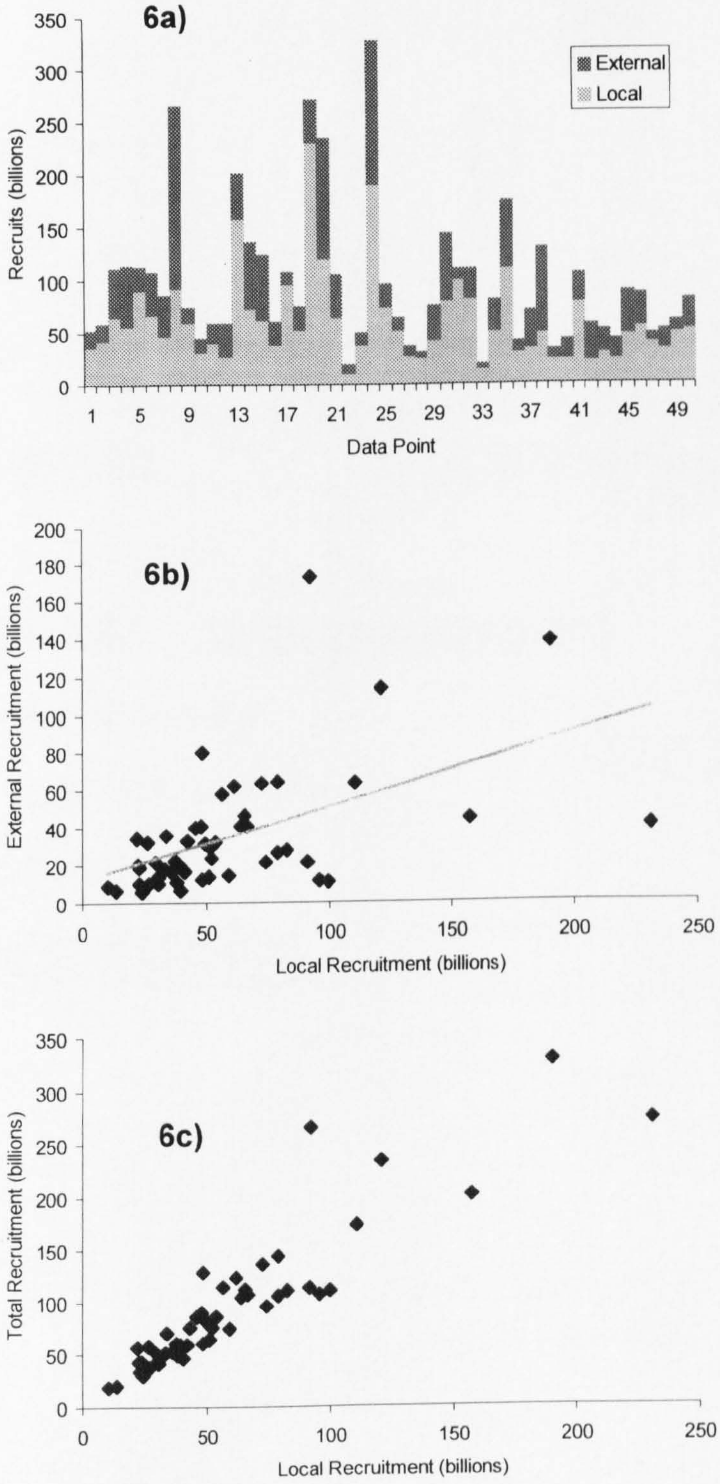


Figure 5.6. Results from recruitment model (Method 1) incorporating local and external recruitment with stochasticity. **a)** Local and external recruitment predicted for 50 SSBs selected at random from the reduced Shetland data set. **b)** External recruitment against local recruitment with trendline. **c)** Total recruitment against local recruitment with trendline.

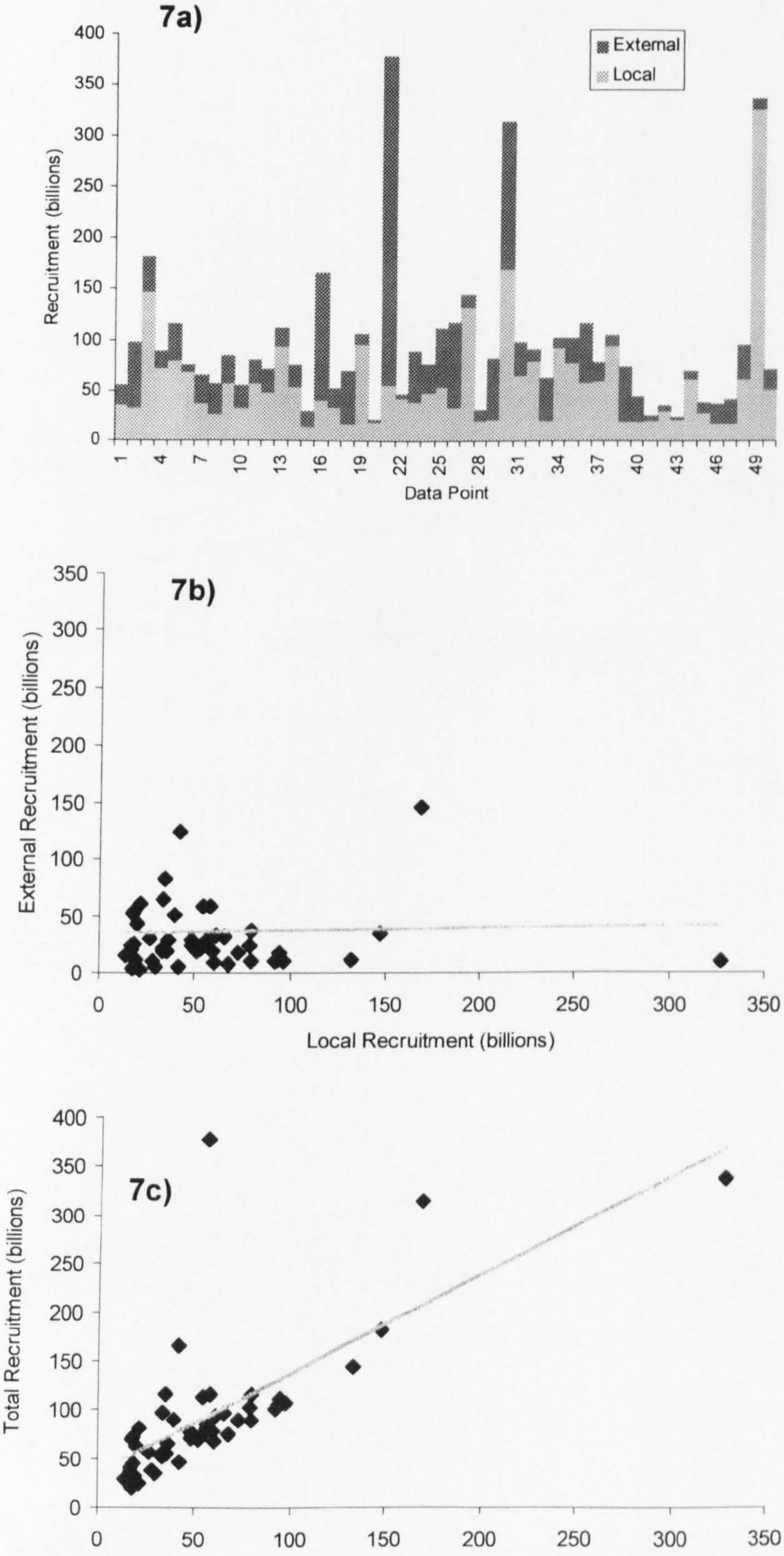


Figure 5.7. Results from recruitment model (Method 2) incorporating local and external recruitment with stochasticity. **a)** Local and external recruitment predicted for 50 SSBs selected at random from the reduced Shetland data set. **b)** External recruitment against local recruitment with trendline. **c)** Total recruitment against local recruitment with trendline.

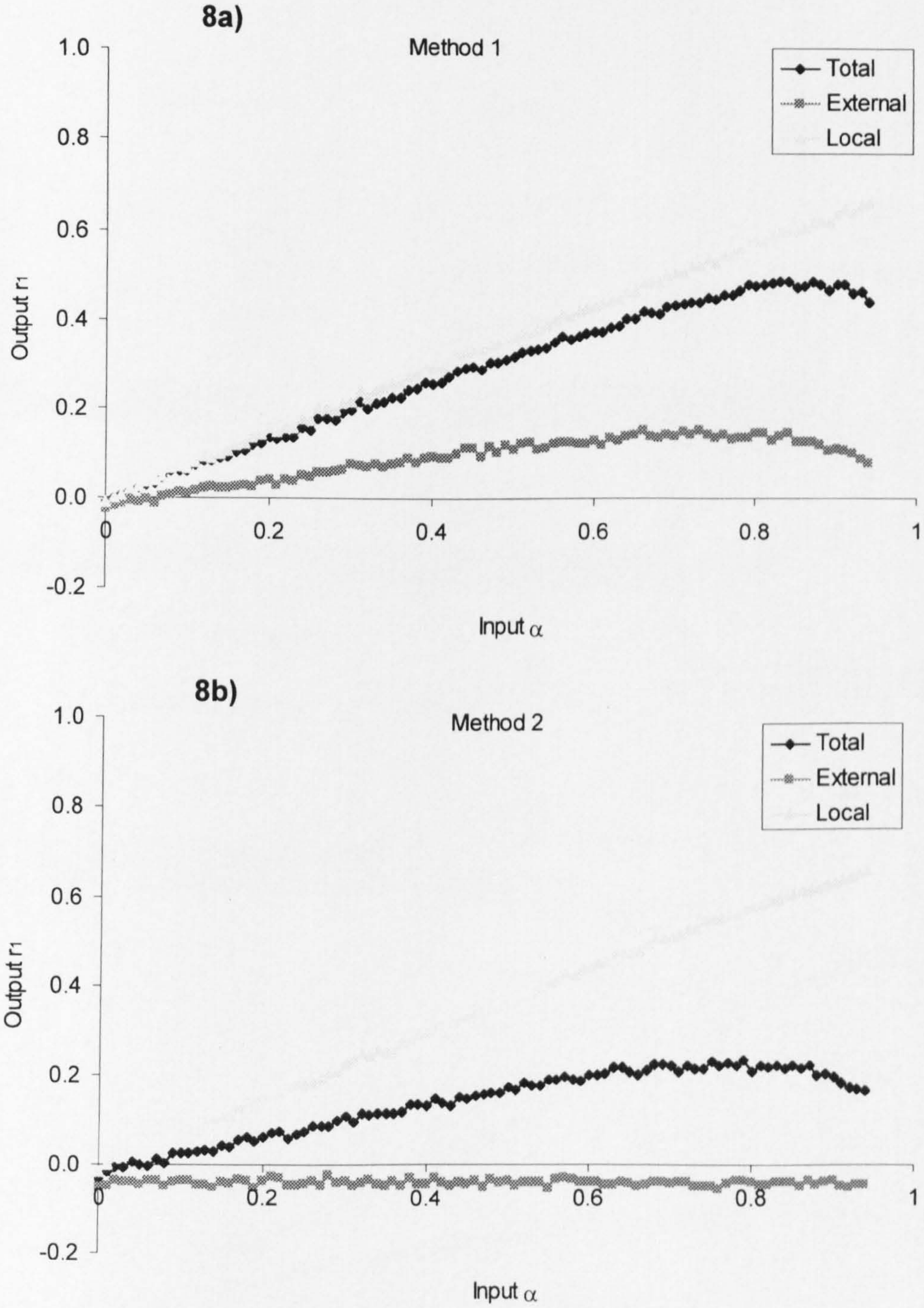


Figure 5.8 Results of stochastic population models for sandeels at Shetland with autocorrelated local recruitment. External recruitment simulated by **a)** Method 1 and **b)** Method 2 (see text). Output autocorrelation, r_1, for ln(total recruit), ln(external recruit) and ln(local recruit) time series against input autocorrelation coefficient, α, for local recruitment model.

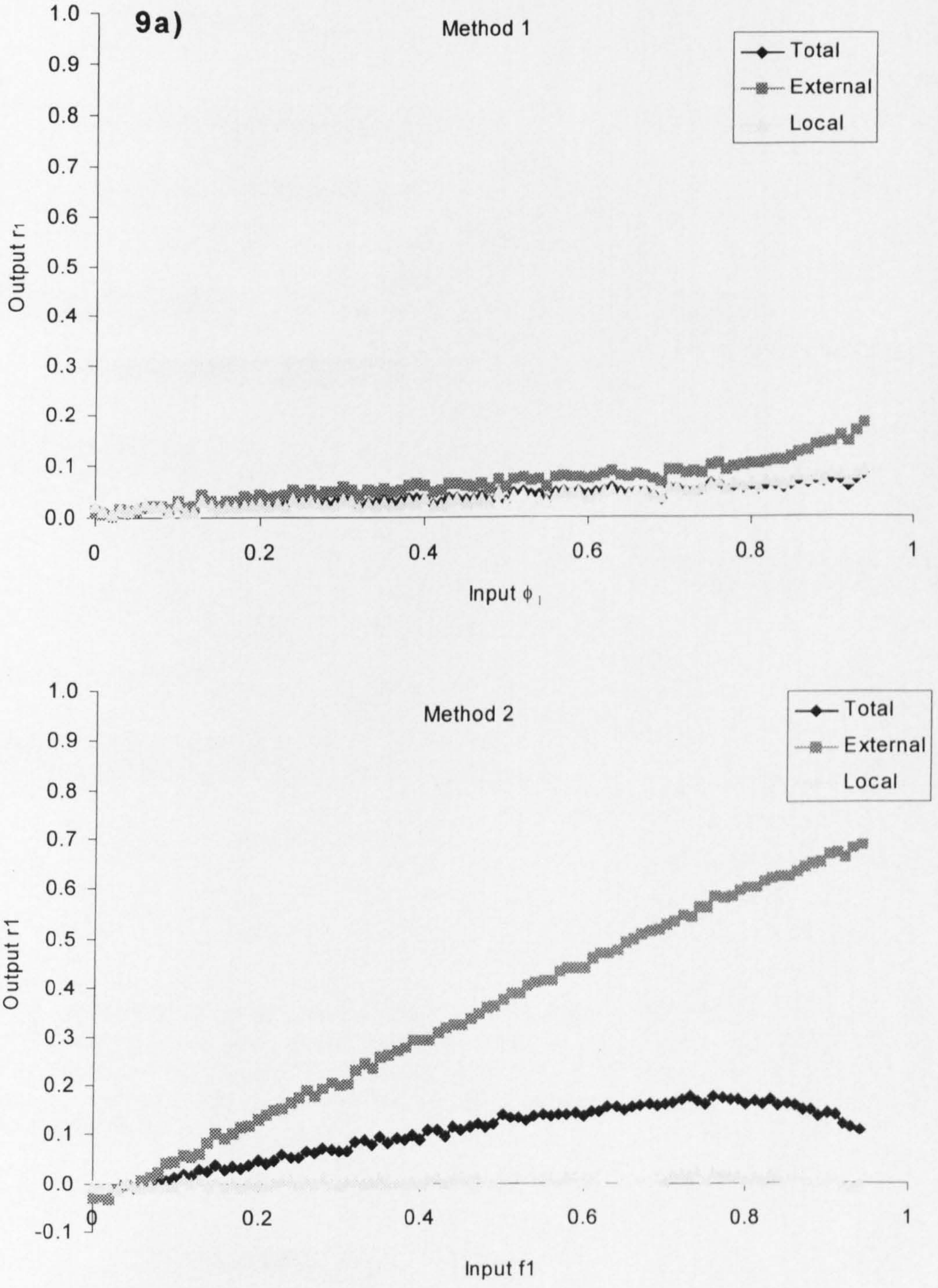


Figure 5.9 Results of stochastic population models for sandeels at Shetland with autocorrelated external recruitment. External recruitment simulated by **a)** Method 1 and **b)** Method 2 (see test). Output autocorrelation, r_1, for ln(total recruit), ln(external recruit) and ln(local recruit) time series against input autocorrelation coefficient, ϕ_l, for external recruitment model.

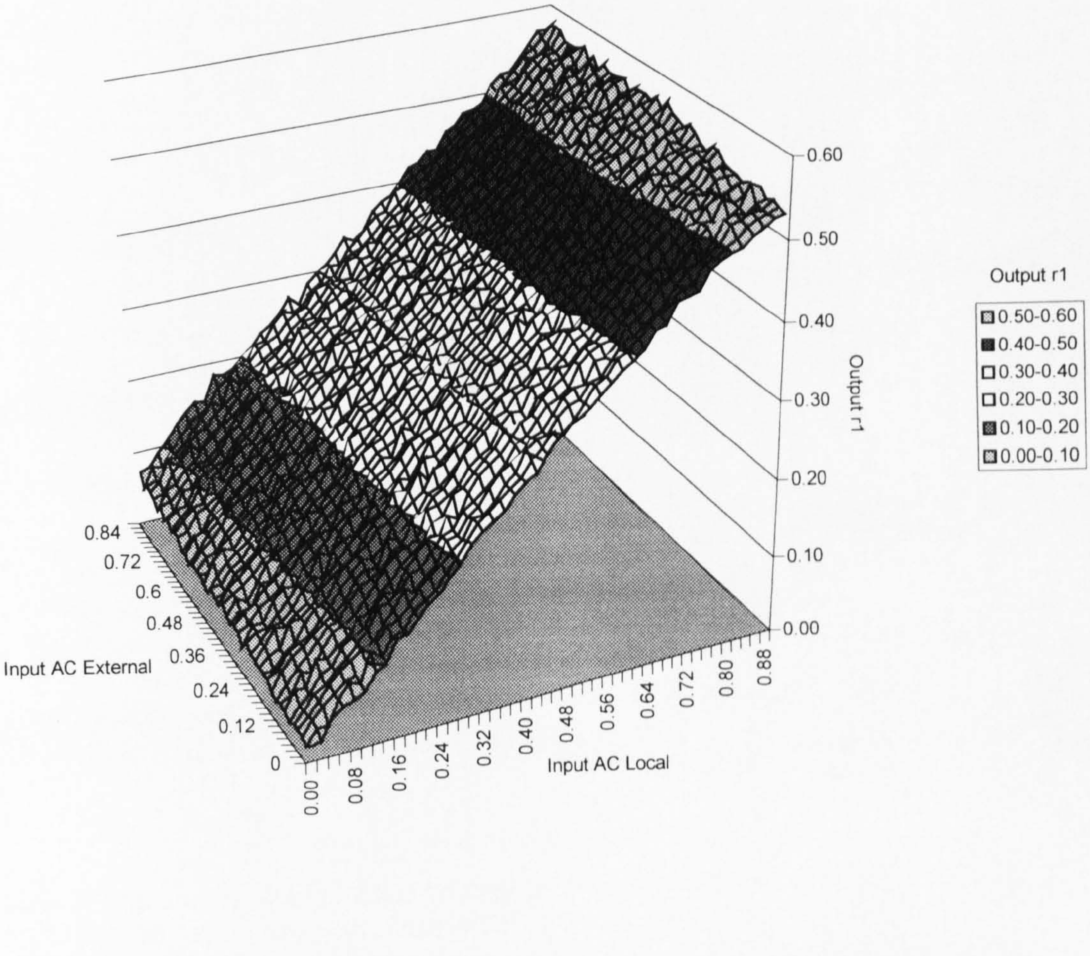


Figure 5.10 Results of stochastic population models for sandeels at Shetland with autocorrelated local and autocorrelated external recruitment using recruitment model Method 1 (see text). Output autocorrelation, r_1, for ln(total recruit), time series against input autocorrelation coefficient, AC, for external recruitment function and local recruitment function.

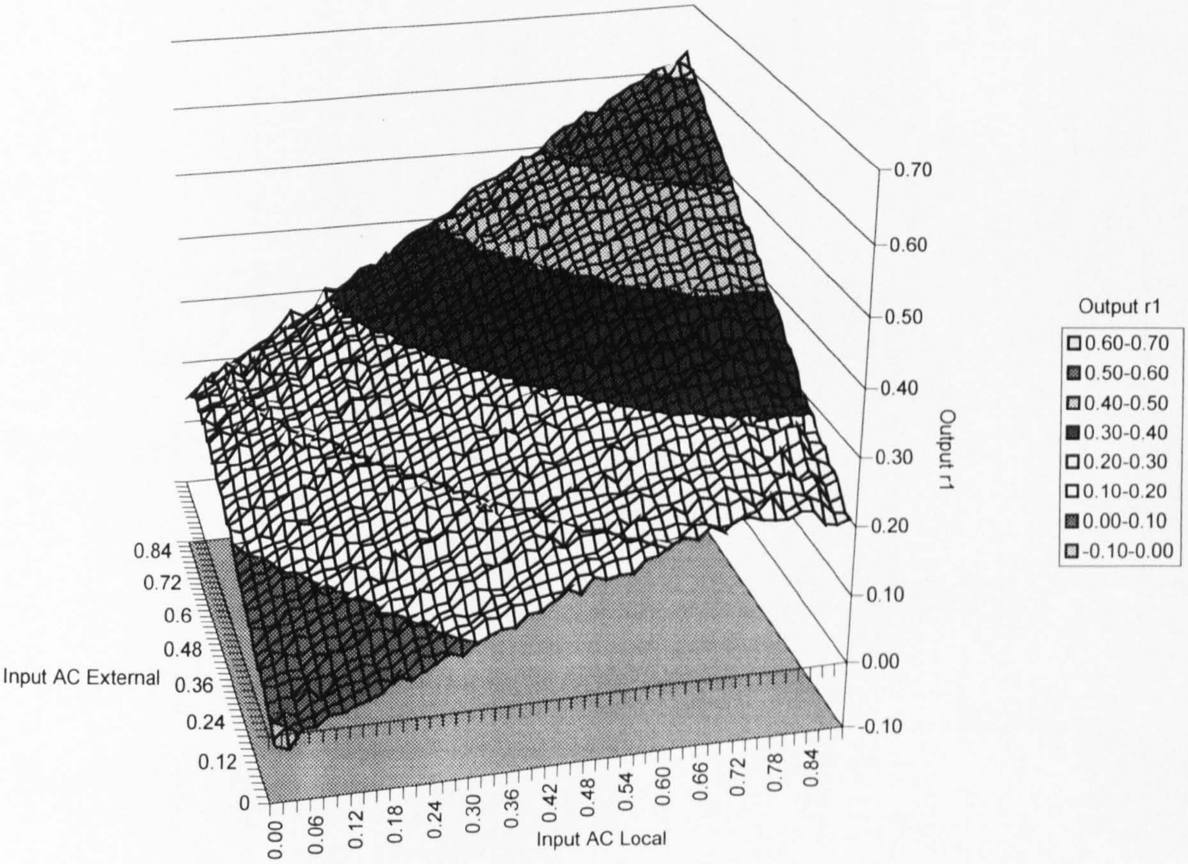


Figure 5.11 Results of stochastic population models for sandeels at Shetland with autocorrelated local and autocorrelated external recruitment using recruitment model Method 2 (see text). Output autocorrelation, r_1, for ln(total recruit), time series against input autocorrelation coefficient, AC, for external recruitment function and local recruitment function.

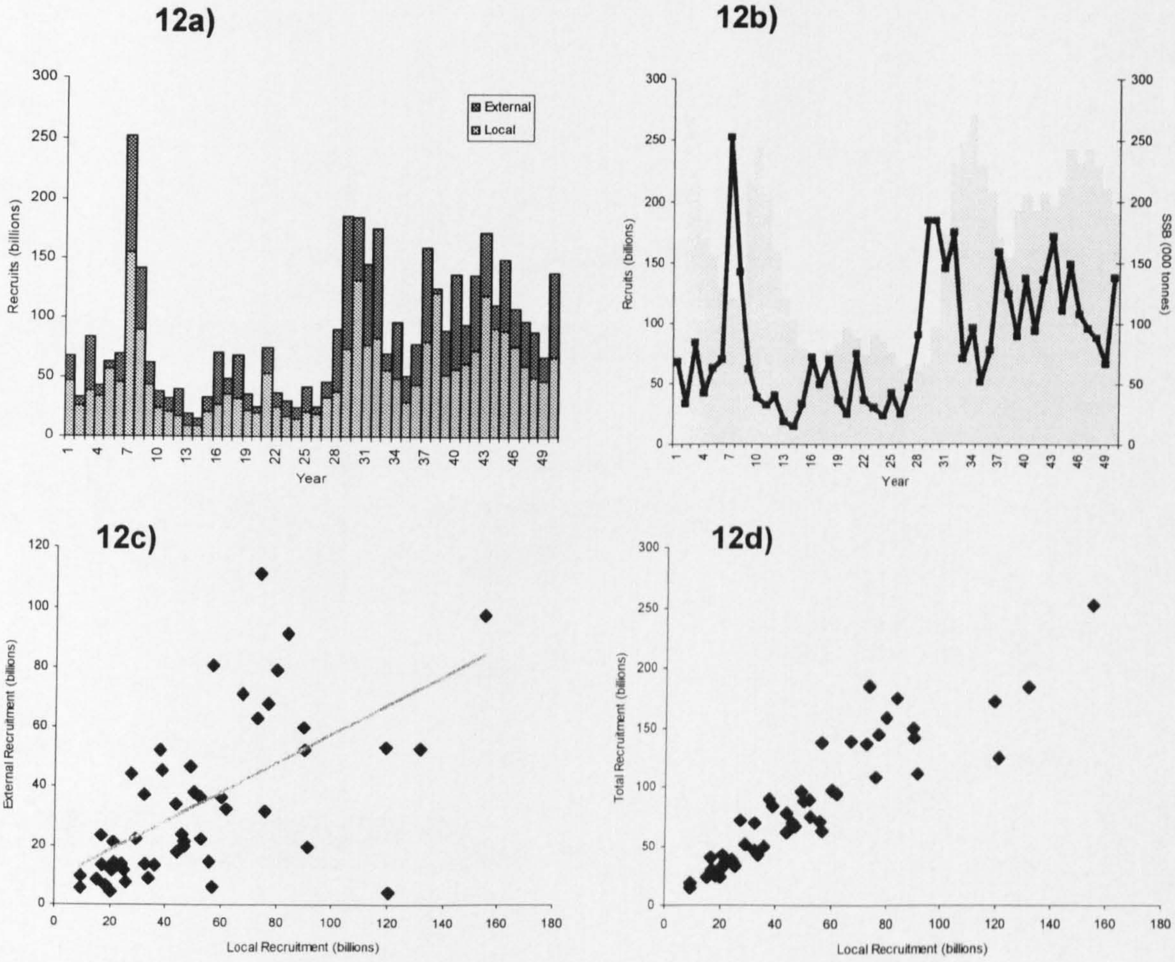


Figure 5.12 Results of stochastic population model for sandeels at Shetland with local and external recruitment simulated using Method 1 (see text). Local recruitment function is autocorrelated with an input autocorrelation coefficient of 0.64. **a)** Local and external recruitment produced in 50 year simulation **b)** Total recruitment and SSB produced by 50 year simulation. **c)** External recruitment against total recruitment, with trendline. **d)** Total recruitment against local recruitment.

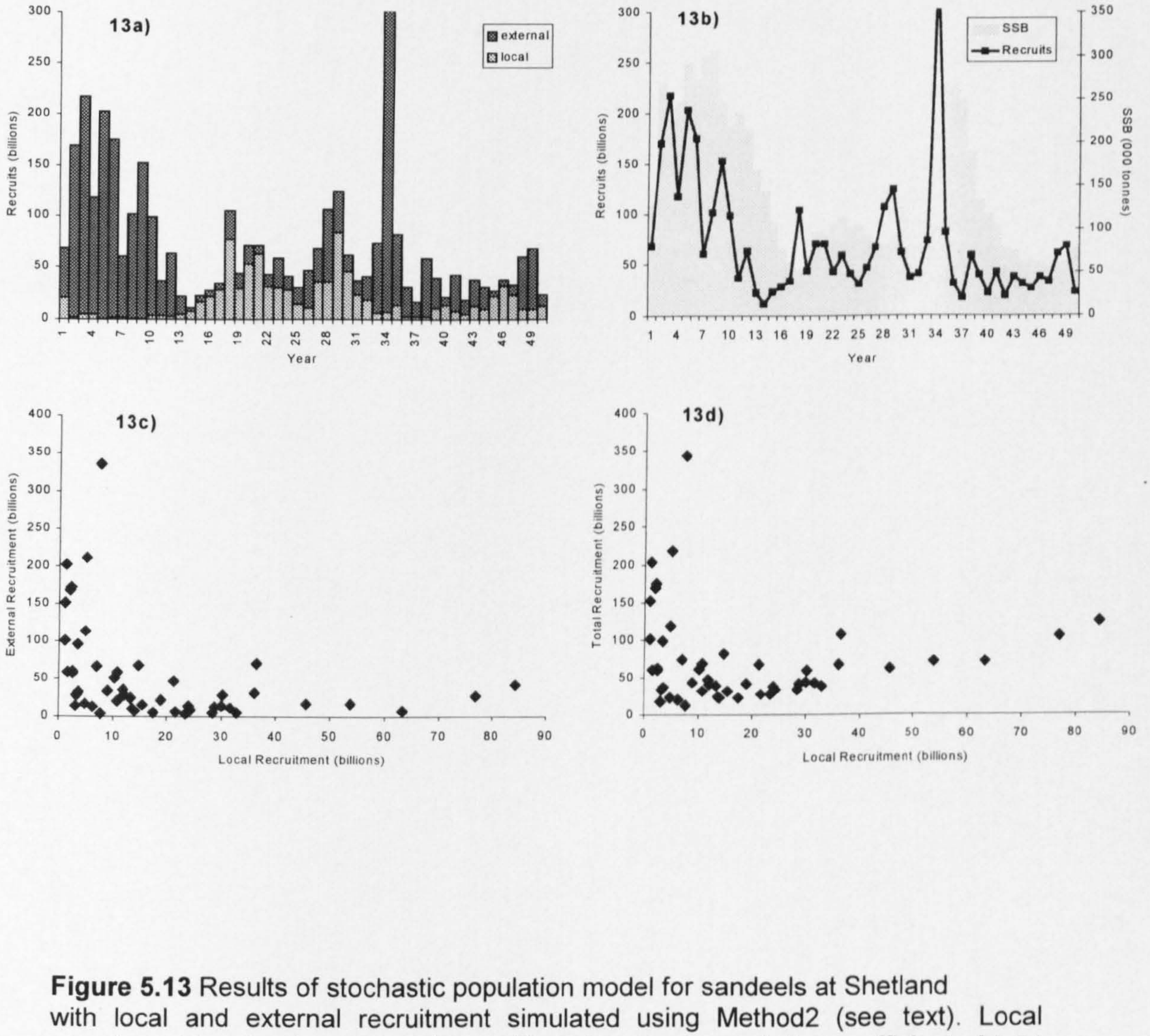


Figure 5.13 Results of stochastic population model for sandeels at Shetland with local and external recruitment simulated using Method2 (see text). Local recruitment function is autocorrelated with an input autocorrelation coefficient of 0.54 and external recruitment input autocorrelation coefficient is 0.6. **a)** Local and external recruitment produced in 50 year simulation **b)** Total recruitment and SSB produced by 50 year simulation. **c)** External recruitment against total recruitment, with trendline. **d)** Total recruitment against local recruitment.

CHAPTER 6

SEABIRD FUNCTIONS AND FISHERY MANAGEMENT

6.1 Introduction

Shetland is considered internationally important as a breeding site for a diverse range of seabird species. According to the RSPB, a million seabirds are thought to nest annually around Shetland. Twenty-one species of seabird breed regularly at Shetland (Dunnet & Heubeck, 1995). As well as more common species such as kittiwakes *Rissa tridactyla*, fulmars *Fulmarus glacialis* and puffins *Fratercula arctica*, species which are rare breeders elsewhere in the UK, such as the great skua *Catharacta skua* and Arctic skua *Stercorarius parasiticus*, nest in high numbers around the Shetland coast. Furness (1990) supplied a table of seabird populations censused in Shetland during 1980-87 and expressed these as percentages of the North Sea breeding total and British plus Irish breeding total. 60% and 77% of the North Sea coast total (67% and 76% British and Irish total), for Arctic skuas and great skuas respectively, nest at Shetland. Even for species more commonly observed around British coasts, such as fulmars and puffins, a high percentage breed at Shetland (68% and 48% of North Sea coast totals and 40% and 18% of British and Irish totals respectively). These percentages can represent high numbers of birds, for example 208,314 fulmars and 125,000 puffins were censused at Shetland over 1980-1987.

At Shetland, many of these birds rely on young sandeels as prey during the breeding season (Furness & Todd, 1984; Blake *et al.*, 1985; Fowler & Dye, 1987; Martin, 1989a; Monaghan *et al.*, 1989; Harris & Wanless, 1990; Phillips *et al.*, 1996; Wright & Tasker, 1996; Furness, 1999). There is thought to be a lack of alternative small fish, which are suitable as a food source, around Shetland (Kunzlik, 1989). During the late 1980s, when sandeel recruitment at Shetland decreased to extremely low levels, the breeding success at many seabird colonies around Shetland also declined (Monaghan, 1992; Dunnet & Heubeck, 1995). In particular, very low breeding success or almost complete breeding failure over these years was observed at Arctic tern (Monaghan *et al.*, 1989; Monaghan *et al.*, 1992) and kittiwake colonies (Harris & Wanless, 1990; Harris & Wanless, 1997) around Shetland. The lack of fledglings from these colonies in the late 1980s was linked to food shortage. Colonies in southern and eastern Shetland were the most strongly affected (Harris & Wanless, 1990; Monaghan, 1992).

It was with regard to the sandeel fishery at Shetland that concerns were first raised about potential impact of sandeel fisheries on the marine ecosystem (Reeves, 1999). It was suggested that the sandeel fishery may have caused local depletion of stocks in the vicinity of seabird colonies (Monaghan, 1992). Further processes by which industrial fisheries could affect foraging seabirds include reducing mean recruitment to the fish stock, increasing variability in recruitment to the fish stock or altering trophic structure in the ecosystem (Tasker & Becker, 1992; Hunt *et al.*, 1996; Furness, 1996; Bax, 1998; Furness, 1999). In 1992, the Sea Fisheries (Wildlife Conservation) Act was introduced which requires wildlife considerations to be taken into account when discharging functions under the Sea Fisheries Act. Management of the Shetland fishery now considers potential effects of the fishery on the availability of sandeels to seabirds. At present, the sandeel fishery at Shetland operates with a closed season during June and July, the peak seabird breeding season, to avoid competition (Reeves, 1999).

Although sandeels are important for other marine predators, such as fish, pinnipeds and cetaceans (Harwood & Croxall, 1988; Bax, 1991; Doyle & Greenstreet, 1999; McConnell *et al.*, 1999), only seabirds will be considered here for various reasons. Firstly, seabird breeding at Shetland is well studied and many of these studies are published. Also, for certain species of seabird there appears to be a relationship between estimates of sandeel abundance and breeding success (Monaghan *et al.*, 1989; Harris & Wanless, 1990; Phillips *et al.*, 1996). It has been suggested that seabird data could provide additional information on fish stock size and/or movements and, in some cases, could even act as indicators of fish abundance (Springer *et al.*, 1986; Cairns, 1987; Montevecchi *et al.*, 1988; Bailey *et al.*, 1991; Cairns, 1992; Montevecchi & Myers, 1996; Litzow *et al.*, 2000). Finally, ecological responses of certain species of seabird could act as an indicator of ecosystem health at Shetland. Sandeels are planktivores which can occur in vast numbers (there was estimated to be 360 billion sandeels around Shetland in 1997; ICES, 1999) so form an important trophic link in the Shetland ecosystem. If seabird species that are considered vulnerable to variation in sandeel biomass are doing well, then it might be reasonable to assume the sandeel stock and the ecosystem are healthy.

6.2 Vulnerability Index

As some, but not all, of the seabird species that breed around Shetland suffered complete breeding failure in the late 1980s when 0-group sandeel abundance was low, it is obvious that certain species could be considered much more sensitive to sandeel abundance then others. Although a diverse range of seabird species breed around Shetland, including all of them in the model is impractical. Instead, species considered particularly vulnerable to sandeel availability, were identified and used as indicator species. If potential breeding success for these species is considered high then it can be assumed that potential breeding success of other seabird species is also good.

What characteristics do seabirds possess that makes them vulnerable to changes in sandeel abundance? The ability of a seabird to obtain food depends on a number of parameters such as the size of the bird, ability to dive and the foraging range (Martin, 1989; Furness & Tasker, 2000). Martin (1989) produced a table of the foraging characteristics of seabirds breeding around Shetland. Part of this table is reproduced in Table 6.1. Martin categorized three foraging characteristics for each seabird: Depth; Range; Body Mass (the categorizations are given with Table 6.1).

The ability of a bird to dive and pursue prey underwater will affect prey availability. During the day, sandeels sporadically migrate vertically through the water column. So a seabird that can only take fish from the sea surface, such as kittiwakes or terns, will have restricted prey availability compared to a bird that can dive deep after fish, such as guillemots. Similarly for foraging ranges, seabirds which forage over a large area, such as fulmars, have more sea in which to find prey then birds which forage near their breeding sites, such as the shag (Martin, 1989; Wanless *et al.*, 1990). Finally, the body mass of a seabird is thought to affect the energy budget - small birds are less able to increase foraging time if prey availability reduces (Pearson, 1968). The species with the poorest breeding season in 1988 (Arctic terns, kittiwakes, Arctic skuas, black guillemots and puffins) were also the smallest in terms of body mass (Martin, 1989).

The foraging characteristics tabulated by Martin were used to develop a "vulnerably index" for these species. This index is a measure of how vulnerable a species is considered to be to sandeel abundance. Each characteristic was ranked and assigned cumulative numbers, with equal steps, which terminated in 1 (Table 6.2). For example for Depth; the numbers assigned were surface=0.25, shallow=0.5, medium=0.75 and deep=1. The closer to 1 the assigned number, the less vulnerable the characteristic is considered to prey abundance. The vulnerability index was determined as 100 x the product of the characteristic values each species given in Table 6.1:

$$\text{Vulnerability Index} = 100 \times \text{Depth value} \times \text{Range value} \times \text{Body Mass value}$$

The results are shown in Table 6.1, birds with the lowest vulnerability indices are considered the most vulnerable to changes in prey abundance. Based on the foraging characteristics given by Martin (1989), terns were identified as the most vulnerable with an index of 1.7, followed by kittiwakes with an index of 3.3. Gannets, with an index of 50, were the least vulnerable. How do these results compare with observations of breeding success in years of low 0-group abundance? Arctic terns appeared to be the most hard hit of the seabirds during the late 1980s judging by breeding success. Very few or no young were fledged during this period (Monaghan, 1992; Monaghan *et al.*, 1992). Similarly kittiwakes, which also have a low vulnerability index (3.3), showed low breeding success during the late 1980s when sandeel abundance was low (Heubeck, 1989; Harris & Wanless, 1990).

Shags, which were ranked 6/10 for vulnerability indices (vulnerability index = 14.9, Table 6.1), generally showed good breeding success during the late 1980s (Okill, 1989) although they appeared to retain a diet exclusively of sandeels (Martin, 1989). Survey data published by Dunnet & Heubeck (1995) show shags nesting at Sumburgh Head (see Figure 6.1) maintained a breeding success of 1.10 – 1.58 young fledged per nest over 1988 to 1993 inclusive, with the exception of 1990 when breeding success dropped to 0.63. Gannets, which have a high vulnerability index of 50, also maintained relatively good breeding success in the late 1980s (Okill, 1989). Dietary studies indicated gannets switched to feeding on herring during the years of low sandeel abundance (Martin, 1989). These birds show two different responses to low prey availability – prey switching and/or increased foraging effort.

Concurrently, Furness & Tasker (2000) also constructed an vulnerability index for seabirds breeding in the North Sea, including Shetland. Furness & Tasker scored six foraging characteristics as opposed to the three that I used above. The extra three characteristics were "High cost of foraging", "Lack of spare time in energy budget" and "Low ability to switch diet". The cost of foraging refers to the energetic cost of flight, for example energetically expensive flapping flight compared to predominantly gliding flight. Spare time in the energy budget is a measure of the amount of time spent chick-rearing, that is the amount of "off-duty" time. Ability to switch diet distinguishes between specialized feeders on a single prey type through to birds taking a wide range of prey.

In contrast to the method developed above, the scoring range was between 0 to 4 in steps of 1 (so each characteristic had five scores) with 0 between awarded to the least vulnerable characteristic. The ten species shown in Table 6.1 were ranked according to the vulnerability index assigned by Furness & Tasker. The vulnerability ranking is similar to the ranking assigned above for the first five species in the list and for gannets (the least vulnerable). There is disagreement between the two methods for four of the species (fulmars, shags, razorbills and guillemots). This is mainly due to the extra categories included by Furness & Tasker (cost of foraging, lack of spare time in energy budget and ability to switch diet) and due to differences in defining categories. Furness & Tasker defined five classes in each category compared to four classes in the Depth category and three in the Range category in the method developed above.

Furness & Tasker then used the vulnerability indices to calculate sensitivity indices to sandeel abundance for seabirds in four areas of the North Sea – Shetland, Orkney, Thurso to Peterhead; Peterhead to Farnes; southern and south-eastern North Sea and north-eastern North Sea. While Furness & Tasker's vulnerability index quantifies the vulnerability of seabirds to prey abundance, the sensitivity index quantifies the vulnerability to sandeel abundance, which will depend on the abundance of alternative prey. The sensitivity index was calculated as the vulnerability index multiplied by the proportion of sandeels in the diet of breeding seabirds, thus producing regional sensitivities to sandeel abundance.

The results for the ten species considered above, in the area including Shetland, produced by Furness & Tasker were ranked according to assigned sensitivity indices (Table 6.1). This decreases the similarity in the results between the method developed above. However, all three methods are consistent in identifying Arctic terns and kittiwakes as the most vulnerable, or sensitive, species to changes in sandeel abundance at Shetland and gannets as the least vulnerable.

6.3 Seabird Functions

Breeding success of certain seabird species at Shetland may be linked to foraging success on sandeels. To provide an indication of potential seabird breeding success in the models an estimate of foraging success, such as biomass of sandeels removed, needs to be determined. The number of sandeels removed by predators is calculated as a function of the natural mortality rate in the models. The natural mortality rate used in sandeel assessments, is defined as mortality due to predation, disease and other natural causes, so includes predation by seabirds (ICES, 1999). The natural mortality rate is set by taking a "qualified guess" based on information such as analysis of stomach contents of predatory fish (Sparre, 1991). I do not have the knowledge of this procedure or the information to determine the proportion of the natural mortality rate attributable to a particular species of seabird. Therefore, alternative approaches were considered to model potential seabird breeding success.

Assuming breeding success of certain seabird species is linked to sandeel availability, "indicator" functions could be constructed to determine potential influence of sandeel abundance on seabird breeding success. These functions would not be used in the sandeel population model to remove sandeels due to predation by seabirds, as this is still incorporated in the natural mortality rate, but applied to the output biomass to identify years with potentially poor foraging success. In other words, for a given year the biomass of the sandeel stock is determined and the potential seabird breeding success is calculated as a function of this biomass. Years when the potential seabird breeding success drops below a threshold level are considered "poor" years.

Firstly, an appropriate parameter from seabird studies needs to be identified to reflect sandeel availability. Cairns (1987) proposed relationships between food supply and seabird population and behaviour parameters, namely adult survivorship, breeding success, chick growth and fledgling weight, colony attendance and activity budgets. All of these were assumed to show curvilinear relationships to food supply. The response to food supply occurs at different time scales and different levels of prey availability for each parameter. For example, adult survivorship is considered to integrate food availability over a year and is sensitive to fluctuations when food supply is extremely scarce. Chick growth is assumed to vary with food supply when this is poor to moderate. Chick growth rate reflects food supply over the chick rearing period therefore this has an integration period of one to two months.

I am concerned with potential adverse affects of the fishery on seabird breeding success, so want to identify years when food availability is considered to be poor to moderate. Cairns (1987) proposed breeding success and chick growth rates as useful indicators over a poor to moderate food availability range. Breeding success is considered to reflect food supply over the breeding season, which is usually two to several months long, whereas chick growth rate reflects food availability over the much shorter chick-rearing period. The sandeel fishery around Shetland operates from April or May to September, although since 1995 the fishery is closed during June and July (Reeves 1999). These months overlap most or all of the breeding periods of seabird species at Shetland (Furness 1990). For example, Furness (1990) estimates kittiwakes are present in Shetland (representing the breeding period) from the middle of February to the middle of August while Arctic terns arrive about the middle of May and depart at the start of August. In view of this, it was decided breeding success would be the most suitable indicator of food availability for the models. Additionally, there are published studies of breeding success at seabird colonies around Shetland.

The indicator functions will consist of breeding success against sandeel abundance but what form should this take? Cairns (1987) suggests a curvilinear (sigmoidal) relationship between food supply and breeding success, so breeding success increases rapidly at moderate food supply then levels off at high food supply. Monaghan *et al.* (1989) indicated a non-linear relationship between Arctic tern breeding success at Shetland over 1980-1986 inclusive and estimates of 0-group sandeel abundance in Shetland waters in 1st July. Phillips *et al.* (1996) fitted a logistic (sigmoidal) curve to the Arctic skua breeding success on Foula over 1986-1993 inclusive against estimates of 0- plus 1-group sandeel numbers in Shetland waters on 1st July. Hence, it was assumed the relationships would be non-linear and would probably be either sigmoidal or asymptotic.

It was decided to look for similar relationships using published estimates of seabird breeding success. Dunnet and Heubeck (1995) published data on annual counts at seabird colonies around Shetland which included breeding success at colonies of kittiwakes and fulmars. According to the vulnerability index constructed above, fulmars (index of 10) could be considered moderately vulnerable to changes in prey availability while kittiwakes (index of 2) could be considered very vulnerable.

Breeding success was plotted against four measures of sandeel biomass in Shetland waters from the stock assessment data (ICES, 1999): 0-group biomass, 0- plus 1-group biomass, 1- to 7-group biomass summed, 0- to 7-group biomass summed. The assessments estimate 1+ group numbers on 1st January and 0-group numbers on 1st July. 1st July represent the date when the majority of recruits enter the exploited stock however, the actual date may very between years depending on environmental conditions. This has implications for breeding seabirds which are dependant on young sandeels to feed their chicks, such as Arctic terns and kittiwakes. If the peak sandeel recruitment is late then chicks may starve and breeding success will be low – even if the subsequent sandeel recruitment is high. However, the models produced here move in yearly steps so the temporal variation in sandeel recruitment will not be explored. Sandeel numbers were multiplied by the mean weight-at-age to find estimates of biomass. It was decided biomass was more suitable measure of prey availability than fish numbers when considering more than one age class of fish as, for example, a 1-group fish is much heavier than an 0-group fish so represents a larger energy source for seabirds.

6.3.1 Fulmars

Dunnet & Heubeck supply a table for breeding success of fulmars at four colonies around Shetland: Sumburgh Head, Troswick Ness and Eshaness (see Figure 6.1) over 1985-1993 inclusive and Westerwick over 1990-1993 inclusive. Breeding success varied between 0.30 (1988 Sumburgh) and 0.59 (1991 Sumburgh, 1993 Westerwick) fledged young per apparently occupied nest. Plots of breeding success against calculated sandeel biomass are shown in Figure 6.2. All four plots show a positive relationship between breeding success and sandeel biomass. Much of the variation, as indicated by extreme data points, occurs in the data series for Sumburgh Head and Westerwick. Counts of apparently occupied nests were small at these colonies (between 18 and 123) compared to counts at Troswick Ness and Eshaness (between 92 and 448).

To remove the influence of count size, a weighted mean breeding success, $\overline{B}$, was calculated for each year over all colonies:

$$\overline{B} = \frac{\sum_{i=1}^{n} N_i B_i}{\sum_{i=1}^{n} N_i} \qquad 6.1$$

where N_i is the number of apparently occupied nests at site i, B_i is the breeding success at site i.

The results are shown in Figure 6.2. This removed some of the variation in the data series. Positive relationships of breeding success with sandeel abundance are seen in three of the four measures of abundance: 0-group biomass, 0- plus 1-group biomass and total biomass. For the first two measures the relationship appears to be asymptotic, breeding success increases at low levels of sandeel abundance and levels off at high levels of abundance. For the latter measure, the relationship appears to be linear.

Accordingly, an asymptotic model (Equation 6.2) was fitted to the relationships with 0-group biomass and 0- plus 1-group biomass (black line, Figure 6.2).

$$\hat{B}_t = \frac{a\overline{B}_t}{b + \overline{B}_t} \qquad 6.2$$

where $\hat{B}_t$ is breeding success predicted by the model in year t, $\overline{B}$ is weighted mean breeding success (Equation 6.1) and a and b are constants.

A linear relationship was fitted to breeding success in relation to total sandeel biomass. The R^2 was calculated for each model as a measure of the proportion of total variance explained by the fitted model. The highest R^2 (0.59) was returned by the model fitted to breeding success against total sandeel biomass. The models of breeding success against 0-group biomass and 0- plus 1-group biomass also had relatively high R^2 values (0.45 and 0.41 respectively).

In the vulnerability index developed above, fulmars were assigned an index of 10 and were ranked sixth out of the ten species considered for vulnerability to sandeel availability. Therefore, fulmars could be considered to be moderately sensitive to changes in prey abundance. Furness & Tasker (2000) developed a more detailed seabird sensitivity index to sandeel abundance and indicated fulmars were one of the least sensitive seabird species to sandeel abundance at Shetland (together with gulls, petrels, cormorants, shearwaters and gannets). Even so, a positive relationship with breeding success was found in three of the four measures of sandeel abundance. It must be remembered that food supply is not the only influence on breeding success, this can also be affected by weather (seabirds may not be able to forage under certain conditions), predation and breeding habitat quality (Cairns, 1987) so the relationship with sandeel abundance may be coincidental.

While there is a positive relationship with sandeel abundance, fulmar breeding success shows limited variation between years (weighted mean breeding success varied between 0.43 and 0.55, Figure 6.2). For the purposes of the model, this spread of breeding success is too low (no poor years). Therefore, fulmars were rejected as an indicator species.

6.3.2 Kittiwakes

Dunnet & Heubeck (1995) also supply a table for breeding success of kittiwakes at six colonies (see Figure 6.1) around Shetland: Sumburgh Head, Troswick Ness, and Eshaness over 1986-1993 inclusive, Kettlaness and Westerwick over 1987-1993 inclusive and an estimate for 1993 at Burra. Most of the colonies (excluding Burra which has no data) showed almost complete breeding failure during 1988, 1989 and 1990 except for Eshaness, where breeding success was moderate (0.45-0.65 young fledged per incubated nest). No or very few young were fledged at Kettlaness between 1987 and 1993 inclusive but Dunnet & Heubeck propose this could be due to predation by great skuas which was observed to be particularly heavy. As I am concerned with fluctuations in breeding success due to food availability, Kettlaness was excluded from further analysis.

As for fulmars, breeding success was plotted against the four measures of sandeel abundance described above (Figure 6.3). There appears to be a positive relationship with all four measures of sandeel abundance. The weighted mean breeding success (young fledged per incubated nest) was calculated for each year using Equation 6.1 and added to the graphs. The relationships of breeding success with 1- plus group biomass and total biomass appear to be linear, therefore linear models were fitted to the data. The R^2 values were calculated for each linear model and this was highest for the relationship with total biomass (0.46).

The plots of weighted mean breeding success against 0-group and against 0- plus 1-group sandeel biomass appeared to decrease rapidly at low sandeel abundance, therefore asymptotic models were fitted to the data (Equation 6.3). The R^2 values were calculated as a measure of the proportion of total variance explained by the fitted models. The relationship between weighted mean breeding success against 0- plus 1-group biomass had an extremely high R^2 value of 0.90. Estimates of weighted mean breeding success were available over a wide range of sandeel abundance for this model. Therefore, the model fitted to these data would provide a useful indicator of potential breeding success of kittiwakes and will be used to analyze output from the sandeel population model.

The vulnerability index developed above, indicated that kittiwakes could be considered as very sensitive to sandeel availability, kittiwakes were ranked second out of ten species. These are small seabirds that are surface feeders and generally forage close to the breeding colony. The vulnerability index and sensitivity index developed by Furness & Tasker (2000) also indicate that kittiwakes are considered very sensitive to sandeel abundance. Low breeding success or almost complete breeding failure was observed at kittiwake colonies around Shetland during the late 1980s when sandeel 0-group availability was low (Harris & Wanless, 1990; Dunnet & Heubeck, 1995; Harris & Wanless, 1997).

Furness (1999) analyzed breeding productivity of kittiwakes from different areas of the North Sea against different measures of sandeel abundance that excluded 0-group fish and found all correlations were positive. Correlations with 0-group fish were found to be negative. The most consistent correlations were found to be kittiwake breeding success with the number of 1+ sandeels on the 1st July. Breeding productivity at Shetland was also correlated with sandeel abundance and showed strong positive correlations with the log of numbers of 1-group sandeels and 1+ group sandeels. A very weak positive correlation was suggested with 0-group sandeel abundance with kittiwake breeding success at Shetland, in agreement with the strong positive relationship found in the data analysed above (Figure 6.3).

Furness (1999) showed positive correlations between breeding success of kittiwakes and sandeel numbers in different areas of the North Sea and negative correlations with 0-group sandeel numbers. However, Furness also showed that the number of 0-group sandeels were negatively correlated with the number of 1-group sandeels in the North Sea. This relationship was also shown for sandeels in the North Sea by S. Arnott (pers. com.) and can be seen in Figure 3.2 of Chapter 3. So as the most consistent correlations with breeding success were with 1-group sandeel numbers, it is not surprising that negative correlations were found with 0-group numbers. Shetland seems unique in showing a positive relationship with sandeel availability. At Shetland, the number of 0-group sandeels is positively correlated with 1-group numbers (see Figure 3.2b in Chapter 3) and the analysis carried out above showed a strong positive relationship with 0-group sandeels.

In conclusion, weighted mean kittiwake breeding success was plotted against measures of sandeel biomass at Shetland. Sandeel biomass was considered a more appropriate measure of prey value than numbers when more then one age class of fish is considered. A strong positive relationship was found between weighted mean kittiwake breeding success and the biomass of 0- plus 1-group sandeels (R^2=0.90). As estimates of breeding success occurred across a wide range of sandeel biomasses it was decided this would be an appropriate indicator function for potential seabird breeding success.

6.4 Breeding success indicator

The indicator function of breeding success against biomass of 0+1-group sandeels developed for kittiwakes at Shetland was used to devise a scoring system for potential breeding success. Four categories were selected: poor, moderate, good and excellent. It was assumed the upper threshold breeding success for the poor category was 0.42 young fledged per incubated nest and this occurred when 0+1-group sandeel biomass was 24,000 tonnes (Table 6.3). Moderate breeding success (0.42-0.61) was assumed to occur over an 0+1-group sandeel biomass of 24-47,000 tonnes. A biomass range of 47-140,000 tonnes was selected for good breeding success (0.61-0.93) and excellent breeding success (0.93+) was assumed to occur when 0+1-group sandeel biomass was above 140,000 tonnes.

The biomass of 0+1-group sandeels, determined from population estimates and mean weight-at-age in the historical data (ICES 1999), was calculated for each year over 1974-1997. The potential kittiwake breeding success category was determined for each year. This indicated that twelve of the years could be considered good for potential kittiwake breeding success and eight years were considered excellent (Table 6.3). Three years were considered poor for potential kittiwake breeding success (1988, 1989 and 1990) and one year was considered moderate (1987). The years of potentially poor and moderate breeding kittiwake breeding success (1987-1990) corresponded to years when many kittiwake colonies at Shetland failed (Dunnet & Heubeck, 1995).

6.5 Simulations with Recruitment Models

A number of recruitment models were developed for sandeels at Shetland: the autoregressive model from Chapter 3, Ricker stock-recruit models in Chapter 4 and Ricker stock-recruit models with external recruitment in Chapter 5. The models represent potential recruitment dynamics at Shetland - due to high uncertainty in our understanding of these processes a number of alternative models were developed. Simulations of these models were carried out with varying rates of fishing mortality to indicate potential affects of fishing mortality on the sandeel population structure, kittiwake breeding success and the catch landed by the fishery.

Firstly, a summary of the parameterised models selected from the previous Chapters is given together with the baseline output. Then fishing mortality is varied and the results analyzed and compared between models.

6.5.1 Recruitment Models

Seven recruitment models were selected in the previous Chapters to simulate recruitment dynamics of sandeels at Shetland. In Chapter 3, a first-order autoregressive model (hereafter AR) was parameterised. This model (Chapter 3, Equation 3.28) uncouples recruitment from SSB - recruitment is simply expressed as a function of recruitment in the previous year. The model produced ln(recruit) time series which, on average, had an autocorrelation coefficient of 0.53 – similar to that calculated for the historical data series (0.51).

Chapter 4 fitted Ricker stock-recruit models to the Shetland data set, assuming no net external recruitment. Firstly, a Ricker curve was parameterised using bootstrap analysis of the complete historical data set. A first-order autoregressive model was incorporated in the Ricker function to produce a Ricker model with autocorrelated residuals (see Chapter 4, Equation 4.20). Simulations were carried out with the model input autocorrelation coefficient set to 0.51 (the value of the autocorrelation coefficient from the historical data series). This produced model output ln(recruit) series which had autocorrelation coefficients of 0.37 on average – less then the target (historical) value. It was found that increasing the input coefficient to 0.73, generally increased the output autocorrelation coefficient to 0.50. As an input autocorrelation coefficient of 0.73 represents extremely high forcing on the stock-recruit relationship, both the model with this input value and with the lesser input value of 0.51 were selected for further analysis (the model with low input autocorrelation coefficient will be referred to as CompleteLow hereafter and the high input as CompleteHigh). The historical time series is only 24 years long so confidence in the calculated autocorrelation coefficient is reduced.

It was found during fitting both Ricker and Shepherd stock-recruit models in Chapter 4, that the four low recruits years which occurred in the late 1980s were strongly influencing model fit. Although there was no biological reasoning to remove these data points, in the face of uncertainty, these data points were excluded from the series and a second Ricker curve parameterised. Simulations were carried out using the Ricker models with autocorrelated residuals and it was found that an input autocorrelation of 0.51 generally produced an output autocorrelation coefficient of 0.36 in the ln(recruit) time series. As before, it was found that an input autocorrelation coefficient of 0.73 was required to produce an average output autocorrelation coefficient of 0.50. As 0.73 represents strong forcing on the stock-recruit relationship both of these models were selected for further analysis (the model with low input autocorrelation coefficient will be referred to as ReducedLow hereafter and the high input as ReducedHigh). .

The final set of models, developed in Chapter 5, included functions for external recruitment. It was assumed that the stock-recruit relationship at Shetland was similar to that in other areas of the North Sea. Therefore, a Ricker model fitted to the North Sea data was scaled down (by area) to represent local recruitment at Shetland. It was assumed that the difference between this model and the Ricker model fitted to the Shetland data set would be due to the addition of external recruits to Shetland. However, the models were surprisingly similar. In addition, the large variance about the Shetland curve was due to the four low recruit years. The models developed exploit the phenomenon of additive variances but it was not possible to produce a model for using these curves that produced this large observed variance.

In order to develop the model, the Ricker curve parameterised using the reduced data set (minus four low years) was used as this was different to the North Sea model. Total (local plus external) recruitment is expressed using the scaled North Sea Ricker model with lognormal variance. The lognormal variance distribution is assumed to be the sum of a lognormal distribution with a mean of zero representing local recruit variance around the stock-recruit curve and a second log-normal distribution which represents "external error". The local recruitment lognormal variance was assumed to be equal to that seen in the North sea data. "External error" accounts for the extra variance due to the addition of external recruits, this is included by adding a second lognormal variance about the stock-recruit curve which had a mean greater then zero. The variance in the total recruit series produced is similar to the variance of the Shetland data about the scaled North Sea Ricker model. Functions for autocorrelation were incorporated into local variance, into external error and into both. It was determined the most feasible model was that with local recruitment autocorrelated with an input autocorrelation coefficient of 0.64 – this model will be referred to as ExtMethod1 hereafter.

The second model was produced which was an adaptation of the first. The distribution of external recruitment produced by simulations of the parameterised first model was determined. In the second model, local recruitment was expressed using the scaled North Sea Ricker curve with lognormal variance and external recruitment was simply selected randomly from the parameterised distribution. Simulations were carried out incorporating autocorrelation in the local recruitment function and autocorrelating the external recruit time series. The most feasible model selected was that with local recruitment autocorrelated with an input autocorrelation coefficient of 0.54 and with the external recruitment series also autocorrelation (input autocorrelation coefficient of 0.6) – this model will be referred to as ExtMethod2 hereafter.

6.5.2 Model Simulations

The population model developed in Chapter 3 was used to carry out simulations with the recruitment models discussed above. The mean and standard deviation for both the ln(recruitment) and SSB series produced for each simulation was output together with the autocorrelation coefficient, r_1, for the ln(recruit) time series. To assess potential kittiwake breeding success, the biomass of 0+1-group fish was calculated for each year and scored against the breeding success categories discussed above (Table 6.3). Finally, the number of fish, hence biomass, caught by the fishery in each age class was also calculated.

Age specific fishing mortality rates were selected as described in Chapter 3 (from a distribution for each rate calculated from the historical data – see Table 3.5, Chapter 3). Eleven levels of fishing mortality were tested - the selected annual fishing mortality rate for each age class was multiplied by a constant *g*. *g* was varied between 0.0 and 5.0 in steps of 0.5. For each value of *g*, 1000 simulations of 24 years were carried for each recruitment model discussed above.

6.5.3 Results

Firstly, the results for *g*=1 will be considered as these represent the baseline models (Table 6.4). The median values for recruitment and SSB varied between models. The models fell into two groups: those parameterised using the complete historical data set (AR, CompleteLow and CompleteHigh) and those parameterised using the historical data set minus four low years (ReducedLow, ReducedHigh, ExtMethod1, ExtMethod2). For the first group the historical median recruitment and median SSB were 48.2 billion recruits and 127 x10^3 tonnes SSB, while for the second group the corresponding values were 70.1 billion recruits and 126 x 10^3 tonnes SSB. Generally, the models produced output values close to the historical values. All models produced mean catches between 22-28,000 tonnes, close to the mean catch of 25,262 tonnes in the historical data over 1974-1986 inclusive (the years for which mean fishing mortality was determined as model input).

To compare potential affect on seabird breeding success, the percentage of years in each biomass category were calculated for each simulation and the average for 1000 simulations was determined (Table 6.4). For the recruitment models in group 1, potentially poor breeding success years occurred with an average frequency of 6-7% and moderate years with a frequency of 12-14%. Conversely, in the historical data poor years occurred with an average frequency of 13% and moderate years with a frequency of 4%. If the ratio of the frequency of occurrence of poor/moderate years against good/excellent years is considered the ratio in the historical data (1:5.2) is similar to the ratios produced by the models in group 1 (1:4.2). If the four low recruit years are removed from the historical data, as for the developing the group 2 models, all the historical years are potentially good or excellent for kittiwake breeding success. The models in group 2 produce very few years, on average, when kittiwake breeding success was poor or moderate.

Simulations were run for each model varying the age-specific mortality rates by multiplying each rate by a constant *g*. *g* was varied between 0 and 5 in steps of 0.5. The median recruitment and median SSB produced by each model for each value of *g* tested are shown in Table 6.5 and Figure 6.4. Although the effect on median SSB is similar between models, the effect on median recruitment varies according to model. As expected, the level of fishing mortality had little effect on the median recruitment produced by the autoregressive model (AR) – recruitment was uncoupled from SSB in this model. For the remaining group 1 models (CompleteHigh and CompleteLow), median recruitment increased to a maximum (>45 billion) when *g* was equal to 1.5-2.0 (CompleteHigh) and 1.5-2.5 (CompleteLow) then decreased. The decrease was slightly sharper in the model with higher autocorrelation.

Median recruitment reached a maximum (>75 billion) for the two models without external recruitment in Group 2, ReducedHigh and ReducedLow, when *g* was in the ranges 1.5-2.5 and 1.5-3.0 respectively. As before, the decrease with high values of *g* was slightly greater in the model with the higher input autocorrelation coefficient. The two models with external recruitment, ExtMethod1 and ExtMethod2, showed different responses to varying *g*. The response by ExtMethod2 was similar to that of the Reduced models but with higher values for median recruitment at low and high values of *g*. Maximum recruitments occur when *g* was between 0.5-2.5 inclusive. This model used the scaled down North Sea Ricker model to simulate local recruitment with a random independent value for external recruitment (which was not affected by SSB). The target series was the reduced historical series – hence the similarity between the models. The higher recruitments at low and high values of *g* are due to the addition of external recruits. The recruitment model, ExtMethod1, was the most sensitive to values of fishing mortality. Maximum median recruitment was returned when *g*=1.5 (74.3 billion), above this median recruitment rapidly declined.

The percentage of years that were considered potentially poor or moderate for kittiwake breeding success for each recruitment model are shown in Table 6.6 together with the percentage produced by each baseline model (*g*=1). The change from the baseline model for each recruitment model is shown in Figure 6.5. The change in the percentage of potentially poor and moderate years increases rapidly for all models once *g*>3. A change of less then 5% occurred over a wide range for all models. The greatest range (0>=g>=3.5) occurred was produced by models ReducedLow and ExtMethod2 (excluding the autoregressive model).

Mean biomass catch (fishery) under varying levels of fishing mortality rate are given in Table 6.7 and shown in Figure 6.6. All models, except AR (autoregressive) and ExtMethod1 (local and external recruitment linked to SSB), show similar responses in mean catch to variation in fishing mortality rate. For all models, maximum catches (>40,000 tonnes) occur when *g*=2 or *g*=2.5 and above.

6.5.4 Conclusions

The recruitment models tested all showed a similar response in median SSB to changes in fishing mortality rate (Figure 6.4b) but differing responses in median recruitment. The autoregressive model (AR) uncouples recruitment from SSB and, although this can reproduce baseline population dynamics of the sandeel stock, it does not provide understanding of dynamics when exploitation levels change. Therefore, the results from this model will not be discussed further. The remaining models fell into two categories, those which were parameterised using the complete historical data set (CompleteHigh and CompleteLow) and those which were parameterised using the reduced historical data set (ReducedHigh, ReducedLow, ExtMethod1 and ExtMethod2). Results from the former group will be considered first.

For the two group 1 models, as input fishing mortality increased the median recruitment increased to a maximum at *g*=1.5-2.0 then decreased. Little change occurred in the percentage of years of poor and moderate breeding success for seabirds (19.4%) in the model output with low autocorrelation (α=0.51) when *g* reduced from 1 to 0.5 or increased to 2.0. There was little change in median recruitment over this period. When *g*=0 (no fishery), the median recruitment decreased from 45/44 billion to 38 billion (CompleteHigh) and 34 billion (CompleteLow), while the percentage low poor and moderate breeding success years increased by 3-5%. Above *g*=2.5, median recruitment drops rapidly for both models as the percentage of poor and moderate seabird breeding success years increases. However, the highest catches by the fishery occurred when *g*=2-4. The increase in catch biomass is due to an increase in the biomass of 1-group fish caught as *g* increases from 0 to 4 (Figure 6.7).

The second group of models also show an increase in the percentage of poor and moderate breeding success years if *g*=0 (n0 fishery) as median recruitment declines slightly. Excluding ExtMethod1 model, the models show optimum recruitments when *g* is in the range 1 to 3, which is also the range of low percentage of poor and moderate breeding success years. However, optimal catches by the fishery occurs when *g* is in the range 2.5 to 4.

Model ExtMethod1 represents a unique case where external recruitment occurs but is linked to local SSB, so if SSB is high then external recruitment is generally low (due to density dependence). However, problems arise where local SSB is reduced due to heavy exploitation so the likelihood of a large local recruitment is reduced as the likelihood of a large external recruitment is also reduced. In this instance it is unlikely that external recruitment is linked to local spawning stock biomass (as the model should be density independent).

In conclusion, considering all models except autoregressive model (AR) and ExtMethod1, optimal fishery catches of 43-56,000 tonnes occur when *g* is in the range 2.5 to 4 – or 0-group fishing mortality rates in the range 0.186-0.298 and a 1-group fishing morality range of 0.635-1.016. A minimal number of poor and moderate years of potential seabird breeding success occurred when *g* was in the range 0.5-2 for all models, lower than the range for optimal fishery returns. Thus, considering all these possible models (except the autoregressive model) removing a catch of 38-46,000 (depending on model) should optimize fishery returns without increasing the potential risk to breeding seabirds. It must be stressed though that these models represent a simplified view of our perceptions of population dynamics – which may be very different.

6.6 Model Simulations – Restricted Fishery

Since the sandeel fishery at Shetland reopened in 1995, fishing is suspended during June and July to avoid competition with breeding seabirds. If the total allowable catch (TAC; at present 7,000 tonnes *per annum*) has not been fulfilled, the fishery may recommence in August. If the TAC is taken before June (or fishing does not recommenced in August) then the majority of the catch will consist of 1-group fish, as 0-groups are thought to recruit to the stock and simultaneously to the fishery from the beginning of June.

To simulate this scenario, the models were rerun with 0-group fishing mortality set to zero – thus assuming all catch is taken before June. For 1+ group fish, eleven levels of fishing mortality were tested as before - the selected annual fishing mortality rate for each age class was multiplied by a constant g. g was varied between 0.0 and 5.0 in steps of 0.5. For each value of g, 1000 simulations of 24 years were carried for each recruitment model selected above, except the autoregressive model. The results were compared with the simulations including 0-group fishing mortality.

6.6.1 Results

The results for the baseline models (Table 6.8) where g=1, are generally similar to those for the models with a fishery on 0-groups (Table 6.4) except for SSB and catch. Median SSB increased for all models by a maximum of 6.2% while mean catch decreased by a maximum of 9.4%. The percentage of years considered potentially poor or moderate for kittiwake breeding success decreased slightly, for example from an average of 1 in every 4.2 years for the CompleteHigh model to 1 in 5.3 years, due to the availability of "extra" 0-group sandeels. The average fishery catch also decreased by a maximum of 9.4% (ReducedLow average catch was 25,810 tonnes for fishery on all age-classes and 23,586 for fishery excluding 0-groups).

The model output values for median recruitment and SSB with varying input values of g are shown in Table 6.9 and Figure 6.7. For all models, SSB decreased as the fishing mortality rate increased, however the rate of decline was less than in the models with a fishery on all age classes (Table 6.5 and Figure 6.4). For the models parameterised using the complete historical data set (CompleteHigh and

CompleteLow), median recruitment was at a maximum (>75 billion) when input *g* was in the range 1.5-2.5 inclusive of CompleteHigh and 1.5-3.5 for CompleteLow. For the remaining models, which were parameterised using the reduced historical data set, the optimal ranges for input g which produced the highest median recruitment outputs varied between models. A input range for *g* of 2-3 inclusive returned the highest median recruitments for ReducedHigh model and similarly, an input range of 2-3.5 inclusive returned the highest median recruitments for ReducedLow. ExtMethod2 (independent external recruitment) returned optimal recruitments under a largest range of input g, 0.5 – 3 inclusive. ExtMethod1 (external recruitment linked to SSB) performed worst of all the models, an optimal recruitment was returned only when *g*=1.5.

The potential affect of kittiwake breeding success, that is years which are considered poor or moderate, is shown in Table 6.10 and Figure 6.8. The change in the percentage of potentially poor and moderate years (% change>5) increases rapidly when *g*>3. All models, except CompleteHigh, showed less then a 5% change in the percentage of potentially poor and moderate years when *g*=0 (no fishery) to *g*=3 inclusive. ExtMethod2 was least sensitive to changes in fishing rate, the percentage of potentially poor and moderate years changed by less then 5% over the range *g*=0 to *g*=5.

6.6.2 Conclusions

The mean total biomass catch by the fishery under varying levels of fishing mortality rate are shown in Table 6.11 and Figure 6.9. The Ricker models with no external recruitment (CompleteHigh, CompleteLow, ReducedHigh, ReducedLow) showed similar responses in mean catch to changes in input fishing mortality. Optimal catches (>40,000 tonnes) for all of these models, except CompleteHigh, occurred when *g* was in the range 2-6.5 inclusive. For CompleteHigh, the optimal range commenced when *g*=2.5. Similarly, ExtMethod2 (independent external recruitment) and ExtMethod1 (external recruitment linked to local SSB) also produced optimal catches when g>=2 but the upper limit of the range for ExtMethod1 occurred when *g*=5.

All models, except ExtMethod1, produced optimal recruitments when *g* was in the range 2.0-2.5 inclusive. This corresponded to catches in the range 37,177 tonnes to 50,989 tonnes, depending on the recruitment model. ExtMethod1 (external recruitment linked to local SSB) produced optimal recruitment when *g*=1.5. As discussed above, problems arise with this model when SSB is reduced due to heavy exploitation so is model is rejected when fishing mortality (*g*) is high. This model is excluded from further analysis of results. Including exploitation of 0-group sandeels reduced the ranges of *g* for optimal recruitments for all models (see Tables 6.5 and 6.9) - considering all models, the optimal range was reduced to 1.5-2.0 inclusive. So removing exploitation of 0-group fish in the models increases the level of fishing mortality required for optimal recruitments. The decrease in SSB was also greater in the models with exploitation of 0-group sandeels.

Removing exploitation of 0-group sandeels greatly increased the range of input fishing mortalities which produced a change of less then 5% from the baseline models (*g*=1) for potentially poor and moderate years of kittiwake breeding success (see Tables 6.6 and 6.10). A input range for *g* of 0.5 - 3 produced the fewest years of poor and moderate breeding success in all models without exploitation of 0-group sandeels. Expanding the fishery to take 0-group fish reduced the optimal range of *g* to 0.5 – 2, when considering all models (except autoregressive and ExtMethod1). For the Group 1 models (CompleteHigh and CompleteLow) having no fishery tended to increase the potential poor and moderate breeding success years by between 3.4 – 6.5%.

Maximum catches (53,936 – 62,987 tonnes) occurred in all models when *g*=4 or 4.5 (Table 6.11). Including exploitation of 0-group fish decreased the maximum catches to between 47,801 – 55,730 tonnes and these occurred when *g*=3.5 or 4 (Table 6.7). The model with independent external recruitment, ExtMethod2, was able to sustain high catches at high exploitation rates, even though median recruitment and SSB decreased.

6.7 Chapter Conclusions

In the models where there were no exploitation of 0-groups, the sandeel population appeared to be more resilient to high exploitation rates compared to populations with a fishery on 0-groups. The populations were also less sensitive to higher exploitation rates, when considering the percentage of potentially poor and moderate kittiwake breeding success years. Not exploiting 0-group fish appears to reduce potential adverse effects on seabird breeding success. Catches were also higher in the models without 0-group exploitation. In conclusion, catches by the fishery of 48-58,000 tonnes have little effect on potential seabird breeding success, if exploitation is of 1+ groups only. As the optimal catch depends on the recruitment model used, as a conservative estimate, the worse case scenario was selected. This was for the model CompleteHigh, where a Ricker model was parameterised using the complete data set and the input autocorrelation coefficient was large

(0.73). The optimal catch, with minimal affects on seabirds, returned by this model was 48,000 tonnes on average.

In conclusion, the models seem to suggest that having no fishery may be worse for potential seabird breeding success then having a limited fishery with moderate exploitation rates. With the data available at present, it is difficult to determine which recruitment model is a good representation of recruitment dynamics. The most worrying model is the independent external recruitment – this can support high levels of exploitation with little adverse affect on potential breeding success of kittiwakes. However, local stock size decreases as exploitation increases but this is masked by external recruitment - if external larval transport mechanisms cease then the local stock may be at too low a level to be self-sustaining.

6.8 Summary

- A index of potential vulnerability of breeding seabirds to sandeel abundance was developed. This indicated kittiwakes and Arctic terns are most vulnerable.
- Functions to indicate potential kittiwake breeding success against measures of sandeel biomass were constructed – strongest relationship was found with 0+1-group sandeel biomass. This was used as an indicator function in the models
- Model simulations were carried out using seven different recruitment models developed in previous Chapters varying input fishing mortality rate. Simulations were repeated removing exploitation on 0-group sandeels
- For all models, the sandeel population as well as potential seabird breeding success were more robust to exploitation rates if there is no fishery on 0-group sandeels.

Table 6.1. Foraging characteristics and vulnerability to prey availability of seabirds at Shetland. Depth, Range and Body Mass are from Martin 1989 (key shown). Depth = ability of bird to dive after prey, Range = *foraging range from breeding colony*, Body Mass = weight of adult bird., Vulnerability Index = index of potential vulnerability to prey availability based on the three foraging characteristics, Rank = rank of vulnerability index, Ranked Vulnerability Index from Furness & Tasker (2000) = index developed by Furness & Tasker for vulnerability to prey availability, indices of 10 species given were selected and ranked, Ranked Sensitivity Index from Furness & Tasker (2000) = index developed by Furness & Tasker for sensitivity to sandeel availability, indicies of 10 species given were selected and ranked

Common Name	Species	Depth	Range	Body Mass	Vulnerability Index	Rank	Ranked Vulnerability Index from Furness & Tasker (2000)	Ranked Sensitivity Index from Furness & Tasker (2000)
Terns (Arctic)	*Sterna paradisaea*	Surface	Near	1	1.7	1	1	1
Kittiwake	*Rissa tridactyla*	Surface	Mid	1	3.3	2	2	2
Tystie (Black Guillemot)	*Cepphus grylle*	Medium	Near	1	5.0	3=	3	6=
Great Skua	*Catharacta skua*	Surface	Near	3	5.0	3=	4=	6=
Puffin	*Fratercula arctica*	Medium	Mid	1	9.9	5	4=	3
Fulmar	*Fulmarus glacialis*	Surface	Far	2	10.0	6	9	9
Shag	*Phalacrocorax aristotelis*	Medium	Near	3	14.9	7	8	6=
Razorbill	*Alca torda*	Medium	Mid	2	19.8	8	6	4
Guillemot	*Uria aalge*	Deep	Mid	2	26.4	9	7	5
Gannet	*Sula bassana*	Shallow	Far	5	50.0	10	10	10

Depth: Surface = <0.5m; Shallow = 0.5-5m; Medium = 5-10m; Deep =>10m
Range: Near =<10km; Mid = 10-50km; Far =>50km
Body Mass: 1=<0.5kg; 2=0.5-1kg; 3=1-2kg; 4=2-3kg; 5=>3kg

Table 6.2 Rank assigned to categories of foraging characteristics of seabirds given by Martin 1989.

Depth	Rank	Range	Rank	Body Mass	Rank
Surface	0.25	Near	0.33	<0.5kg	0.20
Shallow	0.50	Mid	0.66	0.5-1kg	0.40
Medium	0.75	Far	1.00	1-2kg	0.60
Deep	1.00			2-3kg	0.80
				>3kg	1.00

Table 6.3 Characteristics for function to indicate potential breeding success (young fledged per incubated nest) for kittiwakes at Shetland. Sandeel biomass = biomass of 0-group fish on 1st June plus biomass of 1+group fish on 1st January (from ICES 1999), estimated range of sandeel abundance for each breeding success category. Historical Data Score = number of years from the historical data set where the estimated sandeel biomass is within the range for breeding success category. % = percentage of years represented by each historical data score.

Breeding success	Mean young fledged per incubated nest	Sandeel Biomass	Historical Data Score	%
poor	0-0.42	0-24K	3	13
moderate	0.42-0.61	24-47K	1	4
good	0.61-0.93	47-140K	12	50
very good	0.93+	140K+	8	33

Table 6.4 Baseline model output for seven recruitment models in population model of sandeels at Shetland. Group 1 = models developed using the complete historical data set (Historical Group 1, from ICES 1999). Group 2 = models developed using the historical data set minus four low recruitment years which occurred in the late 1980s. AR = autoregressive model developed in Chapter 3, CompleteHigh = Ricker model with high autocorrelation in error terms (0.73) developed in Chapter 4, CompleteLow = Ricker model with low autocorrelation in error terms (0.51) developed in Chapter 4, ReducedHigh = Ricker model with high autocorrelation in error terms (0.73) developed in Chapter 4, CompleteLow = Ricker model with low autocorrelation in error terms (0.51) developed in Chapter 4, ExtMethod1 = Ricker model with external recruitment linked to local SSB developed in Chapter 5, ExtMethod2 = Ricker model with independent external recruitment developed in Chapter 5. Average percentage of years where 0+1 group sandeel biomass is within ranges defined for potential seabird breeding success (poor, moderate, good and excellent) given together with the ratio of poor and moderate years to good and excellent years.

				Group 1			Group 2			
		Historical	Historical		Complete	Complete				
		Group 1	Group 2	AR	High	Low	ReducedHigh	ReducedLow	ExtMethod1	ExtMethod2
	Median Recruitment (Billions)	48.2	70.1	47.9	44.9	43.9	72.3	71.6	73.4	81.6
	Median SSB (000 tonnes)	127	126	118.6	121.2	131.5	136.9	142.1	143.0	149.7
	Mean catch (tonnes)	25262	25262	24485	22256	24036	24958	25810	26336	27866
Seabirds	% Poor	13.0	0.0	6.0	6.9	6.9	0.0	0.2	0.2	0.0
	% Moderate	4.0	0.0	13.3	12.5	12.4	1.6	1.9	1.7	0.4
	% Good	50.0	60.0	43.4	44.0	41.7	43.0	42.4	41.4	35.7
	% Excellent	33.0	40.0	37.2	36.6	38.9	55.3	55.5	56.7	63.9
	Poor/Moderate:Good/Excellent	1:5.2	0:1	1:4.2	1:4.2	1:4.2	1:59	1:47	1:52	1:249

Table 6.5 Output from simulations of population models for sandeels at Shetland. Median recruitment (billions) and median SSB (x10^3 tonnes) produced by seven recruitment models (see Chapter 6 text or Table 6.4 for details) under varying fishing mortality rates. *g* = constant by which each age-specific fishing mortality rate was multiplied by. Values in bold indicate optimal recruitment values: >45 billion for Group 1 models and >75 billion for Group 2 models.

		Group 1			Group 2			
	g	AR	Complete High	Complete Low	Reduced High	Reduced Low	ExtMethod 1	ExtMethod 2
Recruitment	0	**47.5**	37.7	34.3	59.1	57.7	64.8	71.7
	0.5	**48.3**	42.5	39.8	66.7	65.6	71.1	**78.1**
	1	**47.9**	44.9	43.9	72.3	71.6	73.4	**81.6**
	1.5	**47.8**	**46.8**	**46.5**	**76.4**	**77.1**	74.3	**81.6**
	2	**47.7**	**45.1**	**48.9**	**79.0**	**79.6**	72.3	**82.7**
	2.5	**48.1**	41.6	**47.2**	**77.2**	**80.7**	64.0	**80.3**
	3	**49.0**	36.3	42.9	74.2	77.4	55.3	74.0
	3.5	**48.3**	32.7	38.8	68.3	70.1	43.6	67.9
	4	**48.9**	27.8	31.2	54.8	60.1	31.3	63.4
	4.5	**48.9**	19.0	25.0	42.9	48.1	21.5	57.8
	5	**48.5**	13.2	17.4	31.9	34.0	14.1	51.8
SSB	0	175	160	169	177	181	197	204
	0.5	144	139	148	157	162	171	177
	1	119	121	131	137	142	143	150
	1.5	96	102	111	120	123	119	123
	2	80	88	94	103	105	98	102
	2.5	68	71	78	86	89	77	85
	3	59	58	62	70	72	59	67
	3.5	49	47	51	57	58	45	53
	4	43	37	39	44	45	32	45
	4.5	37	29	30	34	36	26	37
	5	32	22	23	27	27	21	30

Table 6.6 Output from simulations of population models for sandeels at Shetland. Average % of potentially poor and moderate years for kittiwake breeding success produced by seven recruitment models (see Chapter 6 text or Table 6.4 for details) under varying fishing mortality rates. % change = change from baseline models (g=1). g = constant by which each age-specific fishing mortality rate was multiplied by. Values in bold indicate cases where the % change in potentially poor and moderate years is less then 5%.

		Group 1			Group 2			
	g	AR	Complete High	Complete Low	Reduced High	Reduced Low	ExtMethod 1	ExtMethod 2
% Poor/Moderate	0	19.1	22.6	24.4	3.4	4.9	2.7	0.7
	0.5	18.7	19.6	20.6	2.0	3.0	1.9	0.5
	1	19.4	19.4	19.4	1.7	2.1	1.9	0.4
	1.5	19.9	19.6	19.2	1.9	1.5	2.2	0.5
	2	20.8	22.0	18.2	2.6	1.4	4.3	0.7
	2.5	21.5	26.3	20.6	3.6	1.9	8.6	1.4
	3	21.4	30.9	24.7	5.8	3.1	14.7	2.5
	3.5	22.3	34.7	28.9	9.6	6.0	23.4	4.8
	4	22.7	38.5	35.5	18.0	11.4	35.7	7.4
	4.5	23.2	46.2	42.2	26.7	20.7	48.3	10.9
	5	24.3	54.2	50.7	36.1	34.4	57.4	16.1
% change	0	**-0.3**	**3.2**	5.0	**1.8**	**2.8**	**0.8**	**0.3**
	0.5	**-0.7**	**0.2**	**1.3**	**0.3**	**0.9**	**0.0**	**0.1**
	1	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**
	1.5	**0.5**	**0.2**	**-0.2**	**0.3**	**-0.6**	**0.3**	**0.1**
	2	**1.4**	**2.6**	**-1.2**	**0.9**	**-0.7**	**2.4**	**0.3**
	2.5	**2.1**	6.9	**1.2**	**1.9**	**-0.2**	6.7	**1.0**
	3	**2.1**	11.5	5.3	**4.2**	**1.0**	12.8	**2.1**
	3.5	**2.9**	15.3	9.5	7.9	**3.9**	21.5	**4.4**
	4	**3.4**	19.1	16.1	16.3	9.3	33.8	7.0
	4.5	**3.8**	26.8	22.9	25.0	18.6	46.4	10.5
	5	5.0	34.7	31.4	34.4	32.3	55.5	15.7

Table 6.7 Output from simulations of population models for sandeels at Shetland. Average catch (x10^3 tonnes) produced by seven recruitment models (see Chapter 6 text or Table 6.4 for details) under varying fishing mortality rates. % change = change from baseline models (*g*=1). *g* = constant by which each age-specific fishing mortality rate was multiplied by. Values in red are considered optimal catches (>40,000 tonnes).

t	AR	Complete High	Complete Low	Reduced High	Reduced Low	ExtMethod 1	ExtMethod 2
0	0	0	0	0	0	0	0
0.5	13757	12828	11885	13594	13039	14307	15208
1	24485	24036	22256	25810	24958	26336	27866
1.5	32327	33839	31268	36730	35397	35682	37314
2	38790	**42413**	38478	**45390**	**44253**	**42645**	**45748**
2.5	**45161**	**47263**	**43554**	**52105**	**49817**	**44685**	**50751**
3	**50023**	**48540**	**45329**	**55584**	**53987**	**45239**	**51787**
3.5	**51863**	**49896**	**47445**	**55731**	**55662**	41779	**52007**
4	**55254**	**47115**	**47801**	**52645**	**52007**	36782	**52073**
4.5	**57905**	**44371**	**44066**	**48227**	**47201**	31164	**50442**
5	**59042**	39302	39542	**41815**	**42242**	27724	**48365**

Table 6.8 Baseline model output for seven recruitment models in population model of sandeels at Shetland with no fishery on 0-group sandeels. Group 1 = models developed using the complete historical data set (Historical Group 1, from ICES 1999). Group 2 = models developed using the historical data set minus four low recruitment years which occurred in the late 1980s. AR = autoregressive model developed in Chapter 3, CompleteHigh = Ricker model with high autocorrelation in error terms (0.73) developed in Chapter 4, CompleteLow = Ricker model with low autocorrelation in error terms (0.51) developed in Chapter 4, ReducedHigh = Ricker model with high autocorrelation in error terms (0.73) developed in Chapter 4, CompleteLow = Ricker model with low autocorrelation in error terms (0.51) developed in Chapter 4, ExtMethod1 = Ricker model with external recruitment linked to local SSB developed in Chapter 5, ExtMethod2 = Ricker model with independent external recruitment developed in Chapter 5. Average percentage of years where 0+1 group sandeel biomass is within ranges defined for potential seabird breeding success (poor, moderate, good and excellent) given together with the ratio of poor and moderate years to good and excellent years.

	Group 1	Group 2	Group 1		Group 2			
	Historical	Historical	Complete High	Complete Low	Reduced High	Reduced Low	ExtMethod 1	ExtMethod 2
Median Recruitment (Billions)	48.2	70.1	43.7	43.0	71.3	69.8	72.9	80.3
Median SSB (000 tonnes)	127	126	127.7	136.2	146.0	147.0	150.7	155.5
Mean catch (tonnes)	25262	25262	20536	22308	23139	23586	24355	25692
% Poor	13.0	0.0	6.9	6.5	0.1	0.3	0.1	0.0
% Moderate	4.0	0.0	11.9	11.9	1.5	1.7	1.6	0.3
% Good	50.0	60.0	43.5	41.6	40.5	40.6	39.2	33.5
% Excellent	33.0	40.0	37.7	40.0	58.0	57.4	59.1	66.1
Poor/Moderate:Good/Excellent	1:5.2	0:1	1:5.3	1:5.5	1:64	1:50	1:60	1:294

Table 6.9 Output from simulations of population models for sandeels at Shetland with no fishery on 0-group sandeels. Median recruitment (billions) and median SSB ($x10^3$ tonnes) produced by seven recruitment models (see Chapter 6 text or Table 6.4 for details) under varying fishing mortality rates. *g* = constant by which each age-specific fishing mortality rate was multiplied by. Bold values indicate optimal recruitments: >45 billion for Group 1 models and >75 billion for Group 2 models

		Group 1		Group 2			
	g	Complete High	Complete Low	Reduced High	Reduced Low	ExtMethod 1	ExtMethod 2
Recruitment	0	38.1	34.8	60.1	57.7	64.5	73.8
	0.5	41.0	38.5	66.0	64.4	69.2	**77.2**
	1	43.7	43.0	71.3	69.8	72.9	**80.3**
	1.5	**45.1**	**45.6**	74.7	74.0	75.1	**82.7**
	2	**46.5**	**48.7**	**78.4**	**78.3**	73.3	**82.2**
	2.5	**46.9**	**47.7**	**80.8**	**79.9**	70.4	**81.4**
	3	42.1	**46.2**	**78.6**	**81.5**	65.4	**78.6**
	3.5	38.5	45.1	74.5	**78.8**	59.4	74.2
	4	34.7	40.3	69.3	73.0	49.1	70.8
	4.5	29.2	35.3	62.5	65.9	38.2	66.0
	5	23.9	29.9	55.4	57.2	28.5	61.1
	5.5	19.3	21.8	44.8	48.1	21.0	58.0
	6	13.3	16.3	33.0	36.6	14.1	53.9
	6.5	11.0	12.3	25.4	28.3	9.6	50.3
	7	7.6	9.6	18.6	18.9	6.6	47.5
SSB	0	161	173	180	182	195	211
	0.5	141	150	162	164	172	182
	1	128	136	146	147	151	156
	1.5	111	120	129	134	132	137
	2	99	108	116	118	111	118
	2.5	87	92	101	103	94	99
	3	72	78	88	91	80	83
	3.5	60	67	73	77	64	71
	4	51	57	63	64	50	59
	4.5	43	47	51	54	39	50
	5	35	39	43	44	31	42
	5.5	29	29	35	36	25	37
	6	23	24	28	29	21	32
	6.5	20	20	27	24	18	28
	7	17	18	22	20	16	25

Table 6.10 Output from simulations of population models for sandeels at Shetland with no fishery on 0-group sandeels. Average % of potentially poor and moderate years for kittiwake breeding success produced by seven recruitment models (see Chapter 6 text or Table 6.4 for details) under varying fishing mortality rates. % change = change from baseline models (*g*=1). *g* = constant by which each age-specific fishing mortality rate was multiplied by. Bold values indicate cases where the change in the percentage of potentially poor and moderate years is less then 5%.

		Group 1		Group 2			
	g	Complete High	Complete Low	Reduced High	Reduced Low	ExtMethod 1	ExtMethod 2
% Poor/Moderate	0	23.6	22.2	4.9	3.0	2.6	0.6
	0.5	21.1	20.0	3.1	2.1	2.0	0.4
	1	18.3	18.8	2.0	1.6	1.7	0.3
	1.5	17.1	18.7	1.6	1.3	1.7	0.3
	2	15.5	18.4	1.1	1.5	2.4	0.4
	2.5	17.3	19.2	1.1	1.6	3.5	0.5
	3	18.0	22.5	1.1	2.7	6.1	0.8
	3.5	20.2	25.7	1.7	4.3	8.9	1.4
	4	23.4	28.2	3.4	6.7	15.2	2.0
	4.5	27.0	32.8	5.9	9.5	24.0	3.4
	5	32.1	37.3	10.2	14.0	33.2	5.2
	5.5	40.4	42.0	15.9	20.8	42.1	6.7
	6	46.2	48.2	25.1	29.7	51.1	8.5
	6.5	52.0	51.0	33.1	36.4	58.3	11.0
	7	55.3	55.7	43.7	43.1	63.0	12.9
% change	0	5.3	**3.4**	**2.9**	**1.4**	**0.9**	**0.2**
	0.5	**2.7**	**1.2**	**1.1**	**0.5**	**0.3**	**0.1**
	1	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**
	1.5	**-1.2**	**-0.1**	**-0.5**	**-0.3**	**0.0**	**-0.1**
	2	**-2.8**	**-0.4**	**-0.9**	**0.0**	**0.7**	**0.1**
	2.5	**-1.0**	**0.4**	**-0.9**	**0.0**	**1.9**	**0.2**
	3	**-0.4**	**3.7**	**-0.9**	**1.1**	**4.4**	**0.5**
	3.5	**1.8**	6.9	**-0.4**	**2.8**	7.2	**1.0**
	4	5.0	9.4	**1.3**	5.1	13.5	**1.7**
	4.5	8.7	14.1	**3.8**	8.0	22.3	**3.1**
	5	13.8	18.5	8.2	12.4	31.5	**4.8**
	5.5	22.0	23.2	13.8	19.3	40.4	6.4
	6	27.8	29.4	23.1	28.1	49.4	8.2
	6.5	33.6	32.2	31.1	34.8	56.6	10.7
	7	37.0	37.0	41.7	41.5	61.3	12.5

Table 6.11 Output from simulations of population models for sandeels at Shetland with no fishery on 0-group sandeels. Average catch (x10^3 tonnes) produced by seven recruitment models (see Chapter 6 text or Table 6.4 for details) under varying fishing mortality rates. % change = change from baseline models (*g*=1). *g* = constant by which each age-specific fishing mortality rate was multiplied by. Bold values indicated optimal catches (>40,000 tonnes)

t	Complete High	Complete Low	Reduced High	Reduced Low	ExtMethod 1	ExtMethod 2
0	0	0	0	0	0	0
0.5	11397	10537	12165	11872	12834	13721
1	22308	20536	23586	23139	24355	25692
1.5	31726	29106	33967	33142	34422	35922
2	**40318**	37177	**43357**	**42592**	**41471**	**43867**
2.5	**46470**	**43755**	**50990**	**50702**	**46991**	**50414**
3	**51841**	**47932**	**57770**	**56017**	**50602**	**54491**
3.5	**55688**	**51346**	**61546**	**59458**	**51513**	**57162**
4	**56440**	**53507**	**62988**	**61550**	**48961**	**58801**
4.5	**56920**	**53936**	**62454**	**61937**	**45493**	**58926**
5	**55515**	**52772**	**59617**	**61407**	**40760**	**58397**
5.5	**48870**	**52337**	**56409**	**57260**	36431	**58831**
6	**45585**	**45637**	**50182**	**51391**	33051	**57568**
6.5	**42268**	**45769**	**45736**	**47225**	28496	**56723**
7	**40122**	**43272**	**39879**	**41162**	26676	**55913**

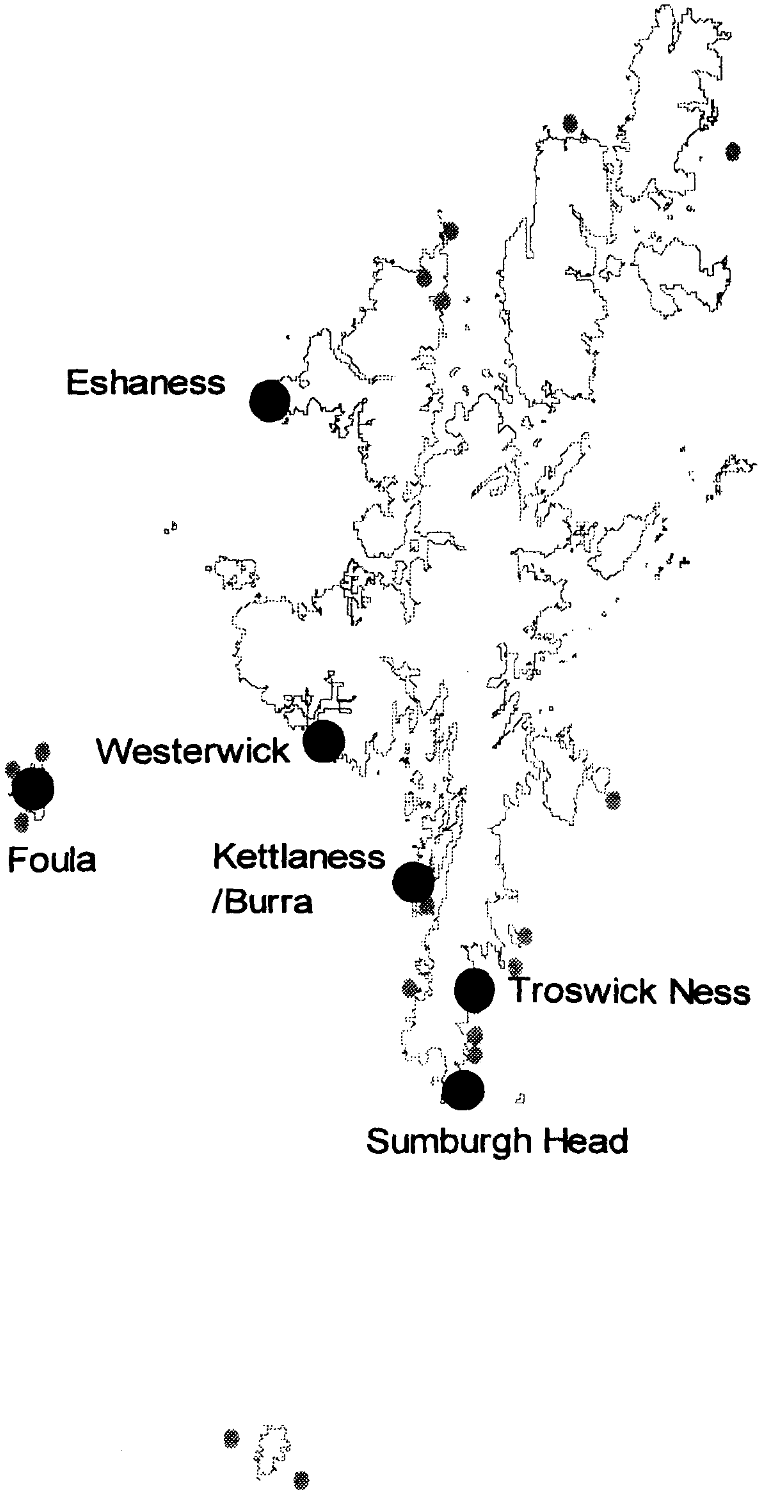


Figure 6.1 Map of Shetland. Black circles indicate seabird colonies mentioned in Chapter 6, Hatched areas indicate sandeel fishing grounds.

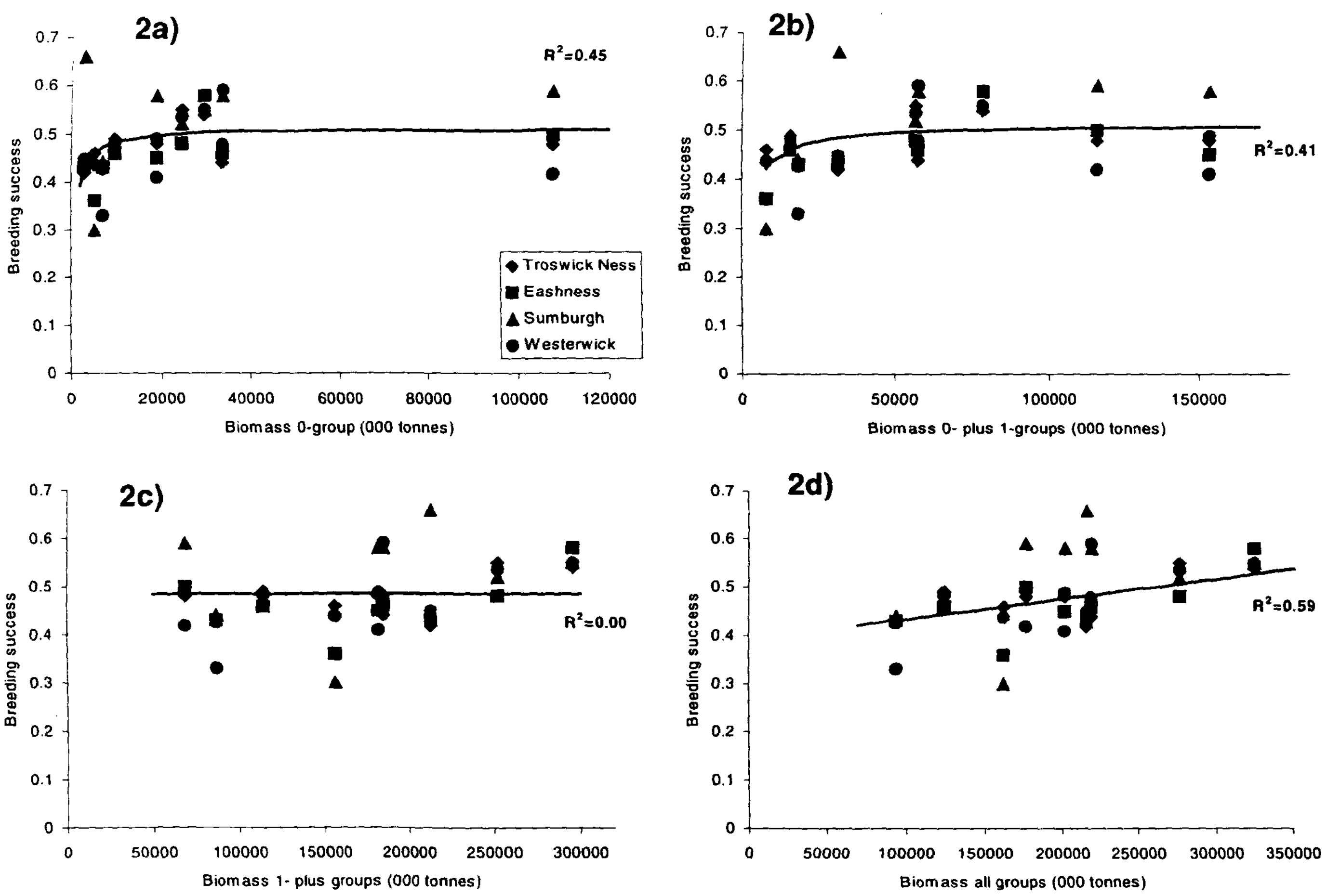


Figure 6.2 Mean fulmar breeding success (young fledged per apparently occupied nest) at colonies around Shetland over 1985-1993 inclusive (from Dunnet & Heubeck 1995) against estimates of sandeel biomass (from ICES 1999). Key to colonies given in **2a**. Weighted mean breeding success across all colonies shown as light circles. Trendline fitted to weighted mean breeding success and resulting R^2 shown for each measure of sandeel availability.

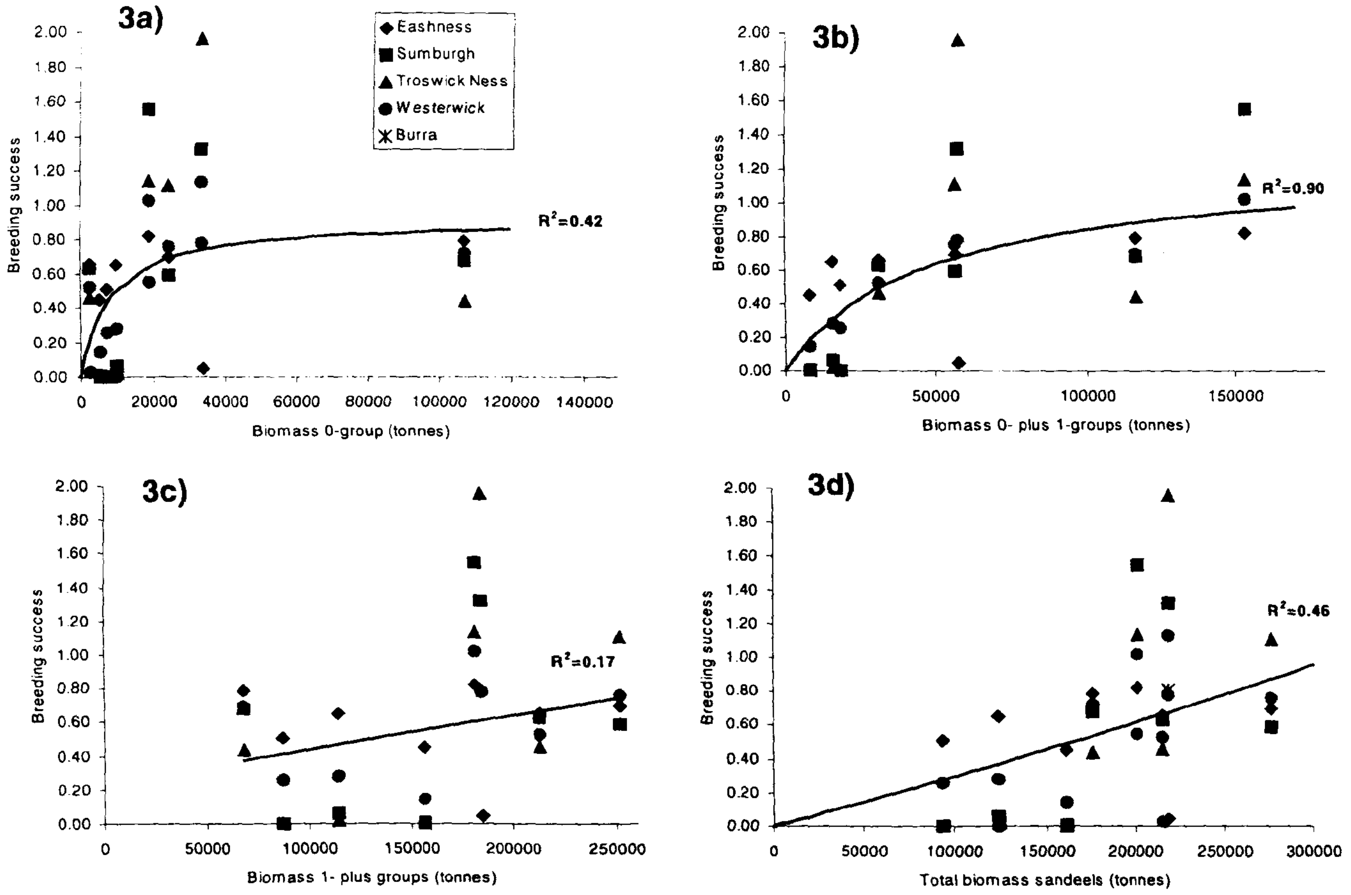
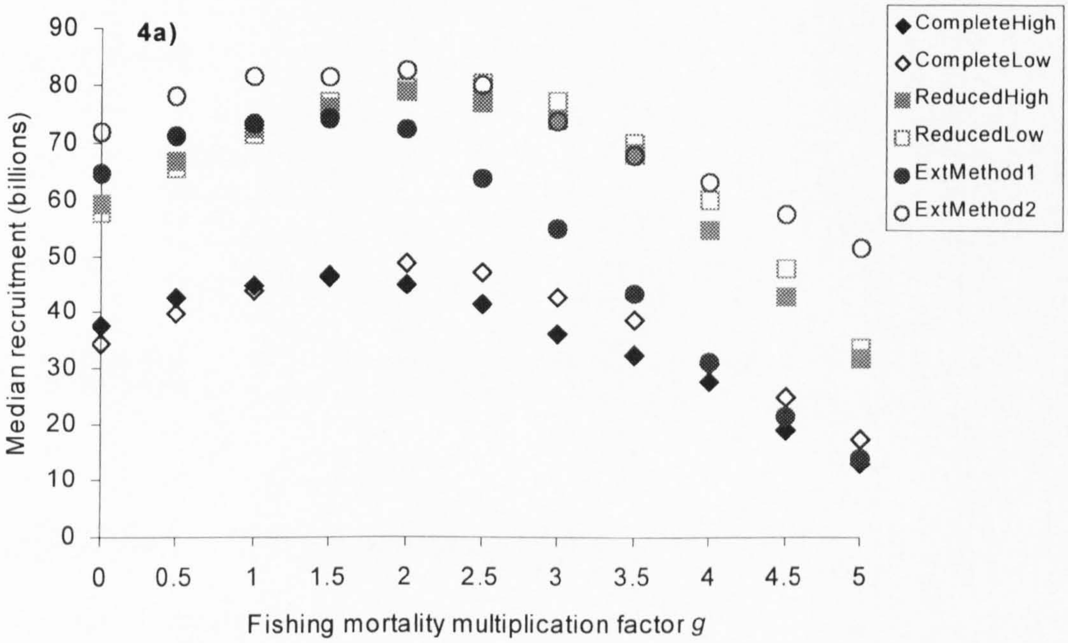


Figure 6.3 Mean kittiwake breeding success (young fledged per incubated nest) at colonies around Shetland over 1986-1993 inclusive (from Dunnet & Heubeck 1995) against estimates of sandeel biomass (from ICES 1999). Key to colonies given in **3a**. Weighted mean reeding success across all colonies shown as light circles. Trendline fitted to weighted mean breeding success and resulting R^2 shown for each measure of sandeel availability.



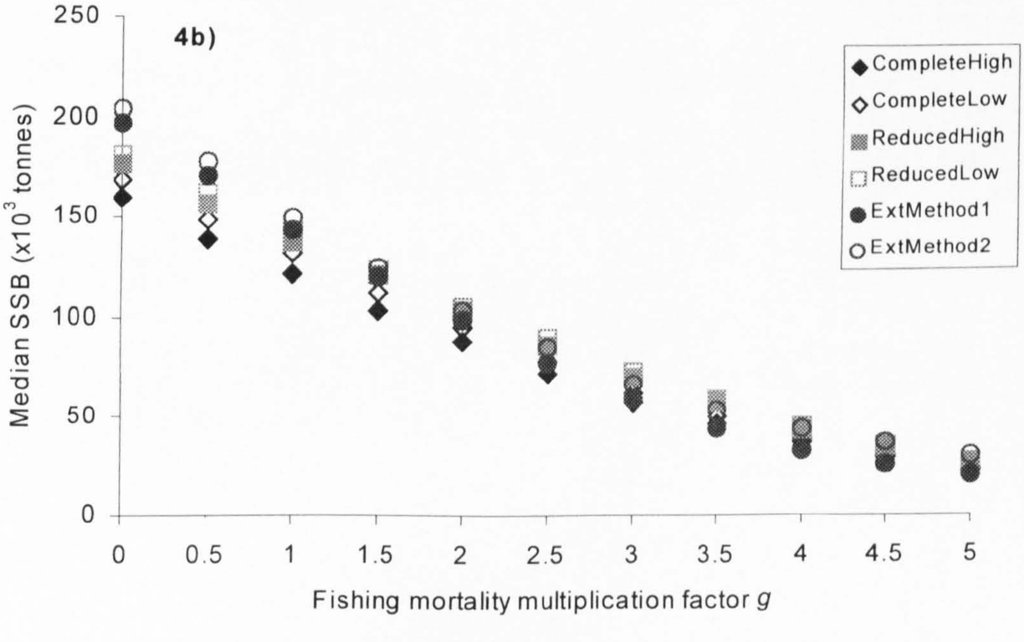


Figure 6.4 a) Median recruitment and **b)** median SSB produced by 1000 simulations of 24 years of a population model with six different recruitment models of sandeels at Shetland (see text for explanation of key) with varying values of *g*. Input fishing mortalities selected from a given distribution for each age class (see Chapter 3, Table 3.5), were multiplied by a constant *g*.

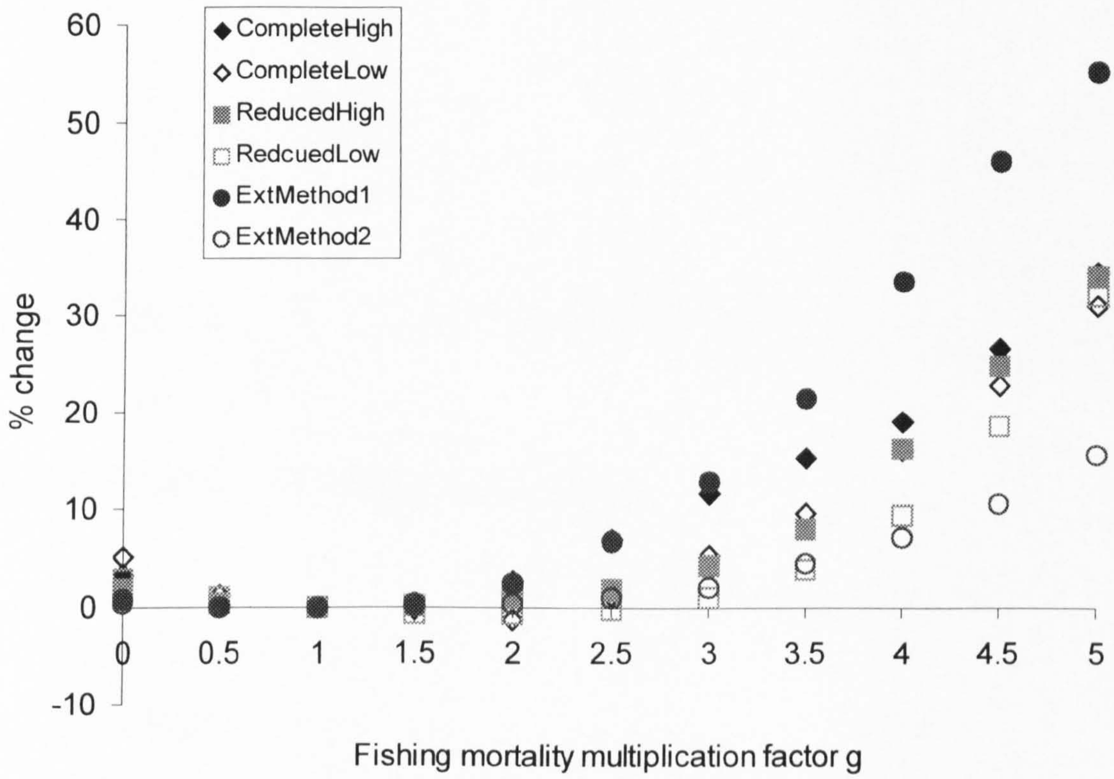
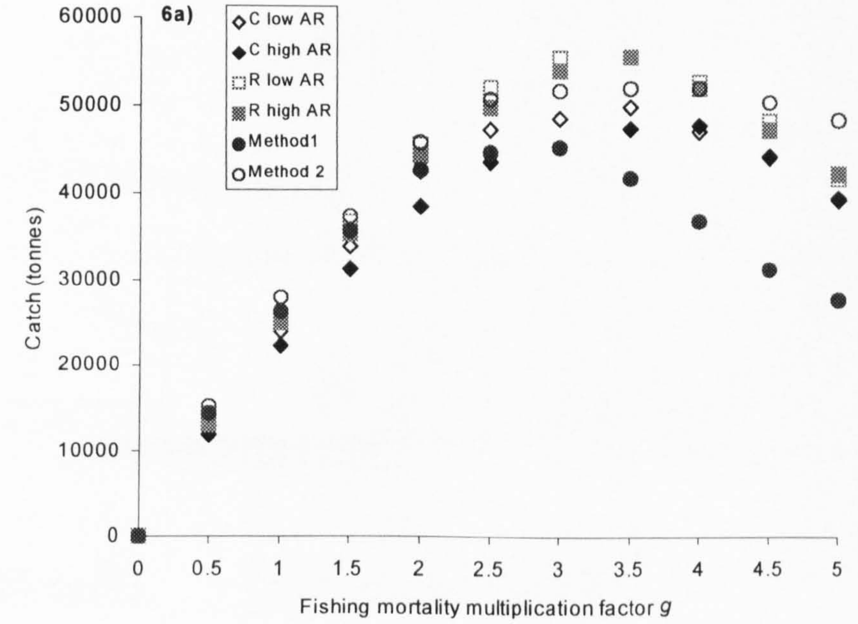


Figure 6.5 Output from 1000 simulations of 24 years of population model for sandeels at Shetland with six different recruitment models (see Chapter 6 for explanation of key). % change from the percentage of potential poor plus moderate breeding success years for kittiwakes at Shetland produced by the baseline model (g=1). Input fishing mortalities selected from a given distribution for each age class (see Chapter 3, Table 3.5), were multiplied by a constant *g*.



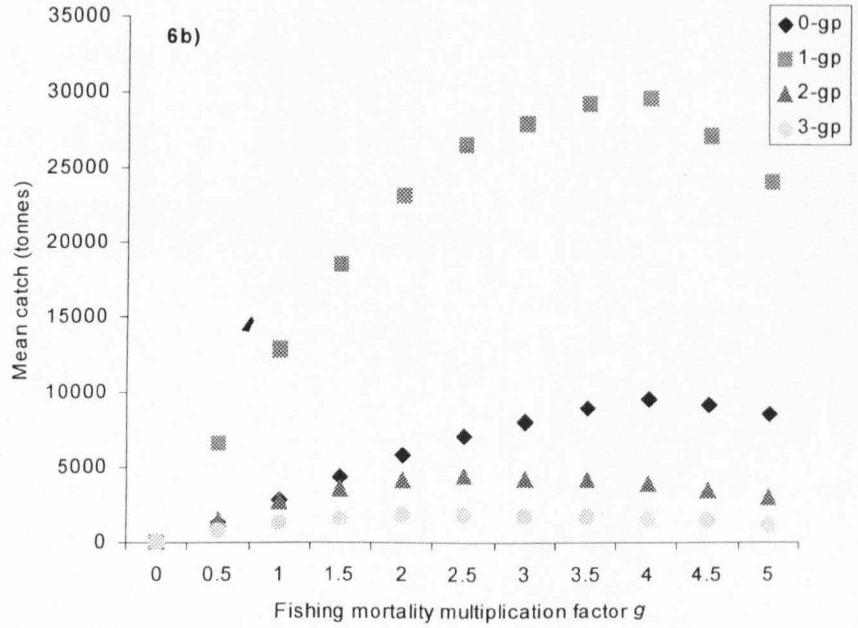
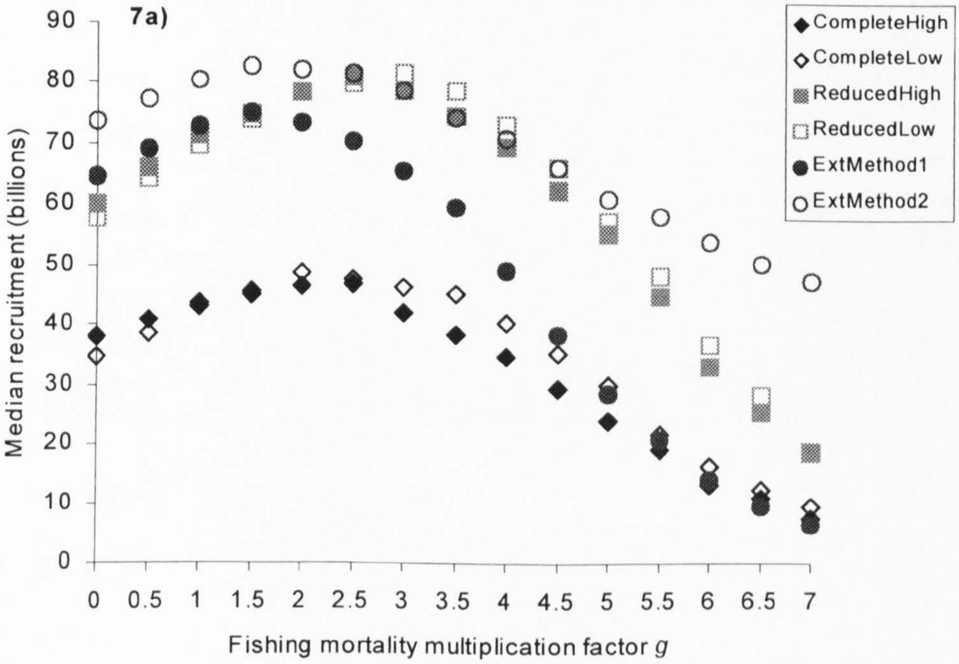


Figure 6.6 a) Mean total catch produced by 1000 simulations of 24 years of population model for sandeels at Shetland with six different recruitment models (see Chapter 6 for explanation of key) and *b)* mean catch of age classes 0-3 inclusive for CompleteHigh model only. Input fishing mortalities selected from a given distribution for each age class (see Chapter 3, Table 3.5), were multiplied by a constant *g*.



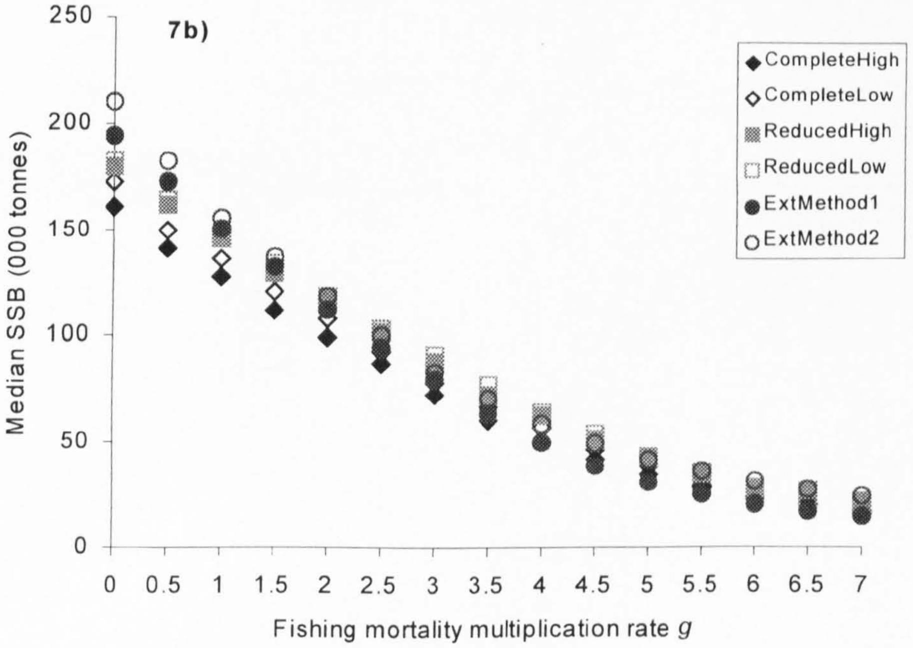


Figure 6.7 a) Median recruitment and **b)** median SSB produced by 1000 simulations of 24 years of a population model with six different recruitment models of sandeels at Shetland (see text for explanation of key) with varying values of *g*. 0-group fishing mortality set to zero for all models. Input fishing mortalities selected from a given distribution for each age class (see Chapter 3, Table 3.5), were multiplied by a constant *g*.

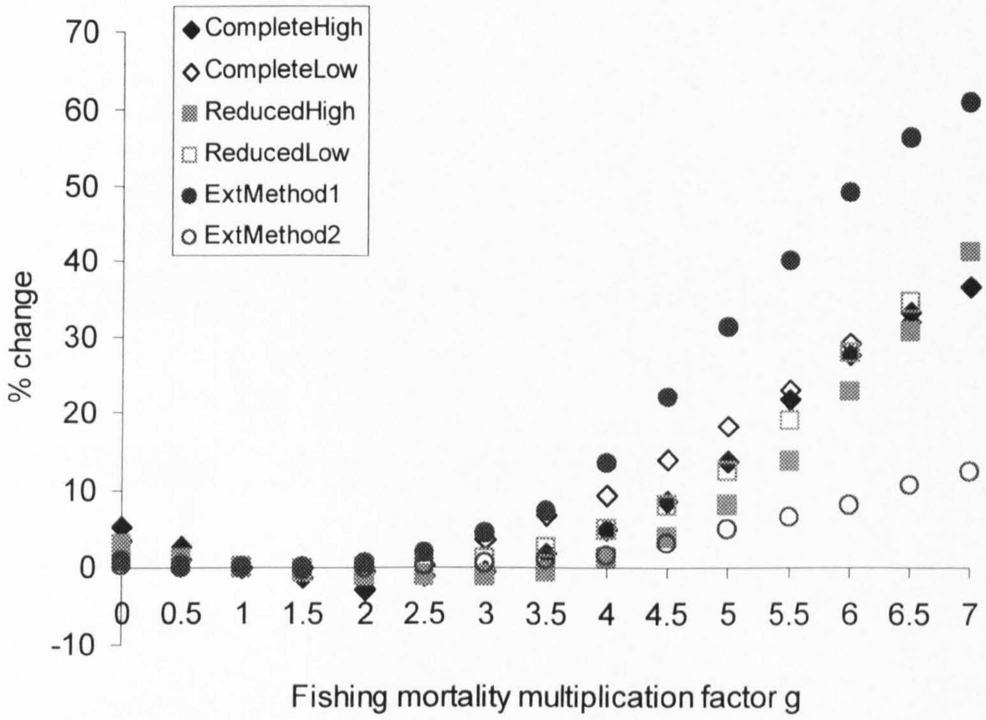


Figure 6.8 Output from 1000 simulations of 24 years of population model for sandeels at Shetland with six different recruitment models (see Chapter 6 for explanation of key) with 0-group fishing mortality set to zero. % change from the percentage of potential poor plus moderate breeding success years for kittiwakes at Shetland produced by the baseline model (g=1). Input fishing mortalities selected from a given distribution for each age class (see Chapter 3, Table 3.5), were multiplied by a constant *g*.

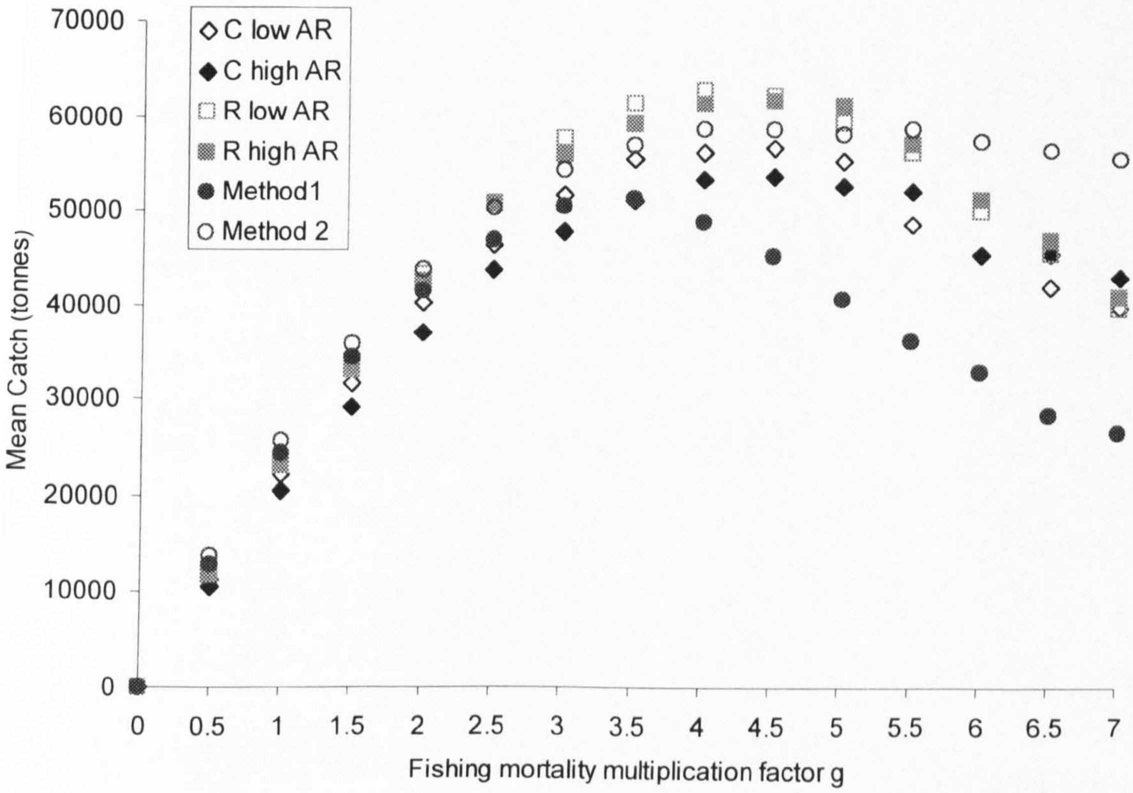


Figure 6.9 Mean total catch produced by 1000 simulations of 24 years of population model for sandeels at Shetland with six different recruitment models (see Chapter 6 for explanation of key). Input fishing mortalities selected from a given distribution for each age class (see Chapter 3, Table 3.5), were multiplied by a constant *g*.

CHAPTER 7

CONCLUSIONS AND DISCUSSION

7.1 Thesis Summary and Conclusions

Since improving our understanding of recruitment dynamics is vital for managing fisheries, this thesis has concentrated on analyzing recruitment patterns and developing models to simulate recruitment. In Chapter 3, recruit time series were analyzed to determine any underlying trends or patterns in the data and forecasting models - autoregressive or moving average models - fitted. Stock-recruit models were then parameterised (Chapter 4) but these highlighted the fact that four low recruit years, which occurred in the late 1980s when SSB was relatively high, were strongly influencing model fits. In Chapter 5, models to represent the hypothesis that net external recruitment occurs were developed. Chapter 6 tested selected models from the previous Chapters, under different fishing mortality rates, to analyze the potential impact on catch biomass and seabird breeding success.

The stock-recruit data used in this thesis were taken from the *Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak* (ICES, 1999). Estimates for population size, SSB and landings, as well as population parameters such as age-specific mortality rates, were given for the years 1974-1997 inclusive for Shetland sandeels and 1976-1996 inclusive for the North Sea stock. Subsequent working groups have provided further estimates for the North sea stock (recruit estimates for 1998 and 1999 and SSB for 1998, 1999 and 2000; ICES, 2001) though not for the Shetland stock.

The Shetland stock is now managed on a three-year basis, so the next assessment review is due in 2001. An attempt was made to update the assessment by the working group in October 2000 (ICES, 2001). This proved extremely problematic for reasons including missing survey data years and the years of closure of the fishery. No updated assessment was produced but survey indices (mean number of fish per 30 minute tow) indicate that 1998 was probably a moderate recruitment year - 559,200 caught 0-groups per 30 minute tow, close to the average of 648,962 from previous years. 1999 was a very good year – 1,166,590 0-groups were caught per 30 minute tow comparable with the 1,009,020 0-groups caught per 30 minute tow in 1991 when recruitment was extremely high (ICES, 2001). However, only 7,920 0-groups were caught per 30 minute tow in 2000 – this is the lowest survey index for 0-groups returned over 1984 - 2000 inclusive (excluding 1987 and 1995 for which no data exists).

Because of high natural mortality rates and few year classes in the fishery, deterministic models are difficult to define for sandeel stocks (ICES, 2000). As cited by ICES (2001): "stock-recruit relationship for North sea sandeels indicates there is no clearly defined relationship between stock and recruitment over the observed stock sizes". Therefore, one of the criteria set within this thesis, namely to simulate recruitment using stock-recruit models proved to be very challenging. In view of the apparent lack of relationship between spawning stock and recruitment, time series analysis was applied to the recruit data to expose patterns in the data. This is an important step to understanding fluctuations in recruitment (Zheng, 1997) and these models can be combined with traditional stock-recruit models.

In Chapter 3, the recruit time series for both the Shetland stock and the North Sea sandeel stock were analyzed for trends and quantitative forecasting models considered. A first-order autoregressive model was parameterised for the North Sea sandeel recruit time series (Figure 3.5a). Based on an estimated recruitment in the North Sea of 198 billion in 1997 (from ICES, 1999), the autoregressive model predicted recruitments of 994 billion in 1998 and 337 billion in 1999. The actual estimates from the latest assessment (ICES, 2001) are 440 billion in 1998 and 874 billion in 1999 – very different to the autoregressive model. Why are the predictions so different to the actual estimated recruitments?

Firstly, the estimate for 1997 (198 billion) on which future projections were based was increased in the later assessment (ICES, 2001) to 349 billion. Substituting this value in the autoregressive model parameterised in Chapter 3, reduces the model projection for 1998 from 998 billion to 683 billion – closer to the actual estimated recruitment of 440 billion. While 440 billion in 1998, predicts a recruitment of 585 billion in 1999, closer to the actual estimate of 874 billion. Secondly, the model assumes an alternating pattern of high and low recruitments, but the historical data does not always follow this pattern (Figure 3.2c). In the early 1990s the pattern changed to a 3-year cycle of 2 high recruitments followed by 1 low recruitment. The high recruitment in 1996 appears to have been followed by two low recruitments in 1997 and 1998. Based on the estimated historical recruitment in 1999 (874 billion) the model predicts a low recruitment of 370 billion in 2000.

For the Shetland data, an autoregressive model was also parameterised to simulate recruitment (Chapter 3, Figure 3.5b). The autoregressive model for Shetland sandeels closely tracked the noise in the series but with a lag, therefore the model could not be used to predict recruitment. However, it was suitable for produce recruitment series in population model simulations.

Although the relationship between stock and recruitment appears weak for both North Sea and Shetland sandeels (Chapter 4, Figure 4.2), it cannot be ignored if exploitation rates increase. It is expected that as SSB is reduced through exploitation, eventually the probability of a good recruitment will be seriously impaired. Therefore, stock-recruit models were considered in Chapters 4 and 5 and were combined with first order autoregressive models to autocorrelate recruitment. The initial intention was to use a Shepherd (1982) stock-recruit model to simulate recruitment at Shetland. However, bootstrap analysis showed that generally no relationship was found between SSB and recruitment for the Shetland sandeel data. Approximately 25-40% of simulations returned a "constant recruitment" model as the best fit, that is there was no influence of SSB on recruitment. The less complex Ricker model was therefore applied to the stock-recruit data.

Ricker stock-recruit models have only two unknown parameters and can be parameterised by simple linear regression (unlike Shepherd models). Bootstrap analysis was also applied to this model and a curve with 95% confidence intervals was parameterised (Figure 4.10a). The lognormal variability about the curve was extremely high (1.01) and this was due to the four very low recruit years (<13 billion) which occurred in the late 1980s when SSB was generally high (76-184 x10^3 tonnes). This prompted the question: are these low recruit years typical of the range of recruitment for the given SSBs or can they be considered outliers?

In 1983, an estimated SSB of 183 x 10^3 tonnes produced an estimated recruitment of 109 billion yet four years later, in 1987, a similar sized SSB of 184 x10^3 tonnes produced an estimated recruitment of only 3.7 billion – a reduction of approximately 97%. On the other hand, an estimated SSB of 153 x10^3 tonnes in 1988 produced an estimated recruitment of 13 billion and similar sized SSBs in 1994 (155 x 10^3 tonnes) and 1995 (152 x 10^3 tonnes) also produced low recruitments of 34 and 23 billion respectively. Therefore, it is difficult to conclude if these data points are outliers.

Removing the four low recruit years enabled a Shepherd model with 75% confidence intervals to be identified, suggesting these years may be extreme values (as they were obscuring the model fit previously). A Ricker curve with 95% confidence intervals was also parameterised using the reduced data set. Biologically, there is no justification for removing the data points, but the 95% confidence intervals indicate the two Ricker curves may not be significantly different. But how much confidence can we have in the model fits?

As discussed by Sparholt (1996), if recruitment is positively autocorrelated then SSB may not be independent of SSB in previous years and so of recruitment. Trends in recruitment may occur before trends in SSB – as is seen in the Shetland sandeel data (Figure 3.1b). This can be seen clearly in Figure 7.1 where the increase and decline in recruitment between 1979 and 1987 is closely followed, at a lag of 3 years, by SSB. This pattern alters when the large recruitment, after several poor years, in 1991 causes a large increase in SSB two years later (not three).

Therefore, the independent variable (SSB) has some dependence on the dependent variable (recruitment) - this violates one of the basic assumptions of linear regression and reduces certainty in the fitted models.

Alternative approaches are being developed to predict recruitment than as a deterministic function of SSB, for example the recruit states mechanism, discussed in Chapter 3, proposed by Gilbert (1997) or the probabilistic approach proposed by Evans & Rice (1988) and further explored by Cook (2000). The deterministic stock-recruit model approach was taken in this thesis as this is a fundamental concept for fishery management which is still widely used today and generally one of the first steps taken when entering this field. Secondly, the relationship between stock and recruitment cannot be ignored especially if SSB reduces with heavy exploitation (Myers & Barrowman, 1996).

Chapter 4 produced models for the Shetland stock which assumed no net external recruitment. But what if there is a sizable input of external recruits into the system? This will obscure stock-recruit relationship at Shetland as not all the recruits originate from the local spawning stock and may have implications for the persistence of the stock and for breeding seabirds. As the frequency and size of external recruitment to the Shetland stock is unquantified the approach taken in Chapter 5 was to identify a measure for local recruitment. It was assumed that the stock-recruit relationship at Shetland was similar to that in other areas of the North Sea, so Ricker models were fitted to the North Sea stock and the mean curve was scaled down for use with the Shetland data. Surprisingly, there was very little difference between the two curves (Chapter 5, Figure 5.5). Two extra years of data (1998 & 1999) are now available for the North Sea sandeel stock and the estimated recruitment in 1997 has been increased from 198 billion to 349 billion. The parameters of the North Sea Ricker model were updated by re-running bootstrap analysis. The new data made very little difference to the mean Ricker curve but decreased the 95% confidence intervals (Figure 7.2).

If the Ricker curve parameterised using the reduced Shetland data set is considered, the average recruitment predicted for a given SSB is higher than that predicted by the scaled North Sea curve (Figure 5.5). This model was selected to develop models with external recruitment the exploit the phenomenon of additive variances. The first method simulates total and local recruitment as a function of SSB, the difference being external recruits. However, external recruitment is linked to local recruitment and SSB in this method, so as the stock reduces the probability of a large external recruitment reduces. It was assumed this was unlikely (for the hypothesis that external recruitment forms an independant significant addition to the

Shetland sandeel stock), so this model was rejected for simulations altering fishing mortality rates. The second method assessed the distribution of external recruits output by the baseline model of the first method and used this distribution to simulate external recruitment. External recruitment is therefore independent of both local recruitment and SSB, so a large external recruitment may occur when SSB is low. However, there will be no affect of density dependence on external recruits at high SSB levels.

Chapter 6 varied input fishing mortality rate in the models and assessed the potential impact on fishery catches and for breeding seabirds. The performance of the recruitment models developed in Chapter 4 and Chapter 5 were tested under a range of input fishing mortality rates. A function was developed to indicate potential breeding success of kittiwakes at Shetland. Two levels of positive autocorrelation were also tested for the models with no net external recruitment (input autocorrelation coefficient equals 0.51 and equals 0.73). It was found that increased autocorrelation reduced the median recruitment, median SSB and mean catch for each recruitment model and increased the proportion of years which were potentially poor or moderate for kittiwake breeding success. As a result of high autocorrelation, low recruitment years were more likely to occur as a series than as a single event.

With a fishery operating on all age classes, it was found that values of F, which were in the range of 1.5 – 2 times greater then the average values of F used in the baseline models (Table 3.5), produced optimal recruitments for all models and increased the potential proportion of poor and moderate kittiwake breeding success years by less than 3%. Mean catches produced by all models in this input F range were between 31,000-46,000 tonnes. The highest catches (48,000-58,000 tonnes) were produced when input F was 3.5-4 times larger than in the baseline models. The models indicate that a substantial catch (31,000 tonnes) could potentially be landed each year with little adverse affect on recruitment or breeding seabirds. Landings of around 52,000 tonnes, the highest on record (1982), may potentially reduce median recruitment by as much as a third for the recruitment models assuming no net external recruitment and parameterised using the complete data set but have less affect in the remaining models.

Simulations were rerun without exploitation of 0-group sandeels. This is assumed to mimic the present strategy of closing the fishery for June and July to avoid competition with breeding seabirds (if all catch is taken before this). Very few 0-groups will be landed before June and fishing only resumes in August if the TAC is not taken. It was found, considering all models, fishing mortality rates in the region 2-2.5 greater than input F in the baseline models optimized median recruitment while increasing the portion of potentially poor and moderate kittiwake breeding success years by less than 1%. The mean catch from the models over this fishing mortality range was 37,000-51,000 tonnes – higher than the mean catches for the optimal F range identified in the models with a fishery on all age-classes and similar to the highest recorded landings of 52,000 tonnes in 1982.

In summary, a number of models were developed to simulate potential recruitment dynamics for sandeels at Shetland – including models with external recruitment. Simulations varying fishing mortality rate indicated a fishery that does not exploit 0-group fish could sustain higher catches with little additional adverse affect on kittiwake breeding success. Depending on the recruitment model selected, optimal catches occur in the range 37,000-51,000 tonnes for this fishery.

These models represent a simplified view of our perceptions of sandeel population dynamics at Shetland. The input data was simply the population parameters and estimates produced by assessments of the stock (ICES, 1999). Therefore, the input data was itself the output of a model and, as stated by ICES (1999), cannot be regarded as absolute levels due to the sensitivity of the models to input data. Conclusions from the models developed in this thesis therefore cannot be taken as absolute levels and must be viewed with caution.

7.2 Further Work

There are two main expansion routes for these models, either temporally and/or spatially, if suitable data is available. There are a number of fishing grounds around Shetland (Figure 2.9) so ideally a spatial model would be based on these grounds. A spatial model could supply insight into fishery management strategies such as closed areas. Lauck *et al.* (1998) propose the use of marine reserves – protected areas – as a method of "bet-hedging" against management limitations thus enhancing long-term sustainable exploitation. Expanding the models to include the Orkney grounds, as suggested by the revised stock divisions proposed Pedersen *et al.* (1999), could improve estimates but little data exists for sandeel populations in this area.

The models could also be developed temporally in order to explore the potential affects of the current management strategy of a closed season in June and July, as well as variation in the availability of sandeels. Evidence suggests that the catchability of larger sandeels is reduced earlier in the fishing season than smaller sandeels (Pedersen *et al.*, 1999). Rindorf *et al.* (2000) present evidence that breeding success in three seabird species: common guillemot, shag and kittiwake, on the Isle of May (Scotland) were related to the availability of 1-group and older sandeels and the timing of peak sandeel availability influenced seabird reproductive output. Additionally, the appearance of external recruits is assumed to occur later than local recruits (Wright, 1996). The timing of this second peak could have important implications for seabird breeding success.

7.3 Discussion

As shown in model simulations in Chapter 6, the occurrence of net external recruitment may be important not only for fishery management and stock persistence, but also for the breeding success of seabirds at Shetland. Potential breeding success of kittiwakes was found to be relatively unaffected over a large range of fishing mortality rates when independent external recruitment was included in the model. The stock could also support relatively high catches by the fishery. This raises concerns as the local SSB may have decreased to such low levels that, if the pre-recruit transport mechanisms fail, the stock may not be self-supporting.

Proctor *et al.* (1998) postulate that larval advection into Shetland waters may be an important factor influencing recruitment. It is expected that a net gain of recruits from outside the Shetland system would obscure the stock-recruit relationship at Shetland and, as seen from the difficulty in parameterising stock-recruit models (Chapter 4), there is no clear defined relationship. However, there is no clear stock-recruit relationship for North Sea sandeels either (Chapter 5) and it is assumed, on a North Sea scale, that immigration to the stock would be negligible.

How much mixing is there between populations? It appears that mixing of sandeels occurs at scales of 200 km or less (Wright *et al.*, 1998 cited by Pedersen *et al*,. 1999). The stock divisions for sandeels in the North sea have been recently revised for assessment purposes based on work on the population structure (Pederson *et al.*, 1999). The new area proposed for Shetland is much larger and includes Orkney and the area North of mainland Scotland. However, little or no information exists on population size and structure outside of commercial fishing grounds including the area around Orkney. If larval advection results in a net gain of recruits to Shetland as suggested by Wright (1996) then the "effective" SSB, that is the SSB in the entire region from which recruits originate (Rothlisberg *et al.*, 1996), for Shetland sandeels will vary between years depending on the larval transport strengths (as the spatial extent of the areas of origin may shrink or expand depending on larval transport mechanisms). This could account for the poor relationship between stock and recruitment for sandeels at Shetland.

What did happen in the late 1980s? Four extremely low recruitment years occurred (<13.1 billion) when SSB, initially, was high (184 x10^3 tonnes; Figure 2.2).

It is now accepted that the decline in the stock was not fishery-induced. Could it be due to a reduction or halt of larval transport mechanisms as discussed above?

In Chapter 2, the recruit time series for sandeel grounds around Shetland were analyzed for synchrony. This indicated that generally the grounds could be considered synchronized – 19 of 105 combinations were significant at P=0.05 for 0-group series and 10 of 105 for 1-group series. There are main three routes by which synchronization could occur – high dispersal, large-scale environmental perturbations or both (Moran, 1953; Ranta *et al.*, 1995). Certainly, high dispersal of recruits is feasible – deployment of drifting drogues indicated that current transport in the vicinity of south-east Shetland may be rapid (Wright & Bailey, 1993).

Large-scale environmental perturbations are also hypothesized to synchronize populations (Moran 1953) and evidence exists that this may occur in fish stocks and is strongest in neighbouring stocks (Ranta *et al*,. 1995; Zheng, 1997; Fox *et al.*, 2000). It would be interesting to see if time series of 0-groups on grounds around Shetland are also synchronized with 0-group numbers in adjoining areas and at Orkney. Unfortunately, this data was not available. However, an indication of sandeel abundance may be found in seabird population data. It has been suggested by a number of authors that seabird data could provide additional information on fish stock abundance (for example Cairns, 1987; Bailey *et al.*, 1991; Cairns, 1992; Montevecchi & Myers, 1996).

In Chapter 6, it was shown that kittiwakes could be considered particularly vulnerable to changes in 0- and 1-group abundance and a function of potential kittiwake breeding success against 0- and 1-group biomass was constructed. Breeding success at many kittiwake colonies around Shetland was low in the late 1980s when sandeel recruitment was very weak (Heubeck, 1989; Harris & Wanless, 1990; Dunnet & Heubeck, 1995). Breeding success of kittiwakes around UK coasts over 1986-1988 was assessed by Harris & Wanless (1990) and a negative relationship was found between breeding success and latitude of colonies in the northern North Sea. In 1988, when the second lowest recorded recruitment occurred (after 1987) and many kittiwake colonies at Shetland failed completely (Dunnet & Heubeck, 1995), the north-south trend in breeding success was significant over the whole length of eastern Britain (Harris & Wanless, 1990). No similar trend was found in the breeding success of colonies on the west coast of Britain. Evidence suggests that food shortage during chick rearing was responsible. Harris & Wanless postulate that this could be result of environmental changes occurring in the North Sea as sea surface temperature around Shetland was extremely high between 1986 and 1988.This warm water extended far down the east coast of Britain in 1988. They conclude that while sea surface temperature alone probably is not a controlling factor, it may be indicative of more profound oceanographic changes.

It is unlikely that a single environmental parameter alone is influencing recruitment and identifying the mechanisms by which the two are related may be difficult. This area was reviewed by Myers (1998) who retested the success of published environment-recruit correlations using new data – only a low proportion were verified on retest. Nearly all the correlations with temperature that held were with populations close to the northern or southern limits of their ranges. Monaghan (1992) showed the sea surface temperatures for Shetland given by Harris & Wanless (1990) were significantly negatively correlated with sandeel recruitment. Arnott (unpublished) showed that sandeel recruitment in the North sea can be considered correlated with the North Atlantic Oscillation (hereafter NAO) – a natural large-scale pattern of disturbance of the atmospheric circulation and climate of the Atlantic-European region (linked to westerly wind flow). How could this impact on sandeel recruitment?

There are considered to be three major northerly routes for the inflow of Atlantic water into the North Sea: through the Fair Isle channel between Orkney and Shetland, southwards along the Norwegian Trench and southwards along the east coast of Shetland (Turrell 1992). Turrell (1992) considers sandeel recruitment as a possible indicator of climate change and suggests the high recruitment at Shetland during the mid-late 1970s may be the result of a reduction of the proposed Atlantic inflow to the east of Shetland. When sandeel larvae are in the plankton, the inflow east of Shetland is predominately wind-driven. A reduction in the strength of the inflow may increase the retention of locally spawned larvae at Shetland. The sea circulation model adapted by Proctor *et al.* (1998) did not support this hypothesis but conversely suggested that larval advection to Shetland is important.

Holliday & Reid (2001) suggest that there is a connection between pulses Atlantic water entering North Sea and ecological changes in the North Sea ecosystem. Two ecological shifts appear to have occurred during the late 1980s (when sandeel recruitment was extremely low) and in the late 1990s - the Continuous Plankton Recorder survey suggests that these events are unusual in a time series of more than 50 years. Around 1988 (the second lowest year on record for sandeel recruitment after 1987), a significant ecological shift is thought to have occurred, as seen in changes of abundance of planktonic species. The incursion of Atlantic water, early in the year in 1988, is thought to have been in the form of a pulse rather then a prolonged period of increased transport. A further incursion occurred late in the year (September onwards) in 1997 (year of highest recorded sandeel recruitment). These pulses happened when circulation in the Rockall Trough was unusual and it has been suggested this is related to the NAO (Reid *et al.*, 1998). Reid *et al.* (2001) demonstrated, using a 3-dimensional mathematical model to measure integrated Atlantic inflow into the northern North Sea, that periodic changes in the plankton records for the North Sea after 1987 are likely to be the consequence of changes in atmospheric circulation reflected by the NAO index.

Is it a coincidence that extremely low recruitments for sandeels at Shetland were recorded during the late 1980s when a marked ecological shift is thought to have occurred in the North Sea bought about by a sharp intrusion of Atlantic water? The regime shift in plankton may affect the trophic structure of the North Sea and therefore may affect the survival of sandeel larvae and recruits. Large increases in the catch of horse mackerel in areas of the northern North Sea coincided with these observed planktonic and environmental changes (Reid *et al.*, 2001). Sherman (1981) presented evidence that an increase in abundance of sandeel species in the north-west Atlantic and North Sea during the late seventies was probably due to changes in the trophic levels of the ecosystem though Sherman suggests this excludes the hypothesis of environmental change. The decrease in herring and mackerel stocks during this period may have resulted in an increased food supply for sandeels through reduced competition and an increased survival of sandeels due to reduced predation.

Planque & Fromentin (1996) and Fromentin & Planque (1996) demonstrated a significant negative correlation occurs between the zooplankton *Calanus finmarchicus* and the NAO in the north-east and the North Sea. *Calanus* is known to be a prey item of sandeels (Reay, 1970). Wright & Bailey (1993) found trends in *Calanus finmarchicus* in the Orkney-Shetland region did generally correspond with changes in sandeel recruitment. They conclude changes in sandeel year-class strength and zooplankton dynamics could be related by an environmental event - nature of which is unclear but the changes in zooplankton have been ascribed to increased Atlantic inflow into the North Sea. However, as sandeel larval advection to Shetland may also ascribed to changes in Atlantic inflow (Wright, 1996), it is likely that a combination of factors are affecting recruitment at Shetland.

If environmental conditions are an important factor producing extremes in sandeel recruitment, deterministic stock-recruit models may not be adequate tools for management – especially in light of current concerns about climate change. As shown in this thesis, development of robust stock-recruit models is difficult without further understanding of processes acting on recruitment. An approach such as that suggested for South African anchovy by Cochrane & Starfield (1991) would be more robust. Anchovy stocks also exhibit extreme fluctuations in recruitment and are short-lived fish (so the fishery is dependent on the lower age classes). Cochrane & Starfield suggest methods to predict recruitment early in the year and demonstrate that if good predictions of recruitment could be made before the start of the fishing season, TAC could be altered accordingly and model simulations indicated this would increase catches theoretically by up to 48%. Although, the increased interannual variation in catch may be detrimental to the fishing industry. Troadec *et al.*, (1980) also suggest a sound management strategy for mackerel and anchovy off California, which exhibit natural long- and medium-term fluctuations, would be to capitalise on good years when they occur.

To conclude, although the TAC for the Shetland fishery is low and SSB appears to be recovering, low recruit years are still occurring. Our knowledge of ecosystem functioning desperately needs to be improved, especially in light of possible climate change. Tragically, reports from the Fair Isle Bird Observatory for this year (2001) tell of mass starvation of Arctic tern chicks – latest reports are that only seven Arctic tern chicks have been fledged from 2,840 breeding pairs (Fair Isle Bird Observatory web site). Breeding guillemots, kittiwakes, puffins and razorbills are also badly affected. It seems that sandeel availability, which appeared to be abundant at the start of the breeding season, has dropped.

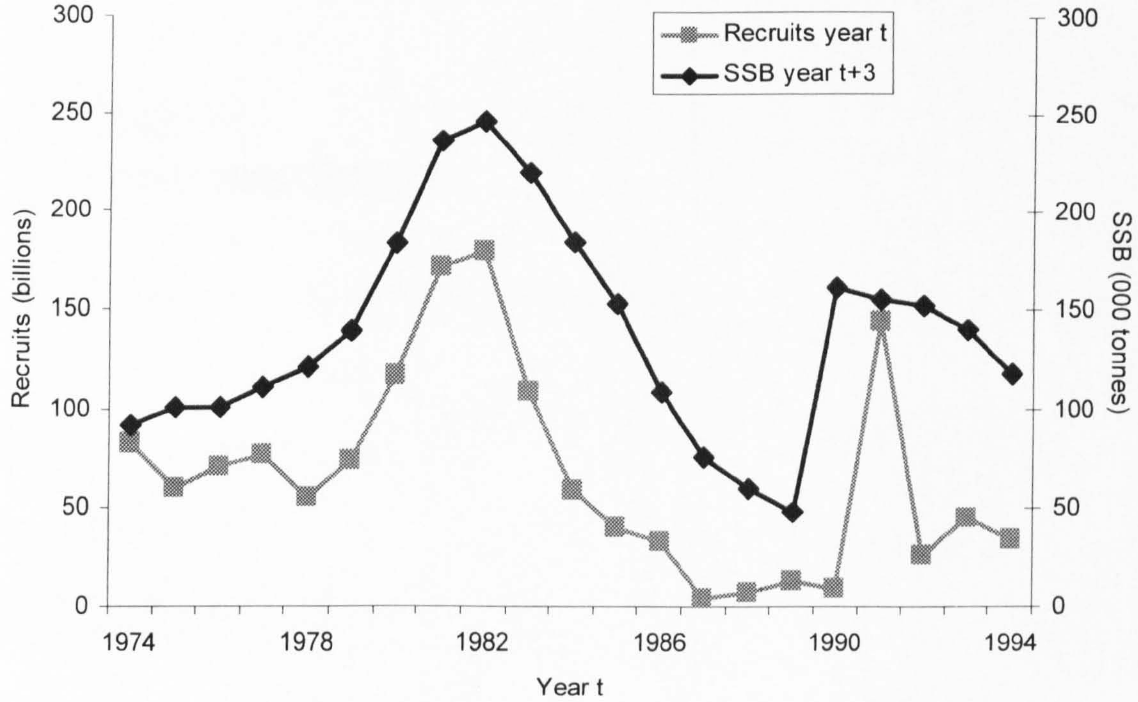


Figure 7.1 Trends in sandeel stock at Shetland (from ICES 1999). Recruitment in year t and SSB in year t+3.

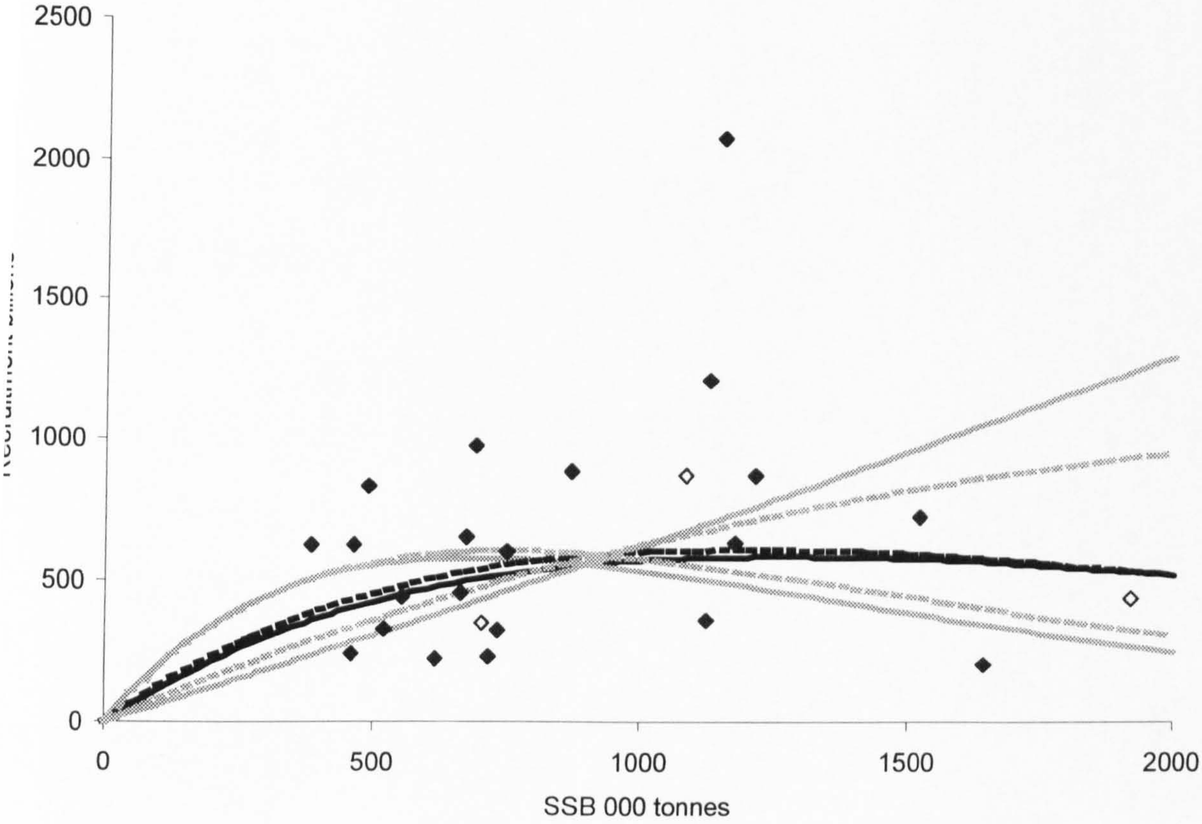


Figure 7.2 Sandeels in the North sea. Ricker model with 95% confidence intervals parameterised using data 1976-1996 inclusive (solid lines; from ICES 1999) and using data 1976-1999 (dotted lines; from ICES 2001).

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