



Effort allocation of the Dutch beam trawl fleet



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Proefschrift

ter verkrijging van het doctoraat in de
Wiskunde en Natuurwetenschappen
aan de Rijksuniversiteit Groningen
op gezag van de
Rector Magnificus, dr. F. Zwarts,
in het openbaar te verdedigen op
vrijdag 25 juni 2010
om 11.00 uur

door

Jan-Jaap Poos

geboren op 25 maart 1975
te Nijmegen

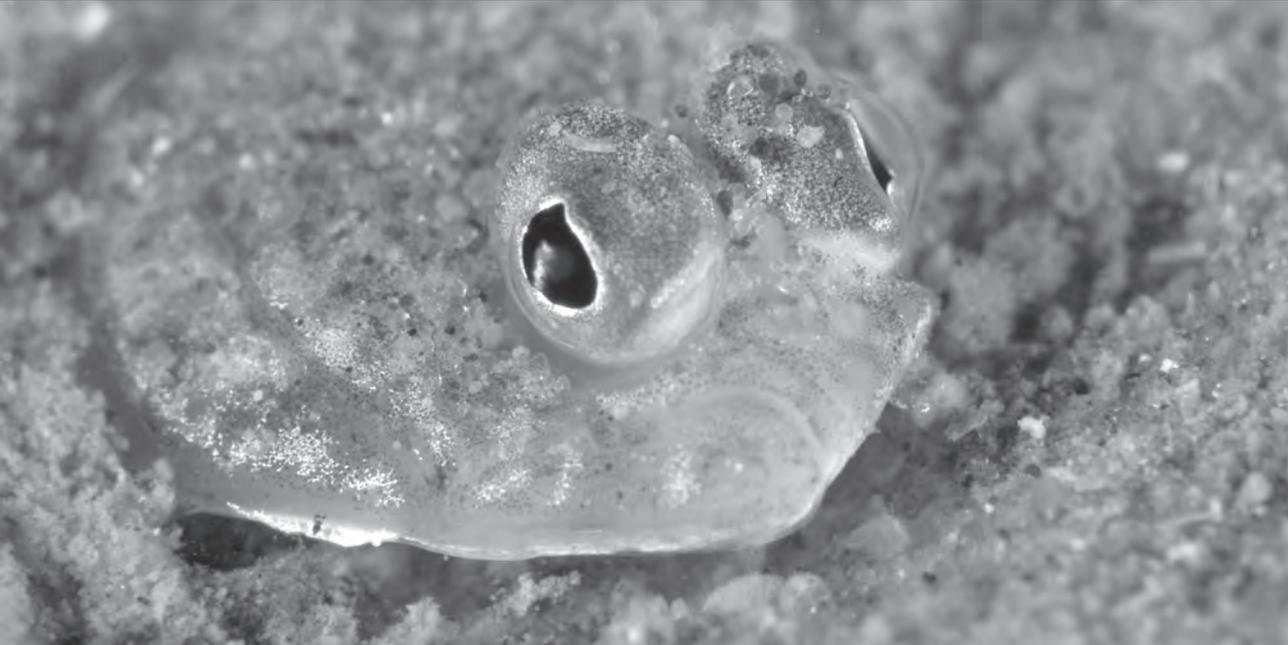
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Chapter 1

Introduction

1.1 Background

Many problems in fisheries management stem from a failure to understand fleet dynamics as caused by the behaviour of individual fishers in response to changes in the availability in the resource as well as to management measures imposed. Some of the world's fisheries crises were not due to poor understanding of the biology of the target species, but to poor understanding of the way fishers operate (Hilborn 1985). Although over the years the importance of understanding the fleet dynamics has been recognised (Clark and Mangel 1979, Gulland 1983, Sampson 1991, Gillis *et al.* 1993, Gillis and Peterman 1998), this issue still receives little attention in providing scientific management advice. One important aspect of the dynamics of fishing fleets, as classified by Hilborn (1985) is the variation in spatiotemporal effort allocation: when to fish, where to fish, and what to fish for. How fishing effort is distributed in space and time has important consequences for the exploitation of marine resources, because it is, in combination with the distribution of the resource, one of the important determinants of the “catchability” (Box 1), the relation between fishing effort and the mortality caused by fishing.

BOX 1 Catchability

Catchability, often denoted q , is a proportionality coefficient linking (i) catch rate and resource abundance, and (ii) fishing mortality and nominal fishing effort (Beverton and Holt 1957). Catchability is thus linked with the assumption of a linear relation between catch rate and resource abundance, similar to a Holling type I functional response (Holling 1959). These links are important in resource management because the catch rate is often used as a direct indicator of biomass while effort regulation may be used to control fishing mortality (Holden 1994, Marchal 1997). For both uses, the catchability should ideally be known, but at least be constant in time.

Catchability is determined by the spatial and temporal overlap between the distribution of the resource and of the fishing effort (Swain *et al.* 1994). Second, the catchability depends on the efficiency of the gear to capture and retain a species. Both the overlap and the efficiency are affected by the behaviour of the species and of the fishery, as well as by physical characteristics of the environment. In this thesis, we mainly focus on how the behaviour of the fishery affects the catchability. One of the main incentives for fishers to change their behaviour and to invest in gear that increases catchability is that they are in competition with each other (Rijnsdorp *et al.* 2008). The continuous increase of gear efficiency (and consequently in catchability) is known as efficiency “creeping” (Marchal *et al.* 2002).

The relation between fishing effort E and fishing mortality F is the base of almost all population and assessment models in fisheries science (Millischer *et al.* 1999). Generally speaking, E is defined as the amount of input in a fishery, often described by simple measures of time fishing, but in trawl fisheries generally adjusted for differences in engine power of the vessels. F is the decay constant expressing the removal rate in the stock, usually in discrete time. The relation between E and F is often assumed to be linear, with an average catchability coefficient q that is constant in time. This assumption of a linear and constant relationship presupposes that fish and fishers are randomly mixed throughout the year, that fishers need no time to process fish before being ready to continue their operation and that there are no density-dependent effects on fish or fishers.

One of the prime deviations from the above assumptions in exploited marine ecosystems is that neither the fish nor the fishers are not randomly distributed. Many processes shape the spatial distribution of individual species. First of all, the distribution of a species is linked to the distribution of its food (Grimes and Finucane 1991, Shucksmith *et al.* 2006) Also, physiological constraints, habitat characteristics and the distribution of predators will affect fish distribution (Amara *et al.* 2001, Brind'Amour *et al.* 2005). Moreover, the reproduction cycle of many fish give rise to long-distance migrations, generating distribution patterns that are not only heterogeneous in space, but also in time (Hunter *et al.* 2003a, Bolle *et al.* 2005, ter Hofstede *et al.* 2007).

The effort allocation within a fishing fleet exploiting such an heterogeneous resource is the result of decisions of individual skippers. As an alternative to the assumption that fish and fishers are randomly mixed throughout the year, one may assume that the distribution of the fishers results from each individual trying to optimize some utility function. This is similar to theoretical approaches in animal ecology, where optimality models are used as a tool to understand the distribution of foragers (as fishing vessels may well be compared with). Optimality models provide a theoretical forager with a set of options, each with its own payoff but measured in a single currency (Stephens and Krebs 1986, Houston and McNamara 1999). The option set is bounded by constraints that can be either intrinsic or extrinsic to the forager. The prediction is that the option with the highest payoff will be chosen.

Traditional optimal foraging models have been used to study two basic problems: which prey to consume, and which patch to use for foraging (Stephens and Krebs 1986). As such, several approaches have been developed within the field of behavioural ecology that may be of direct relevance to our problem of analysing and understanding the dynamics of the choices made by individual fishers. We discuss these in the next section.

1.2 Theoretical models

1.2.1 Ideal Free Distribution

The well-established Ideal Free Distribution (IFD; Fretwell and Lucas 1970) is an optimality model that describes the spatial distribution of animals in relation to their resources based on individual decisions in response to the decrease in intake rate caused by competition. The IFD leans on two assumptions. First, all foragers have perfect (ideal) knowledge about the distribution of their resources. Second, foragers are free, i.e. there are no costs involved in moving to alternative sites (Fretwell and Lucas 1970). Finally, all foragers are identical. The IFD has proven to be the starting point for more specific optimality models, relaxing the two basic assumptions and incorporating incomplete knowledge or travel costs.

Early IFD models assumed that resources were consumed immediately after their input in a patch, leaving no standing prey stocks. A simple system such as this may be rare in the field (van der Meer and Ens 1997), but a classical application is to fish feeding on food items dropping onto the surface of a pond or a stream (Tregenza *et al.* 1996). Individual intake in a patch is directly proportional to the local amount of food available and inversely proportional to the number of foragers present. Because foragers distribute themselves among patches in such a way that they all have equal intake, the proportion of foragers in a patch is equal to the proportion of resources available in that patch. This relationship between resource input and forager density is referred to as the “input matching rule” (Parker 1978).

These early models are also referred to as “continuous input”, but van der Meer and Ens (1997) suggested to label them “immediate consumption” models, because continuous input is also possible in alternative “standing stock” models (Rogers 1992, Lessells 1995). The latter describe animals searching patches of dispersed resources, and are hence limited by search time as well as resource abundance. In this situation, interference competition may occur.

1.2.2 Competition among foragers

The distribution of foragers is influenced by mutual competition. Generally, two types of competition are distinguished: exploitation competition and interference competition. Exploitation competition involves indirect negative interactions arising from the use of a common resource, where each consumer affects others solely by reducing resource abundance (Goss-Custard 1980, Vance 1984,

Marchand 1991). Exploitation competition is irreversible, because a reduction in the number of competitors will not increase the resource abundance, and hence the intake rate will not increase.

Interference competition can be defined as a short-term, reversible decline in intake rate as a result of the presence of others (Goss-Custard 1980). Interference reduces intake rate through mechanisms such as time wasted in interaction with competitors or disturbing prey (Tregenza 1995, Stillman *et al.* 2000). The measure of interference has important consequences for the competitor distribution. In contrast to continuous input situations, a patch with half the density of resources relative to the best patch may not receive half the number of foragers and thus the input matching rule does not apply.

Different models have been used to describe the relationship between competitor density and intake rate. Predictions on the distribution of foragers strongly depend on the assumptions that are made about the effects of interference on intake rate. Two approaches have been taken. The “mechanistical” approach applies simple behavioural models of the predation process assuming a homogeneous environment in each patch. The “phenomenological” approach uses an empirical relationship between searching rate or intake rate and forager density to model the effect of interference. Both approaches result in a set of models (van der Meer and Ens 1997).

In contrast to behavioural interactions among foragers, interference based on prey depression has received relatively little attention. Prey depression occurs when prey are able to respond to the proximity of foragers (e.g. by retreating in a burrow) and can temporarily avoid to predation (Ruxton 1995, Stillman *et al.* 2000). Interference in such a system occurs because, as forager density increases, the proportion of depressed (invulnerable) prey also increases. Vulnerable prey responds to the presence of a forager by switching to the depressed state. This response has a delay time during which the prey can still be attacked. After becoming depressed, each prey has a fixed probability of returning to the vulnerable state. The foragers have no mutual interactions, and interference competition works only because an increase in foragers will result in an increase of prey in the depressed state.

The prey-depression model produces two general predictions that are also produced by interference models based on forager-forager interactions: (1) the measure of interference increases both with increasing competitor density and decreased prey-encounter rate; (2) the outcome is most sensitive to the distance over which interactions occur (Stillman *et al.* 2000).

Differences in competitive ability have substantial implications on forager distribution (Sutherland and Parker 1985, 1992). As in the other competitor interference model, the effect of competitor density is scaled by the interference constant m , but individual differences in competitive weight scale the effect of m . Individuals with a low competitive weight suffer a higher reduction in their intake rate by increased density on a patch than those with a high competitive weight. Importantly, the exact formulation of the effects of interference competition affects the outcome of the spatial distribution of weak and strong competitors (van der Meer 1997).

1.2.3 Diet choice constraints

In the models described above, all foragers are assumed to use a single resource. In practice, foragers are often able to choose from a range of different resources. A forager's diet may be constrained by one or more of the following: toxin intake, nutrient intake, digestion rates, ingestion rates, and limits on feeding time (Pulliam 1975, Stephens and Krebs 1986).

The classical diet choice models assume that the choices of a forager are constant over time, and independent of the nutritional or energetic state of the forager. In order to model such state-dependent decisions, dynamic models have been introduced (Mangel and Clark 1988, Mangel 1992). This technique allows decisions that are influenced by qualitatively different factors based on the value of a single currency, while constraints and choices could be separated in time. Mangel (1992) has shown that rate-maximising and dynamic-programming models yield different results in cases where constraints on a state variable cannot be ignored.

1.3 Optimality models of individual fishers

Optimality models such as described in section 1.2 have been used effectively to gain insight in the spatial distribution of fishing fleets and to understand the decisions of individual fishers (Gillis and Peterman 1998, Gillis 2003). Diet choice models were applied successfully to predict discarding behaviour in the Oregon trawl fleet using dynamic programming (Gillis *et al.* 1995). The availability and economic values of different size-classes of the target species, the trip quota, and the risk of a premature trip termination all influenced decisions through their effect on the final value of the landed catch. At any time throughout a fishing trip, the discarding decision that is most likely to maximise the value of the landed catch varied with the amount of fish already in the hold and the num-

ber of hauls remaining in the trip (Gillis *et al.* 1995). The handling time was assumed to be non-existent, and thus not driving decisions regarding 'prey choice'. Instead, the capacity constraint was the motivation behind the fishermen's diet choice. This constraint was set either by the hold size or the trip quota (Pikitch 1991). The results of the model indicated that discarding size classes with low economic value (high-grading) is more common towards the end of the trip. Furthermore high-grading increased when there is an increase in overall fish availability, a decrease in trip quota, or a decrease in the risk of premature trip termination owing to loss of gear or injury (Gillis *et al.* 1995). However, the model also showed how an increase in the availability of fish may have no effect on, or even reduce, the discarding of intermediately-valued size classes. In addition, the model showed that high-grading may be more common at the beginning of the trip when there is a high probability of the trip quota being filled exclusively by the most-valuable size-class, such as when quota are low.

1.4 Thesis objective

The ultimate goal of the PhD project was to try to understand the patterns in spatial effort allocation by the Dutch beam-trawl fleet (Box 2). This fleet targets two flatfish species, sole and plaice, but has a considerable bycatch of other demersal species (Box 3). The spatial effort allocation of the fleet has important consequences for the exploitation of these marine resources. From the review of foraging theory it is clear that many factors, including knowledge of the distribution of the resources, interference competition, and external constraints, affect the choice of a forager where and when to feed. The same applies to beam-trawl skippers leaving the harbour to fish.

BOX 2 The Dutch beam-trawl fishery

The beam-trawl fishery in the North Sea targets flatfish species, using a heavy fishing gear that allows a number of chains in front of the net that dig into the bottom and thus chase the flatfish out of the sand or mud. The fishery developed in the early sixties, when fishers had noted that otter trawls equipped with tickler chains yielded higher catch rates of highly valued sole and, to a lesser extent, plaice. The negative effect of the large numbers of chains on the spread of the doors triggered the introduction of beams that fixed the net opening. Because the number of chains, beam size and fishing speed depend largely on the engine power of the vessels, beam trawlers became evermore powerful (Daan 1997).

When fishing, two nets are towed over the sea floor behind the vessel in consecutive hauls. The fishing speed depends on the engine power but ranges from 3 to 8 knots (Piet *et al.* 2006). The duration of a haul ranges from 1 to 2.5 hours depending on local conditions. The catch is brought aboard and sorted while the nets are already towed for the next haul. Fishing trips generally start on Monday morning, and last until Friday, when the fish is sold through the auction. The catch consists mainly of plaice (*Pleuronectes platessa*) and sole (*Solea solea*), but includes other flatfish such as, dab (*Limanda limanda*), turbot (*Scophthalmus maximus*) and brill (*S. rombus*). Other fish species such as cod (*Gadus morhua*) and whiting (*Merlangus merlangius*) make up most of the rest of the marketable catch.

One of the main physiological characteristics of the flatfish species is that, besides being flat, they lack a swim bladder. This makes locating high densities through echo-sounders impossible. Hence, beam trawlers have to spend time searching for patches with high catch rates while making exploratory hauls in a broader area, where they expect to find concentrations (Rijnsdorp *et al.* 2000). Also, skippers may share information on their perception of the catch rates in order to reduce searching time.

Owing to competition and the management constraints imposed, the fleet composition has been changing in terms of engine power since the introduction of the beam trawl (Daan 1997, Rijnsdorp *et al.* 2008). During the 1970s, increasingly more powerful vessels outcompeted smaller vessels, and the total fleet size decreased slightly. In the 1980s, both the number of vessels and their average engine power increased, following new investments in the fleet. After 1988, the number of the vessels has slowly declined and their average engine power only grew very little, resulting in a decline in total engine power of the fleet. These changes are likely affected by the management measures taken. Differences in quota management between the Netherlands and other EU countries caused some beam trawlers to re-flag to other member states in order to be able to fish for the quota of the flag state.

BOX 3 The main target species of the Dutch beam trawl fleet

The Dutch beam-trawl fleet targets a number of demersal species, but in general, plaice (*Pleuronectes platessa*) and sole (*Solea solea*) are the most important ones, in both weight and value (Gillis *et al.* 2008). Plaice lives on the sandy

parts of the European continental slopes down to about 100 metres (Wimpenny 1953). There are a number of spawning grounds, where mature fish congregate during the spawning season (between December and March) and high concentrations of eggs may be found (Wimpenny 1953). Thus, plaice perform a migration cycle, with mature individuals migrating from the northerly feeding grounds used in summer, to the southerly spawning grounds in winter (Hunter *et al.* 2003b). During spawning, the female plaice assemble in specific spawning areas and release their eggs to be fertilized by the attendant males. These spawning concentrations result in elevated catchabilities in the fishery, because the spawning areas are well defined and therefore the high concentrations are easy to find and exploit (Rijnsdorp 1993b). The fertilized eggs develop into 7mm long larvae. After approximately thirty days, the left eye begins moving dorsally and anteriorly. Forty-five days after hatching the left eye has reached its final position on the right-side dorsal. During this process, the larvae born in the southern part of the North Sea make their way to the shallow continental coast, where they settle as 0-group. As they grow older, and larger, they move to deeper water, and by the end of age 2 become 15 to 25 cm in length. At these lengths, considerable discarding of plaice occurs, because the distributions of the fish of this size and the fisheries overlap, they are retained by the gear, and the minimum landing size prohibits their landing (See also BOX 5). Females grow faster than males and also reach larger sizes. In the North Sea, females plaice become mature between three and seven years old (Wimpenny 1953, Rijnsdorp 1989). The average age-and length-at-first-maturity differs between different areas. Males mature one to two years earlier than females, and at a smaller size (Rijnsdorp 1989, 1993a). Over the years, there is a trend towards maturation at younger ages and smaller lengths (Grift *et al.* 2007), which is in agreement with the theory that predicts that high selective pressures resulting from size- and age-dependent selection can change maturation schemes (Law 2000).

Although less abundant than plaice, sole is of high commercial importance, because its price being several times higher (Rijnsdorp *et al.* 1992, Taal *et al.* 2007). The species reaches its northern distribution limit in the Irish Sea, the southern North Sea, Skagerrak and Kattegat. Small numbers may also be found in Scottish waters and off the Norwegian south coast (Wheeler 1969). Although sole may be found in shallow waters of a less than 1m, deeper waters are favoured in winter by large fish and especially during severe winters they may form high concentrations in relatively small pits and become an easy target (Horwood and Millner 1998). Sole spawns in spring, with a peak in late May. Spawning appears to be triggered by water temperature (ICES 1965). Most spawning takes place in coastal waters. As a consequence, the catchability of adult sole in the large

beam trawlers decreases, because these vessels are prohibited from fishing in the coastal 12 nm zone and the plaice box (see also BOX 5). The larvae hatch after about 7 to 8 days, and settle at the bottom during metamorphosis at a length of 7-10 mm and about 3 weeks after hatching (Fonds 1979). Nursery areas are confined to shallow sandy to muddy coasts and a depth down to 20 metres (van Beek *et al.* 1989). Approximately 50% of the females mature at age 2 (Van Beek 1985, Mollet *et al.* 2007). Mature individuals migrate to the spawning grounds, and during this migration, they may move away from the bottom at night and travel in midwater and even at the surface (de Veen 1967). Like in plaice, a trend in has been observed towards maturation at younger ages and smaller lengths in sole as well (Mollet *et al.* 2007).

A first step in unravelling the mechanisms behind the allocation is to find out how the patches (i.e. good fishing grounds) of target species are distributed in space, how this spatial pattern changes seasonally and if fishermen are able to detect these patterns (perception) and respond appropriately. Because fishery-independent data on the distribution of target species are restricted to a few surveys, we will have to use commercial catch and effort data. This is not ideal because these data may be subject to bias owing to the behaviour of the fishers and their competitive interactions (Millischer *et al.* 1999, Gillis *et al.* 1995, Gillis and Peterman 1998). In order to be able to react to changes in the spatial pattern of target species abundance, for instance in response to temperature changes, fishermen have to perceive these changes. This perception is strongly dependent on the variance in the catch rate (van Densen 2001). Therefore, we address the questions: are fishermen able to perceive predictable differences in catch rates between fishing grounds?

Within the trip level, the relation between catch rate and abundance also needs clarification, because competitive interactions play a role here. As shown in section 1.2, the nature of this competition - being either interference or resource competition - strongly affects the relation between catch rate and abundance. Interference through depression will be explored and analysed in relation to the implications for the distribution of vessels of different engine power.

A third aspect to be studied concerns the effect of quota regulations on the fishing behaviour, in particular with respect to catchability for target species. The setting of Individual Transferable Quota (ITQs) is part of Dutch management system within which the fleet operates (Box 4), and which consists of measures for input as well as output control and technical measures (Box 5). The management system constrains fishermen in their choice of target species. It may be expected that they alter their fishing pattern in order to use their ef-

fort as effectively as possible, without exceeding quota. Diet choice models may be used to predict their optimal behaviour when operating in a multi-species fishery. The set of options within such a system changes when management constraints change. The efficacy of the effort as affected by the constraints can be estimated using non-linear regression techniques. A skipper who chooses fishing grounds that provide higher catch rates of marketable non-quota species may achieve positive changes in effectiveness (i.e. profit) of nominal effort. The other option is to discard the low-valued fraction of the target species for which a quota has been set (Gillis *et al.* 1995). Using dynamic programming, diet choice models can simulate the spatial behaviour of fishers, given constraints such as uncertainty about catch rates in the period to come and minimum use of energy.

BOX 4 Management of the Dutch beam-trawl fishery

Management measures for North Sea fish stocks have been introduced after World War II, first by the North-East Atlantic Fisheries Commission (NEAFC) and later by the European Union (EU). The current objectives of the management measures, stated in Council regulation (EEC) No. 3760/92 (article 2, par. 1), indicate that exploitation of stocks must be on sustainable basis. Management measures are enforced under the EU Common Fishery Policy (CFP) (Daan 1997). In general, three different categories of management measures can be distinguished: output control through annual Total Allowable Catches (TACs) input control through the Multiannual Guidance Programs (MAGP); and technical measurements (for instance prescribing minimum mesh sizes or restricting the use of particular gears in specific areas).

However, the main tool is output control through TACs. On an annual basis, the EU asks the International Council for the Exploration of the Sea (ICES) to propose TACs, based on “appropriate” scientific advice (i.e. taking into account the condition of sustainable exploitation). After a political lobby in consultation with the industry, the Council (i.e. the responsible ministers of the different countries) decides on the final TACs. The lobby may lead to considerable amendments to the TAC proposals. National quota are defined automatically because the shares are fixed (‘relative stability’). TAC measures may fail meeting the objective of rational exploitation (Daan 1997, Rijnsdorp *et al.* 2008) for two main reasons: (i) the TACs and quota apply to landings, and in a multi-species fishery exhausting the quota for one species may result in increased discarding (and thus a higher fishing mortality than the TAC is intended to achieve) (ii) the TACs set by the Council have generally been higher than the values proposed by ICES.

Input control through MAGPs are aimed to find a balance between fishing capacity and the fish stocks. In practice this means reducing the fishing capacity (i.e. fleet size) available to the extent that the fishing mortality exercised would correspond to the level at which the Maximum Sustainable Yield (MSY) would be obtained. Thus, MAGPs have become a major component of the EU regulations. However, a major problem is the measurement of fishing capacity. The two units chosen (gross registered tonnage and overall engine power) are only indices of the potential of a fleet to catch fish, but there is no direct relation between these two measures and the amount of fish a fleet is able to catch, because this depends on the amount of time spent fishing and the gear used (Holden 1994). Moreover, in a multispecies fishery, the fishing capacity aimed for is necessarily a compromise, because the MSY of each species would require a specific capacity. For these reasons, there is no fixed relationship between the indices of capacity and fishing mortality rates. Nevertheless, their advantage is that they can not lead to dispute among Member States, because they are objectively defined.

The general idea behind the first MAGP (1983 to 1986) was to restructure the fleet, while maintaining existing capacity (Holden 1994). The second MAGP (1987 to 1991) required cuts in capacity, but several member states failed to meet their targets by margins of 11% or more (Holden 1994). Subsequently, further cuts have not been expressed in terms of a reduction of capacity and a decrease in fishing effort. Effort was calculated as a combination of the capacity and the days spent at sea (Holden 1994). However, the targets of the MAGPs, such as a cut in fishing effort on stocks of plaice and sole of 30 %, have rarely been met.

BOX 5 Technical measures

Besides the TAC and MAGP measures described in Box 2, technical management measures have been imposed to maintain fish stocks at a sustainable level. Such measures include minimum mesh-size regulations, minimum landings sizes of target fish, gear restrictions and zones that restrict fishing with certain vessel types. The technical management regulations in the CFP are commonly being updated 2 to 3 times a year (Vervaele *et al.* 1990). Several have an effect of the spatial scale of exploitation:

- A minimum legal mesh size for trawl fisheries on plaice and sole (75 mm) has been introduced after WW II (Beverton and Holt 1957, Daan 1997). However, the selection curve of this mesh size does not match the minimum legal

landing size for plaice (26 cm) and therefore resulted in a high discard rate of undersized fish (van Beek *et al.* 1983). In the late 1980s, the minimum legal mesh size was gradually increased to 100 mm in 1992, but a derogation of 80 mm has been maintained for the sole fishery south of 55 °N (Daan 1997). From January 2000 onwards, this geographical line has been moved upwards in the eastern North Sea, thus allowing usage of 80 mm nets up to 56 °N east of 5°E (Council regulation (EEC) No. 0850/98). The catch of marketable plaice is not affected by a difference in mesh of 80 or 100 mm (van Beek 1990, Holden 1994). The catch-per-unit-of-effort is generally based only on the marketable catch, which is also the amount of interest to the fisherman. Use of any of the two mesh sizes will thus not affect the catch rate of plaice. In contrast, the 80-mm mesh retains considerably more marketable sole than the 100-mm mesh (van Beek *et al.* 1983).

- With the introduction of minimum mesh sizes, also minimum landing sizes had been imposed. The minimum landing size for plaice has varied between 26 and 27 cm, while the size for sole has been 24 cm since 1946.
- Engine power regulations for beam-trawl vessels have been one of the instruments used for effort reduction. An overall limit on the engine power of newly built vessels has been set to 1491 kW (=2000 hp) in 1987 (Salz 1996). Before 1987, vessels with much stronger engines (up to 4500 hp) had become fashionable because they allowed fishing almost independently of weather conditions and offered greater safety (Salz 1996). These vessels were allowed to continue their fishing operations, but were expected to disappear gradually.
- Distinct zones have been defined where vessels with engine power exceeding 221 kW (= 300 hp) have no fishing rights. The area within a 12-mile limit off the coast was closed for the large beam trawlers in the 1970s (Davidse 2001). In addition, the so-called “Plaice box” was founded in 1989 in the south-eastern North Sea. Initially, this area was closed for large beam-trawl vessels only during the 2nd and 3rd quarter of the year. In 1994, the closure was extended to the 4th quarter and from 1995 onwards the box has been closed all year round (Pastoors *et al.* 2000).
- Because the measures set to reduce the maximum engine power of newly built vessels in 1988 would only slowly have an effect, effort reduction was sought in the shorter term by restricting gear dimensions. Catchability is partly determined by the swept area of the gear. Therefore, the maximum total beam length (two nets) for the large beam trawlers has been set to 24 m in 1987, while the maximum total beam length was set to 9 m for the small beam trawlers fishing within the 12-mile zone or the plaice box.

1.5 Thesis outline

Chapter 2 deals with the spatio-temporal patterns in the catch rates of sole and plaice. Predictability in these patterns may be used by fishers to optimize their intake rate by choosing patches with the highest expected returns. The spatio-temporal patterns are analyzed at two scales: a seasonal scale that describes the changes caused by the annual migration patterns in the two species; and a weekly scale that describes the build-up and decay of local hot-spots of resource aggregations.

Chapter 3 addresses the relation between forager density and intake rate, which provides important clues on the competition among vessels. When parts of the North Sea were closed for all trawl fisheries in 2001 for the protection of the cod stock, the EU factually provided a large-scale displacement experiment of fishing effort. Although many factors affecting spatial distribution remained uncontrolled, the closure served as a good way to study the effects of reallocating fishing effort on the intake rates of fishing vessels. To disentangle the effects of area specialization and competition, we analysed the effects for fishers that traditionally had fished in the closed area (“immigrants”) and those that did not have to move (“residents”) separately.

Chapter 4 discusses the implications of unequal competition among vessels through differences in the behaviour of the two target species. Vessels with different engine power may be affected differently because their intake rate is susceptible to these behaviours.

Chapter 5 investigates the effects of quota management on the spatial distribution of the Dutch beam-trawl fleet. Constraints set on landings play an important role in structuring the spatio-temporal distribution of fishing effort and also in varying the rate of discarding of marketable plaice. Such output constraints alter the optimum strategy (with respect to maximum revenues) of fishing fleets. Rather than being solely concerned with instantaneous profit maximization, skippers have to consider the fact that they face the possibility of quota becoming exhausted towards the end of the year.

Chapter 6 shows the implications of the changing fleet dynamics on the exploitation of North Sea plaice, in terms of the changing selectivity-at-age resulting from the changes in spatial distribution of the Dutch beam trawl fleet.

Finally, chapter 7 provides a general discussion of the results obtained. This puts the findings in a broader perspective, discusses some of the important assumptions made, as well as potential avenues for future research that could provide answers to the questions left open.

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Chapter 2

The dynamics of small-scale patchiness of plaice and sole as reflected in the catch rates of the Dutch beam trawl fleet and its implications for the fleet dynamics

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Journal of Sea Research 58 (2007) 100-112

2.1 Abstract

Catch rates of sole *Solea solea* and plaice *Pleuronectes platessa* in the Dutch beam trawl fleet operating in the North Sea show spatio-temporal variation. The variation in catch rates reflects differences in abundance of the species. Up to 45% of the variation in catch rates can be explained by the time of day of the catch, the engine power of the vessel and the migration cycles of the species. Also, spatial covariance was found in the residual variation for both species using variograms and covariance functions. The ranges of the spatial structure were found to be between approximately 20 to 45 nautical miles, indicating patchy distribution of the species. No differences in the ranges of the spatial structures were found between different seasons. Cross-covariance analysis shows the patches lasted up to two weeks. The implication of the spatial pattern in flatfish for the dynamics of effort allocation is discussed.

2.2 Introduction

The development of satellite tracking and global positioning systems (GPS) has made it possible to study the spatio-temporal distribution of fishing vessels in great detail. These studies indicate a patchy distribution of fishing effort, where some parts of the resource space are heavily fished, while others remain unvisited (Rijnsdorp *et al.* 1998, Larcombe *et al.* 2001, Marrs *et al.* 2002).

The patchy distribution of trawling effort may reflect spatial variation in the density of target species as well as the distribution of trawlable grounds. Spatio-temporal variation in fish density may be related to patches of high food availability (Fonds and Groenewold 2000) or spawning locations (Hunter *et al.* 2003) and may change over time owing to the migrations between spawning and feeding grounds (Harden Jones 1968, De Veen 1978, Arnold and Metcalfe 1996, Gillis and Frank 2001), or the migration of a new cohort to the fishing grounds (Beverton and Holt 1957, Harden Jones 1968).

The dynamics of small-scale patchiness in fish distribution may have important implications for the spatial distribution of the fleet. The occurrence of detectable patterns in resource availability is a prerequisite for fishermen to optimise their effort allocation in relation to the resource distribution, affecting the interactions among fishing vessels (Paloheimo and Dickie 1964, Gillis and Peterman 1998) and the relation between fishing effort and fishing mortality, a key issue of fisheries management (Hilborn and Walters 1992).

The objective of this paper is to analyse the spatial and temporal dimensions of the local concentrations of plaice and sole as reflected in the catch rate of Dutch beam trawl vessels. First, the effect of the time of day (De Groot 1971), engine power (Rijnsdorp *et al.* 2000a) seasonal changes in spatial distribution (De Veen 1978, Rijnsdorp and Van Beek 1991) on the catch rates are analysed. Then, the dimensions of the local concentrations in the residual catch rates are analysed, using geostatistical tools such as variograms and covariance functions (Cressie 1993) that have also found application in the evaluation of marine surveys (Freire *et al.* 1992, González-Gurriarán *et al.* 1993, Pelletier and Parma 1994, Petitgas 1997). The results will be summarised in a conceptual model, and the implications of the results for the dynamics of effort allocation, and the use of the catch per unit of effort as an index of the stock abundance, will be discussed.

2.3 Materials and methods

2.3.1 The Dutch beam trawl fleet

The Dutch Beam trawl fleet practices a multi-species fishery, targeting two flatfish species (sole *Solea solea* and plaice *Pleuronectes platessa*) with a valuable by-catch of turbot, brill, cod and whiting (Daan 1997). The gear consists of two nets fitted with chains, towed alongside the vessel. Each of these nets is 12 m wide and held open by a beam. Fishing trips usually last 4 to 5 d, during which there is almost continuous fishing (day and night), with an average duration of hauls of approximately 2 h. The average speed during the tow is equal to 6 knots, resulting in track lengths of approximately 12 nautical miles (Rijnsdorp *et al.* 1998). Owing to their physiology (no swim bladder) and demersal way-of-life, the targeted flatfish species cannot be detected by sonar. Thus, information on local density can only be obtained by exploratory fishing or hearsay (Rijnsdorp *et al.* 2000b).

2.3.2 Data catch rates

Data on the catch and effort were available from a study of the micro-distribution of beam trawl vessels using an automated position recording (APR) system to log the positions of vessels at 6 min intervals with a spatial resolution of 1' latitude and 2' longitude (± 180 m) (Rijnsdorp *et al.* 1998). Some of the vessels provided data on the catch (kg) per haul of the two target species plaice and sole and times of shooting and hauling of the gear (Table 2.1). The recorded catch comprised only fish kept on board (i.e. total length above legal minimum landing size, plaice ≥ 27 cm, sole ≥ 24 cm).

The geographical position of each individual haul was defined by the midpoint of the APR recordings during the haul. Geographical haul positions were transformed to a Cartesian coordinate system resulting in a grid with easting and northing in nautical miles. Spatial covariance structure was estimated using Euclidean distances in this grid.

Only vessels with engine-power exceeding 300 hp were included in the analysis, because the smaller vessels have different fishing rights and thus exhibit different fishing patterns than the larger vessels. The research period spanned 1994 to 1999. Owing to failure of the APR system and gaps in the additional logbook catch data, the total number of hauls differed from year to year and among vessels (Table 2.1). Engine power ranged from 1500 to 3899 hp, with a large part of the observations coming from 2000 hp vessels. Two vessels were refitted with new engines, resulting in higher engine powers in 1999. In total 60,087 valid hauls were recorded.

Table 2.1 Number of valid hauls by year for each of the vessels in the sample.

Ship	Engine power (hp)	Number of hauls						Total
		1994	1995	1996	1997	1998	1999	
1	1500	1152	1152	100	86	73		2563
2	1600		1014		328			1342
	2039						491	491
3	1694				1089		1113	2202
4	1800			1403	1563			2966
	1995						1637	1637
5	1800				79			79
6	1801	657		860				1517
7	1899		1079		1306	515		2900
8	1995		880		1091	1086	1192	4249
9	1999	875	1214	913	1595	991		5588
10	2000	234	1328	1155	969	1158	1410	6254
11	2000	935		452				1387
12	2000	853	953	739	214	798	609	4166
13	2000		538	124	202			864
14	2000		343					343
15	2000			652	774	586	538	2550
16	2000			625	568			1193
17	2286		855				598	1453
18	2364						563	563
19	2400			934	1557	835	869	4195
20	2400				777	906		1683
21	3834		1298	859	1657		1549	5363
22	3899	972		1698	1869			4539
Total		5678	10654	10514	15724	6948	10569	60087

The catch rates for the two target species by haul were calculated by dividing the total weight (kg) by the haul duration (h). To normalise the data, catch rates were \log_{10} transformed. The percentage of non-zero catches in the dataset was 90.4% for sole, and 91.9% for plaice. The spatial pattern of the probability of non-zero values was assumed to have minor effects on the overall distribution of catch rates, and was therefore not modelled in this study.

2.3.3 Statistical analysis

Let $S(l,a,t)$ denote a random variable corresponding to the local catch rate of either target species at location l , year a and week t , where location is defined by Easting (x) and Northing (y) in a two dimensional space and t is defined by the week number within a year. We assume that the spatial distribution of both target species is stable within a week. The process $S(l,a,t)$ can be decomposed into the large-scale component called drift and a stochastic component. The drift is constant over years, and reflects the average seasonal pattern in catch rates. We modelled this drift in a General Linear Model, as Taylor series of location, time and interaction of location and time. The week (of year) component was modelled using a 4th power Taylor series, all other Taylor series use 3rd powers. The GLM-model also accounts for differences in catch rates caused by the year (a_j), the different engine power of the vessels (hp) and time of day (ToD) during shooting (Rijnsdorp *et al.* 2000a):

$$(2.1) \quad \text{catch rate} = a_i + \log_{10}(\text{engine power}) + ToD_j + \sum_{p=1}^4 t^p + \sum_{p=1}^3 x^p + \sum_{p=1}^3 y^p + \sum_{p=1}^3 x^p \sum_{p=1}^3 y^p + \sum_{p=1}^3 t^p \sum_{p=1}^3 x^p + \sum_{p=1}^3 t^p \sum_{p=1}^3 y^p + \epsilon$$

Differences in catch rates between years are mainly caused by changes in stock biomass or changes in the constraint set by the TAC of the species under consideration. Although the recorded time of the APR has a resolution of minutes, the ToD_j values were grouped in two-hour intervals, reducing the degrees of freedom used by this term to 11. The predictor t accounts for differences in catch rates that are caused by seasonal changes in catchability, caused for instance by overlap of the various age groups and fishing effort, or changes in behaviour of the target species (Rijnsdorp 1991). The Taylor series of predictors x and y and t^*x and t^*y reflect the spatial differences in catch rates over the research area, and the yearly changes of this pattern over the seasons. The assumption of a normal error term (ϵ) distribution was tested by visual inspection of the probability plot of the residuals.

Table 2.2 Analysis of variance results for both the GLM model as a whole, and the individual effects in the model. Non-significant explanatory variables were removed from the final model.

Source	Sole					Plaice				
	DF	SS	MS	F	Pr > F	DF	SS	MS	F	Pr > F
Model	47	1649	35.1	525	<.001	36	3383	94.0	1263	<.001
Error	54249	3628	0.07			55186	4107	0.08		
Total	54296	5278				55222	7490			
Year	5	604	120.8	1784	<.001	5	86	17.3	231	<.001
ToD	11	51	4.7	69	<.001					
Log(engine power)	1	40	40.2	594	<.001	1	2	2.3	31	<.001
$\sum_{p=1}^3 t^p$	3	48	15.8	233	<.001	3	430	143.3	1921	<.001
$\sum_{p=1}^3 x^p + \sum_{p=1}^3 y^p + \sum_{p=1}^3 x^p \sum_{p=1}^3 y^p$	14	350	21.8	322	<.001	14	163	11.7	157	<.001
$\sum_{p=1}^3 t^p \sum_{e=1}^3 x^p + \sum_{p=1}^3 t^p \sum_{p=1}^3 y^p$	13	170	13.1	196	<.001	13	288	22.2	298	<.001
colinearity		386					2414			

The spatial variance that is not part of the recurring changes in the spatial pattern found in the GLM analysis is represented by the residuals. Spatial correlation in the residuals was evaluated using semivariograms and covariance functions (Cressie, 1993). Semivariograms $\gamma(h)$ express the variance between samples minus the covariance between samples separated by a distance h . If the semivariogram increases with distance, then there is a correlation structure as closer points in space are more alike than distant ones. As an alternative, the nonergodic covariance function $C(h)$ can be used (Isaaks and Srivastava, 1988). The covariance function can also be used for measuring spatial dependence of attributes that are separated in time. This form of the covariance function is referred to as the cross-covariance function. We preferred using the cross-covariance function rather than the cross semivariogram, because the latter required observations to be collected at the same locations at the two time steps (Deutsch and Journel 1998). This requirement cannot be met in a system where the sampling locations are chosen by economic incentives of fishing vessels. The semivariogram and (cross-)covariance functions were calculated with distance (h) bins of 2.5 nautical miles.

The observed variograms and (cross-)covariance functions were grouped into four quarters of the year. Spherical models were fitted to the data in each of the quarters to describe the range and size of the spatial covariance using a limited set of parameters (Cressie 1993). Each quarter consisted of 3 months, the first quarter starting on 1 January. The spherical semivariogram model used to fit the observed semivariograms has the form (Cressie 1993):

$$(2.2) \quad \gamma(h) = \begin{cases} C_0 + C_s \left(1.5 \frac{h}{a} - 0.5 \left(\frac{h}{a} \right)^3 \right) & \text{if } h \leq a \\ C_0 + C_s & \text{if } h > a \end{cases}$$

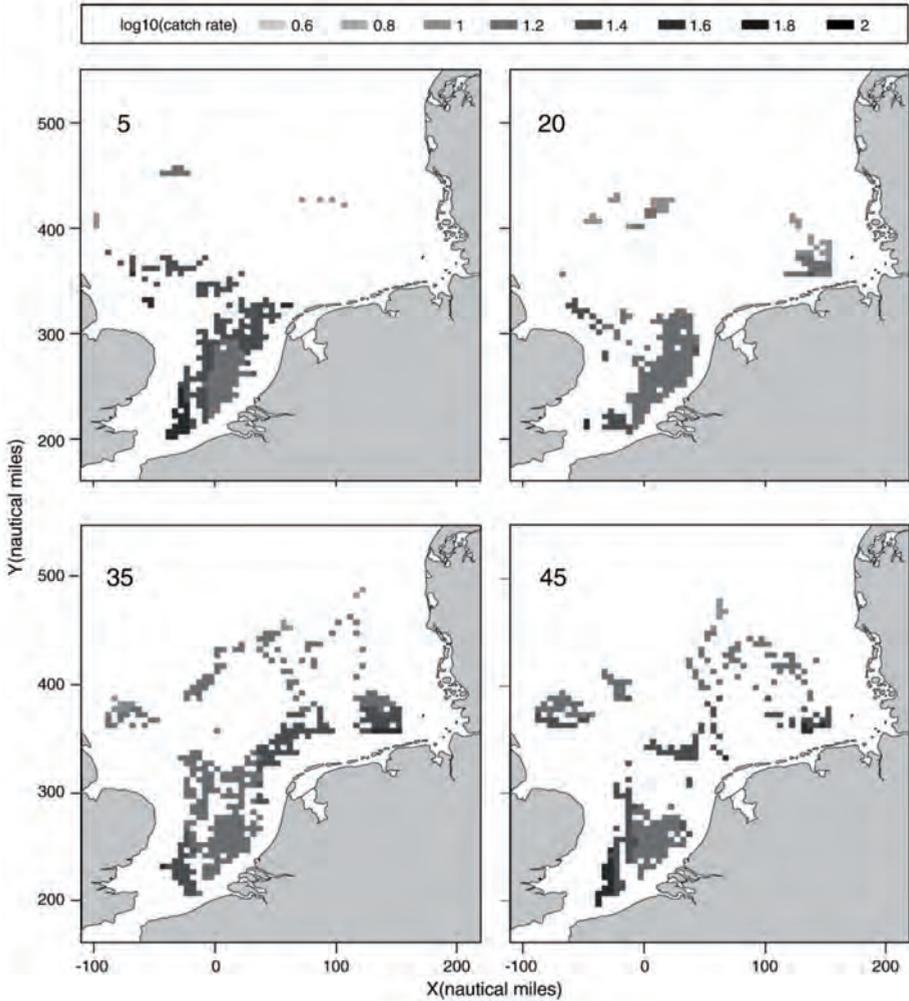


Figure 2.1 Spatial distribution of weekly \log_{10} transformed sole catch rates in the North Sea, as predicted by the General Linear Model. Week numbers of the year are indicated in the upper left corners.

In this model, C_0 defines the nugget effect. The nugget values in the variograms indicate both the measurement error and the variability of the process at very small distances. However, it was not possible to estimate how the nugget effect should be partitioned. The range r is the spatial extent of structure in the data. C_s is the sill minus the nugget effect, where the sill is that value of semivariance at distances equal to and larger than the range. Likewise, the observed covariance values were modelled using a spherical covariance model, of the form:

$$(2.3) \quad C(h) = \begin{cases} s \left(1 - 1.5 \frac{h}{a} + 0.5 \left(\frac{h}{a} \right)^3 \right) & \text{if } h \leq a \\ 0 & \text{if } h > a \end{cases}$$

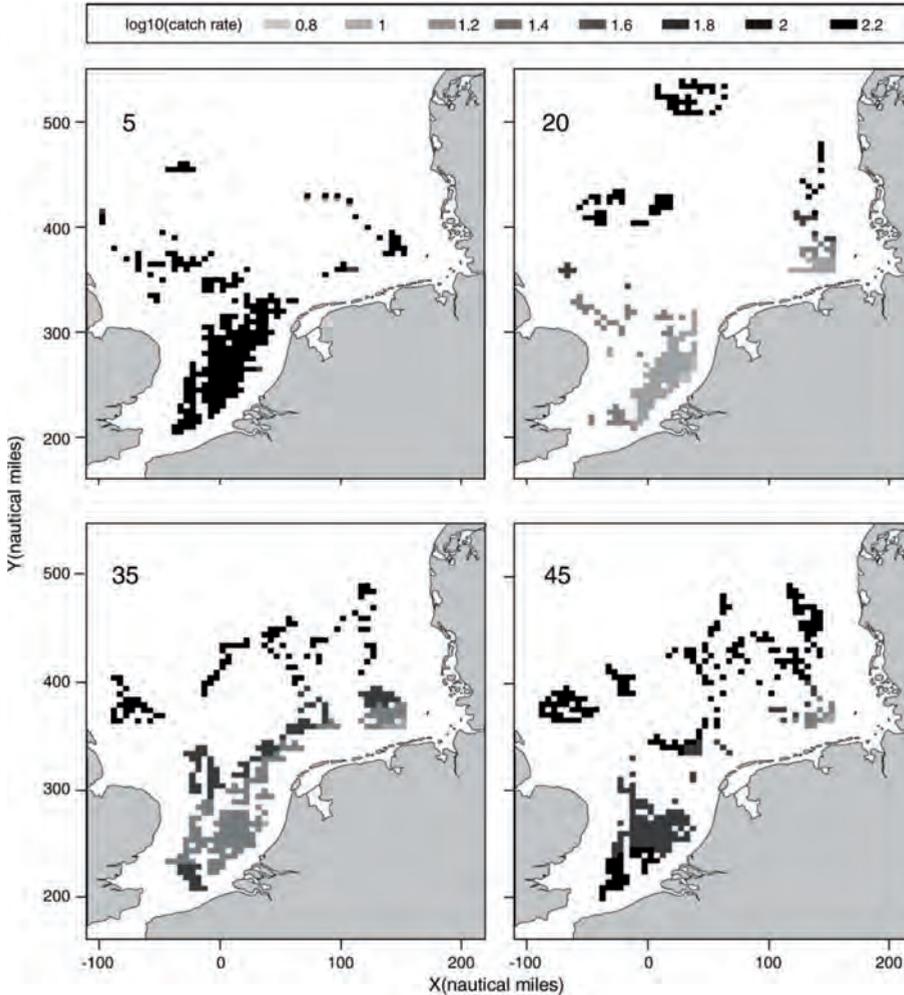


Figure 2.2 Spatial distribution of weekly \log_{10} transformed plaice catch rates in the North Sea, as predicted by the General Linear Model. Week numbers of the year are indicated in the upper left corners.

In this model P is the covariance at very small distances, and r is the range (i.e., the distance at which the covariance function reaches 0). Both the semi-variogram and the covariance function were assumed isotropic (i.e. equal in all directions), and modelled as such. The spherical models were fitted to the empirical variograms and covariance functions using a weighted least squares approximation. For the variogram, each squared residual was weighted according to the number of pairs of points used to compute $\gamma(h)$ and to the inverse of $\gamma(h)^2$ (Cressie, 1993). For the covariance function, each squared residual was weighted according to the number of pairs of points used to compute $C(h)$. All model fitting was done using SAS (SAS Institute Inc. 1996).

2.4 Results

2.4.1 Average seasonal and spatial patterns in catch rate

In the study period between 1994 and 1999, the geometric mean of non-zero catch rates was 18.3 kg h^{-1} for sole, and 40.7 kg h^{-1} for plaice. Catch rates of sole showed a strong relation with year, engine power and, to a lesser extent, time of day, whereas catch rates of plaice did not (Table 2.2). Catch rates of both species were not uniformly distributed in space, but showed a clear spatial pattern that changes over the seasons. For sole (Figure 2.1) this seasonal pattern was less pronounced than for plaice (Figure 2.2). Plaice exhibited high catch rates in the northern part of the central North Sea in spring and summer, and a more uniform spatial distribution in autumn and winter. This is reflected in a significant effect of the predictor variables location and the interaction effect of time of year and location (Table 2.2). Moreover, there was a marked temporal

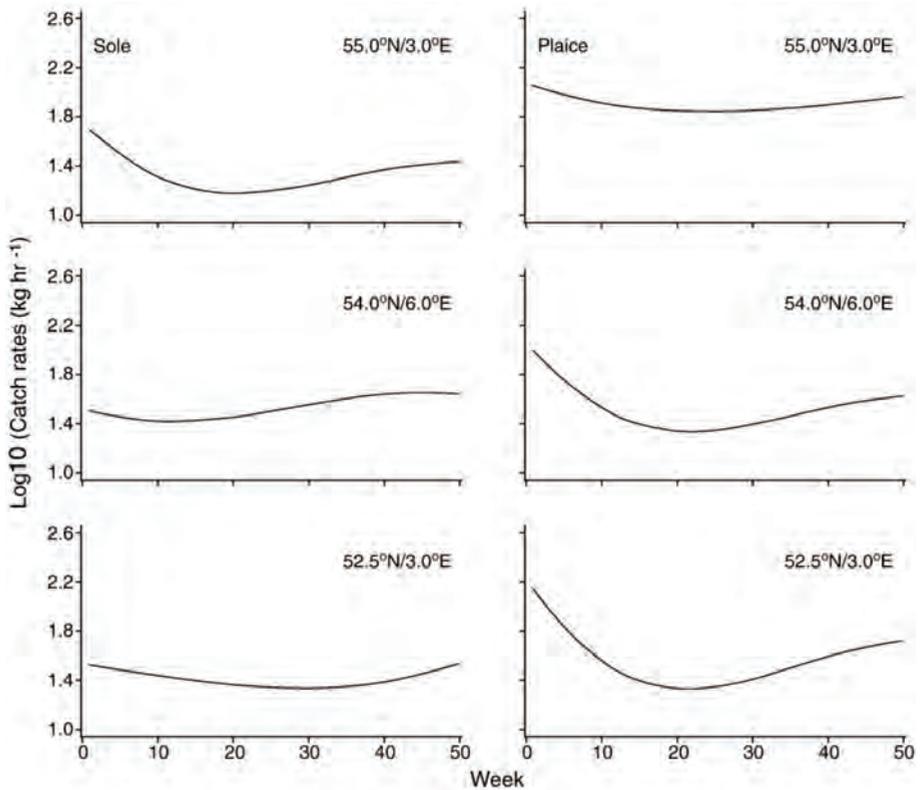


Figure 2.3 Estimated seasonal trends in catch rates for sole (left) and plaice (right) at three different locations in the North Sea, indicated by the position in the top right corner of each panel (° latitude/° longitude).

pattern in catch rate that is independent of the spatial effects, reflected in a significant effect of the predictor variables time of year for both species (Table 2.2). The estimated seasonal trends at different locations are plotted in Figure 2.3. The GLM explained approximately 31.2% of the total variance in catch rates

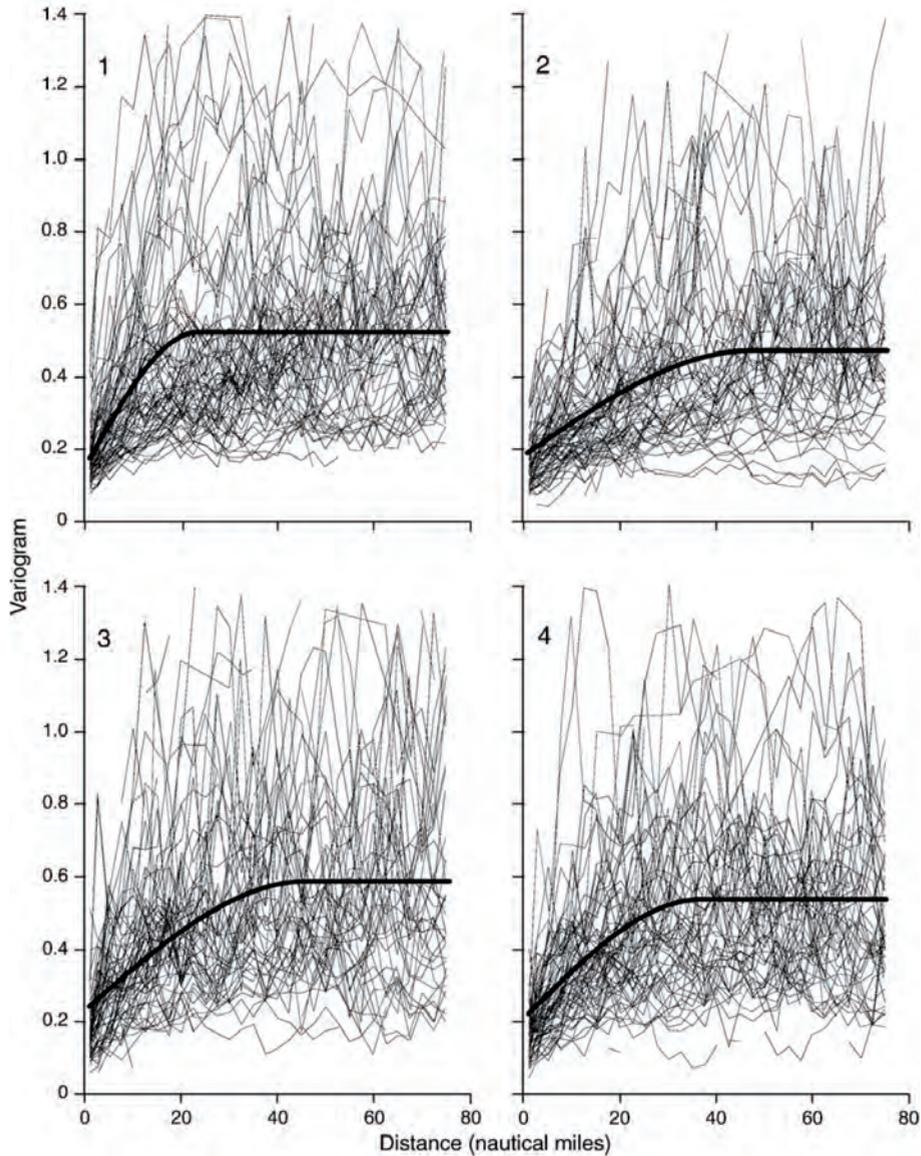


Figure 2.4 Variograms of detrended catch rates for sole, per season, indicating the change in variance over distance. The number of the season is indicated in the upper left corner of each of the panels. Thin lines represent the observed variograms for each of the individual weeks. The solid line gives the fitted variogram modelled as a spherical function.

for sole and 45.2% for plaice. In sole, the collinearity showed that 7.9% of the variance in catch rate cannot be ascribed to a single term. In plaice, collinearity was much higher and accounts for 32.1% of the total variance. This makes it difficult to interpret the contribution of the various terms to the explained variance in catch rate. Nevertheless, there was a strong effect of the time of year on the catch rates of plaice, explaining 5.7% of the total variance in catch rate. This effect was much smaller in the catch rates for sole, where time of year explained only 0.9% of the total variance. For sole, the interaction of time of year and location explained 3.2% of the total variation, while in plaice the explained variance by this term was somewhat higher with 3.9%.

2.4.2 Dimension of local concentrations

On top of the observed seasonal patterns, the geostatistical analysis showed small-scale patchiness. The estimated size of areas with high or low catch rates ranged from 26 to 47 nautical miles for sole (Figure 2.4) and from 32 to 41 nautical miles for plaice (Figure 2.5), as found in the ranges of the semivariograms. The covariance functions yield somewhat smaller ranges for both species, ranging from 22 to 30 nautical miles for sole and from 17 to 32 nautical miles for plaice (Table 2.3). Thus, both approaches indicate patch sizes of 20 to 50 nautical miles. The nugget comprised the variance of catch rates taken at very small distances within a week time, and the measurement error. The ratio between the nugget and the sill indicated the amount of variance explained by the nugget effect. The remaining variance is 'spatially structured'. This spatially structured component is in the order of 0.6 to 0.7 for sole, and 0.7 to 0.8 for plaice, indicating that two hauls taken within close proximity exhibit less than half the variance compared to hauls taken randomly in space as a result of the smallscale spatial structure of the resource.

2.4.3 Persistence of local concentrations

The cross covariance structures indicate that the covariance found within a 40 nautical mile radius is persistent from one week into the next (Figs. 6 and 7). However, the estimate of the local covariance does decrease over time, with the cross-covariance of hauls one week apart being smaller than those within a week, and the cross-covariance of hauls two weeks apart being equal to or smaller than those one week apart. Thus, the local patches exist within a time period of one or two weeks.

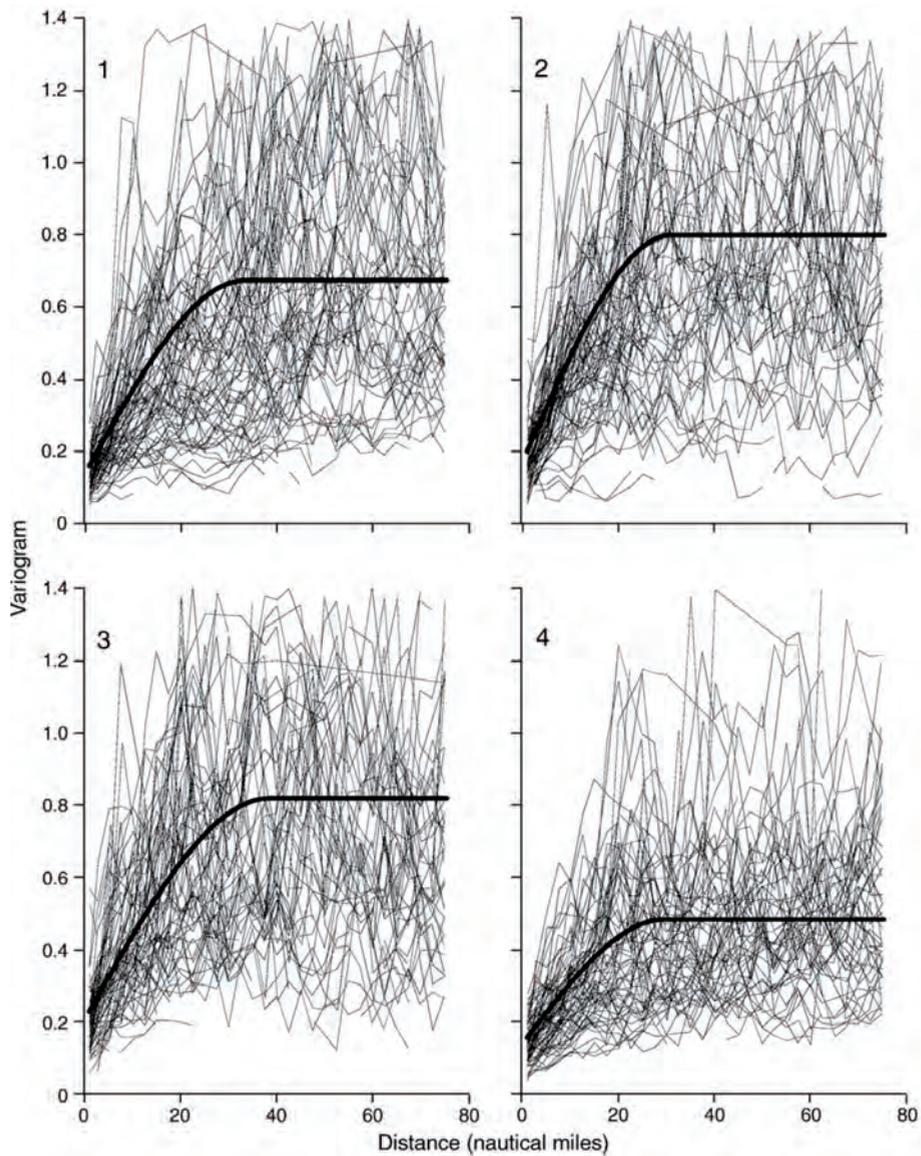


Figure 2.5 Variograms of detrended catch rates for plaice, per season, indicating the change in variance over distance. The number of the season is indicated in the upper left corner of each of the panels. Thin lines represent the observed variograms for each of the individual weeks. The solid line gives the fitted variogram modelled as a spherical function.

2.5 Discussion

The objective of this paper is to analyse the spatial and temporal dimensions of the local concentrations of plaice and sole as reflected in the catch rate of Dutch beam trawl vessels. Although catch rate will reflect the local density of the target species, other factors such as fish behaviour, environmental conditions, fishing power and interactions among vessels may influence the relation between densities and catch rates (Hilborn 1985, Abrahams and Healey 1993, Gillis 2003).

The beam trawl gear used by the Dutch fleet is developed to allow the use of a large number of tickler chains running in front of the ground-rope chasing buried fish from the sea bed (Daan 1997). Such tickler chains especially increase the catch rate of sole (Creutzberg *et al.* 1987). The catch efficiency of the beam trawl depends on the proportion of fish that is within the vertical reach of the gear. Hence animals that are buried below the reach of the tickler chains (Creutzberg *et al.* 1987, Lindeboom and De Groot, 1998), or that have moved up into midwater (De Veen 1976, Arnold and Metcalfe 1996) are not available to the gear. Such vertical migrations may be synchronised to the tidal cycle during the migration to and from the spawning grounds, as is known from plaice (Arnold and Metcalfe 1996, Hunter *et al.* 2004b), or to the day-night cycle (De Veen 1967, De Groot 1971, Casey and Myers 1998).

Table 2.3 Parameter estimates of the spherical models fitted to the experimental semivariograms and covariance functions. The parameters are estimated by quarter. The spatially structured component corresponds to (sill-nugget)/sill.

Sole					Plaice				
Quarter	Range (nautical miles)	sill	nugget	Spatially structured component	Quarter	Range (nautical miles)	sill	nugget	Spatially structured component
Semivariogram									
1	23.3	0.052	0.015	0.71	1	38.6	0.068	0.015	0.78
2	47.0	0.047	0.018	0.62	2	31.0	0.080	0.017	0.79
3	45.5	0.058	0.023	0.60	3	38.5	0.081	0.020	0.75
4	37.5	0.053	0.021	0.60	4	30.6	0.048	0.014	0.71
Covariance function									
1	21.6				1	17.0			
2	23.6				2	30.1			
3	26.4				3	24.2			
4	29.1				4	23.6			

The significant effect of time of day on the catch rates of sole may be related to the diel activity pattern of this species, which shows highest feeding activity during the night (De Groot 1971). No effect of the time of day was observed for

plaice. This could be related to the shift in diel pattern during the spawning and feeding period. De Groot (1971) showed that during the spawning period in December and January, plaice were mainly active at night, whereas in the other months they were mainly active during the day. Moreover, light levels may affect the ability of fish to detect an approaching trawl and influence the catch efficiency (Glass and Wardle 1989, Walsh 1991).

Environmental conditions such as temperature may also affect catch efficiency. At low water temperatures, sole are known to become lethargic and are less likely to be able to escape fishing gear (Woodhead 1964, Horwood and Millner 1998), increasing the catch efficiency. On the other hand, high temperatures may reduce oxygen levels, likely to result in 'passive' behaviour (Doornbos and Twisk 1984), also increasing catch efficiency. Catch efficiency may also be negatively related to fish densities as differences in escapement and capture behaviour were observed at various densities of cod and American plaice in the mouth of a trawl (Godø *et al.* 1999). These effects may contribute to the seasonal pattern found in the catch rates.

The engine power of individual beam trawlers may also affect catch efficiency. Trawlers with higher engine powers will trawl larger areas owing to higher fishing speeds (Beverton and Holt 1957, Rijnsdorp *et al.* 2000a). Moreover, increased towing speed may hasten the onset of exhaustion of swimming fish, reducing their ability to escape (Dahm *et al.* 2002).

Finally, catch rates may be influenced by the density of fishing vessels on a particular fishing ground due to interference competition (Abrahams and Healey 1993, Gillis and Peterman 1998, Rijnsdorp *et al.* 2000a,b).

The observed seasonal patterns of catch rates concurs with the seasonal distribution patterns revealed by tagging studies (ICES 1965, De Veen 1978, Rijnsdorp and Pastoors 1995, Hunter *et al.* 2003), the location of spawning grounds indicated by egg surveys (Harding *et al.* 1978, Van der Land 1991) and the location of nursery grounds indicated by pre-recruit surveys (Van Beek *et al.* 1989). Such seasonal changes in spatial distribution are mainly driven by the migrations between feeding and spawning grounds, and the annual recruitment. Tagging studies have shown that adult plaice migrate southwards in autumn over distances of up to 200 nautical miles towards the spawning grounds in the English Channel and in the southern and southeastern North Sea (Houghton and Harding 1976, Arnold and Metcalfe 1996, Hunter *et al.* 2004a). After spawning they return northwards to feeding grounds dispersed over the North Sea down to a depth of about 100 m. In contrast to the north-south migrations in plaice, adult sole generally migrate over shorter distances along an east-west axis moving into shallow waters to spawn in spring (ICES 1965, De Veen 1967). Recruit-

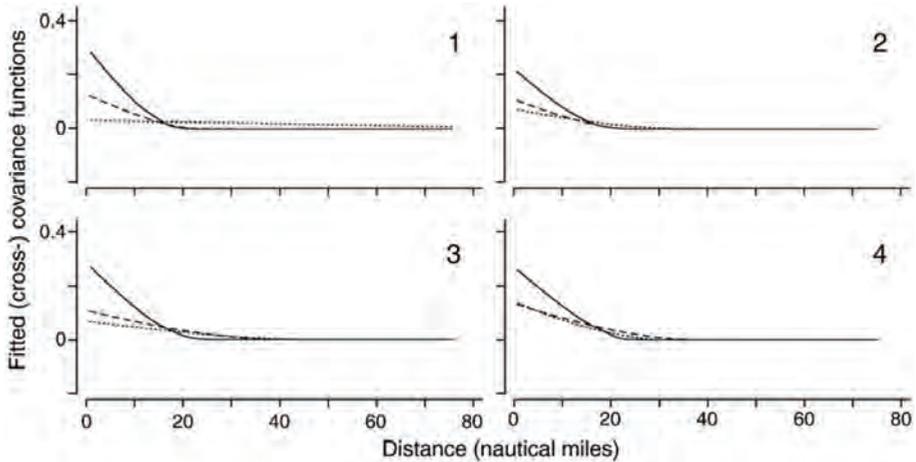


Figure 2.6 Estimated theoretical (cross-)covariance functions for sole, per season, indicating the change in covariance over distance. The number of the season is indicated in the upper right corner of each of the panels. (Cross-) covariance functions with (—) no time lag between observations, (- - -) one-week time lag, (•••••) 2 weeks time lag between observations.

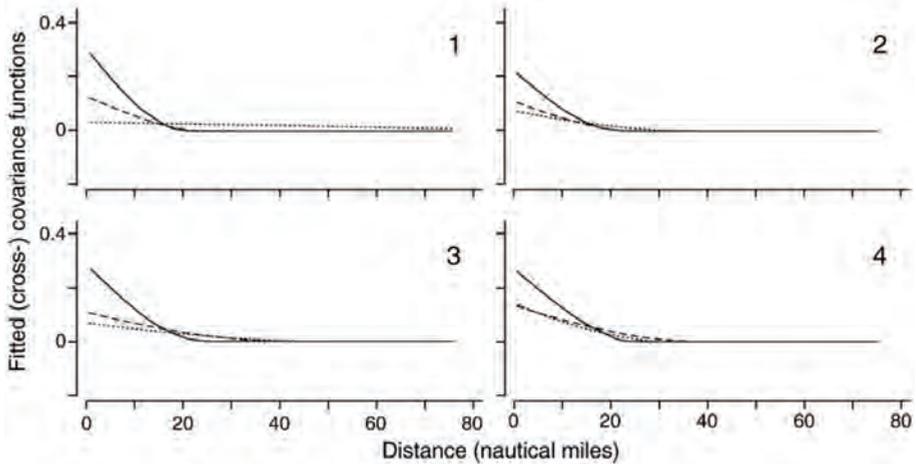


Figure 2.7 Estimated theoretical (cross-)covariance functions for plaice, per season, indicating the change in covariance over distance. The number of the season is indicated in the upper right corner of each of the panels. (Cross-) covariance functions with (—) No time lag between observations, (- - -) one-week time lag, (•••••) 2 weeks time lag between observations.

ment typically occurs in autumn when the recruits leave the shallow coastal waters (Beverton and Holt 1957). The predictable pattern concurs with the pattern in the partial fishing mortality rate observed for both species (Rijnsdorp *et al.* 2006). In conclusion, there is a predictable pattern in spatial distribution

in both plaice and sole that changes seasonally in relation to adult migration patterns and juvenile recruitment. The predictability differs between sole and plaice owing to the higher inter-annual variation in recruitment level, as well as the contribution of the different nursery grounds (Van Beek *et al.* 1989, Fox *et al.* 2000). Moreover, the spatial distribution of sole changes in relation to water temperature when they migrate over larger distances to the deep pits in the western North Sea during cold winters (Woodhead 1964, Horwood and Millner 1998). The larger variation in sole (Rijnsdorp *et al.* 1991) is reflected in the strong year effect on the catch rates of sole found in this study.

Super-imposed on the seasonally changing spatial distribution pattern, local patches occur. The covariance structure indicates that hauls within 20 to 30 nautical miles exhibit larger covariance, whereas hauls that are separated beyond this distance show no additional covariance. The minimum size of the local patches determined in our study is restricted by the track length of one tow (approximately 12 nautical miles). The patchiness of the flatfish species is likely to be related to the patchiness of their food (Shucksmith *et al.* 2006). Marine organisms generally show a patchy distribution (Valiela 1984) and this also applies to Annelida, Bivalvia and Crustacea in the North Sea (Duineveld *et al.* 1991, Kunitzer *et al.* 1992), the main prey species of plaice and sole (Braber and De Groot 1973, Rijnsdorp and Vingerhoed 2001). No systematic difference in the patch size was apparent between the quarters that could be related to biological differences such as spawning or feeding behaviour.

The persistence of the local patches was estimated to be up to 2–3 weeks, which may reflect the time needed for a local concentration of plaice or sole to deplete the local density of its prey. Alternatively, local patches of sole or plaice may be depleted by the fishery.

In our analysis we assumed that a local patch is a stationary phenomenon. This assumption is likely if the patch is related to a feeding concentration on sessile benthic organisms, such as bivalves or polychaetes. However, in some cases, a local patch of plaice or sole may change its position if it is related to feeding on mobile prey, such as sandeel, or to quickly changing environmental conditions. However, it is unlikely that the estimate of the temporal persistence will be seriously biased as a result of this, because plaice and sole mainly feed on sessile prey (Rijnsdorp and Vingerhoed 2001).

The predictability of the spatial and temporal patterns has important implications for fishing behaviour and for the understanding of the effects of fisheries management. The patterns allow fishermen to 'predict' catch rates of target species based on the time-of-year. This conclusion is important when effort management is applied to this fleet, because it implies that fishermen will be able

to actively adapt their fishing behaviour selecting fishing trips in periods with species compositions optimising revenues under effort restrictions.

The persistence of local patches for up to 3 weeks implies that information gathered during a fishing trip may have predictive power for the location of the peaks in the next fishing trip. Hearsay about patches with high target species catch rates in ports is thus a valuable source of information. Indeed in several trips, skippers returned to the local concentration area of the week before (Rijnsdorp *et al.* 2000b). In other fisheries, such fleet response of relocating effort to high catch rates with a lag period of one to several weeks has also been found (Gillis *et al.* 1993, Holland and Sutinen 1999).

The spatial dimension of the local patches corresponds to a distance covered by 2 to 3 hauls. This is in agreement with the fishing patterns described by Rijnsdorp *et al.* (2000b), who showed that the change in direction of successive tows peaked around 0 or 180 degrees when the catch rate was above the weekly average, and around 0 degrees when the catch rate was below the weekly average.

We did not analyse the shape of the local concentrations, in terms of analysing the anisotropy of the variograms. However, beam trawl vessels show preference for certain depth strata (Piet *et al.* 2000), causing elongated shapes in effort distribution in areas with a complex bathymetry. This depth preference may reflect the distribution of the target species, suggesting preference for these depth strata of the fish, or it may reflect an incapability of fishing too steep depth gradients with towed bottom gears.

The results of this study may be summarised in a conceptual model illustrating the relation between the local density of a target species, the distribution of a fishing fleet and the resulting pattern in catch rate. The patchy distribution of the target species may be visualized as undulating landscapes, for which elevation and shape will change seasonally, whereas the location of the peaks and troughs will change over a period of weeks. In such a dynamic resource environment, a fishing fleet will have to detect the peaks of the resource landscape (consisting of a number of target species) in order to maximise its net revenue (catch rate - fishing costs). As the cost of fishing will increase with the distance to the harbour (Sampson 1991), we expect that at increasing distance from the harbour, only higher peaks will be fished. As the resource landscape can only be detected by trial and error, some fishing effort will occur in the valleys. Rijnsdorp *et al.* (2000b) showed that during a fishing week approximately 20% of the tows may be considered as sampling and 80% as exploitation of local concentrations. The sampling tows were characterised by a below average catch rate and occurred in locations that were only fished once. The exploitation tows

occurred in areas that were fished more than five times during the week, and had a catch rate that was approximately 1.15 times the weekly average. The catch rates of individual vessels will reflect the local density of the resource if no interference competition among the fishing vessels occurs. However, if interference interactions occurs, the catch rate will be negatively affected by the number of fishing vessels exploiting the local concentration and will underestimate the local density (Gillis and Peterman 1998, Gillis 2003). There is evidence that interference competition occurs in the beam trawl fleet exploiting flatfish in the North Sea (Rijnsdorp *et al.* 2000b, Poos and Rijnsdorp 2007). Under the assumption of profit maximisation of individual fishing vessels, the beam trawl fleet will distribute itself over the patches such that the net gain in each of the patches is equal for all of the individuals. Exact formulations of the mechanisms of competitive interactions are found to be crucial for predictions of the distribution of the competitors (Van der Meer and Ens 1997). If fishing vessels indeed follow the assumptions of profit maximisation, have knowledge about the spatial distribution of the resource, and interference competition occurs, this has important implications for the relationship between fishing effort and fishing mortality, and for the use of commercial catch per unit of effort data as an index of the population biomass (Gillis *et al.* 1993, Gillis and Peterman 1998).

2.6 Acknowledgements

The study was funded by NWO grant ALW88510104. Comments on an earlier version by Dr. Niels Daan and Dr. Sarah Kraak are gratefully acknowledged.

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Chapter 3

An “experiment” on effort allocation of fishing vessels: the role of interference competition and area specialization

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Canadian Journal of Fisheries and Aquatic Sciences 64 (2007) 304-313

3.1 Abstract

A temporarily closed area established to protect spawning Atlantic cod (*Gadus morhua*) in the North Sea allowed us to study the response of the Dutch beam trawl fleet exploiting common sole (*Solea solea*) and plaice (*Pleuronectes platessa*). A number of vessels left the North Sea 1 month earlier than the normal seasonal pattern. The vessels that continued fishing in the North Sea were concentrated in the remaining open areas. In the first week after the closure, the catch rate decreased by 14%, coinciding with an increase in crowding of 28%. Area specialisation affected the response of individual vessels because vessels without prior experience in the open areas showed a larger decline in catch rate compared with vessels that previously fished in these open areas and were more likely to stop fishing during the closed period. The decrease in catch rate in response to the increase in competitor density allowed us to estimate the strength of the interference competition.

3.2 Introduction

Fisheries management generally does not take into account the response of the fisheries to management measures (Holden 1994), which may lead to unforeseen changes in the exploitation pattern, reducing the effectiveness of the management of the target species, and unexpected implications for the sustainable use of the marine resources (Dinmore *et al.* 2003). To be able to include the response of fisheries to management, knowledge about the processes underlying spatial and temporal allocation of fishing effort is required. This is of paramount importance as a scientific basis for effective fisheries management (Gordon 1954, Paloheimo and Dickie 1964, Gillis 2003).

The dynamics of the spatial distribution of fishing vessels may be studied using the behavioural ecological theory of optimal foraging (Abrahams and Healey 1993), which has been successfully applied to fisheries problems (Gillis *et al.* 1993, Rijnsdorp *et al.* 2000b, Gillis 2003). One of the optimal foraging theories regarding spatial allocation of foragers is known as the ideal free distribution (IFD; Fretwell and Lucas 1970), which predicts how foragers will distribute themselves in relation to their food resources. The IFD assumes that individual foragers (i) are “ideal”, meaning that they are able to choose the area that maximizes fitness rewards, and (ii) are “free”, meaning that they experience no cost of moving between feeding areas. Also, all foragers are assumed equal. In its simplest form where no interactions occur among foragers, all foragers will aggregate in the best feeding area. However, if the intake rate is affected by the presence of other foragers by interference competition (Hassell and Varley

1969; van der Meer and Ens 1997), for instance, owing to interactions among foragers (Goss-Custard 1977) or a response of the prey to the density of foragers (Ruxton 1995, Stillman *et al.* 2000), foragers will distribute themselves over the resources. Hence, the occurrence of interference competition has the potential to strongly affect the spatial distribution of foragers (Sutherland 1983, van der Meer and Ens 1997).

In contrast to animal studies in which the interference interactions among foraging individuals can be observed directly (Goss-Custard 1980), interference competition among fishing vessels is more difficult to study quantitatively. Although the direct interactions among vessels can potentially be quantified (Gillis 1999), the interaction between fishing vessels and their fish resources is difficult to estimate. A decrease in the catch rate of fishing vessels with increasing number of vessels is insufficient evidence as it may reflect interference competition; however, it may also be due to the local depletion of the fisheries resource (exploitation competition).

The evidence for interference competition among fishing vessels is mainly inferred from observational studies: from equal catch rates among vessels exploiting different fishing grounds or from a change in catch rate following a change in vessel density (Hilborn and Ledbetter 1979; Healey and Moms 1992; Gillis *et al.* 1993). To our knowledge, only two studies provided “experimental” evidence for interference competition. Abrahams and Healey (1993) showed that vessel density had a significant influence on the catch rate of Chinook salmon (*Oncorhynchus tshawytscha*) and spiny dogfish (*Squalus acanthias*), but not on coho salmon (*Oncorhynchus kisutch*). Rijnsdorp *et al.* (2000b) showed that the catch rate of flatfish (order Pleuronectiformes) significantly increased during a week when part of the fleet remained in harbor for religious reasons.

The IFD offers a robust starting point for the analysis (Milinski and Parker 1991, Gillis 2003), although the assumptions of the IFD of perfect knowledge, equality among fishing vessels, and no cost of movement among fishing areas will certainly be violated in the real world. Fishers will differ in their knowledge about the location of trawlable grounds and the distribution of the prey (Hilborn and Ledbetter 1979, van Densen 2001). Bottom trawl fisheries, especially, are restricted to areas with soft sediment where the chances of gear loss are small (Rijnsdorp *et al.* 1998, Piet *et al.* 2000). Also, fishing effort allocation will be related to the distance to the home port (Sampson 1991).

The process underlying the spatial dynamics of fishing vessels is generally inferred from the observed dynamics of the system. These observational studies, however, do not allow us to draw unequivocal conclusions on the processes involved. Although experimental research on effort allocation is generally not

feasible (but see Abrahams and Healey (1993)), changes in the management regime may provide an opportunistic experiment. Thus the response of fishermen with respect to catch rates and effort distribution following an area closure may provide answers to the mechanisms involved in effort distribution and their strength.

In this paper, we analyse the response of the Dutch beam trawl fleet to a temporarily closed area focussing on the effect of interference competition and providing an empirical estimate of the strength of the interference competition in a fisheries context. Further, we address the null hypothesis that fishers who lack knowledge of fishing in the remaining open areas will experience lower catch rates than fishers with local knowledge. Insight into these factors will allow us to better predict the response of fishing fleets to management measures.

3.3 Materials and methods

3.3.1 Fishing fleet

The Dutch beam trawl fleet targets common sole (*Solea solea*) and plaice (*Pleuronectes platessa*) (Dam 1997), towing demersal gears fitted with chains at speeds between 5 and 7 nautical miles per hour. Bycatches are comprised of other flatfish species such as turbot (*Scophthalmus maximus*), brill (*Scophthalmus rhombus*), and dab (*Limanda limanda*) and roundfish species such as Atlantic cod (*Gadus morhua*) and whiting (*Merlangius merlangus*). The fishing effort of the fleet shows a patchy distribution owing to the distribution of the target species and the physical characteristics of the sea bed (Rijnsdorp *et al.* 1998). Trips typically start on Monday and end on Friday, during which there is almost continuous fishing. The fleet is comprised of two components: small (1300 horsepower (hp)) and large (>300 hp) beamers. The small vessels are allowed to fish in the coastal zone, from which the large beam trawlers with higher engine power are banned. Vessels in the northern harbours utilize beam trawls rigged with tickler chains and generally have engine powers up to 2000 hp. In the southern harbours, the large beamers typically use chain mats to fish the rough grounds in the southern North Sea, requiring engine powers up to 4500 hp.

3.3.2 Area closure in 2001

To reduce the fishing impact during the spawning period of the heavily depleted North Sea cod stock, two areas in the North Sea were closed for trawling (“closed north” and “closed south”; Fig. 8) between 15 February (Thursday,

week 7) and 30 April (Monday, week 18) 2001. In this paper, the closed period is defined as weeks 8 to 17. With 43% of the fishing effort in the reference years, the two closed areas encompass the main fishing grounds of the Dutch beam trawl fleet. The remaining two areas open for fishing during the closure are referred to as “open north” and “open south”. In addition to the area closure, an effort reduction program was set up by the Dutch Ministry of Agriculture, Nature Conservation and Food Safety (LNV). This program encompassed a voluntary reduction in fishing effort by staying in port for 3 weeks in April. The majority of the large beam trawl vessels participated in the program.

The management measures in 2001 mainly affected the fleet of large beam trawlers, because the small beamers were allowed to fish in the coastal waters (12-mile zone and plaice box). Hence, our study was restricted to the fleet of large beam trawlers representing approximately 50% of the fleet.

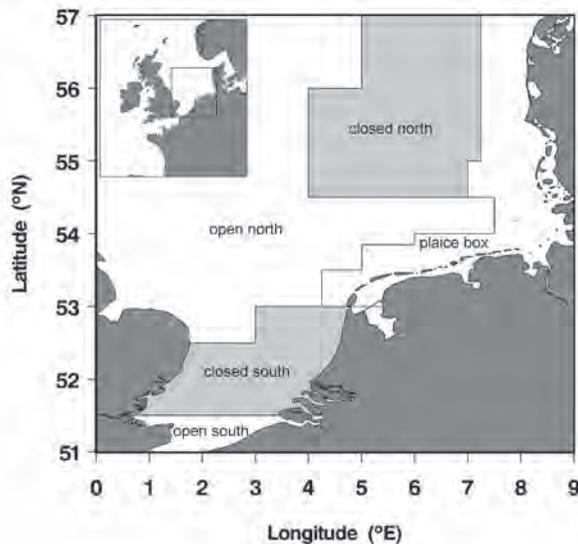


Figure 3.1 Overview of the open and closed areas in the North Sea. The plaice box is permanently closed for fishing vessels > 300 hp. The closed areas indicated in grey were closed between 15 February and 30 April 2001 to protect spawning cod (*Gadus morhua*). The plaice box is permanently closed for demersal trawl fisheries such as beam trawling for vessels with engine power exceeding 300 hp.

3.3.3 Analysis

The analysis is based on the EU logbook data of individual vessels available from the Dutch national catch and effort database. This database comprises data per trip on landings (kg) by commercial fish species, fishing effort (days at sea), ICES

rectangle fished (boxes of 30' latitude x 1° longitude), engine power, and fishing gear. The patterns in effort allocation and catch rates before (1 January - 15 February 2001), during (15 February - 30 April 2001), and after (1 May - 15 June 2001) the closure were compared with the average patterns in the reference years 1999, 2000, 2002, and 2003. The area closure in 2001 started in week 7, preceded by the annual week of prayer, during which part of the fleet stays in port for religious reasons.

Fishing effort was expressed as the number of days at sea and was spatially allocated per ICES rectangle. In addition, the number of fishing trips per week allocated in the different open and closed areas was calculated. The average competition that an individual fishing vessel experiences was quantified by calculating using Lloyd's index of mean crowding (m^*) (Lloyd 1967, Pielou 1969),

$$(3.1) \quad m^* = \frac{\sum f_j^2}{\sum f_j} - 1$$

where f_j is the number of vessels in the j th ICES rectangle. This index expresses the number of vessels with which a vessel shares a fishing area (ICES rectangle) and depends on the total effort. A high m^* value indicates a high level of co-occupation experienced by the individual vessels. The weekly mean crowding indices were calculated for the four study areas, including all recorded fishing trips (Figure 3.1).

For the analysis of the effects of fishing effort on catch rates in the open areas, catch rates from vessels that were not present throughout the entire period were excluded to prevent a possible effect of a change in the composition of the fleet on the catch rate.

In both open areas, different selection criteria were set to the engine power of vessels to increase the homogeneity of the sample. For the open north area, only vessels with engine powers up to 2500 hp were included, whereas for the open south area, only vessels ranging from 2400 to 4500 hp were used, representing the chain-mat beamers that generally fish in this area. These selections result in a study fleet consisting of 124 vessels present throughout the study period, of which 93 vessels have fished in the areas open north versus 13 vessels in the open south during the closure. Based on the number of days at sea recorded in the open areas in the 3 years prior to the area closure, the fleet was further segregated into immigrant vessels (40 days at sea), intermediate vessels (50-200 days at sea), and resident vessels (>200 days at sea; Figure 3.2). Resident vessels thus have spent more time in the respective open areas in previous years and may therefore be more specialized in fishing its grounds. Using this classification, in the open north area, 10 vessels are classified as immigrant in

comparison with 70 residents. In the open south area, six vessels were immigrant and seven were residents.

The effect of management measures on the effort allocation is likely to be mediated by the skipper's response to changes in revenue rather than weight of the catch of individual species. The catch rate was therefore expressed in monetary units (euros) combining the target species to a value per unit effort (VPUE):

$$(3.2) \quad \text{VPUE} = \frac{\sum C_s P_s}{f}$$

where C_s is the catch (kg) of species s , being sole, plaice, or cod, and P_s is the corresponding price (euros per kg). The fishing effort, denoted by f , is expressed in days at sea. Because the VPUE of beam trawl vessels is strongly affected by the engine power (hp) of the vessel (Rijnsdorp *et al.* 2000a), standardization was applied using a general linear model (GLM) to fit the following regression model:

$$(3.3) \quad \log_{10}(\text{VPUE}) = \alpha + \beta \log_{10}(\text{hp}) + \varepsilon$$

Normal distribution of the model was checked using visual inspection of the residuals.

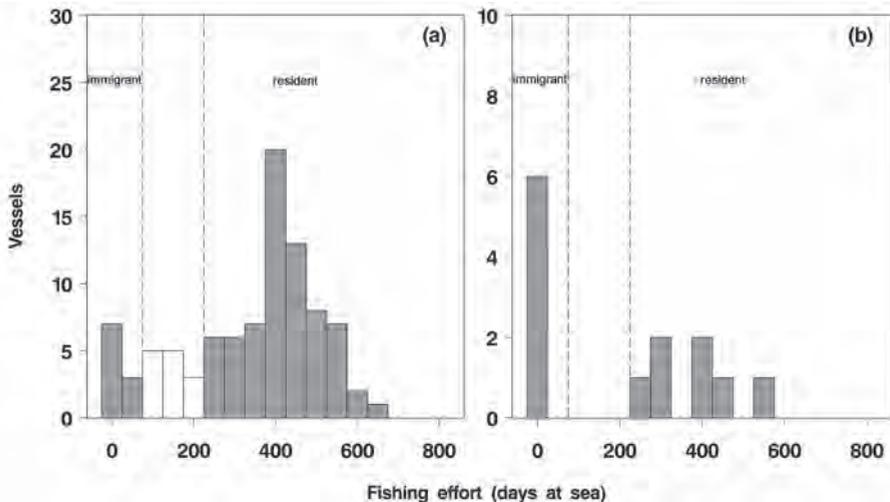


Figure 3.2 The distribution of previous fishing effort allocated (1998 to 2000) by individual vessels fishing in the two open areas during the closure in 2001. The vertical broken lines indicate the separation between the vessels categorized as “immigrants”, “intermediate” and “residents”. The intermediate group is not used for further analysis.

3.3.4 Interference and exploitation competition

The catch rate on a fishing ground is determined by the density of fish and the interference among fishing vessels. The density of fish on a fishing ground will depend on the local biomass and change in time due to (i) immigration and emigration, (ii) removals by fishing, (iii) body growth, and (iv) natural mortality. Over short time periods, e.g., weeks, the changes in local biomass will be mainly determined by the combined effects of immigration and emigration and removals by fishing as natural mortality and body growth will be negligible.

Because interference will act immediately whereas exploitation will act gradually, interference and exploitation competition can be disentangled if a sudden change in vessel density occurs. In a situation without interference, but with exploitation competition, an increase in vessel density will result in a steeper slope of the catch rate. In a situation with interference and exploitation competition, an increase in vessel density results in a sudden decrease in catch rate owing to the lower efficiency resulting from the increased interference and an increase in the slope of the catch rate owing to the higher exploitation rate.

The sudden change in catch rate due to interference at the time of area closure and the change in the slope of the catch rate with time reflecting the net result of fisheries removals (exploitation) and the immigration-emigration from the study area was estimated with the following GLM:

$$(3.4) \quad \log_{10}(\text{VPUE}) = \mu + \alpha \text{ week} + \beta \text{ week closure} + \text{closure} + \log_{10}(\text{engine power}) + \varepsilon$$

where the closure parameter is a class variable that is set to 1 for those weeks when the area closure was in effect and set to 0 otherwise. The regression coefficients α and β estimate the slope in catch rate over a number of weeks. The interaction between the slope and the closure allows for a change in the slope during the closure. The effect of the class variable closure on the catch rate allows estimation of a change in the catch rates resulting from the area closure. The engine power of the vessel is added to the model to account for its effect on catch rates. Finally, ε is the error term of the model. The model was fitted to the data for each year separately from weeks 1 to 13. To exclude effects of area specialization owing to, for instance, differences in local knowledge, only resident vessels were included in the analysis.

3.4 Results

3.4.1 Fishing effort

Following area closure in 2001, the fishing effort in the North Sea shows a decline coinciding with an increase in fishing effort outside the North Sea (e.g., Irish Sea). The low level of fishing effort in week 7 is related to the “bid week” during which a part of the Dutch fleet stayed in the harbour for religious reasons. The increase in fishing effort outside the North Sea starts in the second week of the closed period, much earlier than in the reference years (Figure 3.3). The maximum of 7-10 trips, reached between weeks 12 and 17, is much higher than the maximum of three vessels in week 20 observed in the reference years.

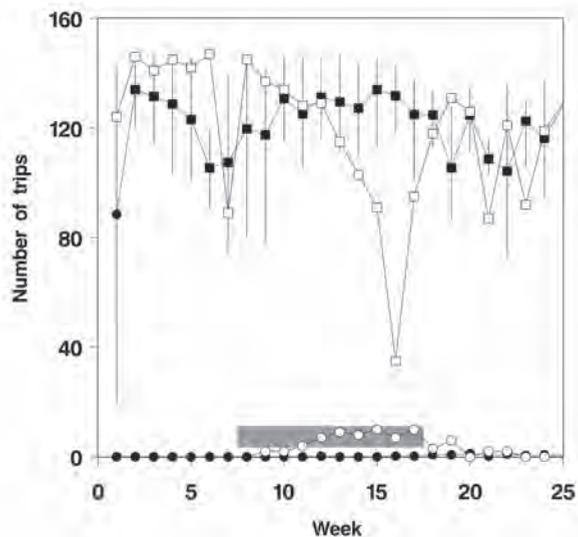


Figure 3.3 Number of fishing trips of Dutch beam trawl vessels (> 300 hp) by week. The number of trips in the North Sea in 2001 (\square) and the average number of trips in the reference years (\blacksquare). The number of trips outside the North Sea in 2001 (\circ) and the average number of trips in the enclosing years (\bullet). The vertical bars indicate the range of the observations within the reference years. The shaded horizontal bar indicates the period of the area closure.

Within the North Sea, the area closure on 15 February 2001 halts fishing in the closed areas. The few trips reported in the closed areas during this period are probably owing to misreporting. The beam trawl effort is mainly redistributed to the open north area (Figure 3.4) in which the number of fishing trips increased from 100 in weeks 1 to 6 to 140 trips in week 8. In the following weeks, the number of trips gradually decreased to reach the preclosure level around

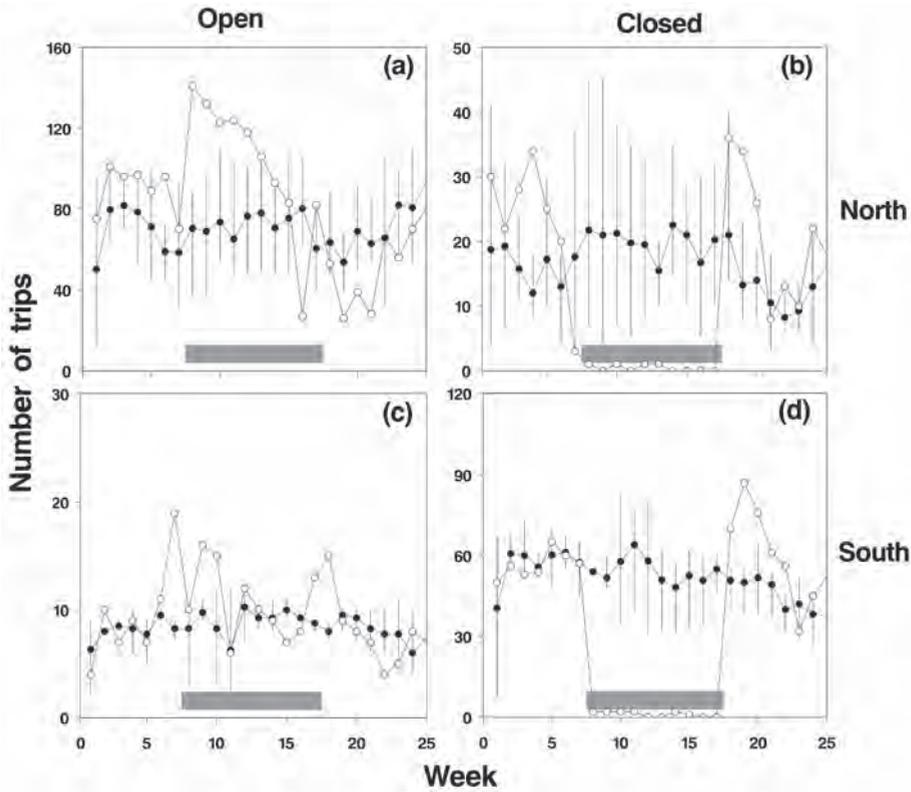


Figure 3.4 Number of fishing trips of Dutch beam trawl vessels (> 300 hp) by week in the four areas in 2001 (○) and the average number of trips in the reference years (●). The vertical bars indicate the range of the observations. The shaded horizontal bar indicates the period of the area closure.

week 14. Fishing effort in the open south area only increased for two weeks following the closure, after which it fell back to the average level of the reference years. This may be owing to the rough grounds in this area that require specialised beam trawls (chain mats). To test whether resident and immigrant vessels differed in their response to the closure by staying in port, the average weekly probability of making a fishing trip was estimated. Resident vessels have a higher probability (p) of making a fishing trip during a week ($p = 0.76$) than immigrant vessels ($p = 0.59$) during the closure ($\chi^2 = 17.17$, $df = 1$, $p < 0.001$).

After the closure was lifted, the beam trawl fleet moved into the previously closed areas. The number of fishing trips in the closed south and closed north areas was higher than in any of the weeks prior to the closure, whereas the number of trips in the open north area was lower than in the weeks before the closure. In the open south area, no decrease in the number of trips was apparent after the closure was lifted.

3.4.2 Mean crowding index

The changes in the index of competition among vessels are shown in relation to the area closure (Figure 3.5). The trends in mean crowding generally corresponded to the trends in the number of fishing trips. Mean crowding among vessels in the open areas reached a peak value just before and during the first half of the closed period, whereas during the second half of the closed period, the mean crowding fluctuated around the level that was observed in the reference years. For about 3 weeks following the end of the closed period, the mean crowding index in the closed north and closed south areas reached peak values that were substantially higher than the reference levels. In correspondence to this, the mean crowding reached low values in the open south and open north areas. The high levels of mean crowding observed during the closed period in 2001, however, fall within the range of values observed in the reference periods, indicating that a strong aggregation of fishing effort is possible under normal conditions unrelated to the area closure.

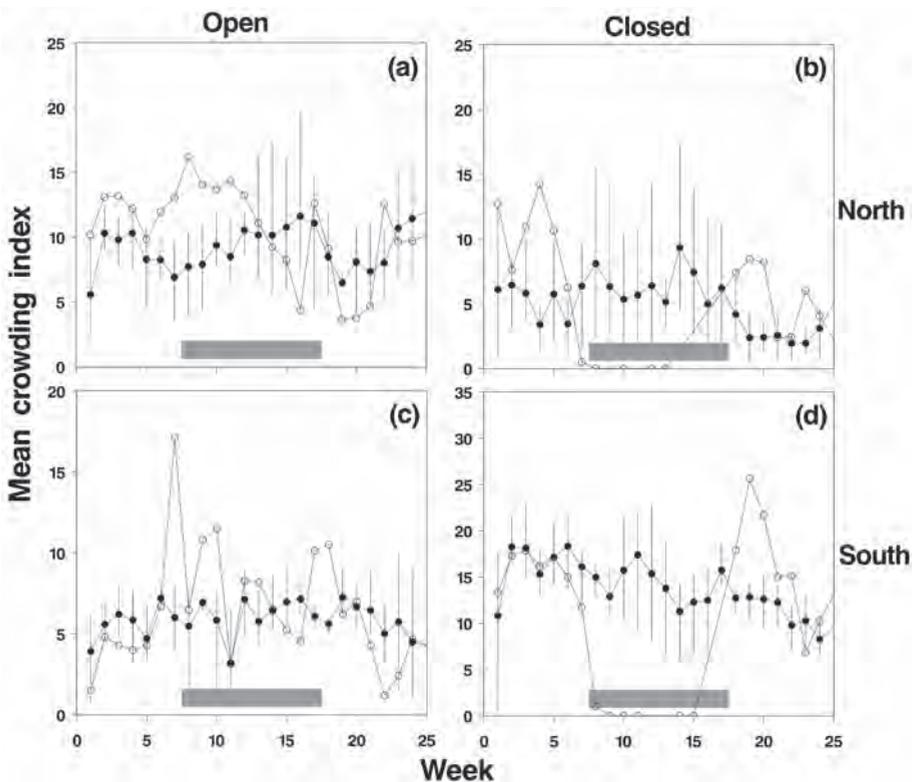


Figure 3.5 Mean crowding index by week in the four areas in 2001 (○) and the average mean crowding index in the reference years (●). The vertical bars indicate the range of the observations. The shaded horizontal bar indicates the period of the area closure.

Mean crowding in the individual areas deviated in minor detail from the general pattern described above. In the open north area, the increase in mean crowding was approximately 28% during the first week of the closure. In the open south area, the index of mean crowding was more variable among weeks, as well as among years. However, there is a distinct peak in the week just before the closure followed by a drop at the onset of the closure and a second peak during the subsequent two weeks.

3.4.3 Revenue rate

Revenue rates (VPUE) were standardised to a vessel of 2000 hp. The regression model used explained 16.5% of the total variance in VPUE ($F = 9063$, $df = 1,45967$, $p < 0.001$). No apparent relation was found between model predictions and residuals or between engine powers and residuals.

In the reference years, the standardised VPUE showed a gradual decline from winter to spring in all four areas (Figure 3.6). In January and early February, the $\log_{10}(\text{VPUE})$ varied around a level of about 3.85, corresponding to a revenue of 7.1×10^3 euros per day. VPUE decreased to a level of about 3.6×10^3 euros per day between April and June. In 2001, however, the results were different. In the weeks prior to the closure, VPUE was at a level similar to that of the reference years, but then dropped in the first week of the closure (week 8) to a level well below that of the reference years. In the subsequent weeks, the catch rates remained below the level of the reference years and reached a minimum in weeks 13 to 15. Only at the end of the closed period did the VPUE reached values comparable to the level in the reference years. In the open south area, VPUE started to decline in the week prior to the closure, coinciding with a peak in fishing effort. The drop in VPUE in the open north area coincided with an increase in the number of trips (from 70 in week 7 to 141 in week 8) and an increase in the mean crowding index. In the open south area, the number of trips increased from 11 in week 6 to 19 in week 7 and 17 and 16 in weeks 9 and 10, respectively.

After the closure was lifted in week 18, the revenue showed distinct peaks of 5.8×10^3 and 4.7×10^3 euros per day in the previously closed areas, which is a 100% and 48% increase compared with reference years, respectively. The catch rate decreased sharply in the second week and reached a level typical for the season in the fifth or sixth week after the areas were re-opened. Revenue rates in both open areas increased simultaneously, coinciding with a 30% decrease in the number of trips in the open north area, whereas in the open south area, the number of trips increased 15% to 15.

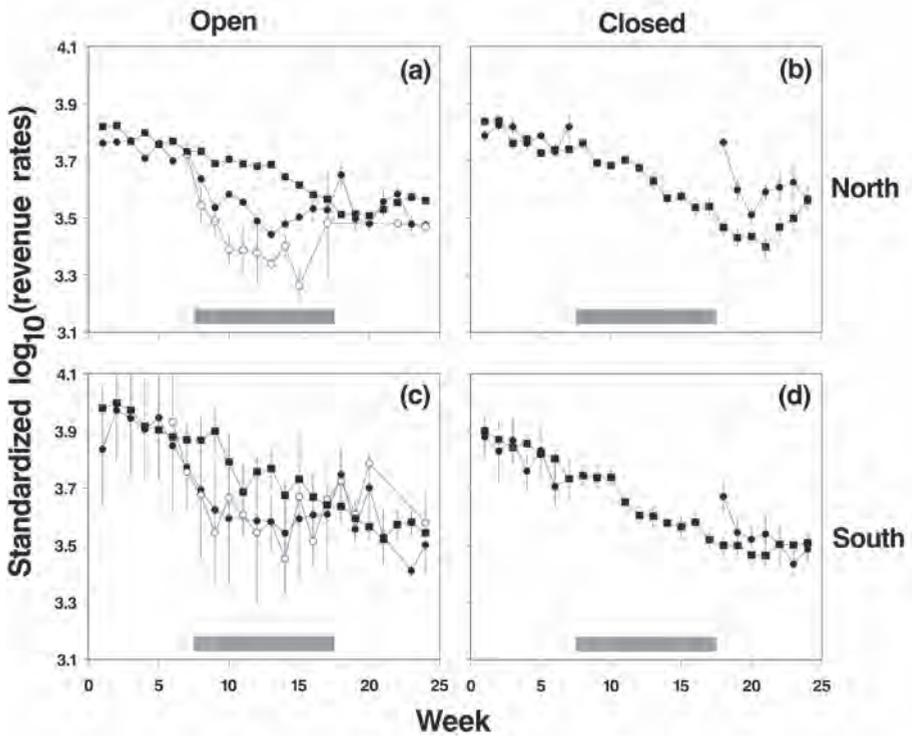


Figure 3.6 Standardized \log_{10} (revenue rate) by week in the four areas for residents (\bullet) and immigrants (\circ) in 2001 and residents during the reference years (\blacksquare). Vertical bars indicate 2 standard deviations. The shaded horizontal bar indicates the time period of the closure in 2001.

3.4.5 Area specialization

Comparison of the VPUE between residents and immigrants indicated that residents performed significantly better than immigrants in the open north area, but not in the open south. The first immigrant vessels enter the open areas in week 7, obtaining catch rates equal to the residents. In the open north area, the average VPUE drops in the subsequent week, when the number of competitors increases. The decline of immigrant VPUE at levels below those of the residents continues throughout the closure, with a maximum difference of 43% in week 15.

3.4.6 Interference and exploitation competition

The drop in VPUE of resident vessels in the first week of the area closure reflects the increased interference among the fishing vessels resulting from the

increased competitor density. This $\log_{10}(\text{VPUE})$ difference of 0.065 reflects a drop in VPUE of 14% (Table 3.1). No significant difference was found in the reference years. A difference in the slope of resident VPUE reflects an increase in the exploitation competition combined with migration effects. The difference in $\log_{10}(\text{VPUE})$ slopes before and during the 2001 closure is estimated to be -0.017, which is the largest difference found. However, significant differences are also found in the reference years, both positive and negative.

Table 3.1 Results of the General Linear Model of the decrease in $\log(\text{VPUE})$ in the area 'Open North' at the onset of the closure ($\Delta\text{closure}$) and the difference in slope of $\log(\text{VPUE})$ before and after the onset of the closure (Δslope). $\Delta\text{closure}$ reflects the interference competition owing to the increase in vessels and Δslope reflects the combined effect of the exploitation of the resources and the immigration and emigration in the area. SE, standard error.

Year	$\Delta\text{closure}$			Δslope		
	Estimate	SE	$p > \chi^2$	Estimate	SE	$p > \chi^2$
1999	0.002	0.011	0.86	0.013	0.003	<0.01
2000	-0.003	0.013	0.79	0.002	0.003	0.51
2001	-0.065	0.010	0.01	-0.017	0.003	<0.01
2002	-0.024	0.016	0.14	-0.009	0.004	0.02
2003	0.013	0.014	0.36	-0.012	0.004	<0.01

3.5 Discussion

3.5.1 Effort re-allocation

The area closure of 2001 resulted in a re-allocation of fishing effort by the Dutch large beam trawl fleet. Compared with the reference years, fishing effort shifted towards the open areas and areas outside the North Sea. In the first weeks after the closure, the number of competitors on the fishing grounds increased at the scale of the ICES rectangles.

During the closure, the total number of trips in the North Sea decreased. The decrease in fishing effort, which is especially noticeable after week 13, is related to the national cod recovery plan between the fishing industry and the government that started in week 13 (Anonymous 2001). The national recovery plan comprised of a vessel lay-up of 3 weeks in combination with the use of more selective fishing gear (large-mesh panel in upper net, lowering of the head rope).

The reallocation of fishing effort within the North Sea resulted in a mixing of vessels with different levels of experience on the open fishing grounds. Vessels with little experience in the open areas showed a lower level of fishing activity during the closure compared with the "resident" vessels that continued fishing

on the grounds on which they fished in previous years. After the closure was lifted, the fishing effort peaked in the previously closed areas, coinciding with a VPUE that was well above the seasonal value in the reference years.

The number of vessels re-allocating their activities to fishing grounds outside the North Sea was relatively small compared with the total size of the fleet, reflecting the shortage of fishing rights (quota) in areas other than the North Sea. The vessels that temporarily fished outside the North Sea appeared to respond to the area closure and left the North Sea 1-2 months earlier than in the reference years.

3.5.2 Area specialization

In the open north area, the decrease in catch rate during the closure is stronger for immigrant vessels than for resident vessels, which indicates area specialization, i.e., vessels doing well in one area but not in the other. Such differences with regard to revenue rates concur with results found in the British Columbia salmon purse seine fleet (Hilborn 1985). The area specialization may be caused by differences in (i) (personal) knowledge of skippers on the resource distribution and the optimal rigging of the gear for the fishing ground (sea bed characteristics, currents), (ii) vessel and gear design, or (iii) possession of individual transferable quota (ITQ) for the various target species. Lacking data about the skipper, the design and the ITQ of vessels hinders disentangling these effects.

Whatever the mechanism behind the area specialization, it does not seem to act in the open south area. A possible explanation may be that its surface area is far smaller than that of the open north area and the sample size (number of vessels) is much smaller. If differences in personal information are the reason behind differences in fishing success between residents and immigrants, then learning could progressively reduce these differences. However, no decrease in the difference between the two categories is found, implying that either the period of the closure is too short for immigrants to gain sufficient knowledge or that difference in information is not the key issue explaining the difference in fishing success.

3.5.3 Interference and exploitation competition

The analysis showed an immediate decrease in catch rate of resident vessels at the start of the 2001 cod closure that is not seen during the same period in the reference years. This decrease of 14% in the open north area coincides with

an almost doubling in the fishing effort and a substantial increase in the mean crowding index in this area. This result provides evidence for the occurrence of interference competition among beam trawlers. It corroborates the conclusion of an earlier study, which documented a 10% increase in catch rate in the week of prayer when the vessel density was substantially reduced (Rijnsdorp *et al.* 2006).

It is likely that interference competition is the result of the targeted flatfish species response to the fishing vessels, known as interference competition through prey depression (Ruxton 1995, Stillman *et al.* 2000). Rijnsdorp *et al.* (2000a) showed that the catch rate of beam trawlers fishing with a slightly lower fishing speed decreased much faster than that of larger vessels fishing at higher speeds. This suggests that flatfish may increase their capability to escape from an approaching gear towed at low speeds. This is supported by differences in observation rates of Greenland halibut during bottom trawls (Albert *et al.* 2003).

We hypothesize that the spatial scale at which the interference competition occurs will substantially exceed the surface area covered during an individual tow. Because the beam trawl fleet concentrates its fishing effort on local hot spots (Rijnsdorp *et al.* 2000a, 2000b) and has tow lengths of about 12 nautical miles, the spatial scale of the ICES rectangles (-30 x 30 nautical miles) at which we could estimate the mean crowding index will be an acceptable proxy for the competitive interaction between vessels.

Ruxton (1995) has formulated a model for describing the relation between intake rates and competitor densities in prey depression situations. The functional response of this model approximates Beddington's equation (Beddington 1975), which, assuming handling time is negligible (Gillis *et al.* 1995), may be simplified to

$$(3.5) \quad I = \frac{an}{1+qp}$$

where I is the intake rate, a is the search efficiency, n is the prey density, q is a parameter expressing the interference, and p is the predator density. For the beam trawl fishery, we can now estimate the interference parameter using the results of the present study and a previous study of Rijnsdorp *et al.* (2000b). To combine these studies, the catch rate data in that study are transformed to euros per day, and the mean crowding index for the fishing effort is calculated, showing that it decreased from 7.5 to 1.95 during the bid week, whereas the catch rate increased by 10%. The predator density is calculated using $m^* + 1$, which adds the predator itself to the competitors with which it shares the ICES rectangle. Fitting the Beddington equation to the combined results of both

studies using nonlinear sums of squares approximation yields a q estimate of approximately 0.035, with 95% confidence limits -0.007 and 0.077 (Figure 3.7). This method estimates the combined response of the three species. However, because sole is the higher-valued species, it probably affects the interference estimate more strongly than plaice and cod.

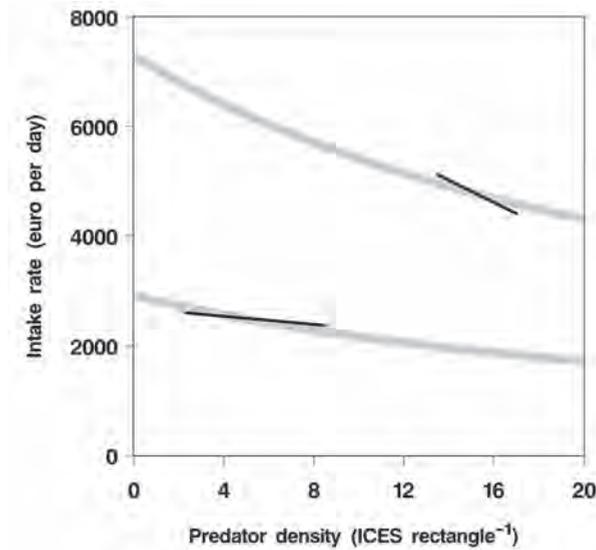


Figure 3.7 Effects of predator density on intake rate for two studies of the North Sea Beam trawl fleet combined. Black lines depict the results from the current study (upper line) and the study by Rijnsdorp *et al.* (2000b) (lower line). Shaded lines are model outcomes of a Ruxton type interference competition model with $h = 0$ and $q = 0.035$ fitted through the observations.

Upcoming techniques may allow us to gain insight in the processes of interference through prey depression at the individual-species level for flatfish. Tagging adult female plaice using data storage tags has proven to record geographical location and depth for individual fish (Hunter *et al.* 2004). Combining these data with the high resolution data of fishing effort allocation provided by vessel monitoring systems (VMS; Rijnsdorp *et al.* 1998; Dinmore *et al.* 2003) may reveal the effect of fishing activity on fish behavior. At present, these data are not available for the total beam trawl fleet, which prevents a more detailed analysis.

The significant increase in the steepness of the slope of VPUE over time during the 2001 closure may indicate a faster rate of depletion of the local prey species (exploitation competition). It should be noted, however, that the slope shows substantial interannual variation, which may be due to the interannual variations in the combined effect of depletion and immigration-emigration.

The high catch rate experienced in the weeks directly following the re-opening of the closed areas may be the result of high survival during the closed period resulting in higher abundance of the resource. Also, the target species may have built up a high density on their preferred feeding grounds in absence of fishing disturbance. The steep decrease in catch rate after the re-opening of the fishery in the two areas may be due to a combined effect of the interference among vessels and the fishing-up of local concentrations.

The presence of interference competition and area specialization has important implications for our understanding of fisheries and fisheries management. Interference competition affects the relation between CPUE and fish stock biomass (Gillis and Peterman 1998) and plays an important role in fishing effort allocation (Abrahams and Healey 1990, Gillis *et al.* 1993). Area specialization affects the choice of fishing grounds by individual fishermen, because their catch rates are negatively affected by moving to areas that they have not fished. This may be the reason for the importance of previous fishing effort on selection of fishing grounds found in studies using random utility models (RUMs; Holland and Sutinen 2000, Hutton *et al.* 2004). Studies on the processes behind both interference competition and area specialization help to understand the spatial allocation of fishing effort.

3.6 Acknowledgements

This study was funded by NWO grant ALW88510104. Comments on a previous draft by Dr. Gejan Piet and two anonymous reviewers are gratefully acknowledged.

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Chapter 4

Spatial segregation among fishing vessels in a multispecies fishery

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ICES Journal of Marine Science 67 (2010) 155-164

4.1 Abstract

Individual decisions of fishers on where to fish in heterogeneous environments may shape the relation between fishing effort and fishing mortality. Fishers may be viewed as individual foragers, whose decisions are aimed at optimizing short-term gain, as in ideal free distribution (IFD) theory. Although IFD assumes all foragers to be equal, they are likely to differ in competitive abilities for different prey types or target species. Here, we present an IFD-like model of a fishing fleet consisting of two components with different competitive abilities for two target species, showing that spatial segregation can result from unequal interference competition, but also in the absence of interference competition. Differences in catch efficiency between vessels for target species in combination with differences in the spatial distribution of target species can result in spatial segregation among vessel groups. The theoretical results are used to interpret the observed spatial segregation of two components within the Dutch beam trawl fleet using observations from a vessel monitoring by satellite system. However, this study cannot pinpoint which of the processes included in the theoretical model is the prime cause of the segregation within the Dutch beam trawl fleet.

4.2 Introduction

A basic problem in fisheries research is to understand the distribution of fishing fleets, a problem closely linked to comprehending the behaviour of individual fishing vessels exploiting fish stocks (Hilborn 1985). Based on the assumption of homogeneous mixing of fishing effort and the fish stock, a linear and constant relation between nominal fishing effort and the mortality generated by fishing is generally assumed. However, individual decisions of fishers when and where to fish may prevent homogeneous mixing, so breaking the linear relation between fishing effort and fishing mortality (Paloheimo and Dickie 1964, Clark and Mangel 1979, Ellis and Wang 2007).

Fishing vessels may be viewed as individual foragers, aiming to optimize gain rates in a single currency (Krebs and Davies 1984): in fisheries, this currency can be assumed to be short-term net revenue (Gordon 1953, Hilborn and Kennedy 1992). Net revenue is affected by local density and price of target species, gear efficiency, and competitive interactions among vessels, as well as fixed and variable costs (Beverton and Holt 1957, Hilborn and Kennedy 1992). The sum of the decisions of individual vessels results in the spatial distribution of the fishing fleet.

Behavioural ecology has a long history of studying and modeling processes affecting the spatial distribution of individual foragers. One of the most influential models is known as the ideal free distribution (IFD; Fretwell and Lucas 1970), which has also found application in fisheries science (see Gillis 2003, for a review). The IFD model assumes that foragers (i) are “ideal”, meaning that each individual forager chooses the habitat that maximizes its fitness, (ii) are “free”, meaning that moving between habitats is free of costs, and (iii) are all alike, genetically and otherwise. If the relation between the gain rate and the number of foragers per patch is known, the distribution of foragers can be calculated.

Interference competition, defined here as a decrease in gain rate at increasing competitor densities, not caused by decreasing local abundance of the prey, will in such a system cause the foragers to spread out over patches. Ultimately, all foragers will have equal gain rates in the equilibrium state of the process. Interference competition may take place through direct competitive interactions among foragers (Ens and Goss-Custard 1984), or it can be the result of prey sensing the presence of predators, and modifying their behaviour to reduce the risk of predation (Ruxton 1995). The latter is known as prey depression. Few studies have attempted to analyse the nature of interference competition in fisheries (Abrahams and Healey 1993). Direct interactions among vessels, reducing fishing efficiency, were suggested for the trawl fishery for silver hake (*Merluccius bilinearis*; Gillis 1999). Prey disturbance by fishing was observed for spawning cod (*Gadus morhua*) in an otter trawl fishery by Morgan *et al.* (1997). A similar mechanism was hypothesized in the trawl fisheries for flatfish in the North Sea, causing interference competition by prey depression (Rijnsdorp *et al.* 2000b, Poos and Rijnsdorp, 2007b).

Although the IFD assumes that foragers are equal, this may not apply in all biological systems. The effect of unequal competitors on the distribution of foragers was first examined by Sutherland and Parker (1985). Subsequent studies by van der Meer (1997), Ruxton and Humphries (1999), and Humphries *et al.* (2001) demonstrated the sensitivity of simulated forager distributions to model formulations. The models in those studies were based on foragers exploiting a single resource species and included direct competition. Depending on the exact formulation of a mathematical model for interference competition, a truncated phenotype distribution may arise, i.e. a distribution where competitors with different competitive abilities occupy different prey patches.

Fishing vessels will differ in fishing power either through differences in vessel size or engine power (Beverton and Holt 1957, Rijnsdorp *et al.* 2000a), age of the vessel (Pascoe *et al.* 2001, Rijnsdorp *et al.* 2006), and skill of the skipper (Hilborn and Ledbetter 1985). Fishing power of bottom trawls will be determined by (i) the swept-area of the gear, (ii) the penetration depth of the gear, and (iii)

the efficiency at catching the fish in the path of the gear (Videler and Wardle 1991, Dahm *et al.* 2002).

An increase in engine power can be used to increase the swept-area per unit of time by increasing fishing speed, width of the fishing gear, or penetration depth of the gear. The latter is relevant to target species, such as flatfish, that bury themselves in the seabed. Fishing speed not only affects the swept-area of the gear per unit time but may also affect catch efficiency, because fish may be less able to escape from gear towed at high speed (Bublitz 1996). Because of the proportion of fish that is accessible to the gear and the differences in fish behaviour, fishing power can differ between species.

Here, we explore the effects of unequal competitive abilities of fishing vessels in a mixed trawl fishery for two species on spatial segregation within fishing fleets. Interference competition is modeled by prey depression influencing the proportion of the population that is susceptible to the gear. The results are described in terms of the spatial distribution of the vessels, with particular emphasis on the resulting spatial segregation among fishing vessels. The model is applied to the beam trawl fishery for flatfish in the North Sea, and the predictions are compared with observations on the distribution of Dutch beam trawlers.

4.3 Material and methods

4.3.1 Model description

Spatial segregation is modelled for two uniform fleets, with 100 small and 100 large vessels that differ in engine power, and hence in their fishing power for two target species (species A and B). Difference in catch efficiency is modelled as the combination of burrowing depth of the species and penetration depth of the gear, species A being a shallow-burying species and species B a deep burying one. The gear towed by small vessels has a shallow penetration depth and that of large vessels a deep penetration depth.

Vessels have the possibility to choose among 20 patches, which differ in the density of species A and B. Different model runs with different numbers of patches (ranging between 10 and 40) indicate that the general conclusions from the model do not depend on the number of patches. The patches are spatially segregated, but the travel cost between patches is assumed to be negligible. Interference competition is modelled by the effect of vessel density on the burying depth of the species, reducing the susceptibility for the fishing gear for higher vessel densities.

The model is used to study the effect of the following factors on the spatial segregation of small and large vessels:

- (i) differences in the spatial distribution of species A and B;
- (ii) difference in the price of species A and B;
- (iii) occurrence of interference competition.

4.3.2 Distribution model without interference competition

To formulate a model without interference competition, we start with the assumption that the burrowing depth of individuals of the species A and B can be described using a normal distribution with different mean depths, μ_A , μ_B , and common variance σ : $\mu_B = \mu_A + \rho$, where ρ is the difference in burrowing depth. We assume that the penetration depth x of the gear depends linearly on the engine power of the vessel type, because large vessels are capable of using more chains, providing them with greater penetration depth (Figure 4.1a). Gear efficiency is defined as the fraction of the population that is vulnerable given the penetration depth. This fraction can be approximated using the cumulative normal distribution function (Sokal and Rolf 1995). The ratio of gear efficiencies for the two species is a declining function of engine power, approaching an asymptote at efficiency ratio equal to 1 (Figure 4.1b). The effects of engine power on the fishing speed and gear width are neglected in the model. The densities, D_A , D_B , of the two species in each patch are linearly related as

$$(4.1) \quad D_B = \beta - rD_A$$

If r is positive, the densities of the two species are negatively related, but if r is negative, the species co-occur. The β parameter scales the overall ratio of the two densities in the system. Each of the species has a price (P_A , P_B) when sold on the market. For simplicity, we assume that the entire catch is landed and contributes to the revenue. The costs of fishing, F , are assumed equal for all patches, and travel costs between patches are assumed to be negligible. Assuming no depletion of the resource, the net revenue T in a single unit of time in a patch for a vessel using gear with penetration depth x can be calculated as the product of gear efficiency, species density, and market price summed over the two species minus the costs of fishing:

$$(4.2) \quad T = \frac{1}{2} D_A P_A \left(1 + \operatorname{erf} \left(\frac{-\mu_A + x}{\sqrt{2}\sigma} \right) \right) + \frac{1}{2} (\beta - rD_A) P_B \left(1 + \operatorname{erf} \left(\frac{-\mu_A - \rho + x}{\sqrt{2}\sigma} \right) \right) - F$$

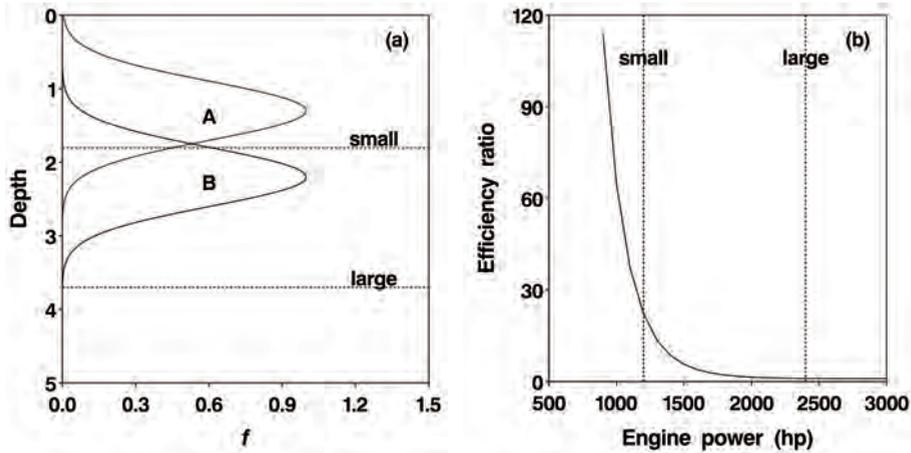


Figure 4.1 (a) Probability density functions of burrowing depth (f) of species A and B. The horizontal lines indicate the penetration depth of small (1200 hp) and large (2400 hp) vessels. (b) Relation between gear efficiency ratio A:B and vessel engine power. The vertical lines indicate the hypothetical engine powers of the two vessel types.

Here, $\text{erf}(z)$ is the error function resulting from integrating the normal probability density function. The terms in parentheses provide an estimate of the proportion of individuals found above the gear penetration depth x . Under the assumption that fishing vessels maximize instantaneous net revenue, the optimal patch for a single vessel is the patch where net revenue T , the sum of the revenues from the catch rates of the two species minus the costs, is highest.

4.3.3 Distribution model with prey depression

In a second step, interference competition through prey depression is incorporated by assuming that the average burrowing depth of a species depends on vessel density in a patch. Analogous to work by Ruxton (1995), prey can move from a vulnerable to a less vulnerable state by increasing burrowing depth by i , i.e. to $\mu_{Av} + i$ and $\mu_{Bv} + i$, respectively. The proportion of prey in the different states depends non-linearly on vessel density v in the patch. The average burrowing depth of prey population A is

$$(4.3) \quad \mu_A(v) = \mu_{Av} \frac{1}{1 + \gamma v} + (\mu_{Av} + i) \frac{\gamma v}{1 + \gamma v} = \frac{\mu_{Av} + \gamma v(\mu_{Av} + i)}{1 + \gamma v}$$

and similarly for population B. The propensity γ of the prey to be in the less vulnerable state encompasses both the probability to enter the invulnerable state upon contact with the gear and the time spent in that state before returning to the vulnerable state again. Individuals cannot burrow deeper than $\mu_A + i$, $\mu_B + i$, reflecting the idea that the avoidance behaviour of the prey is bounded by physiological or energetic constraints.

In the model, vessels enter the environment in a random sequence, choosing the patch with the greatest revenue, taking into account the effect of the prey and vessel densities in the patches. When all vessels have entered the environment, each vessel evaluates the environment in the random sequence again and chooses the patch with the greatest expected net revenue. This step is repeated until no vessel prefers to move. The resulting distribution of the two different types of vessel over the patches is plotted for different combinations of the parameters γ and i .

4.3.4 Spatial segregation in the Dutch beam trawl fleet

We investigate spatial segregation in the Dutch beam trawl fleet in the North Sea. If vessels of different size select different patches, then spatial segregation of the size classes is expected based on the fact that nearest neighbours will be similar in size. Beam trawlers target the flatfish species sole (*Solea solea*) and plaice (*Pleuronectes platessa*; Daan 1997, Gillis *et al.* 2008). A description of the fishing practices and fishing grounds is given by Rijnsdorp *et al.* (1998). Vessels typically make trips lasting 4-5 d in the southern North Sea. Having reached the fishing grounds, the twin beam trawls are shot and fishing commences. A haul lasts approximately 2 h, and after bringing the gear in and emptying the codend, the gear is set again. Dutch beam trawlers typically visit several (neighbouring) ICES rectangles (scale >30 nautical miles), whereas the spatial patchiness of the flatfish resources occurs at a spatial scale of ~20-45 nautical miles (Poos and Rijnsdorp 2007a). In the beam trawl fleet, an increase in the number of chains in front of the groundrope increases the gear efficiency, especially for deeper burrowing species such as sole (Creutzberg *et al.* 1987, Daan 1997). The price of sole in the Netherlands is approximately four times higher than that of the shallower burrowing plaice.

Spatial distribution of beam trawlers is available from vessel monitoring by satellite (VMS) systems, mandatory onboard transmitters that send the GPS data from the vessel to the General Inspection Service. Although initially installed for inspection purposes only, high spatial (0.05') and temporal resolution (~2 h) VMS measurements are available for research purposes with the permission of vessel owners. Changes in the number of owners giving permission resulted in

variable numbers of observations over time, so the period 1 January 2001 to 31 December 2001 was selected for analysis because there were a relatively large number of vessels in the sample. The 57 vessels sampled represent 38% of those active at that time.

To remove vessels that may still be searching for appropriate fishing grounds, or that are moving between ports and fishing grounds (Rijnsdorp *et al.* 1998), only observations between Monday and Thursday were selected. To exclude observations that do not reflect fishing, observations with vessel speeds outside the fishing speed range for this fleet (5-8 knots; Piet *et al.* 2006) were removed.

To test spatial segregation between vessels of different size, the fleet was split into two engine-power size classes. The first size class included vessels with an engine power of 300-1900 hp, and the second those >1900 hp. This boundary for the split was selected as just under 2000 hp to separate the dominant 2000 hp size class from the smaller vessels. The spatial segregation in point patterns of vessels of these two types was tested in 2-h time frames throughout the study period. Of the 57 vessels in the sample, only eight had an engine power <1900 hp. In cases where there were multiple observations of one vessel within a 2-h window, one observation was selected randomly. To prevent conclusions that would be based on very small sample sizes, we subsequently tested only those time frames where >66% of the vessels of both types present in the entire sample were fishing.

The segregation between two groups of vessels was estimated using the test statistic C , which provides an overall measure of spatial segregation, based on the expected classification of the nearest neighbours under the null hypothesis of random labelling of observations (Dixon, 1994). Under random labelling of points, C has a χ^2 distribution with 2 degrees of freedom (d.f.), and the 2-d.f. χ^2 test is used to indicate whether the observed segregation might have arisen from random labelling of points (Dixon, 1994). All statistical testing was done using sequential Bonferroni-corrected a level of 0.05 (Holm, 1979). To prevent autocorrelation of the spatial distributions between time frames affecting the estimate of C , only the time frame between 11:00 and 13:00 each day was analysed.

Data on catches made during the research period were available from EU logbooks that have mandatory catch and effort records (Rijnsdorp *et al.* 2000a). Additional data on gear usage from the fleet were available by fishing haul from detailed logbooks voluntarily completed and submitted by a number of skippers.

4.4 Results

4.4.1 Model results without interference competition

The model outlined in Equation (2) was used to derive optimal patch choice for individual vessels of different size in a spatially heterogeneous environment (D_A varies between patches) in the absence of prey depression. Because in our model the relation between D_A and D_B is linear [Equation (1)] and the efficiency does not depend on species densities, the net revenue depends linearly on D_A . To determine whether the patch with the highest or the lowest density of A would be chosen, we consider the partial derivative of T :

$$(4.4) \quad \frac{\partial T}{\partial D_A} = \frac{1}{2} \left(P_A + P_A \operatorname{erf} \left[\frac{-\mu_A + x}{\sqrt{2\sigma}} \right] - P_B r \left(1 - \operatorname{erf} \left[\frac{\mu_A + \rho - x}{\sqrt{2\sigma}} \right] \right) \right)$$

If this function is positive, then vessels will choose the patch with the highest density of species A. This is true if

$$(4.5) \quad r < \frac{P_A \left(1 + \operatorname{erf} \left(\frac{-\mu_A + x}{\sqrt{2\sigma}} \right) \right)}{P_B \left(1 + \operatorname{erf} \left(\frac{\mu_A - \rho + x}{\sqrt{2\sigma}} \right) \right)}$$

Therefore, the patch choice depends on the relation between the density of the two species r , the prices P_A and P_B , and the efficiencies.

If the two species occur in the same patches ($r < 0$), then the inequality will always be true, because the right side of the inequality in Equation (5) is always positive. Hence, fishing vessels will go to those patches with the highest density of both A and B.

Alternatively, if $r > 0$, there is a segregation in the occurrence of the two species. Now, the patch choice depends on prices and catch efficiencies. To illustrate these effects, we describe several cases assuming $r = 1$. If the prices are equal ($P_A = P_B$), the optimal patch for all vessel sizes is the patch with the highest density of A. The reason for this is that because $\rho > 0$, the efficiency for species A is by definition greater than that for species B. The numerator is hence by definition larger than the denominator, making the inequality true. Therefore, the catches of species B cannot make up for the loss in catch rates of species A when moving towards patches with greater densities of B. This situation is illustrated in Figure 4.2a, where both vessel types would choose the patch with the highest density of species A ($D_A = 1$). If the price of species B is much higher

than species A, e.g. $P_B/P_A = 5$, both fleets choose to fish in patches with the highest density of the deeper-burrowing species B ($D_A = 0$ in Figure 4.2c). However, if the price of species B lies between the ratio of gear efficiencies A:B of the two vessel types, the maximum net revenue for the smaller vessels is found at the patch with maximum abundance of species A (Figure 4.2b). The increased revenue attributable to increases in species B at other patches cannot make up for losses in A because of the inaccessibility of B for those vessels. However, the larger vessels can attain higher revenues at the patches with greater abundances of B through their greater catch efficiency for B. For this reason, the larger vessels will choose the patches with maximum levels of species B ($D_A = 1$ in Figure 4.2b).

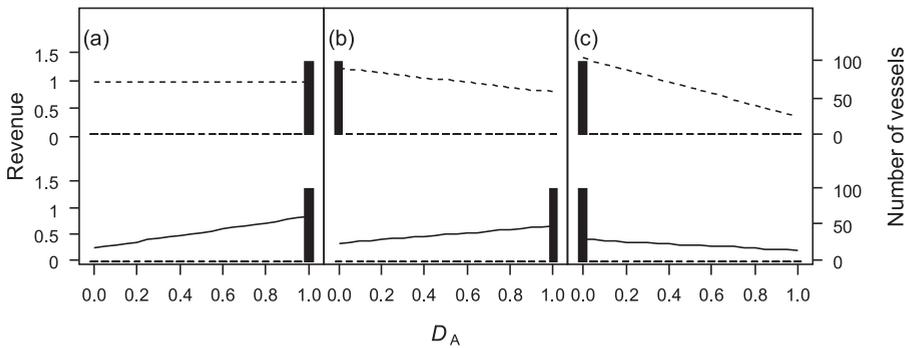


Figure 4.2 The total revenue from two species for large (dashed line) and small (complete line) vessels (left axis) from a patch, for three different price ratios: (a) $P_B/P_A = 1$, (b) $P_B/P_A = 1.625$, and (c) $P_B/P_A = 5$. The patches are ordered in increasing densities of species A ($D_B = \beta 2 rD_A$, $r = 1$). The resulting vessel distribution based on the revenue is represented by the bar graphs in the panels. In each panel, the distribution of the large vessels is represented by the top bar chart and that of the small vessels by the bottom bar chart.

4.4.2 Model results with interference competition

To study the model with interference through prey depression, two distributions of the two prey species were chosen: (i) an environment where species A and B are jointly distributed over the patches, with poor patches lacking both A and B, ranging to good patches with both high densities of A and B ($r < 0$), and (ii) an environment similar to the model without prey depression, with the densities of A negatively related to the abundance of B ($r > 0$). For the two scenarios, the effect of a price difference between the two species on net revenue is analysed.

Model results without spatial segregation of prey species ($r = -1$, $\beta = 0$) are illustrated in Figures 4.3 and 4.4. In the absence of interference competition

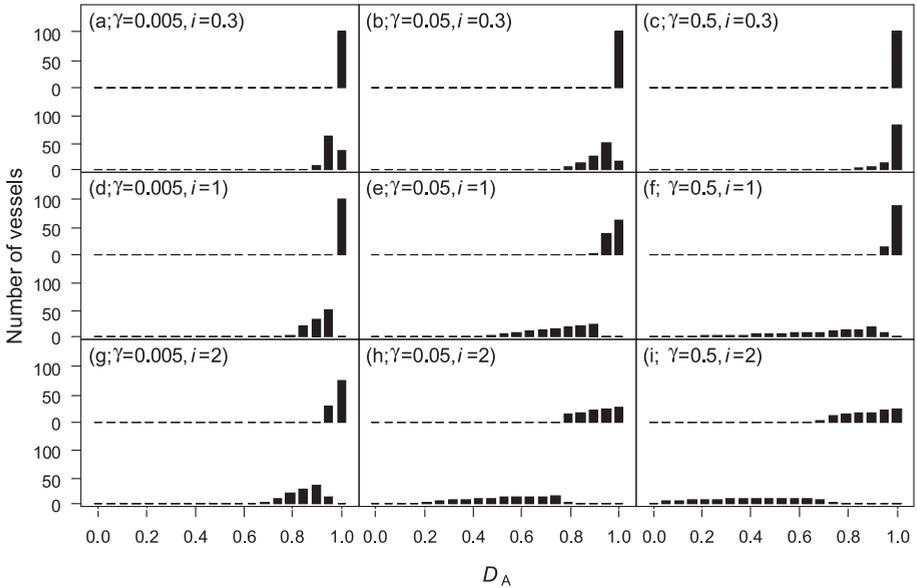


Figure 4.3 Patch choice of large and small vessels in the absence of resource segregation with equally priced species. Each of the panels represents a combination of the two parameters i and γ determining the strength of the competition (see text). In each panel, the distribution of the large vessels is represented by the top bar chart and the distribution of the small vessels by the bottom bar chart.

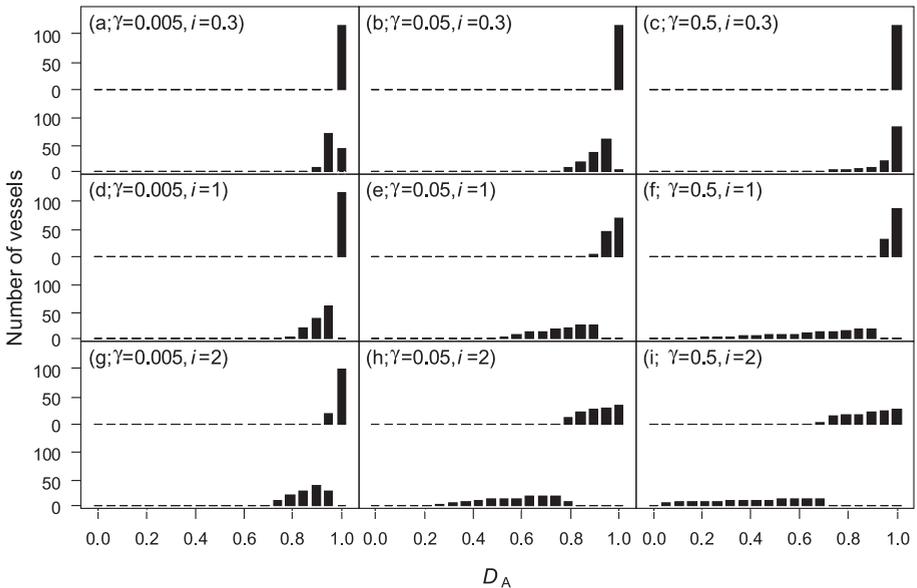


Figure 4.4 Distribution of large and small vessels in the absence of resource segregation with species B being 1.4 times more valuable than species A. The parameters i and γ determine the strength of the competition (see text). In each panel, the distribution of the large vessels is represented by the top bar chart and the distribution of the small vessels by the bottom bar chart.

through prey depression, both vessel types chose the patch with the greatest abundance for both species, irrespective of price differences. If interference competition is added to the model and prices for prey species are equal, large vessels would choose the patches with the greatest abundance of both prey species (Figure 4.3). If the maximum increase in burrowing depth is small, e.g. $i = 0.3$ in Equation (4.3), the effect on revenue obtainable by the larger vessels in the best patch does not affect the choice made by these vessels.

However, smaller vessels cannot access species A in that patch, which burrowed deeper as a consequence of the fishing activity of the larger vessels. The smaller vessels would also choose the patches with lesser abundances of A and B (Figure 4.4a-c). The interference competition within the group of smaller vessels causes their fishing activity to be spread over several of these patches. Under increasing maximum burrowing depths of the prey species (corresponding to increasing i), the effects on revenue rates start influencing the patch choice of the larger vessels, spreading them over patches with lower prey abundances (Figure 4.3d-i). Because of the lower weight of the gear, smaller vessels can no longer fish in the patches occupied by large vessels, similar to the previous situation with lower maximum burrowing depths. Again, smaller vessels fish in a large number of patches with lesser abundance. Difference in prices between the two species does not substantially affect the model results (Figure 4.4).

Model results with segregation of the prey species ($r = 1, \beta = 0$) are presented in Figures 4.5 and 4.6. The model without interference competition shows that both types of vessels choose the patch with the greatest abundance of A, if prices for both species are equal. Adding prey depression to the model changes the distribution of the vessels. If prey depression is small ($i = 0.3$), most small vessels would still choose the patches with the greatest abundance of A and a few vessels select patches with a lesser abundance of A (Figure 4.5a-c). If prey depression increases, e.g. $i = 1$, the two types of vessel become spatially segregated. Large vessels choose the patch with the greatest abundance of A, and smaller ones the patches with lesser abundance of A, because the catch rates in the patch occupied by large vessels have decreased owing to the increase in average depth of prey species A (Figure 4.5d-f). Further increase of the prey depression ($i = 2$) results in a spreading out of the larger vessels over the patches because the average depth of species B now exceeds the reach of the gear in heavily exploited patches (Figure 4.5g-i). The small vessels can only compete with the large vessels in a limited number of patches, preferring the patches with high abundance of A, because species B is not accessible to them. Depending on the strength of the prey depression, a small fraction of the large vessels may choose the patches with low abundance of A and high abundance of B, avoiding competition in the patches with high abundance of A, and being

able to catch a (limited) fraction of B. In that case, the small vessels are forced to choose the patches with intermediate abundance of either prey species (Figure 4.5).

If prey species are segregated, and the deeper-burrowing species B is more valuable than species A, and the effect of interference competition through prey depression is small ($\gamma = 0.005$, $i = 0.3$), then there is strong spatial segregation of fishing effort (Figure 4.6a). The differences in gear efficiency between the prey species in interacting with the difference in price dominate the response. This result is similar to the result of the model without interference competition. However, the interference competition may spread out the two fleets at each end of the resource spectrum. For increasing prey depression, the interference competition between the two fleets results in a situation where the large vessels occupy both ends of the spectrum, leaving only the patches with moderate and more-equal quantities of the two prey species to the small vessels, which again show preference to the patches with a relatively high abundance of A. Hence, the difference in spatial distribution of the fleets that result from price differences between the two species is mitigated by strong interference competition. Therefore, the interference competition may lead to similar distributions of fleets, independent of the price of the species.

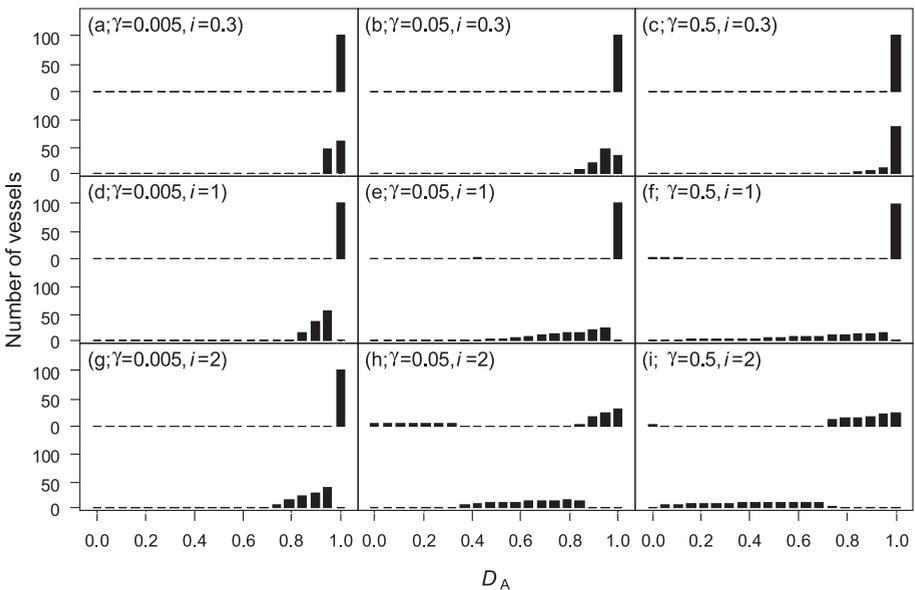


Figure 4.5 Distribution of large and small vessels in the presence of resource segregation and equal prices. The parameters i and γ determine the strength of the competition (see text). In each panel, the distribution of the large vessels is represented by the top bar chart and the distribution of the small vessels by the bottom bar chart.

4.4.3 Spatial segregation in the Dutch beam trawl fleet

In the Dutch beam trawl fleet, the number of chains used in front of the net is positively related to the engine power of vessels >300 hp (Figure 4.7). This observation confirms the hypothesis that the greater power in large beam trawlers is used to increase the penetration of the gear. The large number of chains in the fleet segment <300 hp is linked to legislation prohibiting beam lengths >4.5 m for these vessels. Therefore, those vessels are able to use more chains at lower engine power owing to the shorter lengths of the chains. For vessels >300 hp, the catch rates of the two species lie within the same order of magnitude, with plaice dominant in weight (Figure 4.8) and sole dominant when expressed in terms of value (not shown). Moreover, the contribution of plaice in the catches of the smaller vessels is larger than for the larger vessels, and the opposite is true for sole. As there are no independent data available on the absolute abundances of the species in the patches visited, no conclusion can be drawn on the cause for this difference. However, possible causes could be the differences in gear efficiency or a combined effect of differences in gear efficiency and patch choice.

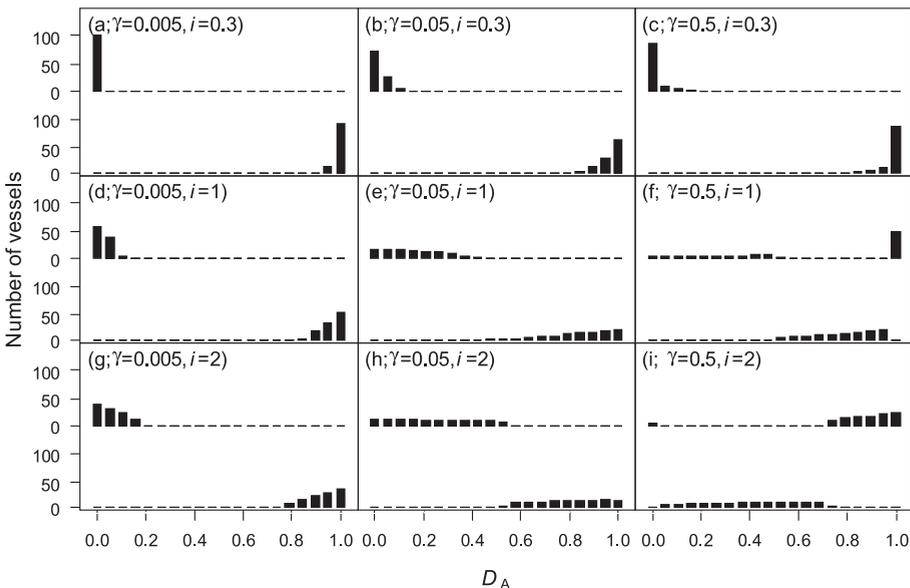


Figure 4.6 Distribution of large and small vessels in the presence of resource segregation and different prices. The parameters i and γ determine the strength of the competition (see text). In each panel, the distribution of the large vessels is represented by the top bar chart and the distribution of the small vessels by the bottom bar chart.

As the sample does not always meet the requirement of having >66% of the vessel types present in the sample at each time-step, some periods were not tested, resulting in a different number of time-steps tested for each comparison of size classes. Also, limited fishing activity in the holiday season between mid-July and mid-August results in a lack of tests in that period. In all, 47 time frames could be used for testing the C statistic. The sequential Bonferroni corrected $\alpha = 0.05$ level for the C statistic for this number of tests was 18.1. In contrast, the uncorrected $\alpha = 0.05$ level for the C statistic was 5.991. The tests show time-steps with significant positive χ^2 values, indicating spatial segregation between size classes (Figure 4.9), but only 4 of the 47 (8.5%) timesteps had significant C test statistics that exceeded the sequential Bonferroni corrected threshold.

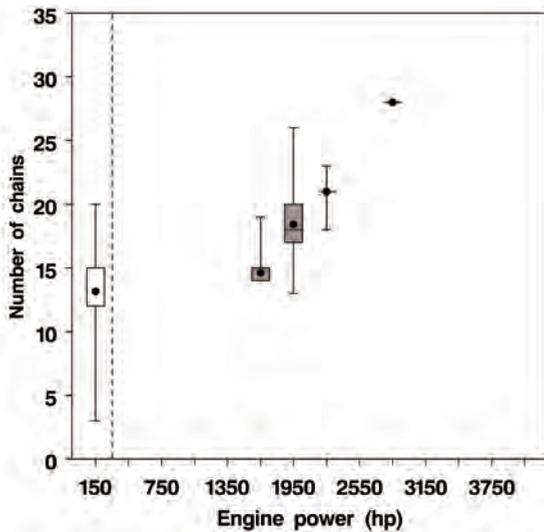


Figure 4.7 Box and whisker plot of the number of chains in the beam trawl gear as a function of vessel engine power. The top and bottom edges indicate the sample 25th and 75th percentiles, the horizontal line drawn within the box marks the median, and the dot marks the sample mean. The whiskers indicate the range. The dashed vertical line indicates the 300 hp limit, and shaded boxes indicate observations for vessels with engine power > 300 hp. Smaller vessels have smaller beam widths by legislation, so may have more chains per horsepower than larger vessels.

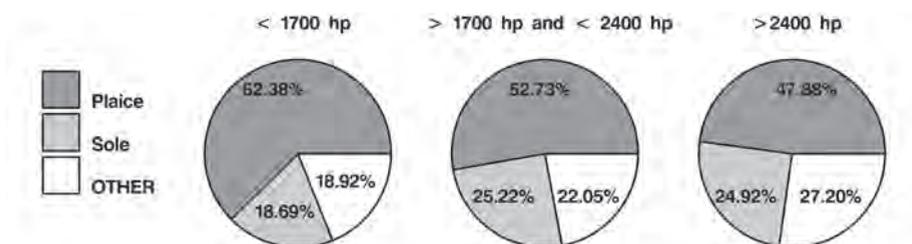


Figure 4.8 Landings composition by weight for three different size classes of Dutch beam trawler fishing the North Sea.

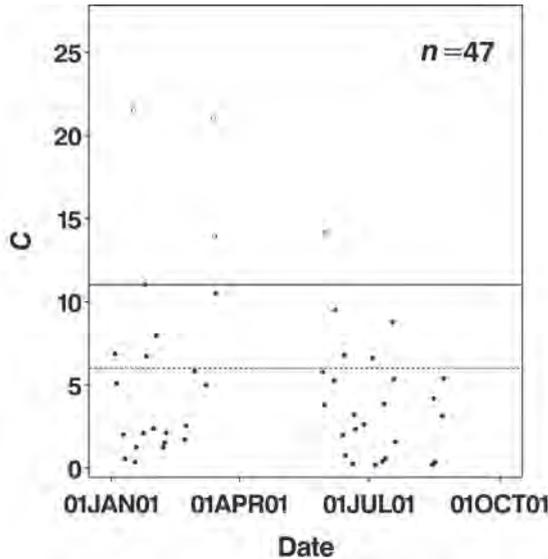


Figure 4.9 Test statistic C for spatial segregation for two size classes of Dutch beam trawl vessels, split at 1900 hp. Each dot represents a single test within a 2-h time frame at noon. Open circles indicate a statistically significant deviation from a random labelling hypothesis using sequential Bonferroni correction. The solid horizontal line indicates the corrected critical value of C , the dotted line the uncorrected critical value of C , and n is the number of tests.

4.5 Discussion

We have presented and analysed a model of possible mechanisms that may result in segregation in the spatial distribution of fishing vessels operating in a multispecies flatfish fishery. The results reveal potential segregation between two fleet segments with unequal competitors through spatial segregation in prey species, price differences, and interference competition through prey depression. In the absence of interference competition, the segregation between fleets depends on differences in the distribution and prices of the prey species, combined with differences in catch efficiency. If the two species are segregated, price differences may lead to segregation in fleets with different efficiencies for the two species. In the presence of interference competition through prey depression, segregation can take place in the absence of price difference or segregation in the prey.

In field data, the prerequisites for segregation deriving from the multispecies nature of the fishery are met. First, the environment in which the beam trawl fleet operates creates opportunities for targeting multiple species. Our results

indicate that sole and plaice indeed comprise a large part of the catch, in both weight and value, corroborating the results in Gillis *et al.* (2008). The larger vessels land more of the deeper-burrowing target species. The exploited part of those stocks is spatially segregated, at least during part of the year (Rijnsdorp *et al.* 2006, Poos and Rijnsdorp 2007a).

The empirical data exhibited segregation in the spatial distribution between the two size classes of beam trawlers. However, the segregation did not seem very strong, some 8% of the observations being significantly segregated. The limited number of significant cases may result from low power of the statistical test, owing to the small sample size of VMS data. Alternatively, factors not included in our model, such as incomplete information and information exchange, travel costs, and management constraints, may play a role in spatial effort allocation and influence the degree of segregation.

Within the Dutch beam trawl fleet, there is substantial variation in the engine power of fishing vessels, and a positive relation between the engine power of vessels and the number of chains used in the fishing operation. Gear efficiency for sole and plaice depends on the number of chains used in front of the net (Creutzberg *et al.* 1987). For sandy seabeds, the slope of this relationship for sole is estimated to be four times steeper than for plaice. Although the exact shape and form of the plaice response is not mentioned in the work of Creutzberg *et al.* (1987), the weak response can be an approximation to the asymptotic value, found for juvenile plaice < 15 cm for a 2-m beam trawl gear in the Wadden Sea (Kuipers 1975). It should be noted that the number of chains in the experiments made by Creutzberg *et al.* (1987) was less than observed within the fleet. Finally, there is a marked difference between the prices of the two species, with the deeper-burrowing sole being approximately four times more valuable than plaice (Rijnsdorp *et al.* 2000a). The catch composition of the vessels shows differences in the contribution of sole and plaice. As expected, sole contribute more to the catches in the large vessels than to the smaller vessels, and the reverse is true for plaice.

Spatial and ecological segregation according to efficiency for different prey has been observed in ecological studies for a wide range of species. For example, oystercatchers (*Haematopus ostralegus*) with different bill lengths specialize differently in feeding techniques and diet (Durell *et al.* 1993). Ecological segregation can also be attributed to ontogenetic diet shifts from small to larger prey species (Daan 1973, Aarnio *et al.* 1996, Vinagre *et al.* 2008).

Our study indicates that the multispecies nature of the Dutch beam trawl fishery in combination with price differences and interference competition is a plausible mechanism for spatial segregation between the two size classes of

vessel. It is not possible to quantify the contribution of price differences or interference competition to spatial segregation. To disentangle the roles of spatial segregation, prices, and interference competition through prey depression, the parameters involved would have to be quantified.

In fisheries, experiments on the depression of target species generally face practical problems owing to the scale of the fishing operation and because observing the effect of the gear on the avoidance behaviour of prey is cumbersome, if not impossible. However, in general, many species exhibit quantified antipredatory behaviour (Lima and Dill 1990). For redshanks (*Tringa totanus*) feeding on *Corophium volutator*, parameter estimates available from Goss-Custard (1970) were used in a model to show that the strength of the competition depends on the search strategy used by the forager (Stillman *et al.* 2000). In the field, redshanks indeed used a search strategy that avoided patches used previously, sustaining high feeding rates (Yates *et al.* 2000).

The effects of fisher behaviour following the IFD assumptions for fish stock assessments have been discussed extensively (Gillis and Peterman 1998). Addition of the mechanisms proposed in this study may also affect the relation between nominal fishing effort and fishing mortality. A previous study has indicated differences in fishing power and susceptibility to interference competition within the Dutch beam trawl fleet (Rijnsdorp *et al.* 2000a). The difference in response of gear efficiency between sole and plaice was also used to explain the race for ever more powerful vessels in the 1970s and 1980s (Daan 1997). One may expect that a fleet evolving towards ever more powerful vessels concentrates on fishing grounds with the deeper-burrowing species, resulting in strong increases in catchability for that species. Such changes have indeed been observed for the Dutch beam trawl fleet over the past five decades (Rijnsdorp *et al.* 2008).

To conclude, weak spatial segregation between vessels of different engine size and gear efficiencies for different species have been found in the Dutch beam trawl fleet. Two alternative mechanistic hypotheses about the beam trawl fishery predict spatial segregation between size classes of vessels. One of these hypotheses depends on the difference in competitive ability between the classes, and the other depends only on the difference in catchabilities of the different target species. Several of the mechanisms involved in the two hypotheses on segregation were indeed found in the fleet studied. The extent to which each of these mechanisms plays a role in effort allocation of the fishery should be determined by carefully designed experiments. In such an experiment, differences in burrowing depth, and in the prey depression resulting from avoidance of the gear, need to be quantified.

4.6 Acknowledgements

The study was supported by NWO grant ALW 88510104 to JJP. The collection of the logbook data was part of the “F-project”, funded by the Dutch Ministry of Agriculture, Nature Management and Food safety. We thank the skippers who voluntarily registered their detailed catch and effort data, and two anonymous reviewers and the editor for their valued input.

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Chapter 5

Individual quotas, fishing effort
allocation, and over-quota
discarding in mixed fisheries

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ICES Journal of Marine Science 67 (2010) 323-333

5.1 Abstract

Many fisheries are managed by total allowable catches (TACs) and a substantial part by individual quotas. Such output management has not been successful in mixed fisheries when fishers continue to fish while discarding marketable fish. We analyse the effects of individual quotas on spatial and temporal effort allocation and over-quota discarding in a multispecies fishery. Using a spatially explicit dynamic-state variable model, the optimal fishing strategy of fishers constrained by annual individual quotas, facing uncertainty in catch rates, is studied. Individual fishers will move away from areas with high catches of the restricted quota species and, depending on the cost of fishing, will stop fishing in certain periods of the year. Individual vessels will discard marketable fish, but only after their individual quota for the species under consideration has been reached. These results are in line with observations on effort allocation and discarding of marketable fish, both over-quota discarding and highgrading, by the Dutch beam-trawl fleet. The models we present can be used to predict the outcomes of management and are therefore a useful tool for fisheries scientists and managers.

5.2 Introduction

Output management in mixed fisheries through total allowable catches (TACs) is not generally successful if fishers continue to fish and to discard marketable fish (over-quota discarding; Daan 1997, Pascoe 1997, Rijnsdorp *et al.* 2007). Only if vessels operate under an observer programme where over-quota catches are recorded and penalized will fishers be forced to redirect fishing effort away from the concentrations of the limiting resource entirely (Branch and Hilborn 2008).

In the EU, many fisheries are managed by annual TACs without a legal restriction on discarding (Holden 1994). Although qualitative information on over-quota discarding does exist (Rijnsdorp *et al.* 2006), the quantities and age structure of discards remain unknown for many fisheries. However, over-quota discarding may have severe implications for estimates of stock biomass and fishing mortality (Cotter *et al.* 2004), in particular where discarding applies to certain age classes (the less valuable market categories).

Bottom-trawl fleets generally engage in mixed fisheries, where a multitude of species contribute to the output of the fishery. As these species differ in habitat requirements and may differ in their seasonal migration pattern, the species composition of the catches will vary in space and time. A heterogeneity in species composition offers fishers the opportunity to influence the species com-

position of their catch, at least to some extent, by redistributing their fishing effort to optimize profits within the constraints set by management (Hutton *et al.* 2004, Branch and Hilborn 2008, Gillis *et al.* 2008).

The North Sea flatfish fishery is a typical example of a TAC-regulated mixed fishery, with catches including the flatfish species sole (*Solea solea*), plaice (*Pleuronectes platessa*), turbot (*Psetta maxima*), and brill (*Scophthalmus rhombus*), each with different seasonal availability patterns (Rijnsdorp *et al.* 2006, Poos and Rijnsdorp 2007a) and prices. Sole and plaice dominate the landings and can be considered to be the main target species (Gillis *et al.* 2008). Adult plaice migrate from the southern spawning grounds to the northern feeding grounds in spring, where they stay until the return migration in autumn (Rijnsdorp and Pastoors 1995, Hunter *et al.* 2004, Bolle *et al.* 2005). On the other hand, sole follow an east-to-west migration cycle that overlaps with the winter distribution of plaice (de Veen 1967, 1978). Sole is the most valuable species, contributing most to the landings expressed in monetary value, and plaice is the second most valuable (Gillis *et al.* 2008).

The TACs for these stocks are set annually after political negotiations, based on stock assessments produced by ICES (Daan 1997). The TAC is subsequently subdivided across EU Member States using a fixed allocation rule based on historical catches and special provisions for areas heavily dependent on fishing (Holden 1994). In the Netherlands, the TACs are divided into individually transferable quotas (ITQs), owned by fishing companies (Salz 1996). ITQs potentially reduce competition and excess investment, while fostering economic efficiency (Squires *et al.* 1998).

Many studies exist in which the effects of individual quotas on discarding are considered (Vestergaard 1996, Turner 1997, Herrera 2005). However, these studies often ignore the flexibility that individual fishers have in modifying the catch composition by changing their fishing pattern in space and time. In this study, we explore the effects of annual individual quotas on discarding, explicitly accounting for spatio-temporal effort allocation, adding a basic dimension of fleet dynamics to the understanding of discarding behaviour.

Dynamic-state variable models offer a powerful tool to study this behavioural flexibility because they allow mixing the timescales between choices and constraints (Clark and Mangel 2000). Previous studies on fleet dynamics using dynamic-state variable models showed that single-species trip quota can lead to highgrading when only the most valuable component of the catch is taken into account (Gillis *et al.* 1995). This single-species approach made use of several market categories, differing in value. Within each haul, the choice made by the individual fisher for each trawl was to discard or to retain the entire catch of

each market category. Another study used a dynamic-state variable model to optimize targeting decisions made by bottom trawlers under management-imposed trip limits on landings of each target species (Babcock and Pikitch 2000). The model predicted that the vessel would fish a single strategy exclusively without trip limits, but would switch between strategies several times under restrictive trip limits. Although that study allowed changes in effort allocation resulting from quota constraints, no discarding was permitted in the model.

We develop a dynamic-state variable model to study the effect of restrictive quotas on the spatio-temporal effort allocation and discarding of marketable fish in the beam-trawl fishery for sole and plaice. It is assumed that a fisher will maximize the economic pay-offs (Gordon 1953, 1954), analogous to optimal foraging theory in animal behaviour (Stephens and Krebs 1986, Krebs and Davies 1984), and will choose the strategy that maximizes annual net revenue given the constraints set by the quota. The strategy consists of a combination of (i) the choice whether or not to go fishing, (ii) the choice of fishing areas with different expected catch rates, and (iii) the choice whether or not to discard the over-quota part of the catch. Choices by month are calculated against annual quota constraints. This study extends the dynamic-state variable models on discarding (Gillis *et al.* 1995, Babcock and Pikitch 2000) by explicitly taking into account the flexibility of discarding and effort allocation in space and time.

5.3 Methods

5.3.1 Model description

A dynamic-state variable model (Clark and Mangel 2000) is used to evaluate the optimal strategy for a fishing vessel under two annual landing quotas, mimicking the mixed fisheries for sole and plaice in the North Sea. Dynamic-state variable models assume that optimal fishing behaviour can be calculated under the assumption that each individual is a utility maximizer. Although many other incentives may play a role in fisher behaviour, there is some empirical evidence for profit as the metric of utility (Robinson and Pascoe 1998). Dynamic-state variable models allow combining the time-scales of short-term choices and long-term constraints such as fishers facing an annual quota system but making daily, weekly, or monthly decisions on where to fish and which fish to keep on board (Clark and Mangel 2000). The individual vessels in the model may be constrained by their quota for the individual species and will respond by changing their fishing pattern in terms of (i) the number of fishing trips, (ii) the choice of fishing areas, and (iii) the choice to discard the over-quota part of their catch.

The problem for the individual is therefore to optimize the utility function Φ , in this case the net revenue at the end of year T . The net revenue is based on total landings for the two species, L_1 and L_2 , total fishing effort and travel time, E , and their respective prices, p_1 and p_2 , and variable costs, p_e , taking into account the total fine D for a vessel exceeding its individual quota for either species:

$$(5.1) \quad \Phi(L_1, L_2, E) = L_1 p_1 + L_2 p_2 - D - E p_e$$

The total fine is calculated as a function of the fine d_1, d_2 per unit of landings, the quotas q_1, q_2 , and the landings:

$$(5.2) \quad D = \begin{cases} 0 & \text{if } L_1 \leq q_1 \text{ and } L_2 \leq q_2 \\ d_1(L_1 - q_1) & \text{if } L_1 > q_1 \text{ and } L_2 \leq q_2 \\ d_2(L_2 - q_2) & \text{if } L_1 \leq q_1 \text{ and } L_2 > q_2 \\ d_1(L_1 - q_1) + d_2(L_2 - q_2) & \text{if } L_1 > q_1 \text{ and } L_2 > q_2 \end{cases}$$

In our model, time passes in monthly steps (t). The expected net revenue at the end of the year needs to be linked to the choices in the preceding months. This is done using the value function, which is the maximum expected net revenue between month t and the end of year T , expressed as $F(L_1, L_2, E, t)$. At the end of the year, this is by definition equal to the net revenue function [$F(L_1, L_2, E, T) = \Phi$]. In the months preceding T , the function depends on the expected net revenue consequences $V_{ijk}(L_1, L_2, E, t)$ of visiting an area i and discarding an excess of j tonnes of the catch of species 1 and discarding an excess of k tonnes of the catch of species 2:

$$(5.3) \quad V_{ijk}(L_1, L_2, E, t) = \sum_{l_1} \sum_{l_2} \lambda_{ij}(l_1, t) \lambda_{ik}(l_2, t) F(L_1 + l_1, L_2 + l_2, E + e_i, t+1)$$

In Equation (5.3), $\lambda_{ij}(l_1, t)$ is the probability that a vessel during a specific time-step (month) will land l_1 tonnes of fish of species 1, given a visit to area i and a choice to discard everything more than j . Likewise, $\lambda_{ik}(l_2, t)$ is the probability that a vessel during a specific time-step will land l_2 tonnes of fish of species 2, given a visit to area i and a choice to discard everything more than k . The parameter e_i is the effort needed to visit area i .

The probabilities $\lambda_{ij}(l_1, t)$ and $\lambda_{ik}(l_2, t)$ can be seen as resulting from a two-stage process. First, the probability of a catch is calculated using discretized normal distributions means μ_{1it}, μ_{2it} , and standard deviations σ_1, σ_2 , respectively for the two species. The reason for choosing a normal distribution is that although the statistical distribution of catches per haul may not be normal (e.g. lognormal),

the sum of the large number of catches per month will approximate a normal distribution. Then, the probability for the actual landings is adjusted by assuming that the catches more than j , k , are discarded. The probability of landings more than these discarding choices j and k are set to zero. Hence $\lambda_{ij}(l_1, t)$ has the following cumulative distribution function:

$$(5.4) \quad \lambda_{ij}(l_1 \leq \chi, t) = f(\chi; \mu_{ij}, \sigma_{ij}, j) = \begin{cases} 0 & \text{for } \chi < 0 \\ \frac{1}{\sigma_{ij}\sqrt{2\pi}} \int_0^{\chi} e^{-\frac{(x-\mu_{ij})^2}{2\sigma_{ij}^2}} dx & \text{for } 0 \leq \chi < j \\ 1 & \text{for } \chi \geq j \end{cases}$$

and $\lambda_{kj}(l_2, t)$ is calculated in a similar manner. Finally, the stochastic dynamic programming equation that provides the optimal choice for the areas to visit and the discarding of marketable fish is

$$(5.5) \quad F(L_1, L_2, E, t) = \max_{ijk} \{V_{ijk}(L_1, L_2, E, t)\}$$

and calculated in a backward iteration because of the recursive nature of $F(L_1, L_2, E, t)$, which depends on $V_{ijk}(L_1, L_2, E, t)$, in turn depending on $F(L_1+l_1, L_2+l_2, E+e, t+1)$. The optimal fishing strategy is an array $H(L_1, L_2, E, t)$ defining the optimal fishing strategy with respect to i, j and k in each time-step, given the state variables L_1, L_2, E . After the backward iteration, the expected distribution of observed decisions can be determined by the forward iteration. This simulates a number of individuals who choose the optimal path, defined by the optimal strategy, given the stochastic nature of the catches.

The model is written in C++, used in a library that is part of the FLR suite (Kell *et al.* 2007) of R (R Development Core Team 2007). The OpenMP paradigm is used in the C++ part of the model to allow parallel computation of the backward iteration on computers with multiple processors (Chapman *et al.* 2007). The probability distributions of the catches for the two species are discretized into 27 bins for each time-step, resulting in 324 discrete states in total for each of the two species. For each of the three areas i , the amount of discarding options j, k is equal to the number of bins per monthly time-step used to discretize the catches. Hence, the discarded fraction of the catch in a single timestep can take a range of values between $[0, 1]$. Staying in port is defined as an additional area, with a zero catch for the two species and no effort. The model was run on an eight-core desktop PC, and a single run (backward and forward calculations for a single set of quota) took < 10 min.

5.3.2 Model parameterization

The Dutch large beam-trawl fleet that is used to parameterize the model described above has been described in detail by Quirijns *et al.* (2008). The spatial distribution of the two resources in the model mimics the North Sea situation. Three different areas are assumed: (i) a northern area (central North Sea), which is part of the summer feeding grounds of plaice with high average catches of plaice (30 t month⁻¹) and low sole catches (1 t month⁻¹); (ii) a central area with intermediate catches for both species 20 t month⁻¹ of plaice and 4 t month⁻¹ of sole); (iii) a southern area (southern North Sea) with low catches of plaice and high catches of sole (8 t month⁻¹ of plaice, 6 t month⁻¹ of sole; Figure 5.1). The market prices used in the model are assumed independent of the total landings and are an approximation of the values observed in the field. Prices differ between species, with the typical first sale price for sole and plaice being €8 per kg and €2 per kg, respectively.

To address the effects of migration of plaice on effort allocation and discarding choices, two different resource distribution scenarios are used. The first assumes a constant mean and variance of the catch rates in the areas over time. The second assumes seasonally varying catch rates for plaice in the northern and the southern area (Figure 5.1, Table 5.1), reflecting plaice migration between southern spawning grounds in winter and northern feeding grounds in summer. Sole migrate along a latitudinal axis, and therefore within areas, rather than between areas. The standard deviations of the catch rates used in the model are taken from a generalized linear model of the monthly catch rates in the three areas between 2001 and 2005. The model assumes normally distributed catch rates with homogenous variance among the areas. The standard deviation for plaice and sole is estimated to be 5.6 and 2.7 t, respectively.

The unit of effort used in the model is a day at sea, consisting of both fishing time and travel time. Independent of the chosen area, fishing time is fixed at 14 d. Travel time, however, differs between areas and is 0, 2, and 4 d for the sou-

Table 5.1 Resource distribution in the model as characterized by μ_{1it} (sole) and μ_{2it} (plaice) for the three areas in the different months t . In the case of only spatial variation in the resource distribution, all μ_{1it} and μ_{2it} are independent of t . In the case of both spatial and seasonal variation, μ_{21t} and μ_{23t} are a sinusoid function of t , reflecting the north-south migration of adult plaice in the North Sea.

Area	Spatial variation		Spatial and seasonal variation	
	Sole	Plaice	Sole	Plaice
North	$\mu_{11t} = 1$	$\mu_{21t} = 30$	$\mu_{11t} = 1$	$\mu_{21t} = 30 + 3\sin(2\pi(t - 5)/12)$
Central	$\mu_{12t} = 4$	$\mu_{22t} = 20$	$\mu_{12t} = 4$	$\mu_{22t} = 20$
South	$\mu_{13t} = 6$	$\mu_{23t} = 8$	$\mu_{13t} = 6$	$\mu_{23t} = 8 + 3\sin(2\pi(t + 1)/12)$

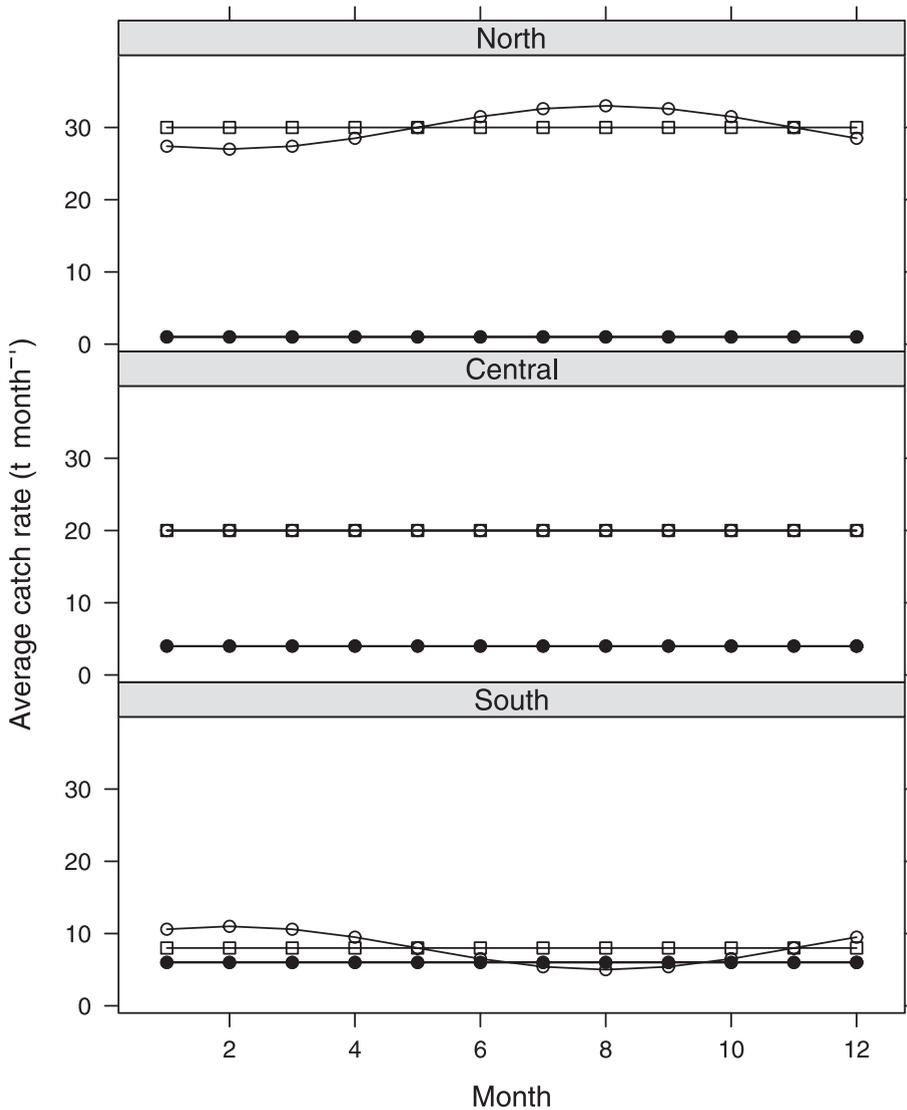


Figure 5.1 Average monthly catch rate of sole (black dots) and plaice in three areas assuming constant spatial distribution (open squares) and seasonal migration between spawning and feeding grounds (open circles).

thern, central, and northern areas, respectively. Hence, fishing in the southern area requires 14 d at sea per month, in the central area requires 16 d at sea per month, and in the northern area requires 18 d at sea per month. These values can be interpreted as the sum of the effort from three trips within a month because the average trip length in the beam-trawl fishery is 5 d, with trips in the north being longer. In the model, it is not possible for a vessel to switch

between areas within a single time-step. Hence, only one area can be selected within a month. In the beam-trawl fleet, a considerable portion of the variable costs of fishing relate to fuel. As an example, in 2006, the average fuel price was €0.41 per litre, and the average fuel costs per day were ~€3500 (Taal *et al.* 2007). Fuel costs make up as much as 55% of gross revenue (Taal *et al.* 2007). To analyse the effects of the variable costs of effort on the dynamics of the system, we analyse scenarios with low variable costs of fishing (€3000 per day) and high variable costs of fishing (€3500 per day). The cost of discarding marketable fish is assumed to be negligible compared with the fishing operation. Discarding, when it happens, would be incorporated into the regular sorting procedure.

In the model, catches and landings of the two species comprise just one market category, but in reality, the fishery lands different size categories, which differ in price. Hence, the discarded marketable fish is likely to constitute the least valuable market category (Gillis *et al.* 1995). In our model, we did not explore the effect of price differences on the discarding of marketable fish (highgrading).

The model is used to analyse the effects of restrictive quotas on spatio-temporal effort allocation and the discarding of marketable fish. We consider the effects of differences in costs of fishing and the migration of the resources in combination with restrictive plaice quotas only because North Sea flatfish fisheries have been more constrained by plaice quotas than by sole quotas since 1990 (Quirijns *et al.* 2008). The model is run for 11 levels of plaice quota ranging between 25 and 400 t. For each run, forward iterations are made for a fleet of 180 vessels (the average fleet size in the period 1990–2004; Quirijns *et al.* 2008). Within a run, all vessels have equal individual landing quotas. Each sole quota is set at 130 t, which cannot be exceeded by any vessel given the maximum sole catches in the simulations. The fine for exceeding the quota is set at twice the price of the two species, sufficiently high to prevent landings from exceeding the quota. Lower fines could result in an incentive for fishers to exceed their quota, but this is not explored in this study.

5.3.3 Data analysis

The outcomes of the model in terms of spatial distribution and discarding can be contrasted against field observations from two different sources.

The first source is the dataset of mandatory logbooks that each fishing vessel must hand into the authorities at the end of each fishing trip. These logbooks have information on the fishing effort distribution of the entire Dutch beam-trawl fleet with a spatial resolution of ICES rectangles (0.5° latitude and 1° longitude) and a temporal resolution of 1 week. Although the logbooks are primarily

used for management purposes, data are made available for research. The data consist of: vessel code, engine power of the vessel, type of fishing gear, ICES rectangles visited, date, time, and harbour of departure, and date, time, and harbour of arrival. The entire dataset spans the period 1990–2007.

From the mandatory logbooks, the centre of gravity (mean) of the fishing effort on the latitudinal axis was calculated by month (Y). The monthly estimates are used as observations in a general linear model:

$$(5.6) \quad Y_i = \beta_0 \cdot m_i + \beta_1 \cdot M_i + \beta_2 \cdot M_i^2 + \varepsilon_i$$

where for the i th observation (Y_i), m_i is the month of the year (as a factor), M_i the time elapsed since January 1990, and ε_i is a normally distributed error term. In this way, the seasonal effect and long term trends in the centre of gravity of the fleet can be disentangled.

The second data source is individual electronic logbooks on fishing effort and catches on a haul-by-haul basis, collected in a collaborative research programme with the fishing industry during 2003 and 2004. Those logbooks allowed for comments by the skippers on their decisions on a haul-by-haul basis. In all, 20 fishers added qualitative information to their haul-by-haul logbooks about factors influencing their fishing decisions, a total of 1029 fishing trips, of which 222 contained comments on fishing tactics and strategy.

The comments were categorized and scored according to several categories, one of which was the mentioning of “discarding of marketable fish”. Other categories included mentioning of gear problems, searching behaviour, weather conditions, restrictive quota, and fish prices. Therefore, from this dataset, spatial and temporal patterns in the occurrence of discarding marketable fish can be quantified from a sample of the fleet. In addition, the reason for discarding marketable fish (restrictive quota, low prices) could be quantified.

5.4 Results

We discuss the model outcomes for four scenarios regarding (i) differences in availability of the two species as a consequence of fish migration, and (ii) the costs of fishing. First, we present model results for fixed spatial then for seasonally varying resource distributions. Within these scenarios, we describe the effects of the different levels of variable (fuel) costs.

5.4.1 Spatial variation in species availability

In the absence of migration, the expected net revenue would be independent of season. The location choice clearly changes with changing plaice quotas (Figure 5.2); high quotas lead to fishing in the central area, for both high and low costs. All catches of marketable fish can be landed and net revenue is largest. A reduction in plaice quota <250 t results in relocation of effort towards the southern area. This is because the southern area becomes more profitable than the central area because of the larger catches of sole and the lower costs. With very low quotas of plaice, the results differ for the two cost scenarios: in the low cost scenario, fishing in the southern area continues, but in the high-cost scenario, vessels spend less time at sea. In scenarios with low plaice quotas and high costs, fishing effort is allocated at the beginning of the year only (Figure 5.3).

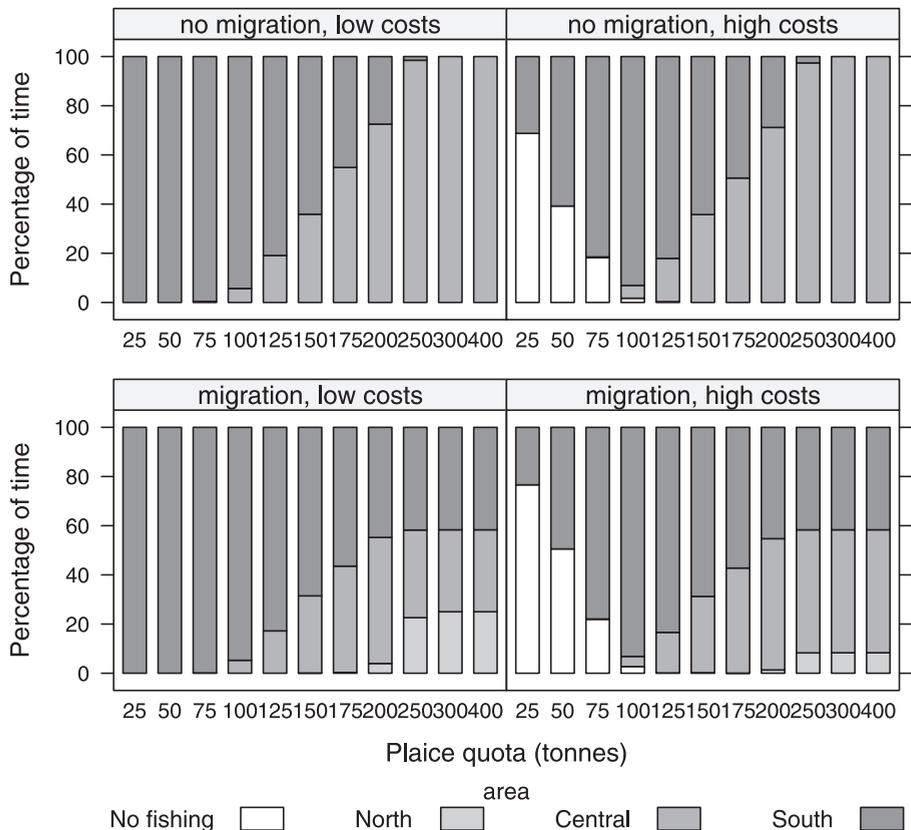


Figure 5.2 Modelled spatial allocation of fishing effort (percentage of time spent fishing in the different areas, or staying in port) for different levels of plaice quota assuming constant distribution of fish and low fishing costs (top left panel) and high fishing costs (top right panel), or assuming seasonally varying distribution of fish and low fishing costs (bottom left panel) and high fishing costs (bottom right panel).

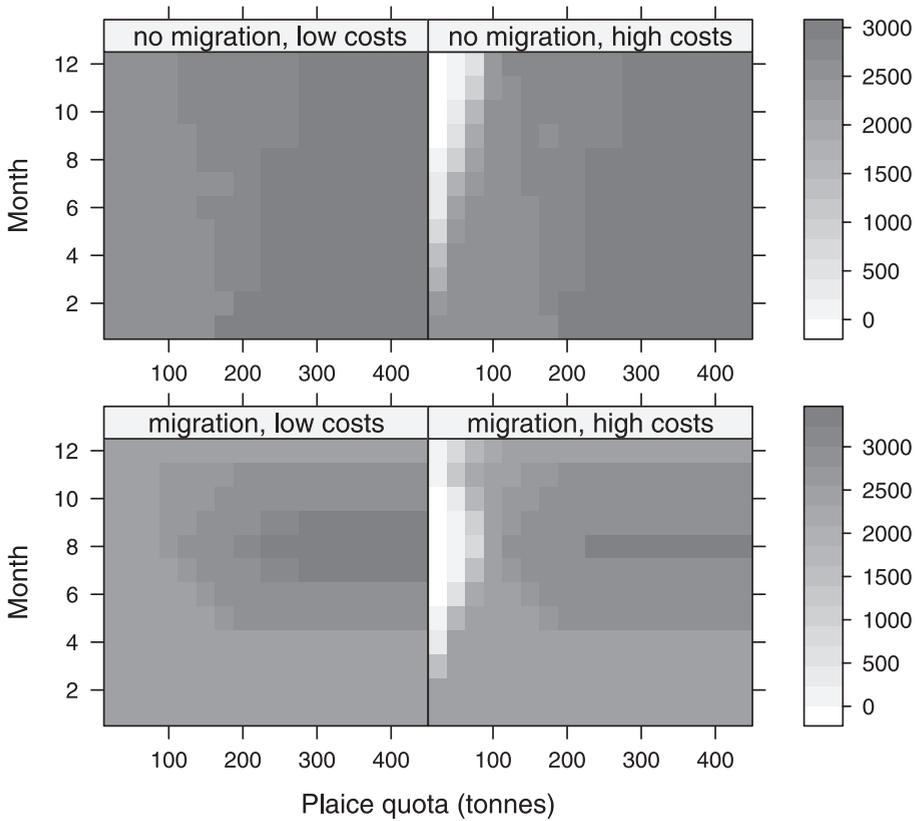


Figure 5.3 Modelled seasonal pattern in fishing effort (days at sea) for different levels of plaice quota assuming constant spatial distribution of fish and low fishing costs (top left panel) and high fishing costs (top right panel), or assuming seasonal varying distribution patterns and low fishing costs (bottom left panel) and high fishing costs (bottom right panel).

The annual catch composition of the two species changes according to the reallocation of fishing effort (Figure 5.4). At levels of individual plaice quota >250 t, the quotas do not affect the catches or landings of either sole or plaice. Below 250 t plaice quota, the average annual catch of plaice decreases, following the level of the quotas, coinciding with a decrease in effort. As fishing effort is reallocated to the southern area with less travel time, sole catches increase. In this multispecies fishery, therefore, a decrease in plaice quota results in an increase in the apparent catchability of sole because the ratio of total sole catch over total fishing effort increases, at equal stock biomass.

At very low quotas of plaice, the effects of quota reductions differ between the two cost scenarios: at low costs, plaice catches become independent of the plaice quota, and all catches of marketable plaice that exceed the quota are

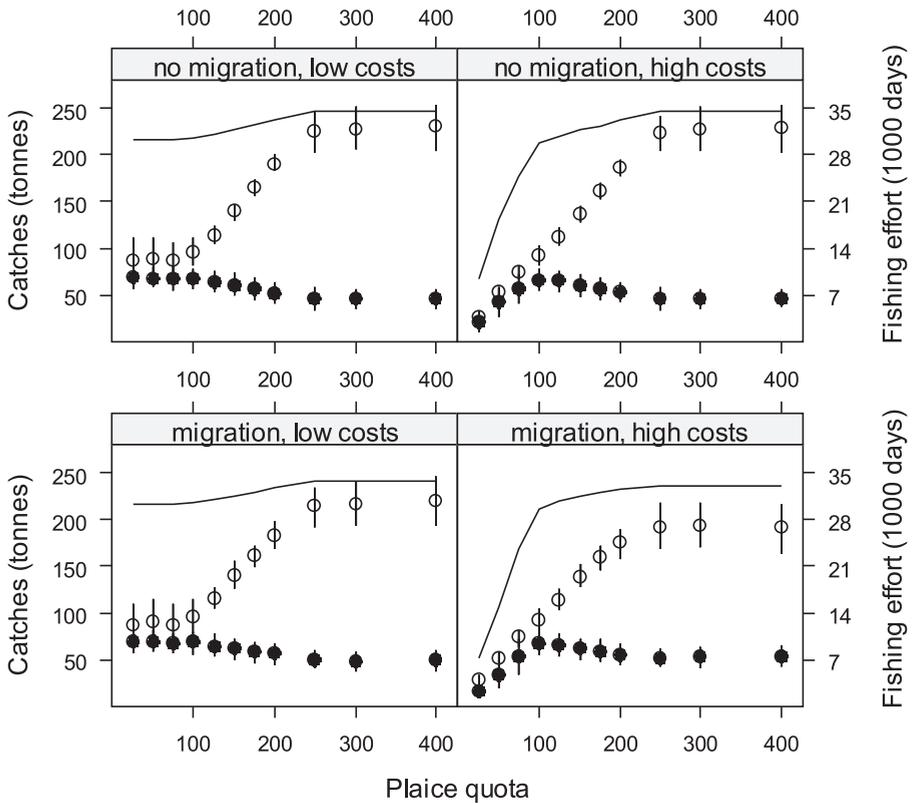


Figure 5.4 Modelled average annual catch per vessel of sole (black dots) and plaice (open circles) and fishing effort of the total fleet (line) at different levels of individual plaice quota, assuming a constant spatial distribution of fish and low fishing cost (top left panel) and high fishing costs (top right panel), or assuming seasonally varying distribution patterns and low costs per unit of effort (bottom left panel) and high costs per unit of area (bottom right panel). Error bars of the annual catches represent the 10 and 90% quantiles.

discarded at the end of the year (Figure 5.5). The optimal strategy is to land all plaice caught until the vessel's quota is reached. Despite the vessel's low quota of plaice, fishing can continue on sole and still be profitable. Continued fishing also ensures high catches of sole. Alternatively, at high cost, very low quotas of plaice will result in a reduction in fishing effort at the end of the year, and hence very little discarding (Figure 5.5).

Owing to the stochasticity in the model, the time of year when the quotas are reached differs among fishers. This is caused by differences in cumulative fishing success resulting from the stochastic monthly catches.

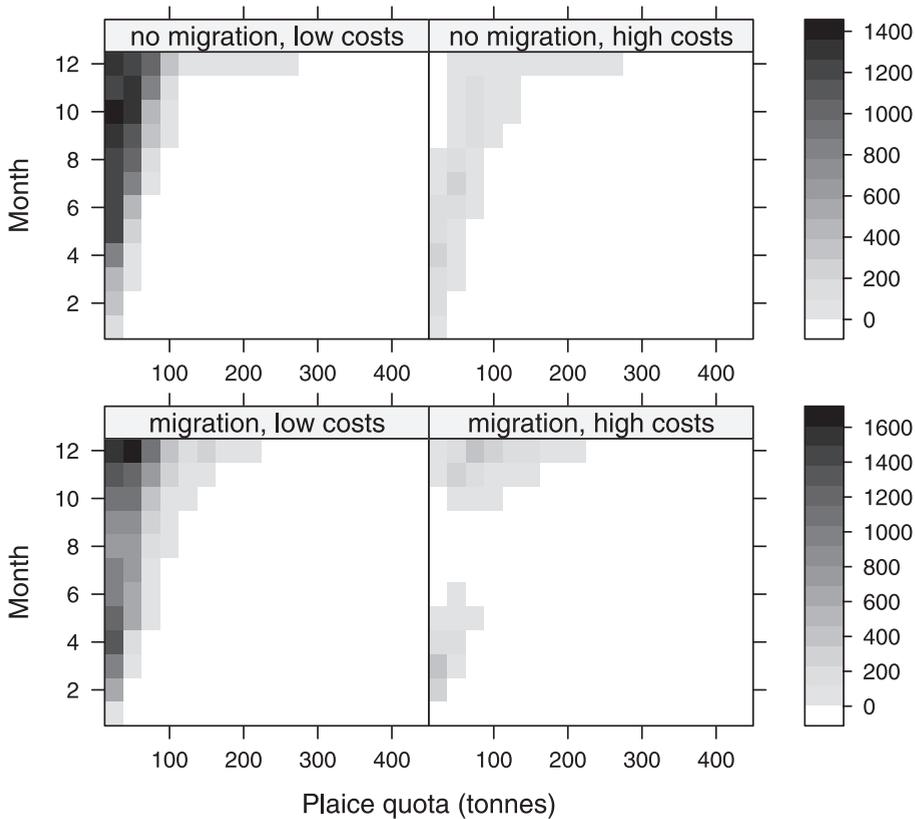


Figure 5.5 Modelled seasonal pattern in total over-quota discarding (t) of marketable plaice for different levels of plaice quota assuming constant spatial distribution of fish and low fishing costs (top left panel) and high fishing costs (top right panel), or assuming seasonally varying distribution of fish and low fishing costs (bottom left panel) and high fishing costs (bottom right panel).

5.4.2 Seasonal and spatial variations in resource availability

A seasonally changing distribution of fish has a clear effect on the distribution of fishing effort. With high quotas of plaice, fishing effort is allocated over all three areas (Figure 5.2). Effort allocation in the northern area is concentrated around month 8, when plaice availability peaks and catches are sufficiently high to offset the higher travel costs of visiting the area. The total amount of effort in the north depends on the cost per unit of effort, with the low cost scenario resulting in more effort being allocated in the area than under a high-cost scenario. Also, the southern area is visited at the beginning of the year when plaice availability peaks there. If the plaice quota decreases, total effort in the northern area decreases and effort allocation patterns increasingly resemble

those found in the absence of migration, with fishing effort concentrated in the south.

The spatio-temporal distribution of fishing effort reflects the choice of individual vessels to visit different areas throughout the year (Figure 5.3). With high quotas of plaice, monthly totals of fishing effort increase in late summer, when vessels tend to visit the northern area. The duration of that period depends on the costs of fishing effort. If costs are low, the northern area is visited for 3 months, but if costs are high, the period lasts just 1 month. At the beginning and the end of the year, fishing effort is low because the southern area is more profitable, requiring less travel time. With decreasing levels of plaice quota, fishing effort shifts to the southern area, similar to the models in which no migration was assumed. However, a decrease in fishing effort associated with high costs of fishing takes place at the end of summer, after which effort increases again in winter. This temporal pattern in effort allocation is caused by the seasonal density of plaice in the southern area.

In general terms, the effect of plaice quota on catch and effort in the presence of plaice migration are similar to the situation without plaice migration. Decreasing plaice quotas leads to a decrease in plaice catches and an increase in sole catches, caused by the changes in catchability attributable to the redistribution of effort (Figure 5.4). At very low plaice quotas, catches of the two species may decline or level off, depending on the costs of fishing. However, in contrast to the situation with no migration, the average catch rates for plaice when plaice quotas are high depend on the costs of fishing: if costs are low, more fishing effort is allocated in the northern area, with its higher catch rate of plaice.

In the presence of migration, the temporal distribution of total discards of marketable plaice with very low quotas of plaice is bimodal. The two periods with high discarding concur with the high catches of plaice in the southern area (Figure 5.5). At the level of the individual fisher, the optimal strategy again is to retain all marketable plaice until the vessel's plaice quota is reached.

5.4.3 Observations

Data from the mandatory logbooks provide insight on the centre of gravity of fishing effort of the entire fleet between 1990 and 2007. The mean latitude varies seasonally and ranges between 52.5 and 54.58 (Figure 5.6). The simple linear model disentangling the seasonal and long-term trends in all 216 observations explains some 71% of the variance, using 13 degrees of freedom. Each term in the model has a p-value <0.01 . The seasonal pattern estimated by the model indicates that the fleet starts fishing in the southern areas in the first few

months of the year and that as the year progresses, the spatial distribution of fishing effort shifts north, then is followed by a southward movement towards the end of the year. Since 1990, fishing effort has shifted gradually south by more than a half degree of latitude, a trend that was especially strong in the 1990s.

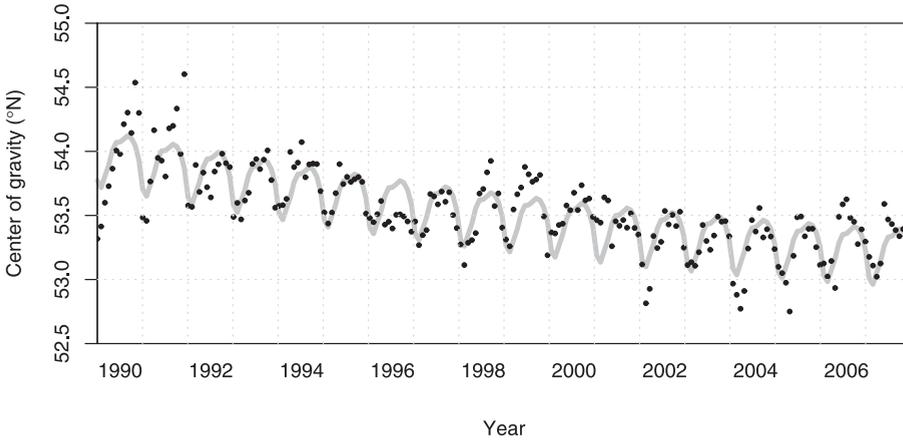


Figure 5.6 Time-series of the monthly centre of gravity of the Dutch beam-trawl fleet latitudinally. Each dot represents the centre of gravity in a single month, calculated from the mandatory logbook data. The grey line represents monthly predictions of the centre of gravity, using a simple generalized linear model, as described in the text.

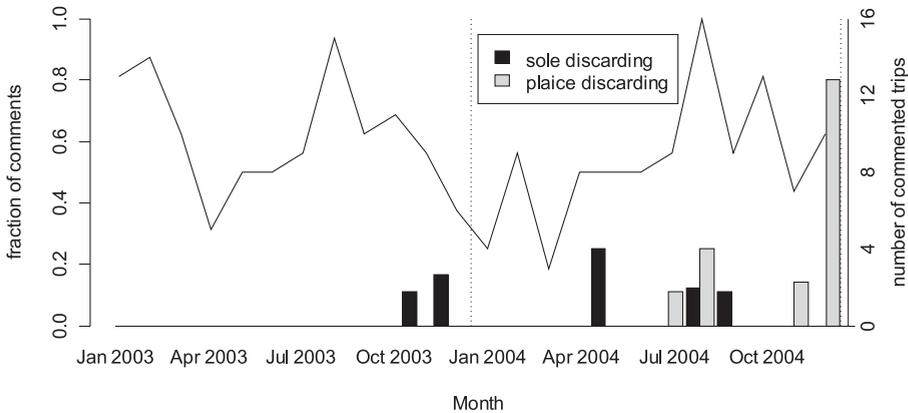


Figure 5.7 Time-series of the number fishing trips indicating discarding of marketable plaice and sole. Each bar represents the fraction of comments that mention discarding in the voluntary logbooks in a given month (left y-axis). The drawn line indicates the total number of trips for which a comment exists per month (right y-axis), and the vertical dotted lines the start of the year.

In the voluntary electronic logbook data, 8 of the 20 fishers reported discarding of marketable plaice or sole in 21 trips (sole 7; plaice 14) out of the total of 222 trips that had comments added to haul data (Figure 5.7). The probability of a comment in the logbook mentioning discarding of marketable fish increased towards the end of the year, indicating that marketable fish are discarded mainly then. In December 2004, 80% of the comments indicated discarding of marketable plaice in the trips reported ($n = 10$). In all five cases where the reason for discarding marketable plaice was reported, fishers stated that they discarded because of their lack of sufficiently large quota. In two cases, along with the lack of sufficiently large quota, low fish price was given as a reason. For sole, no reason for discarding marketable fish was given.

5.5 Discussion

This study has characterized spatio-temporal effort allocation and discarding in a multispecies fishery managed by single-species individual quotas using a dynamic-state variable model. The results of the model clearly show that individual quotas on one species (plaice) influence effort allocation and discarding by individual fishers and as a consequence may affect the catchability of another species (sole). Constraining the quota of one species will result in a shift of fishing effort away from areas with high catches of that species towards areas with profitable catches of other species that are not constrained by quota. Hence, in a multispecies fishery, increasing the quota restrictions for one species may reduce the catchability for that species and increase the catchability for other target species. In the North Sea beamtrawl fishery, decreasing individual quotas for plaice result in reallocation of fishing effort to the southern areas, where plaice catches are smaller and sole catches bigger. The model predictions of seasonality in spatial effort allocation, and the southward shift of effort allocation in the 1990s when the individual plaice quotas became increasingly constraining (Quirijns *et al.* 2008), are confirmed by observations of the fleet. The findings are consistent with the notion that targeting by the beam-trawl fleet between 1990 and 2005 varied in relation to quota restrictions (Quirijns *et al.* 2008).

Also, constraining quotas for one species may result in more discarding of marketable fish. In the situation explored here, the fleet was to some extent capable of reducing over-quota discarding by reallocating fishing effort and increasingly targeting the species for which the quota limits were not restrictive. Also, over-quota discarding depends on the net revenue that can be generated by fishing while only landing those species for which the quotas have not been depleted. In general, over-quota discarding will occur towards the end of the year, as our model results indicate. However, at very low levels of quota, many fishers will

have exhausted their quotas early in the year. In the specific case studied here, the discarding is in the southern area, used by the fishery because of the high catches of “alternative species”. The model results are in line with the observations of discarding of marketable plaice in the Dutch beam-trawl fishery in 2004, when discarding of marketable plaice in the second half of the year peaked in December. This discarding practice coincided with the period when plaice quotas were highly restrictive (Quirijns *et al.* 2008). The comments made by fishers revealed that their reasons for discarding were mainly insufficient quota and perhaps low fish price.

It should be noted that the discards modelled in this study are part of the marketable catch. This form of discarding differs from minimum landing size (MLS) discarding that consists of the nonmarketable part of the catch. MLS discarding may in itself already constitute a large part of the catch (Rijnsdorp and Millner 1996, van Beek 1998). The marketable fish in the model are represented as one homogeneous group and are discarded as such. In the real fishery, the marketable catch consists of several classes that differ in value, and the fish with the lowest value will probably be discarded first. This type of discarding, based on market value, is known as highgrading (Anderson 1994, Gillis *et al.* 1995, Kingsley 2002). In the fishery on which this study is based, there can be such highgrading, because differences in price between market categories may be as much as 100% (Taal *et al.* 2005). In autumn, the fish of low value are the smallest size classes, whereas in winter and early spring such fish may be the largest fish, including spent females of low condition and watery flesh. Such differentiation in classes of different value may influence the temporal distribution of discarding. Low-value fish at the beginning of the year will be discarded to save quota for high-value fish at the end of the year, so giving results different from those obtained by our model, which assumes a single value for all marketable fish. In the electronic logbooks, fishers reported discarding specific size classes of marketable fish, consistent with the notion of highgrading. Moreover, fishers reporting highgrading of marketable plaice continued to land plaice in subsequent weeks, implying that they optimized according to price differences within the species. Our model was unable to evaluate highgrading within a species because each species was modelled as a single homogeneous group.

The effort reallocation found under decreasing plaice quotas depends on the parameters defining the difference in profitability between the various areas. For example, if the difference in prices between species was larger, fishing in the southern region would be more profitable when plaice harvest is unconstrained. In that case, fishing effort would be allocated in the southern area independent of quota size. The maximum plaice catches would be lower, but the temporal discarding pattern would be similar to that found in this study. If the spatial distribution of species were to differ, discarding of plaice might be

greater because the reallocation of fishing effort to areas with lower catches of plaice, higher catches of sole, and lower fishing effort requirements depends on the spatial distribution used in the model.

The assumption of maximizing economic performance has been evaluated before. The response of fishing vessels to catch rate has been shown in, for example, British Columbia salmon seining (Hilborn and Ledbetter 1979) and shrimp trawling (Eales and Wilen 1986). The response has been used to formulate models predicting the distribution of fishing vessels (Gillis *et al.* 1993).

Our model uses a similar assumption, but takes into account a broader behavioural context by incorporating discarding behaviour and the requirement to respect the rules set by fisheries management. It is clear that restrictive quotas influence the spatial distribution of fishing effort and discarding behaviour. The latter allows fishers to continue fishing in a multispecies fishery if one of the quotas is exhausted, depending on the costs of fishing effort.

Our model assumes that fishers have perfect information about the distribution of catch rates in many areas. The knowledge of individual fishers on the distribution patterns of target species depends on the predictability of the resource distributions (van Densen 2001), as well as the level of information sharing within the fleet. The predictive value of observations in the beam-trawl fleet appears to be relatively high (Poos and Rijnsdorp 2007a), in particular with regard to the seasonal migration of adult fish (de Veen 1976, Hunter *et al.* 2003, Bolle *et al.* 2005) and the recruitment of the incoming year class (Beverton and Holt 1957). To increase knowledge of the spatial distribution of catch rates, fishers may exchange information. The role of information exchange in acquiring knowledge of the distribution of the target species has been discussed by Curtis and McConnell (2004).

The effects of the size of individual quotas on catchability of all target species and over-quota discarding have serious implications for fisheries management. First, increased catchability for species not restricted by quotas may be the undesired result of setting individual quotas in a multispecies fishery. Second, if a part of the catch is not landed, a bias may be introduced in the analytical stock assessments supporting the management of many fisheries (Rijnsdorp *et al.* 2007). Because the discarding of marketable fish is concentrated at the end of the year and is mainly associated with vessels with relatively small individual quotas, it is difficult to estimate the level of this form of discarding from the current North Sea discard sampling programmes that combine low sampling levels (< 1% of the trips) with regularly spaced samples throughout the year (van Keeken *et al.* 2004, STECF 2008).

The high fines for exceeding the quota resulted in vessels remaining in port when quotas were low because over-quota fish did not contribute to their economic revenue. However, in reality fishers may assess the potential benefit of the economic return of over-quota landings against the cost of running a risk of being penalized for misreporting. Non-compliance could lead to a higher over-quota catch of plaice. Our results assume high fines in combination with strong enforcement. High fines can also be interpreted as fisher desire to respect a quota. Additional analysis could give insight into the relation between the level of the fines and the compliance with the quota. If over-quota discarding is to be reduced, high fines on over-quota discarding could be implemented, as in a discard ban. However, such a measure is considerably more difficult to enforce than individual landing quotas. Assuming that strong enforcement is possible, the effects of a discard ban can be analysed in the present model by removing the discard options to the vessel.

The individual optimization models presented here ignore the possibility that the behaviour of other members in the fisher population affect the choices of the focal individual (Clark and Mangel 2000). This has two important implications for the results presented in this study. First, the model ignores exploitation or interference competition affecting the catch rates as a result of high vessel density. Such competition may decrease the catch rate as a function of the number of competing vessels in an area (Fretwell and Lucas 1970, van der Meer and Ens 1997). Interference competition may play a role in fisheries worldwide (Gillis 2003), including the Dutch flatfish fishery (Rijnsdorp *et al.* 2000, Poos and Rijnsdorp 2007b).

Second, the model does not allow for transferability of quotas between fishers: quotas cannot be leased from one vessel to another during a year, although this is one of the key points of ITQ systems. Conditions may exist where the transfer of a quota is beneficial for two individuals: given the stochastic nature of catches, one fisher may have reached his quota before the end of the year, because of a sequence of good catches, whereas another may realize he will not reach his quota, because of a sequence of poor catches. A transfer in ITQ will increase the net revenue of both vessels. If all vessels are equal, this effect could be especially strong at quota levels close to maximum catch levels. At a higher quota, no vessel will be restricted by it, and there will be no incentive to transfer quota. At a lower quota, all vessels will be restricted by its level, and no vessel will have excess quota to transfer. Such a hypothesis needs careful testing using robust models. The extension of dynamic-state variable models with frequency dependence has been described (Clark and Mangel 2000), and the method should be considered in future to analyse the effects of transferability of quota on discarding behaviour.

The discarding of marketable fish under conditions imposed by management, mitigated by the spatio-temporal distribution of resources, has important implications for fisheries management. Over-quota discarding will disrupt the link between catches and landings in mixed fisheries and may corrupt the basis of scientific advice and increase the risk of stock collapse (Rijnsdorp *et al.* 2007). This can be tested by using the model described here in studies evaluating fisheries management, employing the framework developed in the International Whaling Commission (Kirkwood 1997, McAllister *et al.* 1999). In such a framework, the population dynamics of fish stocks and the dynamics of fishing fleets are modelled (Butterworth and Punt 1999, Punt *et al.* 2002). The biological detail is often very high (Kell and Bromley 2004), but the response of the fleet to the constraints applied has generally been captured in simplistic assumptions, such as fixed catchabilities for the species being modelled, with all excess catch being discarded (Pastoors *et al.* 2007). The model presented here allows calculation of the economic optimum strategy for fishing fleets under input or output constraints. Hence, it has the potential to add detailed fleet response to management rules, predicting effort, catch, and discard levels in evaluation frameworks.

5.6 Acknowledgements

We thank Willem Vermin for analysis of the original C++ code and adding the OpenMP paradigm, funded by NCF grant NRG-2002.01, the skippers that contributed to the F-project for the invaluable information they provided in voluntary electronic logbooks, and the anonymous referees for their constructive comments. The study was supported by NWO grant ALW88510104 to JJP and funding from the EU project SSP8 022644, Capacity, F and Effort (CAFÉ) to JAB, and an NSERC Discovery Grant to DMG.

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Chapter 6

Comprehensive discard
reconstruction and abundance
estimation using flexible selectivity
functions

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ICES Journal of Marine Science 66 (2009) 763-771

6.1 Abstract

The additional mortality caused by discarding may hamper the sustainable use of marine resources, especially if it is not accounted for in stock assessment and fisheries management. Generally, long and precise time-series on age-structured landings exist, but historical discard estimates are often lacking or imprecise. The flatfish fishery in the North Sea is a mixed fishery targeting mainly sole and plaice. Owing to the gear characteristics and a minimum landing size for these species, considerable discarding occurs, especially for juvenile plaice. Discard samples collected by on-board observers are available since 1999 from a limited number of commercial fishing trips. Here, we develop a statistical catch-at-age model with flexible selectivity functions to reconstruct historical discards and estimate stock abundance. We do not rely on simple predefined selectivity ogives, but use spline smoothers to capture the unknown non-linear selectivity and discard patterns, and allow these to vary in time. The model is fitted to the age-structured landings, discards, and survey data, the most appropriate model is selected, and estimates of uncertainty are obtained.

6.2 Introduction

Discarding is the practice of returning an unwanted section of the catch back to the sea during fishing operations. Discards not only include non-commercial species, but also commercial species that are below minimum landing size (MLS) or less profitable owing to market conditions and quota restrictions (Catchpole *et al.* 2005). Most of the fish that are discarded do not survive the catching and sorting process (van Beek *et al.* 1990, Kaiser and Spencer 1995). This additional mortality may hamper the sustainable use of marine resources, especially if it is not accounted for in fisheries management (Alverson *et al.* 1994, Crowder and Murawski 1998, Rijnsdorp *et al.* 2007).

Accounting for discards in the exploitation of fish stocks starts with their estimation and use in stock assessment. Discard surveys in recent years reveal that discards may correspond to a substantial part of the catch, and for some stocks, they may even exceed the landings (ICES 2008). However, the existing discard estimates often cover a small fraction of the fleet and may therefore be imprecise.

Punt *et al.* (2006) developed a flexible, statistical catch-at-age model that incorporates discard estimates into stock assessment. The method also facilitates discard reconstruction for years lacking discard data, assuming that discard selectivity is constant in time, but what if fishing and discard selectivity-at-age changed over time? Here, we propose an alternative method for estimating

discards and assessing the demographic state of the population. The method is based on a statistical catch-at-age model (Fournier and Archibald 1982, Deriso *et al.* 1985, Gudmundsson 1994, Fryer 2002, Punt *et al.* 2006). Spline smoothers are used to capture the unknown non-linear selectivity and discard patterns, using only few parameters. Hence, we do not have to rely on simple predefined shapes for this important fishing process. By making the parameters in the spline smoothers dependent on time, the method is also able to deal with time-variant selectivity and discard patterns. An additional advantage of statistical catch-at-age models is that both parameter estimates and standard errors for these estimates can be provided. Hence, the uncertainty in the stock development estimate can be shown and be used in managing the fisheries. Finally, the maximum likelihood estimation of the model parameters makes it possible to use information criteria as an objective way to compare models.

We apply the statistical catch-at-age model using landings, discards, and scientific survey data for North Sea plaice (*Pleuronectes platessa*). This species is caught in the North Sea demersal flatfish fishery, which is a mixed fishery targeting a range of flatfish species (Daan 1997, Poos and Rijnsdorp 2007). Changes in market conditions, costs of fishing, or management measures such as the establishment of the “plaice box” (Pastoors *et al.* 2000, Dinmore *et al.* 2003) have led to changes in gear efficiency and seasonal and spatial dynamics of the fleets. In particular, the Dutch beam trawl fishery has seen a displacement of fishing effort from the northern to the southern North Sea (Quirijns *et al.* 2008), the latter characterized by higher concentrations of sole (*Solea solea*), but also juvenile plaice. The small mesh sizes necessary to fish for sole combined with an MLS for plaice of 27 cm leads to considerable discarding of mostly juvenile plaice (van Beek 1990, van Keeken *et al.* 2004).

An extensive scientific discard sampling programme using on-board observers was initiated in 1999 (van Keeken *et al.* 2004). The programme estimates discards from several fish stocks in the countries around the North Sea. Because of the high costs of these observer programmes, sampling effort in the individual countries is generally low compared with the number of fishing trips. For the years preceding the observation programme, discards were estimated following a slight modification of the approach of Casey (1996). This approach is based on prerecruit growth rates, selectivity characteristics of the fishery, and XSA (Shepherd 1999) estimates of fishing mortality (van Keeken *et al.* 2004, ICES 2005). Not only is this method criticized for its conceptual complexity, but its deterministic approach also ignores uncertainty. In the statistical catch-at-age model proposed here, the reconstruction of both historical discards and stock development are estimated consistently and concurrently.

6.3 Methods

6.3.1 Data

Landings, discards, and survey tuning data for North Sea plaice were available from ICES (2008). The combined landings-at-age data from different countries were available from 1957 on, spanning ages 1–15. Discard estimates were available for the period 2000–2007, containing samples from the Netherlands, Denmark, and the UK. There was a marked difference between the spatial distribution of the fishing effort of those countries' fleets. This difference causes different age structures in the landings and discards, because of the spatial distribution of juvenile and adult plaice, and because of the different mesh-size regulations that apply in different areas of the North Sea. The tuning index data were available from three surveys: (i) BTS-Isis, (ii) BTS-Tridens, and (iii) SNS (Rogers *et al.* 1997). These surveys take place in different areas of the North Sea in the third quarter of the year. Because of the large number of zero observations in the survey data for ages 10+, only data for ages 1–9 were used. However, the discards were only estimated for ages 1–8, because all data at age 9 or older were zero. Likewise, because of the limited survey data availability before 1985 for ages 4–9, the estimation model is constructed from 1980 on, such that at least part of the earliest cohorts was covered by the survey data at older ages.

6.3.2 Model description

The model is a traditional discrete-time age-structured population dynamics model

$$(6.1) \quad N_{a+1,t+1} = N_{a,t} e^{-Z_{a,t}}$$

where $N_{a,t}$ are the numbers at age a at time t , and $Z_{a,t}$ the total mortality, which is composed of the instantaneous natural mortality rate M and the fishing mortality rate $F_{a,t}$.

6.3.3 Natural and fishing mortality

Natural mortality is assumed to be constant (0.1) in time and equal for all ages. Fishing mortality $F_{a,t}$ is the result of catchability q , annual fishing effort e_t , and the selectivity pattern $f_{a,t}$, such that

$$(6.2) \quad F_{a,t} = qe_t f_{a,t}$$

Catchability q is the extent to which a stock is susceptible to fishing. The fishing effort e_t is the total amount of fishing in a year, and varies each year (hence the subscript t). With the available data, it is only possible to estimate the product of these two. The selectivity pattern $f_{a,t}$ defines the relative likelihood that an individual of age a in the population is caught and is constrained to have a maximum of 1. This age-dependent selectivity is the result of several processes. First, younger fish are generally smaller, and more likely to escape through the meshes of the net. In contrast, older fish may be able to avoid being caught, e.g. by outswimming the gear. Finally, age-specific differences in the spatial and temporal overlap between the fish and fishery influence the probability of individuals coming into contact with the fishing gear, affecting the selectivity pattern. The above processes make the fishing selectivity a complex function of age, and specifying an *a priori* shape may not fully address the multitude of processes that take place in shaping its functional form. Therefore, we used a smooth function of age, constructed using four b-spline basis functions $h_k(a)$ (de Boor, 2001). These functions can be viewed as four transformations of the explanatory variable a . Each b-spline basis function is a cubic polynomial of the explanatory variable, but it is only non-zero within a certain range (defined by so-called knots) of the explanatory variable. Next, each basis function $h_k(a)$ is weighted by a constant $b_{k,t}$. Summing these weighted functions results in the complex smooth function of age:

$$(6.3) \quad f_{a,t} = \text{logit}^{-1} \left(\sum_{k=1}^4 b_{k,t} h_k(a) \right)$$

In this function, logit^{-1} is $\exp(\cdot)/(1 + \exp(\cdot))$ and ensures that $f_{a,t}$ takes values between 0 and 1. One could also use a polynomial function of age. However, because of the local nature of the basis function, the fit of the smooth function in one range of the data (e.g. at low ages) is independent of its fit at the other extreme (e.g. at high ages). Similar to many other assessment techniques, we assume that the fishing mortality of the last age class is equal to the fishing mortality of the preceding age. Temporal changes in the spatial overlap between fishing effort and the different age classes of the fish population can result in changes in the selectivity pattern. This is captured by modelling the weighting constants as a function of time, hence the subscript t in $b_{k,t}$. To prevent over-parameterization, only a linear function for the temporal changes in selectivity was inspected, i.e.

$$(6.4) \quad b_{k,t} = \beta_{0,k} + \beta_{1,k} t$$

6.3.4 Discards and landings

The expected catch $C_{a,t}$ for age a and year t is calculated from

$$(6.5) \quad C_{a,t} = \frac{F_{a,t}}{Z_{a,t}} N_{a,t} (1 - e^{-Z_{a,t}})$$

The catch consist of discards $D_{a,t}$ and landings $L_{a,t}$. We assume that an age-dependent fraction $d_{a,t}$ of the catch is discarded, such that

$$(6.6) \quad \begin{aligned} D_{a,t} &= d_{a,t} C_{a,t} \\ L_{a,t} &= (1 - d_{a,t}) C_{a,t} \end{aligned}$$

Although landings data are generally available, discard data are often lacking or, as in our study, only available for the most recent years.

Several model formulations for the discard fraction $d_{a,t}$ are fitted and compared: (i) a linear function of age on the logit scale assuming a time-invariant discard pattern:

$$(6.7) \quad d_{a,t} = \text{logit}^{-1}(\beta_0 + \beta_1 a)$$

(ii) a time-invariant smooth function of age [similar to Equation (6.3)], (iii) a smooth function of age that varies linearly in time [similar to Equations (6.3) and (6.4)], and (iv) a smooth function of age where each smooth parameter [see Equation (6.4)] is modeled as a second-order orthogonal polynomial function of time. The mathematical form of the orthogonal polynomial can be found in Ismail (2005), and its implementation in R is described in Chambers and Hastie (1992).

6.3.5 Survey tuning series

The tuning series data for plaice are collected over a short period (August–September) of each year. Because the survey vessel catches are a very small part of the population, it is assumed that these catches do not affect the mortality of the population as a whole. The population size $N_{a,t}$ represents the population size on 1 January of year t . When the scientific survey takes place later in the year, the population size may be reduced considerably by fishing and natural mortality. To correct for this, the mean population size during the time of the

survey $N_{a,t}^U$ is estimated as

$$(6.8) \quad N_{a,t}^U = N_{a,t} \frac{e^{-\kappa Z_{a,t}} - e^{-\lambda Z_{a,t}}}{(\lambda - \kappa) Z_{a,t}}$$

where κ and λ are the start and end, respectively, of each survey expressed as a fraction of a year. Consequently, the catch of survey $U_{a,t}$ of age a in year t can easily be calculated as

$$(6.9) \quad U_{a,t} = s_{u,a} N_{a,t}^U q_u$$

where q_u is the efficiency, which is survey vessel u -specific, and $s_{u,a}$ the age-specific selectivity of the survey vessel u . Again, we model $s_{u,a}$ as a smooth function of age [similar to Equation (6.3)].

Survey selectivity $s_{u,a}$ is assumed to remain constant in time, based on the observation that the gear, the timing, and the spatial distribution of the scientific surveys have not changed.

6.3.6 Likelihood function

The available datasets for parameter estimation are (i) landings-at-age, (ii) discards-at-age, and (iii) tuning series from three surveys. Conforming with most other statistical catch-at-age assessment methods (Fournier and Archibald 1982, Deriso *et al.* 1985, Gudmundsson 1994, Fryer 2002, Punt *et al.* 2006), the data are assumed to be lognormally distributed, with means and age-specific standard deviations predicted by the model. Visual inspection of the residuals indicated that they were approximately normally distributed. There were five zero values in a total of 715 observations in the three datasets. These zero values were replaced by half of the lowest value observed in the dataset where each occurred. This approach guards against zeros in the likelihood function by taking account of the scale of the data. The total log-likelihood ℓ is then

$$(6.10) \quad \begin{aligned} \ell &= \ell_D + \ell_L + \ell_U, \\ \text{where } \ell_D &= \sum_{a,t} n \left(\log(D_{a,t}); \log(\hat{D}_{a,t}), \sigma_a^D \right), \\ \ell_L &= \sum_{a,t} n \left(\log(L_{a,t}); \log(\hat{L}_{a,t}), \sigma_a^L \right), \\ \ell_U &= \sum_{a,t} n \left(\log(U_{a,t}); \log(\hat{U}_{a,t}), \sigma_a^U \right). \end{aligned}$$

Here, $n(\log(D_{a,t}); \log(\hat{D}_{a,t}), \sigma_a^D)$ is the normal probability density of the log of the observed values $D_{a,t}$, with mean $\log(\hat{D}_{a,t})$ and standard deviation σ_a^D . Residual plots for the initial model runs suggested that the variability in the residuals differed with age. To capture this effect, the values of σ_a are modelled as the exponent of an orthogonal polynomial function of age, with 2 d.f. (Chambers and Hastie, 1992). The standard deviations are constrained to be at least 0.05, to facilitate convergence of the minimizer used to find the maximum likelihood.

6.3.7 Parameter estimation and model selection

All model fitting was done in R (R Development Core Team 2008), using the FLR package (Kell *et al.* 2007). The negative of the likelihood function in Equation (10) was minimized using the Broyden–Fletcher–Goldfarb–Shanno (BFGS) quasi-Newton or variable metric algorithm. Several starting values were selected randomly from a uniform distribution within appropriate boundaries, leading to different parameter estimates. This suggests that the likelihood function had several local maxima. We therefore selected the parameter estimates corresponding to the highest maximum likelihood among multiple runs (>50 times). The model often converged to these parameter estimates, and we assumed that these correspond to the global maximum. Also, all eigenvalues of the numerically differentiated Hessian matrix at the parameter values presented here were positive, indicating that the parameter values indeed represented a maximum of the log-likelihood function.

Models with different fishing and discard selectivity functions described above were fitted to the data. The Akaike Information Criteria (AICs) of the model fits were compared, and the model with the lowest AIC was retained for further analysis and inference of the population dynamics and abundance. However, different functional forms of the different model assumptions with respect to selectivity and discarding patterns are presented too, to explore the effect of different model assumptions on these patterns.

6.3.8 Quantifying uncertainty

Minimizing the negative of Equation (10) results in maximum likelihood parameter estimates and the variance–covariance matrix that is derived from the inverse of the Hessian. For estimating parameter uncertainty, we selected random values (10 000) from a multivariate normal distribution with those parameter means and variance–covariances. The resulting random realizations are then used to estimate 95% confidence intervals for population and fisheries characteristics of interest, using the percentile method.

6.4 Results

6.4.1 Selectivity functions

As a reference, the full model containing both a time-variant fishing and discard selectivity function was fitted first. The AIC of this model (862; see Table 6.1) was compared with a model with time-invariant fishing and/or different discard selectivity functions. Based on the AIC, the full model (with time-variant fishing and discard selectivity described by a polynomial timevariant spline) outperformed the simpler models. This model will be used for further comparison and inference.

Table 6.1 Model selection; model number, description of fishing and discards selectivity curves, and log-likelihood (LogL). The number of model parameters (P), the total number of observations (Obs), and the AIC are also given. The lowest AIC value is emboldened.

Model	Selectivity	Discarding	-LogL	P	Obs	AIC
1	Time-variant spline	Polynomial time-variant spline	318.8	112	715	862
2	Time-variant spline	Time-variant spline	333.6	108	715	883
3	Time-variant spline	Time-invariant spline	346.5	104	715	901
4	Time-variant spline	Time-invariant linear function	375.2	102	715	954
5	Time-invariant spline	Polynomial time-variant spline	325.0	108	715	866
6	Time-invariant spline	Time-variant spline	346.1	104	715	900
7	Time-invariant spline	Time-invariant spline	371.2	100	715	942
8	Time-invariant spline	Time-invariant linear function	402.8	98	715	1002

The best fitting model for the fishery on North Sea plaice has a slightly dome-shaped selection curve, with fishing mortality highest on ages 3 and 4. This is similar for the models with a time-variant and a time-invariant fishing selectivity pattern (Figure 6.1). Clearly, there has been a trend to exploit the older ages less in recent years, and the selection pattern is lower for ages 6+. These model estimates corroborate the southward shift in the spatial distribution of the fishery, increasing its overlap with the younger ages of plaice. The time-variant discarding model indicates an increase in selectivity for the young ages (ages 1 and 2) in the most recent years.

The discard fraction is a decreasing function of age in all models (Figure 6.2). The discard fractions of the catch for each age changed little in time, but nevertheless significantly (based on AIC, see Table 6.1). The younger ages (ages 1 and 2) were discarded substantially (>80%). Our results suggest that a relative larger proportion of ages 4–7 was discarded in the early years (1985). Although the discard fraction at age may have been relatively stable in time, the absolute levels of discards have not, because the amount of discarding also depends on

the age-specific selectivity pattern, fishing effort, and population size. Changes in any one of these, such as the observed changes in fishing selectivity, will directly influence the observed discards.

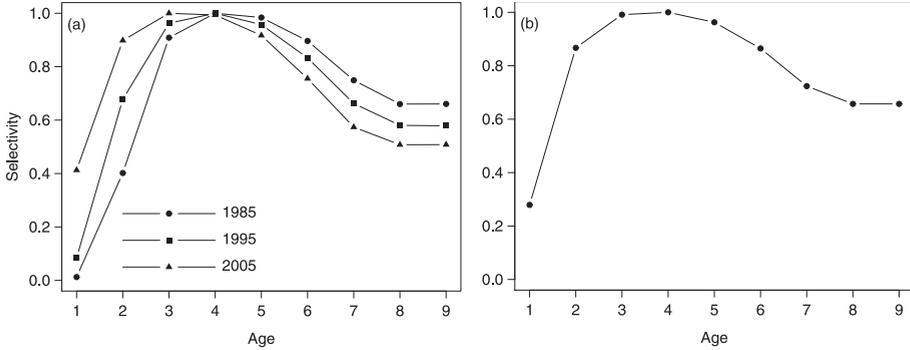


Figure 6.1 Selectivity of the catch for three different years (1985, 1995, and 2005) based on (a) the time-variant (Model 1 in Table 6.1), and (b) time-invariant (Model 5 in Table 6.1) fishing selectivity models.

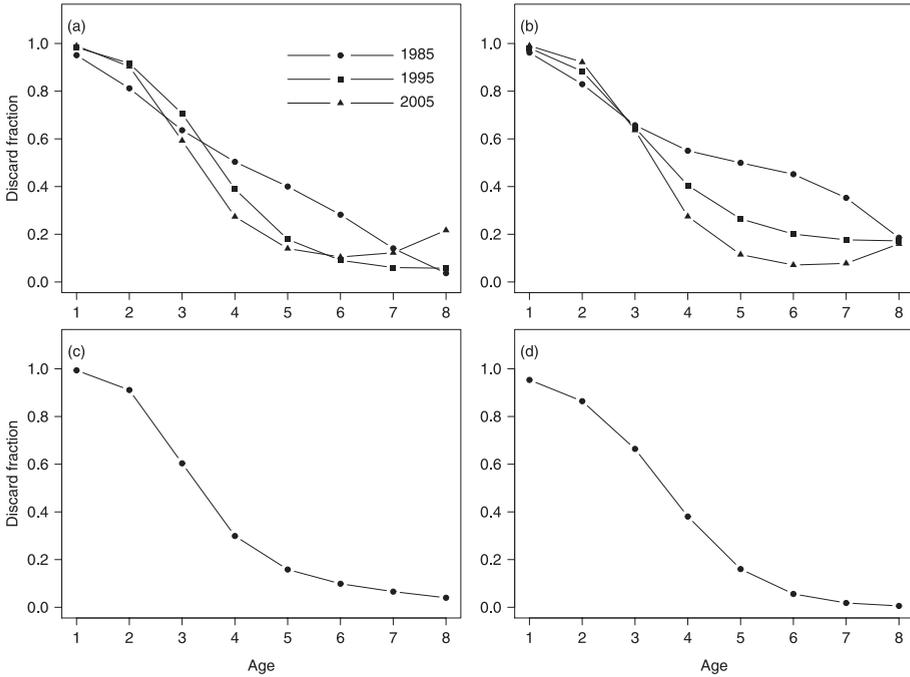


Figure 6.2 Fitted discard selectivity functions based on (a) a polynomial time-variant spline model (Model 1 in Table 6.1), (b) a linear time-variant spline model (Model 2 in Table 6.1), (c) a time-invariant spline model (Model 3 in Table 6.1), and (d) a time-invariant model where the discarding is a linear function of age on the logit scale (Model 4 in Table 6.1).

The selectivity curves for the surveys are key in estimating fishing mortality and discarding in the period where only landing data were available. Both BTS-Isis and SNS surveys showed declining catchability with age, but for BTS-Tridens, it was increasing (Figure 6.3). The BTS-Isis and BTS-Tridens surveys use a similar gear and take place at the same time of year. Hence, the estimated large difference in catchability at age was most likely caused by the survey location. The BTS-Isis survey is closer to shore, whereas the BTS-Tridens is more offshore. The SNS survey is a coastal survey, sampling mainly 1- and 2-year-old fish. For older ages (6þ years), the BTS-Tridens, showed different patterns in catchability depending on whether a time-variant or time-invariant discard selectivity model was fitted. This indicates that there was either strong cross-correlation with other stock or fishery characteristics, or that there were insufficient data to support the functional form of the tuning catchability curves for these older ages.

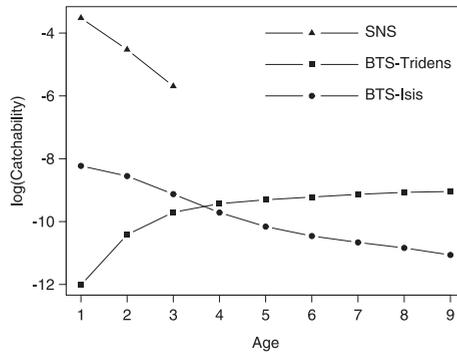


Figure 6.3 Estimated catchabilities of the three surveys (SNS, BTS-Tridens, and BTS-Isis) based on the full time-variant discard and fishing selectivity model (Model 1).

6.4.2 Model residuals

The residuals for landings, discards, and the tuning series indicated how well the assumed population dynamics, model fitted the data.

The residuals for the estimated landings are larger in the very young animals (Figure 6.4). Also, for age 1, there are large negative residuals for 1987 and 1988 in the landing estimates, corresponding to the years where the original data contain zero values. All other ages seem to have random residual patterns. The residuals of the discard estimates are generally larger than those of the landings, especially for older ages. Only for very young ages are the discard residuals smaller than the landings residuals. The large difference in the residuals by age may be caused by the low discard estimates for the older ages. The model also shows a tendency to have positive residuals in discard estimates for

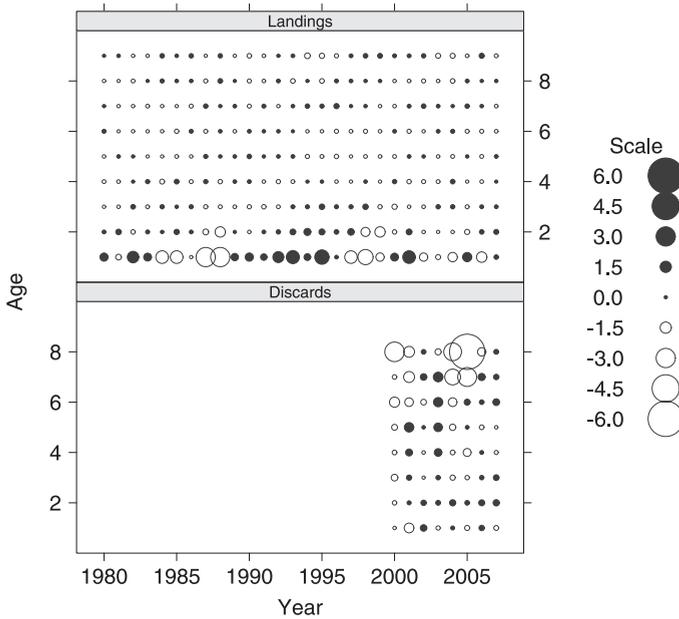


Figure 6.4 Log-residuals of landings and discard for the full time-variant fishing and discard selectivity model (Model 1).

age 2 that may be caused by insufficient flexibility to model the discard pattern over ages. This results in an underestimation of discards at age 2 while fitting the model according to other ages.

A striking pattern in the survey residuals (Figure 6.5) is the abrupt change in the SNS residuals in 2000, which were consistently lower than model expectations, resulting in negative residuals for all ages. In the same period, BTS-Tridens indices observed for ages 1–3 were consistently higher than the expected juvenile population. This resulted in positive residuals for those ages since 2000.

6.4.3 Population and fishery summaries

The summary plots of the historical population dynamics (Figure 6.6) show that the estimated landings increased up to 1988, after which a steep decline took place. Another striking aspect is that the model closely fits the data, which is also supported by the uncertainty estimates being very small, especially for the most recent years. The estimated discards in the most recent years match those of the actual observations reasonably well, but there seems to be some underestimation. Except the discard peak that coincides with the high recruitment in 1986, the model estimated higher discards in the historical part of the time-se-

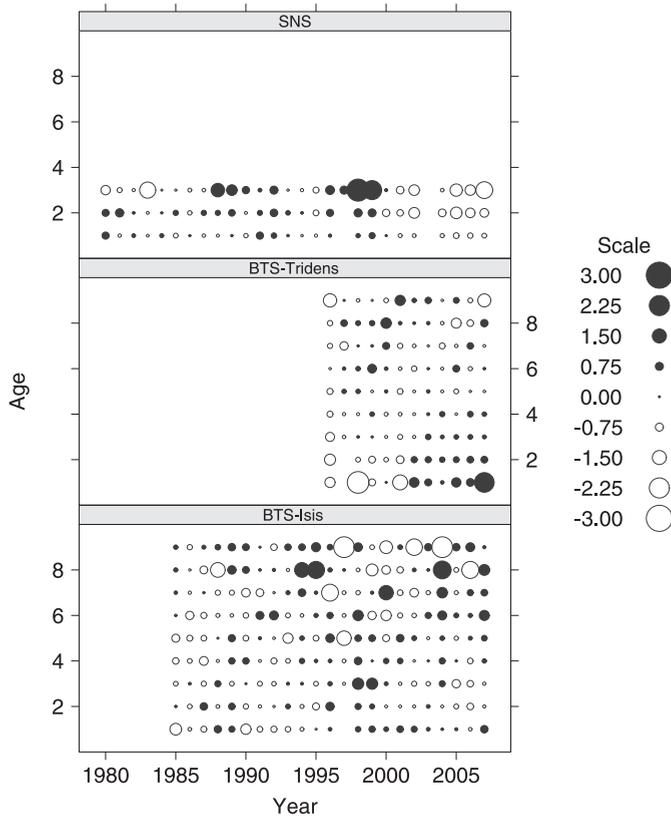


Figure 6.5 Log-residuals of the survey indices for the full time-variant fishing and discard selectivity model (Model 1).

ries than the reconstruction used by the ICES Working Group. Notably, the lows in the reconstructed discards around 1994 were not supported by our stock assessment model estimates. The uncertainty of the total discarding estimate was several times larger at the beginning of the time-series than the most recent estimates. Recruitment showed very similar patterns between the different models, with strong recruitment in 1986, 1997, and 2002. Except for those peaks, there was a clear overall decline from the 1980s on. The mean fishing mortality of ages 2–6 increased up to 1997, after which there was a steep decline.

Spawning–stock biomass (SSB) estimates were high in the 1980s and declined in the 1990s. This resulted from the higher recruitment in the 1980s, combined with a fishery that targeted older individuals. After a low in 1997, SSB appeared to be slightly increasing again, and it is currently fluctuating around 220 000 t. As a result of the uncertain discard estimates at the beginning of the time-series, the uncertainty of the SSB estimates at the same time was larger than the uncertainty towards the end of the time-series.

Overall, the results correspond to the results of the XSA assessment done by the ICES Working Group, except the fishing mortality in most recent years. The model presented here indicates a strong decline in fishing mortality to ~ 0.3 in 2007, whereas the latest ICES estimate (for 2007) is 0.39. It should be noted that the uncertainties presented here are conditional on model formulation and do not incorporate model uncertainty.

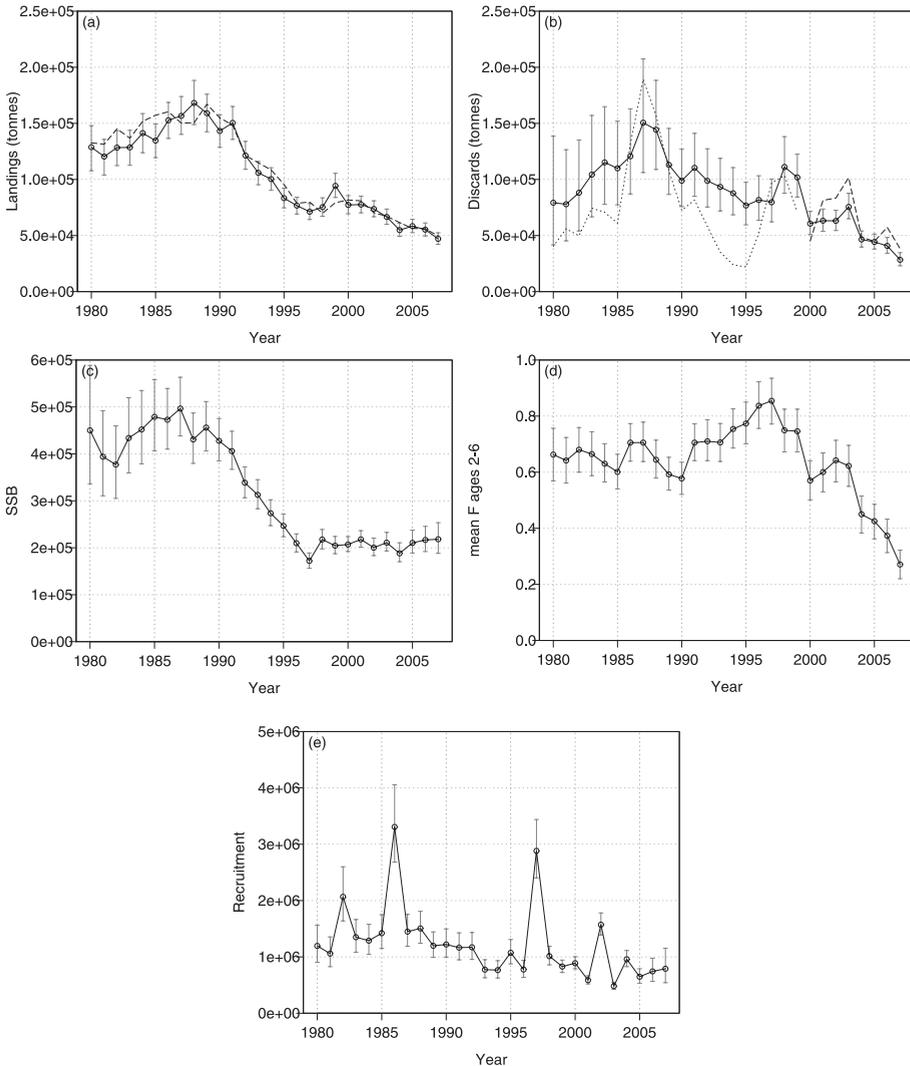


Figure 6.6 Model estimates (95% confidence intervals): (a) landings, (b) discards, (c) SSB, (d) mean fishing mortalities at ages 2–6, and (e) recruitment for the full time-variant fishing and discard selectivity model (Model 1). The dashed lines in panels (a) and (b) represent the landings and discard observations. The dotted line in panel (b) represents the current discard reconstruction used by the ICES Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak.

6.5 Discussion

The results of this study provide estimates of historical discarding and stock development of North Sea plaice. The estimates are based on fitting a simple age-structured population dynamics model to landings, discards, and survey indices. The estimation of missing discard values was integrated with the assessment of the demographic state of the population. Using an information criterion (AIC), different assumptions on trends in selectivity pattern were tested, preventing the formulation of an overly complex model that was not supported by the data (Cotter *et al.* 2004).

Our model differs from alternative approaches in the literature. Casey (1996) used a mechanistic approach to estimate discards using landings-at-age data from the fishery, together with species-specific mesh selectivity parameters, assuming that the size distribution in the population was known or could be inferred. Those discard estimates were subsequently used in a VPA stock assessment. The method was developed for a situation in which absolutely no discard data were available, and in the absence of any information on discarding practices, it is assumed that the primary reason for discarding fish is to comply with MLS regulations. A second approach (Punt *et al.* 2006) used a statistical catch-at-age model, similar to the approach presented here. Although more biological detail was incorporated in the population dynamics part of the model, gear selectivity was estimated using a logistic and a dome-shaped function (of length) and was assumed constant in time. This may suffice for many fisheries where selectivity patterns are constant, but in the North Sea demersal fleet, the selectivity pattern has changed owing to changes in the spatial distribution of the fleet, e.g. with the establishment of the “plaice box” (Pastoors *et al.* 2000).

The statistical catch-at-age model used here considers four types of discard selectivity pattern. Discard selectivity was modeled as a linear function of age, or as a more flexible function of age, with two functions allowing discard fractions to change over time. Our results indicated a sharp decline of discarding with age. This is due to the MLS for plaice resulting in discarding individuals, 27 cm (Daan 1997), which in general will be the younger fish. The discard-at-age curve for the time-variant discard models suggested that, historically, adults in the mid-range of the age distribution were discarded more frequently. Indeed, discarding patterns may have been different in the past because of different MLS values, different growth, different spatial distributions of fish (van Keeken *et al.* 2007), or market conditions (Rochet and Trenkel 2005). Although highgrading was most likely higher from the 1960s until the early 1970s, it is not a likely explanation for our bigger discard estimates of subadults in the 1980s (Rijnsdorp *et al.* 2008).

The extent of discarding in a fishery does not only depend on the discard levels at age, but also on gear selectivity. Therefore, quantifying changes in gear selectivity over time is crucial to historical discard reconstruction. Our results show that the gear selectivity pattern changed over time. In more recent years, older fish were less likely to be caught than in the earlier period. Such changes in selectivity are in line with the redistribution of fishing effort. In recent years, fishing vessels came closer to shore to target sole (Quirijns *et al.* 2008). These coastal regions are characterized by relatively larger numbers of juvenile plaice (Wimpenny 1953, Rijnsdorp and van Beek 1991). Indeed, the selectivity of 1-year-old fish has increased from < 0.05 in 1980 to 0.4 of the maximum selectivity in 2000, and almost all will be discarded.

The discard estimates obtained from the time-variant discard model resemble the actual observations in the past 7 years. In contrast, the time-invariant discard selectivity model suggests lower-than-observed discarding in those years. This may suggest that discards-at-age were lower historically, depressing estimates for the most recent years, but this pattern is not reflected by the time-variant discard selectivity curve. Compared with the current reconstructed discards (van Keeken *et al.* 2004), our estimates showed similar highs and lows (reflecting the level of recruitment in the preceding year), but the extremes levelled out and, overall, our historical discard estimates were higher. These differences may result from the fact that our approach did not take account explicitly of the observed changes in mean body growth of the cohorts, in contrast to the deterministic reconstruction. Highgrading alone will not account for this difference in discard levels, because the absolute discard levels are mostly driven by 2- and 3-year-old fish.

Can we accurately reconstruct historical discards? One of the major limitations with many stock assessment models is that different sources of mortality cannot be separated from each other. In the case presented here, natural mortality was set at a fixed value for all years and age classes, consistent with the ICES procedure that is used to estimate stock size. Although this may be a reasonable assumption for older ages that are susceptible to considerable fishing pressure, it is questionable whether the fixed natural mortality assumption will hold for the younger fish that constitute the discards. Variation in natural mortality can be caused by changes in predation pressure, because plaice can be preyed on by birds, fish, and seals (Leopold *et al.* 1998). Also, unobserved additional fishing mortality may exist, in the form of unreported landings or fish escaping from the net (Sangster *et al.* 1996). If no historical discard data are available, increases or decreases in these mortality rates will be ascribed to the reconstructed discards. When discussing the absolute levels of discards in time, this will be a problem, but for stock assessment purposes it may not. The ultimate objective is to quantify accurately the population processes such as mortality rate. As long

as changes are quantified correctly and consistently, it may not matter whether discards are labeled inappropriately. Some historical discarding data exist, but these data cover only the Dutch beam trawl fleet, and have not been raised to the population level (van Beek, 1990).

This and other studies have shown that statistical catch-at-age models can make use of a wide variety of data sources (Fournier and Archibald 1982, Deriso *et al.* 1985, Gudmundsson, 1994, Fryer 2002, Punt *et al.* 2006). Incorporating additional model components is straightforward if they can be linked to data, and providing their effects are separable from other model components. For example, high fishing pressure has led to rapid changes in age at maturation and individual growth. Although most fishery processes (e.g. mesh size, selectivity ogives, MLS) operate on length, most stock assessments are only age-structured. Punt *et al.* (2006) showed how length-related processes (e.g. the Bertalanffy growth equation) can easily be incorporated into statistical catch-at-age models. Although increasing model complexity can easily lead to loss in model parsimony (Cotter *et al.* 2004), selecting a particular type of model does not need to be based on speculative theories, but it can be based on objective information criteria. An ability to include more biological and fishery-related processes and objectively test for their significance makes statistical catch-at-age models a useful tool to test biological hypotheses and further understand fish demography. Finally, the models do not only provide estimates of stock size, but they also estimate uncertainties, valid for the model and the data used. For fisheries with substantial discarding, the catch data from on-board sampling are prone to substantial uncertainty because of small sample sizes (Heales *et al.* 2003). Model mis-specification and noisy data often lead to biased estimates of population size and fisheries characteristics, but their effect on uncertainties are still poorly understood (Dickey-Collas *et al.* 2007). We noticed that the SSB estimates and their uncertainties varied considerably for different model specifications. Consequently, we believe that use and interpretation should go together with testing a large variety of different models, before they can be used for management purposes.

Statistical catch-at-age models have a large number of advantages, and one may wonder why they have not been used to their full advantage. Traditional statistical catch-at-age models often estimate an age-specific selectivity and implicitly assume that selectivity does not change over time. When this assumption is violated, one can estimate a selectivity pattern for different periods independently. When the biological and fishery processes are complex and poorly understood, we suggest using spline smoothers instead. They do not rely on a priori simple selectivity patterns, but allow for flexible fishing and discard selectivity that can change over time, using only a small number of parameters. Other stock assessment models, such as those described by Gudmundsson (1994), Lewy and

Nielsen (2003), and Schnute and Richards (1995) have been successfully applied to the same problem. However, the current model was designed specifically for reconstruction of both historical discards and stock dynamics of plaice in the North Sea. It provides a basis for extension with additional biological processes, but it can also easily be adapted to estimate the development for other fish stocks where discarding plays a considerable role.

6.6 Acknowledgements

We thank A. Rijnsdorp, S. Kraak, R. Fryer, and an anonymous reviewer for critical comments on earlier versions of this manuscript. The Commission of the European Communities Directorate General for Fisheries contributed to the development of the estimation model and the writing of the manuscript under the contract “Operational evaluation tools for fisheries management options” (“EFIMAS”; SSP8-CT-2003-502516).

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Chapter 7

General discussion

This chapter first provides a summary of the findings of the thesis. Next, the assumptions and uncertainties involved are discussed in some detail, followed by an outlook of the challenges to fill in important gaps in our current knowledge. The chapter ends with some concluding remarks about the implications for fisheries management.

7.1 Summary

The research is aimed at the understanding of the spatial effort allocation by the Dutch beam-trawl fleet, and of its effects on the exploitation of the target species. Historically, much of the research in fisheries ecology has focussed on the biology and population dynamics of the species affected by fisheries (Hilborn 1985). Although the dynamics of the fleet itself are equally important for understanding the effects of management regulations, these have gained much less attention. Hilborn (1985) classified these fleet dynamics into four elements: (i) investment/disinvestment; (ii) spatiotemporal effort allocation: when to fish, where to fish, and what to fish for; (iii) harvesting efficiencies: the elements of the fishing process, competition, interference, facilitation, and learning; and (iv) retaining and discarding: the selection of the part of the catch worth keeping. The different chapters address only the latter three elements.

In dealing with this broad range of topics, I have mainly borrowed from the theory on foraging ecology theory and associated models, while ignoring other relevant scientific domains. Although anthropological and psychological sciences contribute greatly to our understanding of fleet dynamics (Anderson 1997, Smith and Wilen 2003, van Ginkel 2007), these approaches are largely outside of the scope of the thesis.

A bipartite approach has been taken: First, existing data were analyzed to identify the processes that affect the spatial distribution of individual vessels. Second, (profit) maximization models were developed using ecological and economical processes and constraints. The findings indicate that the spatial and temporal effort allocation of the Dutch beam trawl fleet is mainly determined by the local densities of the main target species sole (*Solea solea*) and plaice (*Pleuronectes platessa*) as well as by management constraints. Within these constraints, optimization of revenues, discarding, competition, and learning shape the resulting fishing effort distribution.

The spatial distribution of two target species differs, with sole being present almost exclusively in the southern North Sea, while plaice is found also in the

central and northern North Sea. Both species showed changes in their spatial abundance patterns over the seasons (**chapter 2**), but the seasonal pattern was less pronounced for sole than for plaice. Plaice exhibited high catch rates in the northern part of the central North Sea in spring and summer, and more uniformly distributed catch rates in autumn and winter. This seasonal variability reflects annual migration cycles of the adult population as well as the annual recruitment of a new cohort from the coastal nursery grounds. Consequently, the general pattern is predictable and can be used by fishers to select their fishing grounds. Superimposed on these seasonal patterns, local aggregations of fish may build up, which may exist for only one or two weeks. Their limited persistence allows the fleet to concentrate on these hotspots, because fishers build up local knowledge on the resource distribution through exchange of information. However, interference competition depresses the catch rates in areas with high vessel densities (**chapter 3**). Interference competition is assumed to result from avoidance behaviour of the fish. Differences in catchability can result in spatial segregation among vessels of different engine powers (**chapter 4**).

Meanwhile, the TAC system - the main management tool for the fisheries in the North Sea –appears to affect the optimum location choice in this dynamically variable environment (**chapter 5**). Assuming that individual vessels optimize their annual net revenue, individual fishers have to make a sequence of choices throughout the year on where to fish and which part of the catch to retain by evaluating revenues and costs of each choice. Thus, restrictive TACs affect both the effort allocation and discard rate at the national fleet level. **Chapter 5** shows that the restrictive quota for one target species may affect the catchability of the fleet for several other species.

The processes evaluated in the model study indeed seem to have occurred in the Dutch beam-trawl fleet over the last decade. The severe reduction in the plaice TACs since the beginning of the 1990s (Quirijns *et al.* 2008) has changed the effort allocation, which has increasingly been applied to target sole. This spatial shift has had important implications for the exploitation pattern of the plaice, because the fleet is now exploiting the younger ages more intensively than previously (**chapter 6**). Also, marketable plaice has been discarded, thereby reducing the effectiveness of restrictive TACs (ICES 2009)

7.2 Discussion

Because the emerging spatiotemporal patterns are derived from field observations, it is difficult to pinpoint the exact nature of the behavioural processes involved in the dynamic allocation of fishing effort by individual skippers. In trying to elucidate these processes, some key assumptions need to be discussed in more detail.

7.2.1 Do fishers maximize profit?

The profit-maximization assumption has been used in many studies of fleet dynamics (Gordon 1953, Hilborn and Walters 1987, Gillis *et al.* 1995, Babcock & Pikitch 2000), and is supported by observations and interviews (Hilborn and Kennedy 1992, Robinson and Pascoe 1998). However, the assumption has been questioned in the context of fisheries (Eggert and Martinsson 2004, Salas and Gaertner 2004, Abernethy *et al.* 2007). In many fisheries, the prime decision on where to fish is made by the skipper or owner of the vessel. The question is whether these indeed try to maximize their (long-term) profit.

One of the methods to find out about the objectives of fishers is to use questionnaires and interviews (Robinson and Pascoe 1998). However, it is difficult to get unbiased information about the objectives directly from fishers, because the attitude expressed may differ from the observed behaviour (Wicker 1969).

One alternative hypothesis would be maximization of landings – catch as catch can -, irrespective of the costs and penalties that may apply when overshooting landings quota. Traditionally, in the situation without stringent output control, filling the fish hold may indeed have been the most important incentive for fishers. However, the restriction on landing rights has halted their freedom to market everything they catch. As a consequence, skippers are not evaluated anymore on the size of their catch (van Ginkel 2007). Although it still seems true that ‘Who actually ends up with more money at the end of the year does not seem to have the same status as who was at the top of the table for amount of fish landed for the week’ (Connolly 1997), the penalty for overshooting quota is too severe to allow a landings-maximization strategy to survive.

After analyzing interviews of North Sea, Irish Sea, and the English Channel fishers, Robinson (1998) concluded that in all three surveys the overriding motivation during fishing operations appears to be mainly profit-orientated, given weather constraints. In some cases, fishers did not try to maximize their short-term revenue, but for instance their use of the available quota, or to secure quota for future years. Two of the studies analyzed by Robinson indicated that

constrained optimisation, subject to non-monetary considerations, could best explain the findings. Likewise, Abernethy *et al.* (2007), combining interviews with catch information, concluded that West Indian artisanal fishers that they were not always switching to the most profitable option, for instance for lack of skill or to avoid conflict. Other fishers indicated that they traded off revenue against increased risks or even leisure time. A study on the conch and lobster fishery in the Caribbean indicated that pressure from peers and social status related to different options affect the fishing choice of individuals (Béné and Tewfik 2001).

The above examples of profit “satisficing” can be interpreted as an alternative strategy to profit maximization: deciding on a course of action that satisfies non-monetary goals, subject to some minimum level of profit (Cyert and March 1963). Such behaviour can be considered an appropriate model for many fishers whose aim is to remain in the industry, but not necessarily to be a top-skipper (Robinson and Pascoe 1998). One of the main problems in using this type of behaviour in explanatory models is that the trade-offs between monetary and non-monetary goals are difficult to express in a single currency, and thus the priorities are difficult to assess.

In the debate on profit maximization, the time scales on which fishers seek to optimize their profit are an important aspect in validating the underlying assumption. The “fitness” function of the individual vessels in a fleet is presumably related to their propensity to stay in the fishery. This propensity depends on the short-term gains, but also on many medium- and long-term considerations. In the beam-trawl fleet, the constraints imposed by annual individual quota for the target species have to be taken into account, because overshoots lead to fines at the end of the year. The dynamic state-variable model shows that vessels allocate their fishing effort differently depending on whether the quota are restrictive. Also, situations do occur where discarding parts of the marketable catch (clearly not profit maximizing in the short term) is the optimal choice. A similar medium-term consideration is evident in interviews with several English skippers fishing in the North Sea (Frost *et al.* 1993), who indicated that their main objective was to take the quota. This is important to fishers who want to maintain their future earning potential by guaranteeing their shares, and is thus consistent with long-term profit maximization (Robinson and Pascoe 1998).

Although the profit-maximization assumption may not include the full complexity of all monetary and non-monetary incentives in the decision-making process by skippers, it serves as a satisfactory working hypothesis as long as appropriate time scales are considered. The response to economic signals can be deduced from the model study (**chapter 5**), which generates results that match observations on spatial effort allocation and discarding in the Dutch beam-trawl

fleet. I therefore agree with the conclusion of Robinson *et al.* (1998) that there is strong grounds for using the profit maximization assumption for the purpose of predicting fisher behaviour.

7.2.2 The mechanism of interference competition in fisheries

The presence of interference competition in fishery systems and the nature of the underlying mechanisms are generally difficult to prove unequivocally. The reason is that ecological studies of interference competition essentially require that the behavioural mechanisms involved are observable, while in order to disentangle interference competition from patch choice, forager densities should be controllable within a single homogeneous patch. Neither of these conditions are met in studying fishery systems.

The concept is derived from studying predator-prey systems, where the underlying mechanism can be observed directly. For example, controlled laboratory experiments revealed that interference competition in red knots (*Calidris canutus*) is caused by the increase in the time spent on vigilance and searching with increasing forager density (Vahl *et al.* 2005). In oystercatchers (*Haematopus ostralegus*), interference competition is mainly caused by fighting with conspecifics (aggressive behaviour) and stealing their prey (Ens and Goss-Custard 1984). In these examples, interference competition is caused by interactions among competitors. However, interference competition may also occur when foragers induce avoidance behaviour in the prey: as forager density increases, the proportion of prey in “avoidance” state increases and the intake rate of foragers decreases (Stillman *et al.* 2000). Interference through prey depression has been found in redshank (*Tringa totanus*) feeding on a burrowing amphipod crustacean (Selman and Goss-Custard 1988). The mechanism has been revealed by making a captive redshank walk over a patch of mud, which inhibited the *Corophium* to come to the surface for several minutes after a bird had passed (Goss-Custard 1970).

Of course, carefully designed experiments with fishing vessels to measure interference competition and unravel the mechanisms are virtually impossible. However, the relocation of fishing effort in response to the establishment of a temporarily closed area in 2001 can be viewed as an opportunistic experiment that allows an evaluation of the effect of increased vessel densities in the open area compared to previous years. The results in chapter 3 indicate that during the closure fishing vessels exhibited a reduction in catch rates associated with the increase in vessel density. The reduction was stronger in those vessels that had not normally visited the open area, and thus may have had less knowledge of the fishing grounds located there. The large and sudden decrease in catch

rates right at the start of the closure makes interference competition a likely contributor to the reduced catch rates. The further decline during the closure compared to the expected seasonal pattern can more likely be attributed to the increased competition through exploitation. However, even this opportunistic experiment does not allow to take all possible factors influencing catch rates into account, particularly those related to fish density. There is at least one more example of a manipulative field experiment (Abrahams and Healey 1993), the results of which indicated that as vessel density increased, the catch rates of one species decreased, while those of another increased.

In fact, much of the work done on interference competition has focused on analyzing existing catch and effort data from normal fishing operations (Gillis 1999, Rijnsdorp *et al.* 2000). Therefore, it is not surprising that the mechanisms involved are generally unknown, and can only be hypothesised about. In fisheries such as purse seining, direct interactions may play a role, for instance if two purse seiners attempt to catch the same school. In trawl fisheries, vessels may have to deviate from their favoured course when fishing grounds become really crowded. However, the effects of this is probably small, and in chapter 5, the assumption is made that there are no direct interactions among beam trawlers. Rather, the interference competition is assumed to be indirect through the behaviour of the target species, similar to the prey–depression mechanism. Indeed, fish species may react to the presence of vessels, moving away because of the sound (e.g. cod, herring and capelin; Mitson 1995) or the disturbance caused by the fishing gear (e.g. cod, haddock; Morgan *et al.* 1997, Ona and Godø 1990). Upon the passage of a gear, the structure of cod shoals changed up to 200–400 m on either side of the trawl path, and the effect lasted for more than an hour (Morgan *et al.* 1997). Avoidance behaviour of flatfish has been shown for Greenland halibut (*Reinhardtius hippoglossoides*) using underwater video recordings. Individuals escaped either beneath the ground rope or by ‘outriding’ the gear (Albert *et al.* 2003). Direct observations on plaice or sole are absent, the existence of avoidance behaviour in fish in general makes prey depression at least a plausible mechanism for interference competition.

7.3 Challenges

As has been done in other studies, the profit-maximization assumption for the Dutch beam fishery might be tested in interviews. Care should be taken that these interviews contain the “right” questions and are explicit about the trade-offs that can exist between short-, medium- and long-term profits. Alternatively, and possibly more effective, the incentives for individuals operating in fisheries can be determined using “prospect theory” (Kahneman and Tversky 1979).

As an alternative hypothesis, prospect theory might be applied (Holland 2008). This prospect theory successfully explained human behaviour in the face of uncertainty. The difference between profit (or utility) maximization and prospect theory is explained in Camerer (2003). Shortly, decisions that result in uncertain outcomes with probabilities are valued in utility theory according to the sum of the products of outcomes and probabilities. The option with the maximum value is chosen. In contrast, the decisions in prospect theory are valued by a nonlinear weighting function of the probabilities, giving higher weights to low probabilities and lower weights to high probabilities and a value function exhibiting diminishing marginal sensitivity to deviations from a reference point. The value function is convex for losses and concave for gains. The use of a reference point rather than the final status (as in utility maximization) is called the framing effect (De Martino *et al.* 2006). The value function also exhibits loss aversion if the value of a loss is larger in magnitude than the value of an equal-sized gain (Camerer 2003). As an extension to prospect theory, cumulative prospect theory was formulated, where *cumulative* probabilities are transformed, rather than the probabilities itself (Tversky and Kahneman 1992). As a result, extreme events occurring with small probability are given higher weights, rather than small probability events irrespective of the outcomes.

Empirical studies of the validity of prospect theory include betting on horse races and working hours of cab drivers (Camerer 2003). The study on horse races found that cumulative prospect theory fitted much better to the data than the utility theory (Jullien and Salanié 2000). In particular, the bettors exhibit a form of risk aversion for losses, owing to the cumulative weighting. Their estimate of the probability weighting function for probabilities of gain is almost linear, but the weighting function for loss probabilities overweighs low probabilities of loss (Jullien and Salanié 2000, Figures 3 & 4). The results may explain a bias toward betting on long-odded horses (Griffith 1949, Camerer 2003). Bettors dislike favourites because they like to gamble but are disproportionately afraid of the small chance of losing when betting on one. Another example of the explanatory power of prospect theory on human behaviour is found in an empirical study on taxi drivers (Camerer *et al.* 1997, Crawford and Meng 2009). The correlation between hours and earnings per hour is strongly negative for inexperienced drivers, indicating that drivers set a daily income target and quit when they reach that target. Therefore the drivers work less on days when earnings per hour are high, contrary to what is expected from a utility theory. The results can be explained by assuming that (i) the income target is a reference point, to which the drivers respond, and (ii) there is “loss aversion,” in that the drivers are more sensitive to changes in income below the reference point than above it (Crawford and Meng 2009). Experienced drivers did not exhibit a negative correlation between hours worked and earnings per hour, suggesting that inexperienced drivers use a daily income target, but those who do either quit or

learn by experience to shift toward driving a fixed number of hours (being more in line with utility maximizing theory).

The use of prospect theory could potentially improve our understanding of the fundamental incentives of fishers, adding realism to the models that can be used to predict fleet dynamics, as was suggested by (Holland 2008). However, this approach requires robust estimation of the nonlinear weighting function of the probabilities and the value function for which no general functional form is known, and no mechanism for the form, or its parameters. This would first have to be dealt with. Also, the existence of behaviour that does not follow utility maximization is an interesting subject. In animal ecology, it is generally assumed that evolution has led to fitness maximization strategies (given the environment). One would wonder why the same principle does not apply to human behaviour. Optimal strategies would lead to more offspring (evolution of genes), or spread as ideas (evolution through memes). Such evolution of strategies is already apparent in the taxi driver example, where experienced drivers use a fixed working-hours strategy rather than a fixed-income strategy, which will lead to a higher average income per hour. Interestingly, a recent study found that preferences inconsistent with prospect theory may have an origin in evolutionary psychology (McDermott *et al.* 2008).

The usefulness of using prospect theory in contrast to utility maximization assumptions should be studied. One way forward could be to hold more interviews, but we have seen that these suffer from some drawbacks, such as the difference between expressed attitudes and observed behaviour (Wicker 1969). As an alternative to having interviews, one could consider the use of games, where subjects make choices about fishing strategies in controlled environments. As an example, subjects could be asked to make location choices in a system with a revenue/risk trade-off.

7.3.1 The mechanism of interference competition

To find out whether the mechanism underlying interference competition is related to the behaviour of the fish, one could try to set up experiments with an artificial seabed, and measure the burrowing depths of sole and plaice before and after the passing of a commercial gear, or even only the sound of a passing gear or a passing vessel. Also, the efficiency of a second pass with the gear can be estimated (because the densities in the controlled environment will be known), and the reaction to the gear estimated, dependent on the time lapse between two gear passes. The mechanism may also be related to an increased “vigilance”, fleeing away from the approaching gear earlier, and thus having a higher chance of escape. This type of behaviour might be detected using under-

water video, or, if the water is too turbid, using a Dual-frequency IDentification SONar (DIDSON). If there are no detectable behavioural effects on the catchability of the fish, then it might be worthwhile to investigate the possibility of direct interference competition among vessels more closely.

7.3.2 Extending dynamic models to game-theoretical approaches

In the dynamic model presented in **chapter 5**, each individual vessel acts independently of the choice of other individuals. A worthwhile extension would be to include a frequency dependence by taking the choices of competing individuals into account. This would allow to study the effect of interference competition on the distribution of vessels maximizing their annual profit while accounting for individual quota. In addition, the effects of quota trading on effort allocation and discarding could be studied. Modelling the effects of quota trading on the size composition in the discards of the target species is of particular interest because the prices of the different market categories of plaice and sole may differ considerably. Leaving out such complications in the models may give rise to incorrect conclusions (Kingsley 2002). Game theory is difficult to incorporate in dynamic state variable models, but a heuristic method that does allow for interaction among players may be found in the genetic algorithm (Holland 1992, Haupt and Haupt 2004). This is a search technique based on natural selection and genetics. Replacing individuals by vessels, genes by different behavioural decisions and fitness by annual net revenue might allow to find out which strategy is optimal.

7.4 Implications

One of the important changes for the Dutch beam-trawl fleet has been the increasingly constraining level of the plaice quota over the last decade (Quirijns *et al.* 2008). In addition, the fuel costs, the major component of the variable costs, have risen substantially during that period. As a consequence, vessels tend to minimize steaming time and stay closer to the harbour. Thus, the centre of the overall effort distribution has gradually moved south. This spatial shift has important implications for the exploitation pattern of the plaice stock, because the fishing mortality on the younger ages has increased substantially (Aarts and Poos 2009). Moreover, the restrictive quota created strong incentives for discarding the less profitable parts of the marketable catch. The model has shown that setting restrictive TACs leads to discarding of marketable fish and not necessarily to an effort reduction. Unfortunately the model used could not

distinguish between fish of different market categories or values, and therefore only predicts discarding of marketable fish after the quota have been exhausted. Extensions of the model are required to chart the magnitude of the incentive to discard marketable fish for vessels that still have quota. Since 2009, the European Commission has actually prohibited the discarding of marketable fish in the North Sea for vessels that have not yet met their quota (Council Regulation (EC) No 43/2009).

Changes in spatial effort allocation also affect the catchability of the different species, the parameter that links fishing mortality at the level of the population and the nominal effort exerted by the fleet, because the spatial and temporal overlap between the fleet and each species changes. In particular, the catchability of young plaice and sole has increased. Changes in catchability of different species in fisheries as a result of changes in the management constraints are not limited to the economically important target species, but may be positive or negative depending on where the main concentrations are found.

Over the years, the number of vessels in the Dutch beam-trawl fleet has decreased substantially from 230 large cutters in 1993 to 175 in 2007 (van Wijk *et al.* 1999, Taal *et al.* 2008), and accordingly, the density of vessels on the fishing grounds. The effects of interference competition should have become less, the efficiency of individual vessels should have been enhanced, and the catchability of the target species has become higher.

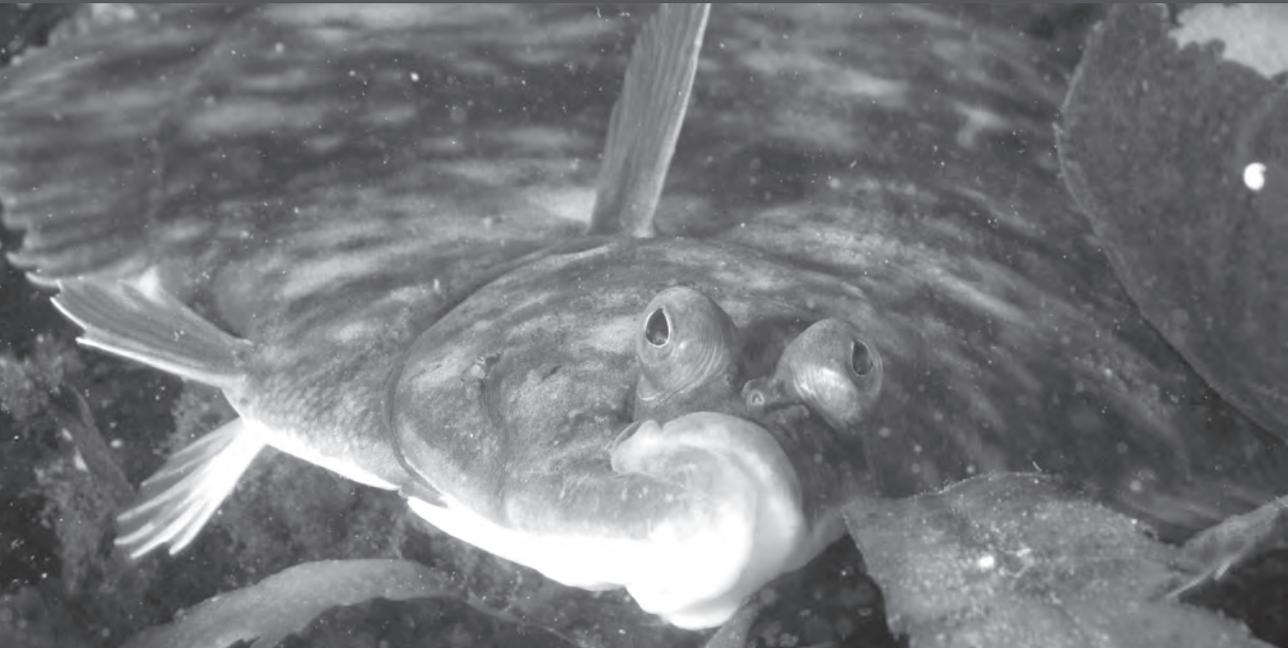
Management measures change the trade-offs and constraints shaping the choices of individual fishers, resulting in unforeseen changes in spatial distribution of the fleets as well as other aspects of fleet behaviour. Such changes should be anticipated and preferably taken into account when designing fisheries management systems.

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Finally...

Summary

This thesis addresses the question how fishers allocate their activities in space and time. Understanding the mechanisms governing the dynamics of fishing fleets is important to understand how fishers respond to management measures and changes in their environment. This knowledge can be used by fisheries managers to design efficient management measures. The study focuses on demersal fisheries exploiting a mixed bag of bottom dwelling flatfish.

The results in the thesis shows that the fisheries respond to the seasonal changes in distribution of their main target species sole and plaice. Area specialization of fishers as well as interference competition among vessels play a role in shaping the spatial distribution of the fleet within the constraints put by management. A dynamic state variable model was developed to study the effect of management constraints on fishing effort allocation and discarding. The model evaluates the trade-offs and constraints that individual skippers face in their fishing operation.

Management measures change the trade-offs and constraints shaping the choices of individual fishers, resulting in changes in spatial distribution of the fleets as well as other aspects of fleet behaviour. It is shown that the beam trawl fleet has shifted its fishing effort increasingly south, as a result of the increasingly restrictive plaice quota. This has resulted in an increased catchability for sole and young plaice, and an incentive for individuals to discard marketable fish.

Samenvatting

Dit proefschrift gaat in op de vraag hoe vissers hun activiteiten verdelen in ruimte en tijd. Het begrijpen van de mechanismen die de dynamiek van vissersvloten bepaalt is van belang om te begrijpen hoe vissers reageren op maatregelen in het kader van visserijbeheer en veranderingen in de omgevingsvariabelen. Deze kennis kan gebruikt worden door visserijbeheerders om effectieve beheersmaatregelen te ontwerpen. Het onderzoek richt zich op demersale visserijen die een aantal soorten tegelijkertijd exploiteren.

De resultaten in het proefschrift laten zien dat de visserij reageert op seizoensveranderingen in de ruimtelijke verdeling van hun doelsoorten schol en tong. Gebiedsspecialisatie en interferentiecompetitie tussen schepen spelen een rol in de totstandkoming van de ruimtelijke verdeling van de vloot, binnen de beperkingen die er opgelegd worden door het visserijbeheer. Er is een 'dynamic state variable model' ontworpen om het effect van beperkingen als gevolg van visserijbeheer op de ruimtelijke en temporele verdeling van visserijinspanning en discarding te bestuderen. Dit model evalueert de trade-offs en beperkingen waar individuele vissers mee geconfronteerd worden in hun visserij.

Beheersmaatregelen beïnvloeden de trade-offs en beperkingen die het individuele gedrag van vissers vormgeven, wat resulteert in veranderingen in de ruimtelijke verdeling van vissersvloten en andere aspecten van vloot dynamica. In het geval van de boomkorvloot laat het onderzoek zien dat de visserijinspanning als gevolg van de verlaging van het scholquotum zuidwaarts is verplaatst. Dit heeft tot gevolg gehad dat er een toename is geweest van de relatieve vangbaarheid voor tong en jonge schol, en een drijfveer voor vissers om marktwaardige vis te discarden.

Dankwoord

Als je zoals ik meer dan 10 jaar doet over het schrijven van een proefschrift, dan kom je veel mensen tegen die ieder op zijn of haar manier bijdraagt aan het uiteindelijke resultaat. Ik probeer hier iedereen te bedanken voor die bijdrage en het is een hele lijst geworden.

Allereerst natuurlijk Adriaan Rijnsdorp, zonder wiens inzicht, doorzettingsvermogen en inventiviteit dit werk nooit tot stand was gekomen. Eigenlijk was je natuurlijk een waardeloze begeleider, die altijd vol enthousiasme zowel de verdieping als de verbreding opzoekt. Zelf heb je aan 8 specialismen eigenlijk niet genoeg. Je combineert een tomeloze drang tot het onderzoeken van de ecologische processen in vis en visserij met een onbegrensd gevoel voor empathie en menselijkheid. Ik ben blij dat ik uiteindelijk kan promoveren bij zo'n rode rakker die geboren is onder de rook van het kasteel.

Aan de universiteit in Groningen hebben twee professoren dit proefschrift mogelijk gemaakt. Wim Wolf heeft succesvol het SUSUSE prioriteits programma ingediend, waar mijn proefschrift een onderdeel van was. Rudi Drent was de promotor die mij in de initiële fase gesteund heeft.

Een proefschrift schrijven bleek gelijk aan talloze avonden, weekenden en vakanties in IJmuiden. Daar vond ik gelukkig de nooit aflatende smile van Erwin Winter. Terugdenkend aan het schrijven van dit proefschrift denk ik toch ook aan de avonden dat we ons na de Chinees verdiepten in "Scratch" en "Rize". Misschien dat die avonden ervoor hebben gezorgd dat het zo lang geduurd heeft. Aan de andere kant was het juist Erwin die mij in de laatste fase heeft weten te overtuigen dat het nu echt af was.

Ik ben blij dat ik straks te midden van mijn twee paranimfen Michiel Vos en Jan-Geert Hiddink mijn verdediging kan voeren. Het is een erekwestie geworden dat ik de mannen die voor mij synoniem zijn aan mijn studie mariene biologie, nu kan vragen om me bij te staan.

De klimmers wil ik bedanken voor de avonden en vakanties die het mogelijk maakten om volledig gefocust op andere zaken dan het onderzoek tot rust te komen, de leukste boeken en films te bespreken en te filosoferen over van alles en nog wat. Gerjan Piet, Nicola Tien, Floor Quirijns en Niels Hintzen heel erg bedankt. Ik blijf uitzien naar onze donderdagavonden en weekendjes.

Alle vrienden, de Groningers, de Westersingelaars en de enige echte Brunssumer: excuses voor alle loze beloften dat ik "toch echt binnenkort weer eens langs zou komen". Marieke, Peter & Maartje, Mitch & Elze, Roger & Marleen,

Piet & Zollo, Julia & Ynte, Jan-Geert & Fem, Roel & Masako, hopelijk vinden we binnenkort tijd om het eens uitgebreid goed te maken.

My co-authors Darren Gillis, Floor Quirijns, Hans Bogaards, and Geert Aarts: many thanks for all you have contributed to the papers that are the foundation of this thesis. I have sincerely enjoyed researching and writing with you. While writing the synthesis of the thesis, I realized how much I like writing as a team effort over doing it in complete isolation. It is a great gift to have competent, critical and fun collaborators. In this light, I also want to thank Niels Daan, who has repeatedly been of great help in editing my texts, especially towards the end.

Ik doe het licht uit bij “het interferentieclubje”. Ik ben nog steeds erg dankbaar voor de uitnodiging van Wouter Vahl om eens langs te komen. Het ritje met de trein was een kleine moeite voor alles wat ik geleerd heb. Uiteraard wil ik ook alle andere vaste deelnemers aan het interferentieclubje bedanken: Isabel Smallegange, Anne Rutten, Romke Kats, Jaap van der Meer en Bruno Ens.

Somewhere in 2002 I visited Canada to work on my thesis, kindly invited by Darren. I remember having a fun time and meeting many great people. I can't remember all names, but I do remember the hospitality offered by Elmer Wade, Doug Swain, Doug Watkinson, Chris Taggert and all the zoology students at the University of Manitoba.

Several years after I was supposed to deliver this thesis I visited IIASA, where I learned some of the skills needed to feel confident in writing down some of its missing parts. Åke Brännström, I am still grateful for what I learned from you. My visit to IIASA was also memorable for the great bunch of youngsters I met. Katja Enberg, Mia Eikeset, Alessandro Colombo, Erin Dunlop, Daniel Falster, Varvara Fazalova and Davnah Urbach: you always made me giggle, and often made me smile.

Ik heb met veel plezier gewerkt bij RIVO/IMARES en heb het nog steeds erg naar mijn zin. Mijn parttime aanstelling naast het AIO werk was achteraf gezien misschien niet de beste keus, maar ik heb daardoor wel veel verschillende kanten van het onderzoek aan visserij kunnen bekijken. Ik heb door het werk naast mijn proefschrift ook beter leren waarderen dat mensen kunnen uitblinken in gebieden buiten de “technische” aspecten van het onderzoek. Floor Quirijns en Martin Pastoors, jullie zijn hierin wel de meest uitgesproken voorbeelden. Ik benijd jullie wel eens om jullie vaardigheden, maar ik ben vooral heel dankbaar dat ik dankzij de niet aflatende inspanningen van Floor gegevens over de vis-

serij heb kunnen gebruiken die ik anders niet had kunnen hebben. Dat geldt natuurlijk ook voor iedereen die zich in de loop der jaren heeft ingezet voor het verzamelen van de enorme berg gegevens die beschikbaar is bij IMARES.

Ik wil iedereen bedanken die mij de afgelopen jaren een “thuis” heeft geboden. Vooraleerst wil ik mijn ouders bedanken, bij wie het altijd goed uitrusten is. Willemien, eindelijk kan ik bellen dat het af is.

Dat er nu een “echt” boekje ligt, is voor een groot gedeelte te danken aan Rachel van Esschoten, die bereid was om in korte tijd alle opmaak te doen. Veel belangrijker is, dat ze heeft geholpen met de strakke planning die nodig was om alles op tijd af te hebben. Het zal een raar gegeven geweest zijn om te moeten haasten voor iemand die zelf al meer dan vijf jaar te laat is.

Katell, I look forward to a life together without theses while on the same side of the globe. I am eager to learn what it is like.

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Finally...

Colophon

ISBN:

978-90-367-4412-6

Author:

Jan-Jaap Poos

Effort allocation of the Dutch beam trawl fleet

Rijksuniversiteit Groningen

Graphic design cover and inside:

Rachel van Esschoten (www.divingduck.nl)

Photography:

Joris Geurts van Kessel: cover (bottom), p. 8 (bottom), p. 54 (bottom),
p. 76 (bottom), p. 100 (bottom), p. 128 (bottom),
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Marcel de Vries: p. 30 (top), p. 54 (top), p. 76 (top), p. 100 (top),
p. 128 (top), p. 166 (top)

Printed by:

Wöhrmann Print Service, Zutphen (www.wps.nl)

