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The current state of knowledge on the ecology and interactions of North Sea Herring within the North Sea ecosystem

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1. Summary

The high phenotypic plasticity in Atlantic herring (Jennings & Beverton, 1991; McQuinn 1997) makes the influence of the environment fairly strong on most characteristics of the North Sea herring population (Cushing, 1967). It also results in many substock components (Heinke, 1898; Redeke & van Breemen, 1907; Cushing, 1955; Zijlstra, 1958; Blaxter & Hall, 1960; Bridger, 1961) that interact with each other and are influenced in different ways by the environment (Wallace, 1924; Antony & Forgarty, 1985; Hulme, 1995). There are also strong density dependent effects in the population characteristics (Cushing & Bridger, 1966; Hubold, 1978; Winter & Wheeler, 1997) that are currently very pertinent as the population has increased substantially in the late 1990s (Nichols, 2001; ICES 2004). Whilst most studies on North Sea herring refer to winter rings rather than ages, for simplification the term age and year will be used in this work. (However remember that for most North Sea herring spawning occurs at age –1). Surveys used to study herring life stages are listed in appendix 1.

2. Life History Traits

Life span to between 17-20 years (38-39 cm length; RIVO data). North Sea herring currently mature at between 2 and 3 years although this changes over time (3-5 years in 1950-60s, Cushing, 1967) with population size and individual year class strength (ICES, 1965; 2004; Burd, 1978; 1984). Mean length at maturity also expresses a trend of rising from the 1930 to the 1970s and then declining (mean length mature 25-27cm at age 2, 26-28 cm at age 3, Saville, 1978). Atlantic herring is a synchronous determinate batch spawner (Bowers & Holliday, 1961; Blaxter & Hunter, 1982).

3. Spawning

Spawning of the main North herring population begins in the north of the North Sea in September and then progresses southwards with time, ceasing in January in the eastern English Channel (Boeke, 1906; Cushing & Burd, 1957, Zijlstra, 1969; Burd & Howlett, 1974; see Figure 1). Smaller coastal populations tend to spawn in the spring (Redeke & van Breemen, 1907; de Groot, 1980; Fox, 2001, Roel, *et al.*, 2004). The number of spawning sites varies with stock size (Burd, 1985; Corten 1999a; 2001a) with a decline in spawning sites at lower biomass of North Sea herring. Due to the phenotypic differences exhibited by herring associated with each spawning site or spawning season (Baxter 1959; 1963; Cushing, 1958; Almaraz & Bailey, 1989; Hulme 1995), the fecundity and egg size and obviously the associated sea temperatures result in larvae with different characteristics and energetic requirements (Sinclair & Tremblay, 1984; Heath *et al.*, 1997). From here on these different groups will be referred to as sub-components of the stock. Atlantic herring spawn benthic eggs that stick to the substratum or each other (Blaxter & Hunter, 1982; McPherson *et al.*, 2003). In the North Sea, herring use gravel beds that are generally between 20-40m depth (see Cushing & Burd, 1957; Parrish *et al.*, 1959). In thicker egg mats mortality due to oxygen deficiency can be high (Parrish *et al.*, 1959; Aneer, 1985) and the mats attract predators (spurdog, haddock, mackerel, lemon sole and other herring; Hempel & Schubert, 1969; de Groot, 1980; Skaret *et al.*, 2002, and personal observations).

Atlantic herring are spatial repeat spawners (McQuinn, 1997) and this behaviour is either caused by natal returns to the "home" spawning bed or adopted behaviour (Harden Jones, 1968; Wheeler and Winters, 1984; McQuinn, 1997 and references cited therein). Like Pacific herring, Atlantic herring are assumed to spawn in waves (temporally discrete cohorts, see Ware & Tanasichuck, 1989; McPherson *et al.*, 2003), but the evidence to support or reject this idea is weak. Recruits from one spawning will not necessarily mature in synchrony (McQuinn, 1997; Brophy & Danilowicz, 2003). Studies devoted to spawning and reproduction of North Sea herring are described and listed in appendix 2.

4. Feeding

The main feeding time of North Sea herring is from April to June (Hardy, 1924; Savage 1937). Feeding intensity reduces in the build up to spawning and little feeding occurs over winter (Hardy, 1924). As the majority of North Sea herring are autumn and winter spawners, they exhibit a different energy-strategy than Norwegian spring spawning herring (Isles, 1984; Winters & Wheeler, 1996; Slotte, 1999). Herring mostly feed by foraging and targeting prey items, with perhaps very limited filtering at low light intensities (Hardy, 1924; Batty *et al.*, 1986; 1990).

The prey of North Sea herring varies by location (Savage, 1937), season (Hardy, 1924) and year (Last, 1989). Larvae feed on nauplii and micro-zooplankton (Checkley 1982), moving onto *Pseudocalanus*, *Paracalanus* and *Temora* copepodites and small meroplankton and then the adults feed on *Calanus*, *Temora*, *Oikopleura*, Schizopoda, Amphipoda and juvenile *Ammodytes* spp (Hardy, 1924; Savage, 1937; Last, 1989). In the north of the area the gastropod *Limacina* is also prominent in the diet. The seasonality in stomach contents is clear, fish eggs are present in the very early spring (when the feeding rate is low; Daan *et al.*, 1985; RIVO unpublished data) and in June (Savage, 1937). *Calanus* is eaten in large numbers in the spring, and then the smaller copepods begin to dominate the diet by summer. In years when post-larval and juvenile sandeels are present in the stomachs (about 50% in the southern and western North Sea), they are present in substantial biomass in February through to April (Hardy, 1924; Savage, 1937; Last, 1989).

It is generally agreed that adult North Sea herring feeds in similar areas, whatever the subcomponent; to the north of the North Sea. Harden Jones (1968) suggested that there were subtle differences between the subcomponents but limited empirical proof has been found to support this hypothesis. It is clear that the distribution of feeding shoals is correlated with plankton abundance; herring shoals are rarely found near diatom blooms (Savage and Wimpenny, 1936), and their distribution whilst feeding is invariably associated with zooplankton abundance (Maravelias & Reid, 1997; Maravelias, 2001). Variability in spatial structure of these shoals tends to be at a scale of 6.5 and 20 nautical miles (Maravelias *et al.*, 1996), ignoring the unresolved small scale variability. The distribution of the feeding herring shows very strong affinity with the southerly incursion of *Calanus* and *Limacina* into the North Sea every year (Bainbridge and Forsyth, 1972), both of which are influenced by the Atlantic inflow. In years when the *Calanus* peak is further north, herring catches are also further north (Corten 2001b). The ratio between zooplankton production in the Buchan area, compared to the NE North Sea is also thought to influence where the herring feed (Bainbridge and Forsyth, 1972), as years with poor zooplankton production in the Buchan areas were also years when the herring moved further north (as determined by catches). Herring feeding shoals are often associated with feeding mackerel.

5. Wintering

The location of overwintering is based on knowledge from historic herring catches, however, detailed information, in the form of maps, is lacking. Harden Jones (1968), Burd (1978) and Corten (2000) assumed that overwintering occurs to the south west of Norway in most years. This is only applicable to those fish that have already spawned (the Shetland, Buchan and Banks components) as the Downs component is still spawning at this late stage in the year (Figure 3). Corten (2000) suggested that an early onset of *Calanus* production to the SW of Norway, results in a delay in the fish leaving this area to migrate to the normal feeding grounds. There is very little in the way of survey data to support the positions or the dynamics of the populations during the overwintering period and in recent years there is no fishery data on the overwintering fish to the east of the North Sea at winter time.

The location of overwintering may change over longer time scales (Alheit & Hagen, 1996; 1997; Corten, 1999b and references therein) when Open Skagerrak Periods or Bohsl n herring periods take place. These are when some of the overwintering herring enter the Skagerrak in wintertime.

6. Larval Drift and Nursery Areas

Due to the herring laying demersal eggs, the yolk sac larvae are highly associated with the spawning grounds (Postuma & Zijlstra, 1974). The abundance of young larvae is clearly linked to spawning potential (e.g. SSB) with a slight influence of temperature at time of spawning (Postuma & Zijlstra, 1974; Saville, 1978). Larval drift is thought to be driven by wind induced flows (Heath & Rankine, 1988; Heath *et al.*, 1997). The larvae drift up to 9km a day (Heath & Rankine, 1988). MIK (Methot Isaacs-Kidd) net surveys of post larvae show a general movement of the larvae in an easterly direction (Figure 4, ICES 2004). The abundance of herring post-larvae in the MIK net survey shows a strong relationship to the following associated recruiting yearclass at age 2 (ICES 2004; Nash and Dickey-Collas *in press*) suggesting that the year class strength is mostly determined between the larvae and post-larvae stages (see Anthony & Fogarty, 1985). Most post larvae metamorphose between April and July (Heath & Richardson, 1989). Variability in larval growth is thought to be largely temperature dependent with added variability from prey availability (Heath *et al.* 1997; Fiksen & Folkvord, 1999; Johannessen *et al.*, 2000). In terms of larval abundance, the North Sea is not isolated, as larvae originating from the west of Scotland are also introduced by the Scottish coastal current into the northern North Sea (Heath & Rankine, 1988; Heath 1989).

The metamorphosed juvenile 0 group fish begin to appear in the eastern North Sea (German Bight and Skagerrak) in the third quarter of the year (International Bottom Trawl Survey (IBTS) results shown in Heath *et al.*, 1997) and appear to stay there (and to a much lesser degree in other coastal areas) until they are 2 year old when they join the feeding adult population through

active migration (Wallace, 1924). Recruiting to the adult population is probably size and maturity dependent (Brophy & Danilowicz, 2003). Burd (1984) suggested that at age 1 the population is most likely to exhibit density dependent effects on growth, but Heath *et al* (1997) suggest that these differences in length come from variability in growth during the larval stages. The length of fish at age 1 has a great influence on their length at later ages (Hubold, 1978). Recent year classes of North Sea herring (e.g. 2000) are apparently exhibiting density induced decreases in growth and maturation rate (ICES 2004).

The main co-occurring species on the nursery grounds are whiting, sprat, juvenile cod, sand eel and more recently anchovy.

7. Migrations

The migrations of North Sea herring have been broadly mentioned in the sections above and can be summarised by figures 3 and 5. As stated above, the characteristics of and mechanisms for overwintering are more vague than the spawning and feeding information. The occurrence of different migration patterns based on phenotypic differences of the subcomponents is currently thought to adhere to the Adopt-Migrant hypothesis (McQuinn, 1997), where generally stocks mix in the nursery areas and the summer feeding grounds, but migrate with others of their size as they approach the need to spawn. Isolated migrants (fast growers or slow growers) can join other subcomponents, and dispersal is more prevalent when established populations become unstable (after collapse or a recruitment boom, McQuinn, 1997; Corten, 2001a). Repeated imprinting of migration intensifies the spatial patterns making straying less likely with spawning experience. However evidence from the west of the British Isles (Brophy & Danilowicz, 2002; 2003) suggest that whether fast or slow growing, and from different nursery grounds, Celtic Sea maturing herring all return to their broader spawning area, suggesting natal homing (see Harden Jones, 1968).

8. Long Term Trends

The North Sea herring fishery has a long history, with countries going to war of the rights to fish and land their catches (England and Holland in 1652-1654). The fishery was known to be variable and the variability in yearclass strength lead to the 18th century idea that North Sea herring were part of a 'mega' stock that migrate to the Arctic in the winter and a variable proportion of the mega-stock return every year to the North Sea. This was discredited in the late 19th century. However it was often noted that variability in year class strength in the North Sea was considered less than in the Baltic (Cushing, 1996) and this is the case (Myers, 2001). It was also noted early on that the recruitment patterns from sub-components of the stock were different (Bjerkan, 1917; Cushing 1992).

In the 20th century, mechanisation of the fishery lead to severe impact by humans on the stock for the first time (Hodgson, 1936; Cushing & Burd, 1957; ICES 1965; Burd, 1978; 1985; Cushing, 1992; Nichols, 2001), as the stock went from a spawning stock biomass of over 2 million tonnes to below 50,000 tonnes. This was a real collapse as recruitment became highly impaired. The fishery was closed from February 1977 to Oct 1981 (Burd, 1985). The collapse affected different components of the stock in different ways, with the southern components declining before the northern components (Burd, 1985; Cushing, 1992). As the stock declined, spawning became restricted and many spawning grounds became abandoned. Recovery was slower than predicted but the stock was considered healthy again by the early 1990s, however as decline in biomass occurred again in the mid-1990s and a swift response by management ensured that the stock did not collapse (Nichols, 2001). Currently the stock is now perceived to be above 2 million tonnes and density dependent effects are being detected again. It is widely accepted that the recruit to stock relationship is domed for herring and that productivity per spawner is impaired at high spawning biomasses (Anthony & Fogarty, 1985; Zheng, 1996; Fox 2001) but overall stock size or area size may influence this density dependent effect (Winters and Wheeler, 1987). In the last 25 years, only 20% of year classes of North Sea herring have failed to correspond to a virtually linear relationship between spawning potential and recruitment strength at age 1 (Nash & Dickey-Collas *in press*).

9. Recent Characteristics

The production of larvae is increasing, but the ichthyoplankton surveys may no longer be covering the whole stock, as stock recovery leads to spawning on grounds away from the main centres (e.g. on Dogger Bank). The higher temperatures in the southern North Sea at present are apparently not restricting the spawning of herring in the area (ICES 2004). Recent work has concentrated on the interaction between the North Sea herring stock and the western Baltic spring spawners. The juveniles of these stocks mix in the Kattegat during their nursery phase.

The mean weights at age are still declining from the high in the 1970s. Apart from the variability between the relative proportions of the subcomponents of the stock, there is no reason to suggest that the current migrations are different from those described throughout the 20th century.

10. Potential Environmental Influence

Corten (2001a) suggests that many recent fluctuations in the distribution of North Sea herring are driven by stock increase, changes in the zooplankton production and variability in the Atlantic inflow by the Fair Isle Current. The interaction of year class strength and environmental signals (combined imprinting effects on individual, hence lag effects on the population) may make the interpretation of the influence of environment difficult (Corten, 2001a). There appears to be a relationship between the changes in the distribution of overwintering herring and the North Atlantic Oscillation (NAO), as seen in the Open Skagerrak Periods (Alheit & Hagen, 1996; 1997; Corten, 1999b) and the location of the feeding grounds in relation to areas of high zooplankton abundance (see above).

The spatial nature of the life cycle has never been accounted for in an MSVPA (Multi-Species Virtual Population Analysis) type of approach (ICES 2003), hence realistic multispecies interactions are difficult to assess. An attempt to consider the spatial nature of North Sea herring dynamics was begun relatively successfully by Heath *et al.* (1997). Overall, the evidence suggests that changes in horse mackerel and sand eel abundances, as well as *Calanus*, *Temora* and *Pseudo/Paracalanus* production (Beaugrand, 2003; Reid *et al.*, 2003) will impact on herring production and distribution (Bainbridge & Forsyth, 1972), and *visa versa*. The increased abundance of herring, combined with a reduction in zooplankton, will increase the impact of herring on the egg survival of plaice and cod (Ellis and Nash, 1997; Segers *et al.*, in prep). Sprat and herring appear to have a complex relationship with some sympatric signals (Tortensen & Gjøsaeter 1995) and divergent signals in other areas (Corten 2001a).

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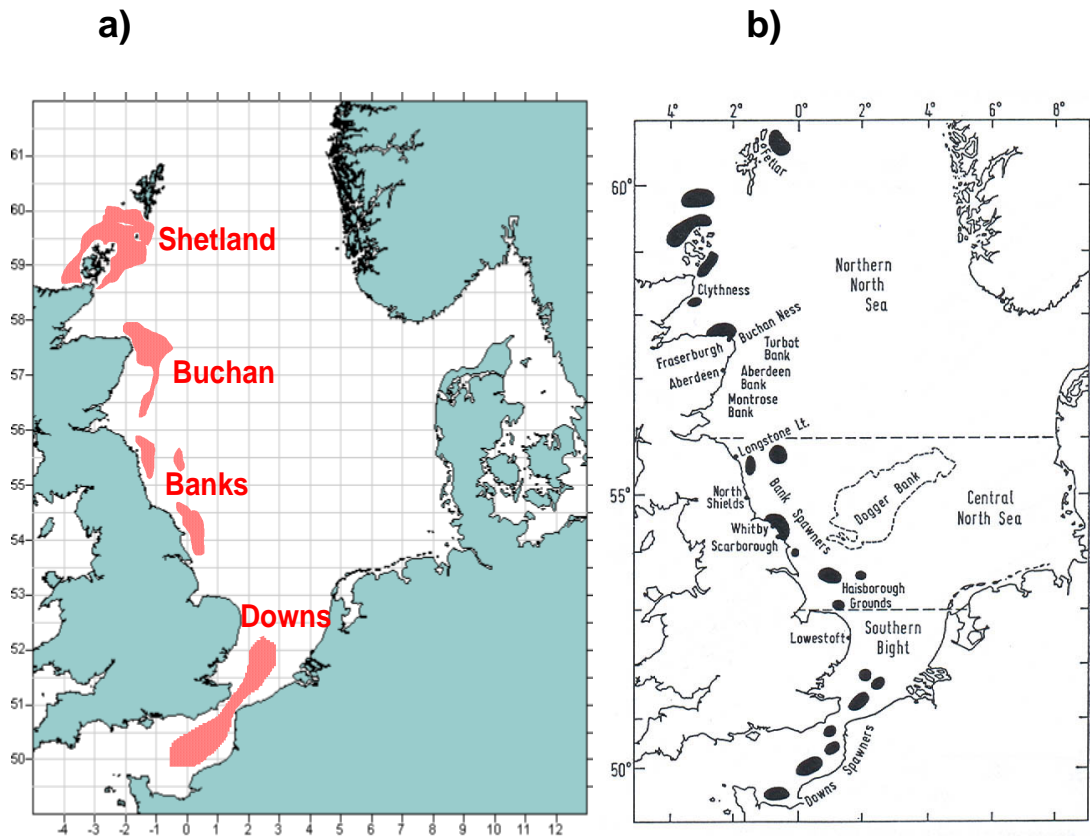


Figure 1. North Sea herring. Generalised major spawning grounds.

- a) inferred from the presence of newly hatched larvae in the ICES herring larval survey (1996 to 2003) and labelled by stock sub-components
- b) from Burd & Howlett (1974).

Spring spawning coastal populations are not shown. Recent ICES surveys do not cover the Dogger Bank area (see figure 2).

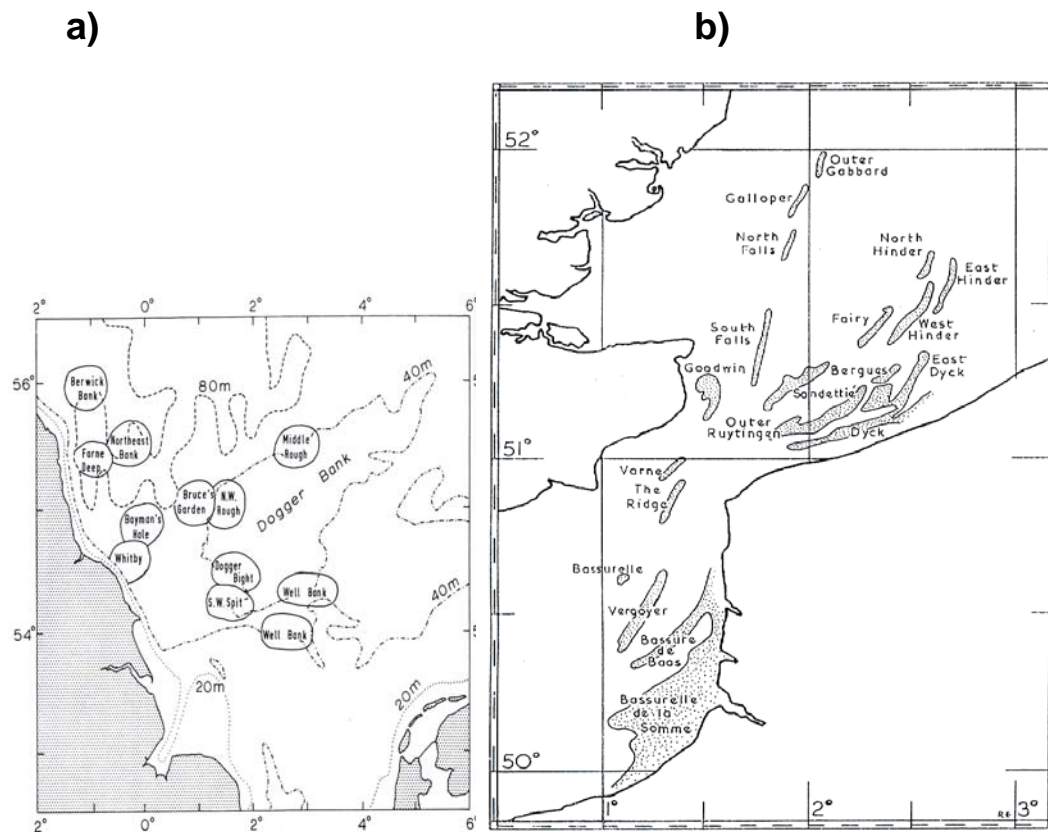


Figure 2. North Sea herring. Specific spawning grounds of Banks and Downs sub-components of the North sea herring stock

- a) The Banks sub-component (from Cushing & Bridger, 1966), spawning does not occur at all of the grounds.
- b) The Downs sub-component (from Cushing & Burd 1957).

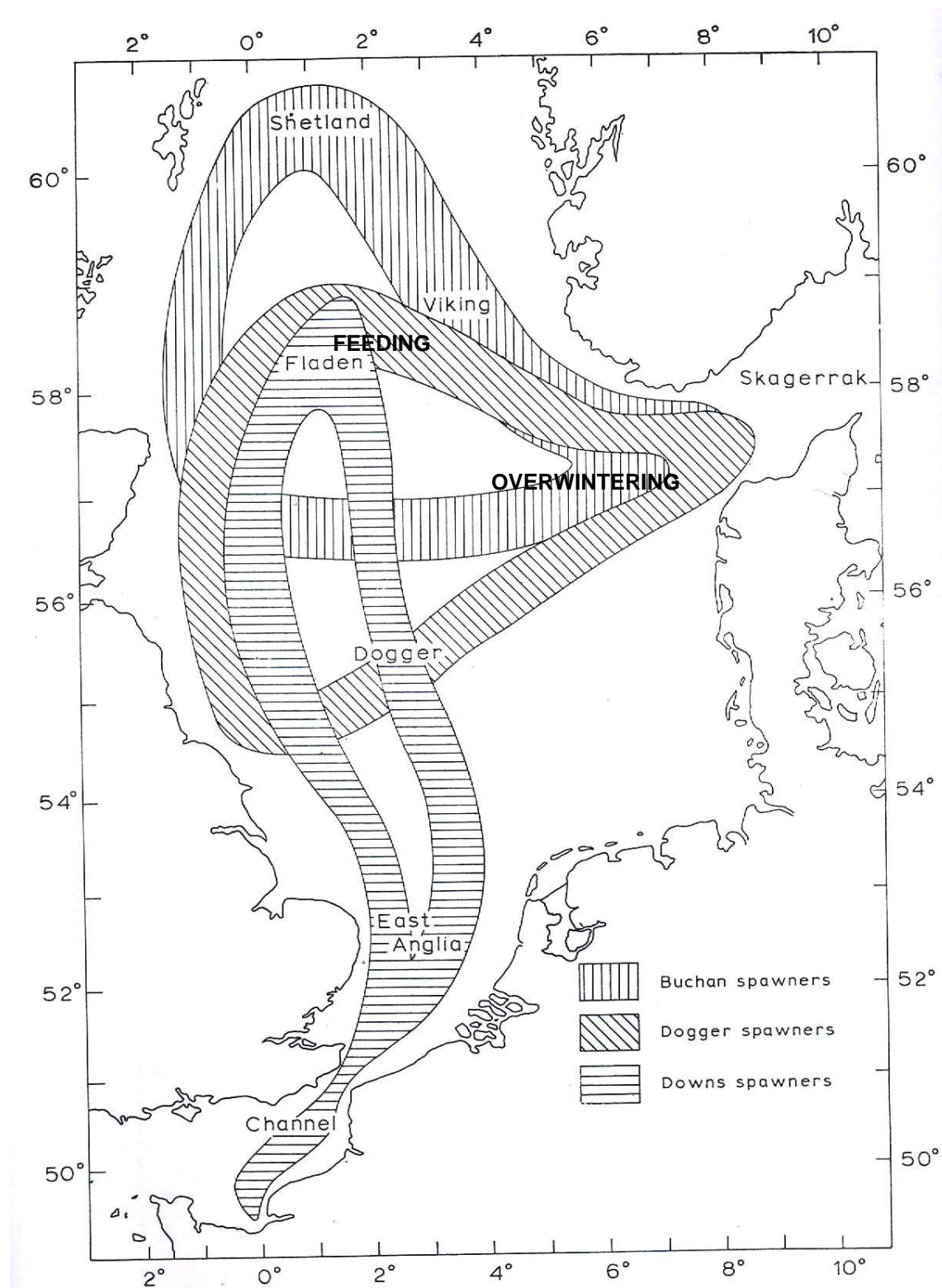


Figure 3. North Sea herring. Suggested migrations routes of three subcomponents of the North Sea herring stock. From Cushing and Bridger (1966).

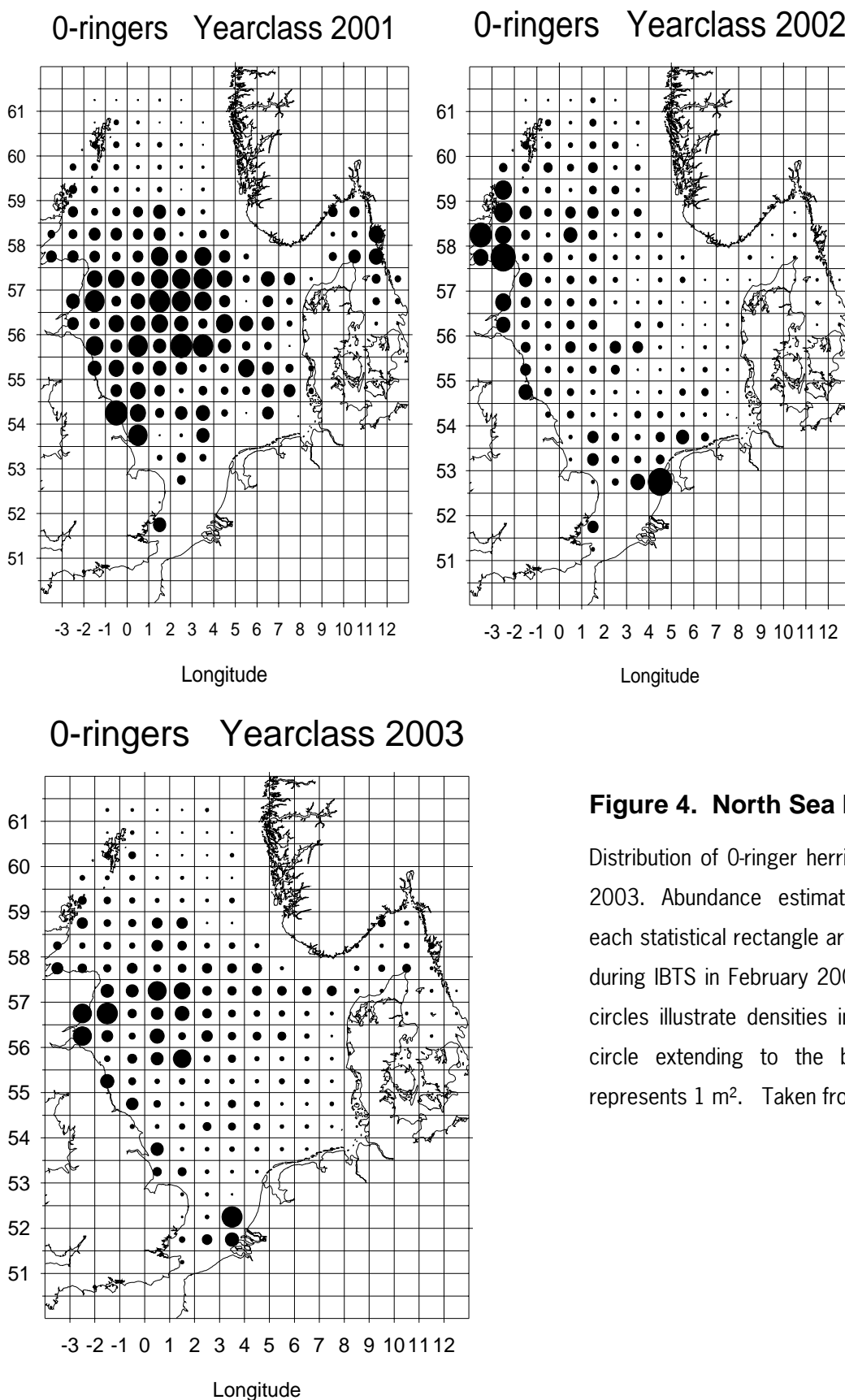


Figure 4. North Sea herring.

Distribution of 0-ringer herring, year classes 2001-2003. Abundance estimates of 0-ringers within each statistical rectangle are based on MIK catches during IBTS in February 2002-2004. Areas of filled circles illustrate densities in no m^2 , the area of a circle extending to the border of a rectangle represents 1 m^2 . Taken from ICES (2004).

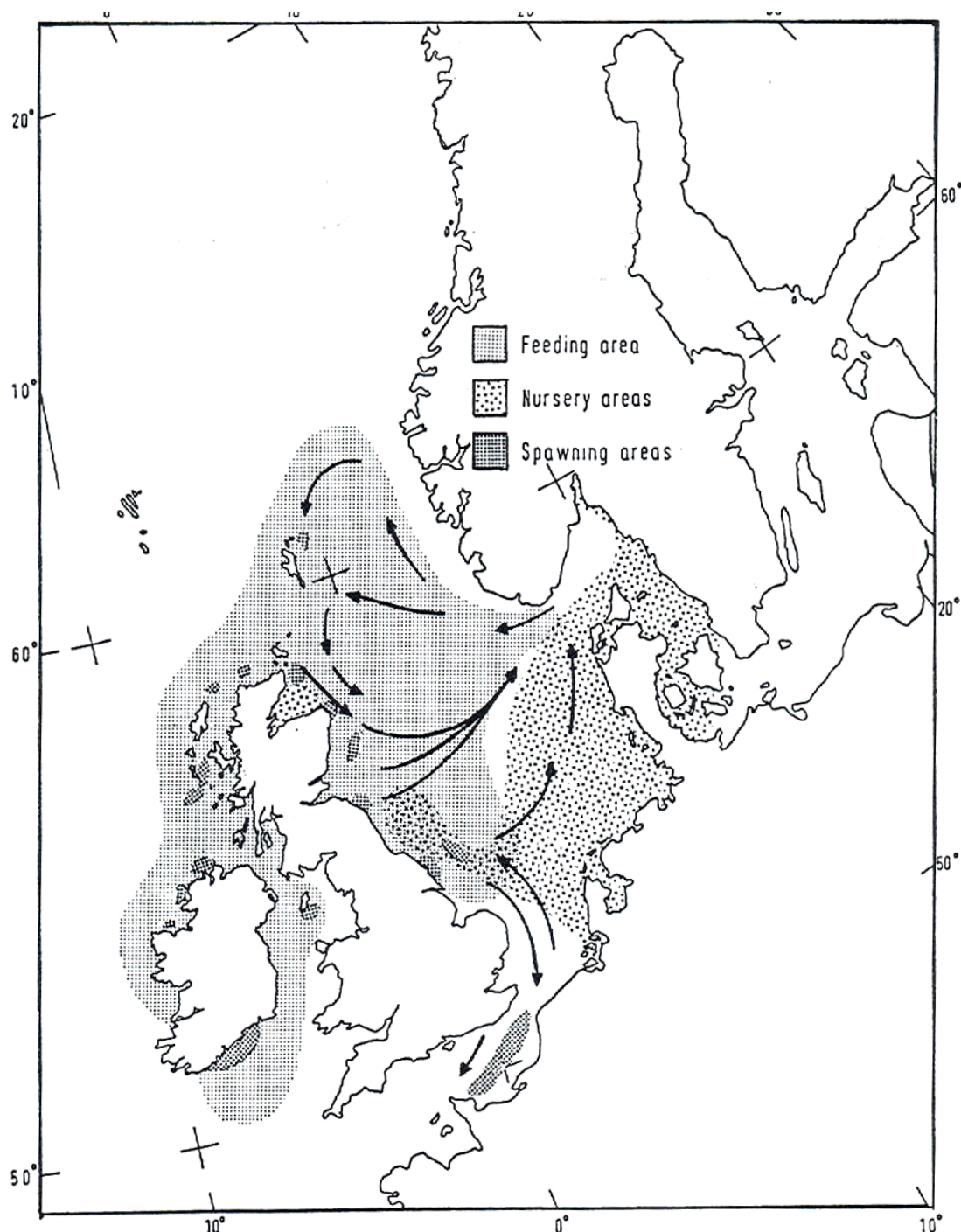


Figure 5. North Sea herring. Schematic summary of generalised migration patterns of North Sea herring, taken from Burd (1978).