Evaluating and optimizing stock enhancement of a natural flatfish stock

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Chapter 1

General introduction

1 General introduction

Costal fishery for marine fish in the inner Danish waters has for centuries been an integrated part of the Danish cultural history. The fishery has used passive gears such as gillnets and traps primarily targeting cod (*Gadus morhua*), herring (*Clupea clupea*), eel (*Anguilla anguilla*) and flatfish. After the industrializing the need for coastal fishery as income supplement to e.g. farming was reduced, but many continued to fish on a leisure or recreational basis. Today around 33.000 people carry out some kind of recreational fishery with gillnet and/or traps in Denmark. Similar too many commercial fisheries around the world, Danish recreational fishermen have also observed decreasing catches, changing species composition and a smaller average size of the fish caught (Pauly et al., 1998; Daan et al., 2005).

Figure 1. Denmark and the inner Danish waters. The squares are the locations where hatchery reared turbot were released at North Zealand (NZ) during the years 1991-1998. The triangles represent the releases in Aarhus Bay (BV) between 2000 and 2006. The circles show the locations where artificially bred turbot was released in Aalborg Bay (AB) during the years 1998 and 1999.

To reverse the trend of decreasing catches the proactive methods of releasing artificially bred individuals has been implemented in a corporation between recreational fishermen and the Danish Institute for Fisheries Research (DIFRES). The goal is to increase the stock size and hence to avoid the need for further implementation of traditional management tools, such as restrictions in catches or regulations of the individual fisher's behaviour and fishing practice. A national program for stock enhancement in Denmark was initiated in 1987, together with a legislation that obliged anglers and recreational fishermen to purchase a fishing license in order to legally carry out their fishery (Rasmussen and Geertz-Hansen, 2001). The funds generated were used for stock enhancement and restocking projects, of both inland and marine species such as turbot (*Psetta maxima*) (Fig.1).

The decision to enhance the turbot stock by releasing artificially reared individuals was based on three considerations: 1) Turbot could be obtained from hatcheries at a reasonable cost; 2) turbot is an appreciated consumption fish and thus considered to be a "good catch" by fishermen and 3) compiling knowledge on turbot population dynamic and general knowledge on flatfish recruitment provided a solid theoretical basis, thus improving the likelihood that stock enhancing would be successful.

1.1 Scope and objectives

The overall aim of this thesis is to analyze, evaluate and optimize releases of turbot for stock enhancement. In total six objectives can be identified:

1. *To discuss criteria for stocking with special reference to flatfish*
2. *To analyze spatial and temporal variation in age-0 turbot cohort size*
3. *To evaluate a large scale stock enhancement experiment using recapture data*
4. *To evaluate habitat suitability by analyzing stomach content of the wild population*
5. *To provide a methodology for estimating post-release mortality and spreading of released turbot applying a diffusion model*
6. *To manipulate size of the turbot released and apply a method for conditioning prior to release in order to minimize post-release mortality*

These six objectives are dealt with in such a way that I first give a general introduction to turbot, its biology and lifecycle. This section will be followed by one on stock enhancement, wherein I will deal with those factors involved in the success of increasing the stock size when releasing artificially reared individuals, such as the post-release mortality and factors involved in the regulation of the cohort size. This chapter is followed by five original papers and one manuscript (chapter 2-7). In **chapter 2** I will discuss general criteria, with special reference to flatfish, which should be fulfilled in order to increase the likelihood for success when stock enhancing a natural population. The focus in **Chapter 3** is on analyzing the spatial and temporal variation in the age-0 turbot cohort size and to identify which factors that are involved in generation the spatial and temporal variation in age-0 cohort size in the wild population. In **chapter 4** a large scale stock enhancement, in which a considerable number of juvenile turbot was released between 1991 and 1998, is evaluated. Growth and mortality are addressed and comparisons between wild and released individuals performed. The objective of **chapter 5** is to evaluate release habitat suitability. The growth of released individuals from three different habitats was analyzed and the stomach content and abundance of the wild population found. The objective of the last two chapters was to address the problem of loss of released fish during the post-release period. In **chapter 6** a method for estimating post-release mortality and spreading of released turbot applying a diffusion model is presented. Finally the objective of **chapter 7** is to manipulate size of the turbot released and test the effect of conditioning prior to release on post-release mortality. These six chapters will be followed by a general discussion in **chapter 8** where I will recapitulate all experiments performed and synthesize the result into a common discussion.

1.2 Turbot

1.2.1 Biology and Fishery

Turbot (Fig. 2) is a flatfish species belonging to the *Scophthalmidae* family together with around 9 other species, all of which live in the North Atlantic Ocean or adjacent waters (Munroe, 2005). Turbot is a valuable species with a typical price at the fish auction of around 10 € per kilo depending of season. Already at age 0 turbot occur as bycatch in the *Crangon crangon* fishery (Berghahn and Purps, 1998). Within EU no minimum landing size (MLS) exist (Anon., 1998), but in Denmark the MLS is set to 30 cm. In Denmark a total of *c.*40 tons is annually landed in Kattegat predominantly as a bycatch in the sole (*Solea solea*) gill-net fishery. In the North Sea the catches are somewhat higher and a total of 4500 tons are landed annually, mainly as by-catch in the Dutch beam-trawl fishery and a Danish directed gill net fishery (Boon and Delbare, 2000).

The geographical distribution of turbot extends from the Black Sea, through the Mediterranean, up along the west coast of Europe, to the British Islands and the Faeroe Island and further into the Baltic Sea and up along the Norwegian coast (Muus et al., 1998). Genetic differences between the Baltic turbot and the North Sea turbot are present and have been proposed to be linked to the strong salinity gradient from the North Sea to the inner Baltic waters (Nielsen et al., 2004). The Kattegat area, where the releases have been carried out, is believed to serve as a transition zone between the two genetically different turbot stocks, which is supported by tagging/recapture experiments of wild fish (Bagge, 1987). These tagging experiments showed that wild turbot tagged and released in the Kattegat/Skagerak area stayed there for as long as 5 years after release. However, a recent study on the Baltic turbot east of Bornholm was not able to show any genetic differences and found higher between year variation in the genetic signal than between areas (Florin and Höglund, 2007).

Figure. 2. Tubot (From Muus et al., 1998)

Turbot can reach a maximum size of 25 kg and larger individuals exclusively rely on fish as diet (Rae and Devlin, 1972, Jones, 1970, Wetsteijn 1981). Turbot is an ambush hunter relying on its agility and speed when stalking a prey after detection (Holmes and Gibson, 1983). It is depending on a visual identification of its prey and is predominately active during the day (de Groot, 1971). Turbot reacts to at least three cues when attacking a prey; dimension, movement and sand grain disturbance (Holmes and Gibson, 1986).

1.2.2 Lifecycle

The lifecycle of turbot can be divided into three ontogenetic stages which are characterized by a change in distribution and habitat association (Fig. 3). First there is a planktonic stage where the egg and the neustonic larvae are transported from the offshore spawning grounds onto the coastal zone wherein the turbot settles (Riley et al., 1981). After settling the juveniles stays in the shallow coastal zone but gradually increase their preferred depth as they increase in size. At around age 3-4 years, depending on sex, turbot matures and undergoes offshore spawning migrations.

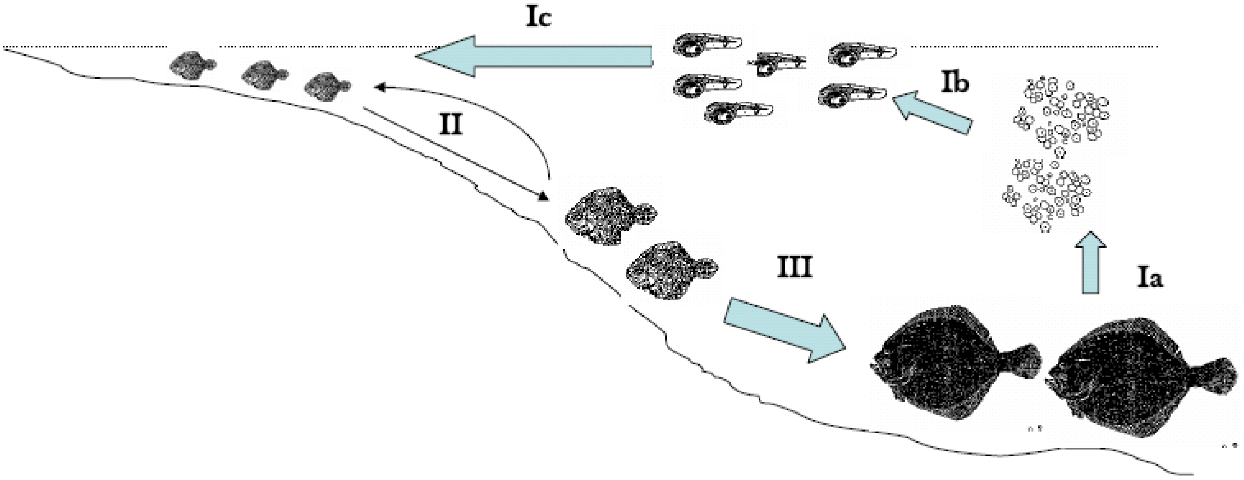

Figure 3. A schematic overview of the lifecycle of turbot. Stage Ia shows the spawning, which takes place somewhere offshore. The eggs and larvae (Ib and Ic) are planktonic. Larvae are transported to the coast by wind driven current. Stage II is the juvenile stage in the nursery. There is seasonal determined migration between shallow and deeper waters and as the size of turbot increases and mature (stage III) they gradually move to deeper waters (Figure with courtesy of J.G. Støttrup)

Spawning and the planktonic life stages

Like other flatfish, turbot females produce a large amount of small eggs that are spawned during the spring/summer (Jones, 1974). The spawning grounds for turbot are believed to be located out offshore but little is known on the exact position within the Kattegat area. In the Scottish areas of the North Sea the spatial distribution of ripe and spent turbot seems diffuse and the same pattern is seen for the distribution of larvae (Rae and Devlin, 1972). An equally diffuse distribution of eggs is observed in the German Bight (van der Land, 1991).

The actual fertilization of the eggs takes place in the water column. The minimum temperature required in order to get a successful hatching of turbot eggs lies around 10 ºC (Jones, 1970; Kühlmann and Quantz, 1980; Iglesias et al., 1995). The embryonic development time is very temperature sensitive and is doubled when water temperature is increased from 12 ºC to 16 ºC (Gibson and Johnston, 1995a). Contrary to e.g. *Pleuronectidae* turbot has a swim bladder during its larval stage (Evseenko, 1981) which has important implications for the transport of larvae from offshore spawning grounds to coastal nursery areas (Riley et al., 1981). The time from hatching to metamorphosis varies according to ambient temperatures, but even with a constant temperature large plasticity in development time is present. For a North Sea batch reared at 14-16 ºC metamorphosis was completed at day 45 for the first individual but not until day 72 for the last (Jones, 1973a). This variation in time from hatching to metamorphosis has the potential to influence the distribution of newly settled turbot since metamorphosis and settlement coincide for turbot like for most other flatfish (Nash and Geffen, 2005).

Juveniles and the nursery area

The distribution of juvenile turbot is associated with shallow, sandy and wind exposed areas (Gibson, 1973; Riley et al., 1981) and since these areas are responsible for the majority of recruits to the mature population they fall within the definition of a *nursery* area (Gibson, 1994; Beck et al., 2001 through Abel et al., 2005).

Turbot settles in the coastal nurseries from June/July and until September at a size around 3 cm (Jones, 1973b; Gibson and Johnston, 1995b). During the period within the nursery area turbot undergoes two ontogenetic changes in their diet, which are important both in terms of increasing growth and avoiding inter-specific competition (Nissling, et al., 2007). The diet of the smallest turbot (< 3 cm) contains planktonic prey items such as calanoid copepods and later polychaeta is included. This diet resembles the diet found for the much more abundant flounder (*Platichthys flesus)* but as the length of the turbot increases the fraction of mysids in the diet also increases and the overlap with flounder decreases. Finally, when they reach a size of 3 – 10 cm, they start feeding on fish and larger crustaceans. The exact size at which fish is included in the diet differs between geographical areas probably as a result of differences in prey availability. In the Baltic, juvenile gobies (*Pomatoschistus* spp.) are found in the diet of turbot as small as 3-5 cm (Aarnio et al., 1996) but along a Spanish coast the inclusion of fish e.g. sandeel (*Ammodytes tobianus*) does not occur until the turbot reach a length of 10 cm (Iglesias et al., 2003). The fish species in the diet of North Sea turbot larger than 21 cm is mainly sandeel and to a lesser extend sand goby (Rae and Devlin, 1972; Braber and de Groot, 1973; Wetsteijn, 1981). Differences in diet are not only observed between geographical areas but also within (Nissling et al., 2007).

As for several other species with a large geographical distribution [e.g. Silversides, *Menidia beryllina* (Conover and Present, 1990)] turbot show counter gradient growth, where fish from high latitude populations has a faster growth than fish from low latitudes (Imsland et al., 2000). The counter gradient growth is caused both by a higher energy intake and a more efficient food conversion (Imsland et al., 2001). The high latitude populations also show a higher temperature optimum for growth, 23 ºC compared to *c.* 17 ºC for a more southerly population (Imsland et al., 2001). These temperature optima for growth is ontogenetic determined and decrease with increasing fish size (Imsland et al., 1996). With increasing size juvenile turbot gradually increases its depth distribution and hence decreases its association with the costal nursery and recruits to the adult part of the population.

1.3 Stock enhancement

Releases of artificially reared individuals into a natural habitat can be grouped into one of three categories: *restocking*, *stock enhancement* or *sea ranching*. A definition of these concepts was proposed at the Third International Symposium on Stock Enhancement and Sea Ranching in Seattle 2007 by Bell et al. (*In press*) as:"

- ***"Restocking** - the release of cultured juveniles into wild population(s) to restore severely depleted spawning biomass to a level where it can once again provide regular, substantial yields. This may involve re-establishment of a species where it is locally extinct to rebuild a fishery, or for conservation purposes."*

- ***"Stock enhancement** - the release of cultured juveniles into wild population(s) to augment the natural supply of juveniles and optimize harvests by overcoming recruitment limitation. Note that recruitment limitation is the rule rather than the exception for marine species with pelagic larvae in open ecosystems, even when spawning biomass is at the desired level."*

- ***“Sea ranching*** *- the release of cultured juveniles into unenclosed marine and estuarine environments for harvest at a larger size in ‘put and take’ operations. Note that the released animals are not expected to contribute to spawning biomass, although this can occur when harvest size exceeds size at first maturity or when not all the released animals are harvested.”*

The releases of turbot in the Danish water fall within the definition of stock enhancement. In the Kattegat area where the releases have been carried out, a natural, self producing turbot population already exists.

Stock enhancement is an interdisciplinary field, building on theory and experiences from ecology, aquaculture and economics and several considerations have to be taken into account to assure the likelihood of success (Blaxter 2000). Among these are: ***1) Viability of producing individuals in the aquaculture***. It is obvious that an efficient production of individuals in the aquaculture is a prerequisite for a cost-efficient stock enhancement. But it is important to stress that stock enhancement should not be viewed as only being a question of efficiently producing as many individuals as possible only to release them into nature at random. **2) *Populations regulating factors.*** When adding artificially reared individuals to a population the goal is to increase the population. In order to evaluate if this goal can be met or not, knowledge on other factors responsible for regulating the population is needed. It is important to identify which density dependent and independent factors regulate the population size and at which stage in the lifecycle. **3) *Release locality and season*.** At some point when setting up a stock enhancement experiment it has to be decided when and where the artificially reared individuals should be released. Synchronizing the release with a season providing optimal growth condition, such as available food and correct temperature, should be a goal. Some areas might not provide the released fish with sufficient food and protection against predators with the consequence of high mortality and low growth. For flatfish this has to be given special attention since flatfish are concentrated during their juvenile stages into nurseries. **4) *Post-release mortality.*** The mortality in connection to the release should be evaluated. The transition from the very homogenous environment experienced during the time in the hatchery to the heterogeneous natural habitat is likely to represent a critical period for the fish and hence an increased mortality during this period can be expected.

1.3.1 Viability of producing fish in aquaculture

Aquaculture production of turbot in Denmark has steadily increased since the 1980s, similar to the global trend in aquaculture production (Fig. 4). The production of turbot on a commercial basis obviously makes it attractive from a stocking point of view, since supply can be expected to be reliable and the economics reasonable. The price is depending on the size of the fish but a 10 cm individual coast *c.* 1.5 €. Another aspect that makes turbot attractive as stocking species is that is possible to induce turbot spawning artificially by manipulating the photoperiod and temperature and hence produce individuals of a desired size any given time (Howell and Yamashita, 2005).

1.3.2 Density dependent and independent regulation of flatfish age-0 cohort strength

It is important, within a stock enhancement context, to distinct between density dependent and independent factors involved in the regulation of the population biomass. The reason why this distinction should be made is that releasing fish into a stock simply suffering from density independent mortality and/or growth will have a predictable result. The likelihood of success will be proportional to the growth in biomass and hence a question of balancing the cost of releasing an individual with the expected gain. In principle the number of individuals released can be as high as manageable. Releasing fish into a stock where density dependent mortality and/or growth takes place will have a different result since the increase in the population numbers will increase the mortality and/or decrease the individual growth. Hence, balancing the coast of releasing an individual with the gain will be different depending on how many individuals that are released.

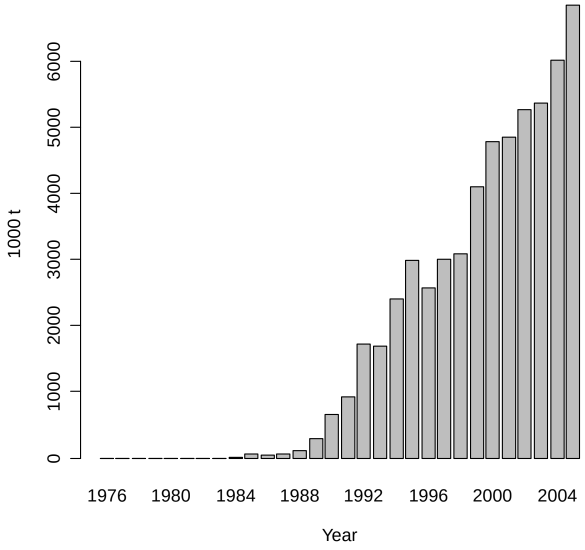

Figure 4. The world annual production of turbot in aquaculture. Data are from FAO (www.fao.org).

For flatfish as well as for other marine species the overall age-0 cohort size is likely to be regulated by density independent factors such as hydrographically conditions acting during the larval stage. But for flatfish, density dependent regulation of the cohort size may also take place somewhere between spawning and the recruitment to the fishery. The first indication of this is that flatfish in general demonstrates a lower variability in recruitment signal compared to other marine fish species (Rijnsdorp, 1994; van der Veer and Leggett, 2005), which has been ascribed to the fact that most flatfish species concentrates during the juvenile stage into specific nursery habitats, i.e. the "*Concentration hypothesis*" (Beverton, 1995, Iles and Beverton, 2000). Secondly, there is a strong correlation between the size of these nursery areas and the size of the adult stock, a relationship often referred to as the "*Nursery size hypothesis*" (Rijnsdorp et al., 1992; Gibson, 1994; van der Veer et al., 2000a).

One mechanism behind the "*Nursery size hypothesis*" is that the numbers of larvae successfully transported into a suitable nursery is proportional to the size of it, i.e. a density independent regulation of the population size. But this will not explain why the recruitment variability for flatfish in general seems lower than for non-concentrating species. An alternative explanation could be that the concentration of individuals into a restricted area will lead to intra-specific competition for resources, propagating that density dependent mortality or growth starts to regulate the population size. With increasing stock size the carrying capacity will eventual be met and the net population biomass growth will be zero (MacCall 1990).

From a stock enhancement point of view the concentration of individuals into a limited habitat leads to two crucial considerations that one should reflect on prior to adding new individuals: 1) Does density dependent regulation of the cohort size takes place at some stage during the life cycle and if so; 2) are the artificially reared individuals released before or after this life stage? The ultimate fault of a stock enhancement program will be to release artificially reared individuals into a population where the carrying capacity has been reached and hence the net population growth will remain zero no matter how many new individuals that are added.

For flatfish some studies have put forward evidence for density dependent growth within the nursery (Rijnsdorp and van Leeuwen, 1992; Modin and Pihl, 1994; Bolle et al., 2004) while other studies have not (van der Veer and Witte, 1993; van der Veer et al., 2000a). The reason for this discrepancy is probably that density dependent growth within the nursery is hard to detect, since the average stock size is to small to induce any competition between individuals This might be even more pronounced nowadays since the spawning stock sizes are small, as most stocks examined are all highly exploited and hence there population size is well below carrying capacity. This is supported by the fact that both Rijnsdorp and van Leeuwen (1992) and Bolle et al. (2004) used historical data and found that an increase in the growth of juvenile plaice happened in the 1960's and 1970's. Modin and Pihl's (1994) study was not based on historical data but actual observations from a small semi-enclosed bay. Hence it seems as if density dependent growth is not a steering factor in the regulation of the cohort size at present day stock sizes but can occur locally in certain areas.

If density dependent growth within a turbot cohort occur it will most likely occur during the very early demersal stages, since the available habitat are smallest during this period. The habitat that. *3* cm turbot settles into is very restricted since depths shallower than 1 m are preferred, whereas individuals as large as 10 cm have increased their preferred habitat to a depth of 5 m. For the coast of North Zealand the area shallower than 1 m only constitutes around 10 percent of the total area down to 5 m, i.e. the habitat size is increased up to 10 times when the turbot growth from 5 to 10 cm.

Whether the mortality risk experienced in the nursery is density dependent or not has also been subject of several investigations. Indications of an increased mortality with increasing density have been put forward for plaice (Beverton and Iles, 1992a). Whether this applies for turbot as well is unknown but mortality during the juvenile stage seems to be comparable to what is found for the much more abundant plaice (Beverton and Iles, 1992b). For plaice, density dependent mortality is caused by density dependent *Crangon crangon* predation on individuals smaller than 30 mm (van der Veer and Bergman, 1987). Further, abnormal high abundances of plaice coincide with years characterized by an absence of *Crangon crangon* (van der Veer et al., 2000b). The increase in predation pressure with increased abundance is caused both by a numerical increase of *Crangon crangon* and an increase in their preference for plaice. It is unlikely that *Crangon crangon* can have the same effect on turbot. Plaice reaches a refuge at a size of 30 mm and since plaice settles at 10-20 mm (van der Veer et al., 1990) the window of predation is much larger than for turbot that settles at a somewhat larger size of c.30 mm (Jones, 1973b; Gibson and Johnston, 1995b).

Other types of mortality such as cannibalism can lead also to density-dependent regulation. However, there is no evidence that this plays an important role in flatfish, which is important in the context of stock enhancement. Density independent mortality is probably also smaller for flatfish compared to e.g. round fish since flatfish are believed to reach a refuge from predators at a small size due to its body shape (Fig. 5; Ellis and Gibson 1995).

Figure 5. A *Larus marinus* having problems swallowing a juvenile flatfish. (Foto by Sune Riis Sørensen)

1.3.3 Release locality and timing

Several studies have shown the importance of choosing the correct season for release. For Japanese flounder (*Paralichthys olivaceus*) timing of the release with the abundance of the dominating prey (Mysids) increased both the stomach index and decreased the numbers of fish with empty stomachs (Tanaka et al., 2006). For striped mullet (*Mugil caphalus*) the recovery rate differs significantly between release seasons, probably as a result of changing mortality (Leber et al., 1997). In a mass-release of hatchery reared *Paralichthys olivaceus* the number released was so high that the release area apparently no longer was able to support the released fish with suitable prey items. As a consequence an abnormal high occurrence of empty stomachs occurred both in the released and in the wild population in the first few weeks after the release but did not affect the long term growth trajectory (Tanaka et al., 2005). For artificially reared flounder the release habitat had a significant effect on the dispersion (Andersen et al., 2005) and for *Mygil caphalus* releases into an area not being a nursery resulted in no recaptures probably due to mass mortality event (Leber and Arce, 1996).

1.3.4 Post-release mortality

After the release two periods of contrasting mortality risk can be identified. The first period is immediately after the release, also referred to as the post-release period. During this period mortality is typically increased to a level far above what is seen for the wild counterparts. The second period succeeds the post-release period and during this period the mortality will be determined by the density dependent and density independent factors described in previous section and presumably the mortality level will be on the same level as what is found for the wild counterparts.

Since the very first releases of artificially bred finger-nail sized plaice by Shelbourne in the 1960'ies, a high mortality during the first period after release has been suspected (Shelbourne, 1964). The magnitude of the mortality and its influence on the outcome of stock enhancement has been suggested to be high. Several reasons for an increased mortality during the first period after release have been proposed: physical damage of the fish intended for release; handling in the hatchery; transport to the release location; and release of fish into an impropriate environment (Leber and Arce, 1996). But proposed by most is a lack of behavioural skills such as predator avoidance (Howell, 1994; Hossian at al., 2002), which has been supported by several e experimental studies (Kellison et al., 2000; Fairchild and Howell, 2004). The apparent connection between mortality and predation is further supported by a number of studies that points towards the importance of the size-at-release in reducing mortality rate (e.g. Yamashita et al., 1994; Leber, 1995; Tominaga and Watanabe, 1998). Unfortunately, reliable quantitative estimates on the post-release mortality and the duration of the post-release period are unavailable from field experiments, due to methodological constraints in separating the lower probability of capture of a released individual due to the changing spatial distribution from the reduction in numbers caused by mortality. Within the field of analyzing releases of hatchery reared individuals this problem has been recognized (e,g, Leber et al., 1996) and attempts to solve it by applying different spatially based sampling strategies have been made (e.g. Furuta et al., 1997). As for other stock enhancement programs, the post-release mortality was not estimated for the Danish turbot releases during the first years. Estimating and analyzing this post-release mortality was one of the major objectives of the present thesis.

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Chapter 2

Can stock enhancement enhance stocks?

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Can stock enhancement enhance stocks?

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Abstract

Successful stock enhancement or restocking requires a thorough understanding of the ecological processes that provide a potential for stocking within different ecosystems, i.e. determine which factors define the potential for stocking, such as population dynamics, economic cost-benefits, fisheries management and socio-economic impacts. Stocking is not simply a question of aquaculture logistics (i.e. the ability to produce a sufficient number of fry relative to the magnitude of the natural recruitment within the system), nor should it be a new outlet for aquaculture production. Quantitative targets should be set and the expected performance of the stocking tested. Potential loopholes, such as post-release mortality and habitat requirements related to the release, should be examined and resolved. If properly managed, stocking may lead to an increase in population, contribute to the local fishery and/or lead to an increase in the spawning stock biomass. The criteria for stocking are discussed in this paper using examples from flatfish and cod stocking programmes within specific ecosystems.

Keywords: Stocking; Stock enhancement; Flatfish; Turbot; Cod

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1. Introduction

The decline in many commercially important fish stocks has speeded up the search for improved management tools, including the shift towards ecosystem-based fisheries management, the introduction of Marine Protected Areas (EC decision on the Common Fisheries Policy [EC/2371.2002]; ICES, 2004a,b) or closed boxes such as the 'plaice box' in the North Sea (ICES, 2004b) to protect fish populations during critical life-stages. These management regulations have, however, proved difficult to apply and have achieved limited results. The genetic implications are barely understood and socio-economic aspects need to be incorporated. Common to these management approaches is restriction of an activity that will, at best, allow the fish population to proliferate by removing one of its pressures. However, for stocks under multiple pressures where major environmentally induced bottlenecks for recruitment are compounded by overfishing, slightly reducing the fishing pressure may be insufficient to improve conditions within management or political timeframes. In some cases, stock enhancement or restocking may offer the opportunity for proactive action. Stock enhancement is here defined as repeated releases of fish to even out natural fluctuations in recruitment and thus stabilise the fisheries. In the literature this is also referred to as sea ranching. Restocking is here defined as multiple releases of fish to a stock chronically suffering from poor recruitment with the aim of increasing both fishery recruits and the spawning biomass. For stocking to

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actually result in an increase in recruits or spawning stock biomass, the scientific approach must be appropriate. It should take into account both major environmental drivers and genetic, socio-economic and management aspects, and implications for the particular species within the ecosystem in question (Blankenship and Leber, 1995; Støttrup, 2004).

Embracing stocking as a tool in fisheries management requires a thorough understanding of the ecological processes that provide a potential for stocking within different ecosystems. The potential for stocking is not derived solely from whether or not the species can be cultured in sufficient quantities relative to the magnitude of the natural recruitment, although ultimately this may be important. The potential for stocking is primarily related to the population dynamics of the species within a given ecosystem, economic cost-benefits, fisheries management and socio-economic impacts. The expected performance of stocking should be tested against quantitative goals as was also suggested by Bannister and Howell (2005), and specific problems such as post-release mortality should be examined and resolved (Furata, 1996). There is a need to explore the potential for utilising stocking to sustain natural stocks that are under pressure due to adverse natural or anthropogenic environmental conditions. This is already the case for some species. For example the International Council for the Exploration of the Sea (ICES) has recently changed its views on stocking and now recommends large-scale stocking of European eel *Anguilla anguilla* as a long-term measure to preserve that population (ICES, 2005).

The criteria for stocking are reviewed and discussed in this paper using examples from flatfish and cod stocking programmes within specific systems to illustrate these criteria and highlight differences. The genetic consequences of stocking also need to be taken into consideration but are not discussed in this paper. A review on this issue is provided by for example Cross (1999).

2. Aims of stock enhancement and restocking

Stock enhancement is employed to even out the natural fluctuations in recruitment thereby stabilising the fisheries. The Japanese stock enhancement programme running since 1963 is an example of stock enhancement with an annual production of 32 different species of fish, shellfish and other invertebrates (Imamura, 1999). The Norwegian cod *Gadus morhua* stocking programme (1990-1997) is another example of stock enhancement (Svåsand et al., 2000). Also referred to as sea ranching, the release of fish is expected to increase the numbers recruiting to the fisheries, especially during years with poor supply of juveniles to the nursery grounds. It implies that the recruitment bottleneck occurs prior to the nursery life-stage and that there is ample prey and few predators during the juvenile stage.

Restocking can be applied to stocks that are chronically suffering from poor recruitment and where the spawning stock biomass is well below the Biological Safe Limit set for that stock (sensu ICES, 2004a). In such cases stock recovery is urgent. The aim of restocking is to increase fishery recruits as well as to increase the spawning stock biomass. Restocking should be part and parcel of fishery management, including recovery plans, for depleted stocks.

3. Criteria for stocking

Stocking, whether for enhancement purposes or restocking, cannot always be successfully applied and there are several criteria that need to be fulfilled before stocking can be a potential tool for enhancing recruitment to fisheries:

1. There should be a *distinct* recruitment bottleneck, not primarily due to overfishing.
2. There should be ample (excess) food for the released fish and following life-stages.
3. There should be a low predation pressure for the size released and larger fish.
4. There should be an economic cost-benefit, or at least quantifiable objectives for this.

Each of these criteria will be dealt with separately, illustrated by results from releases for stock enhancement purposes of flatfish in Denmark (Støttrup et al., 1998, 2002), or cod in Norway (Svåsand et al., 2000), or from a theoretical study on the potential for restocking the Eastern Baltic cod in ICES Subdivision 25 (Støttrup et al., 2005a,b).

3.1. Recruitment bottleneck not primarily due to overfishing (stocking criterion no. 1)

In most temperate flatfish species, recruitment is believed to be limited during the pelagic stage (Van der Veer et al., 1991; Henderson, 1998), or during or just after settling (Tanaka et al., 1989; Rijnsdorp et al., 1992; Gibson, 1994; Van der Veer et al., 2000). High predation pressure during the egg and larval stages, starvation during the early larval stage, and poor supply to the nursery grounds due to adverse wind and current conditions may result in the nursery areas being undersupplied with juveniles. Flatfish species, such as turbot *Psetta maxima*, due to their restricted depth distribution, occupy a relatively limited nursery area (Gibson, 1994; Van der Veer et al., 2000). If these habitats are undersupplied, a potential for stocking the larger juveniles exists. The results from yearly releases of age–0 and age–1 turbot off the exposed coastline of North Zealand (Fig. 1) showed that this highly dynamic habitat was able to provide a suitable habitat for the released fish (Støttrup et al., 2002; Table 1). Mortality was observed to be similar in wild and released turbot (Støttrup et al., 2002). Age–0 turbot released during the autumn grew significantly faster the following summer than did their wild counterparts (Paulsen and Støttrup, 2004). No indication of displacement of the wild fish was found compared to the catches of wild and released fish of the same size groups (Støttrup et al., 2002). Thus, a main conclusion was that the turbot releases in North Zealand had the potential to increase the local population of this species. It was not possible to examine the contribution to the fishery since this species was caught as by–catch in the local sole *Solea solea* fishery. Stocking of other flatfish species has been reported to contribute to the local fishery. For example, stocking the Japanese flounder *Paralichthys olivaceus* on the south-west coast of Hokkaido prefecture in Japan was shown to contribute between 11 and 23% of the commercial landings in four markets studied (Ishino, 1999).

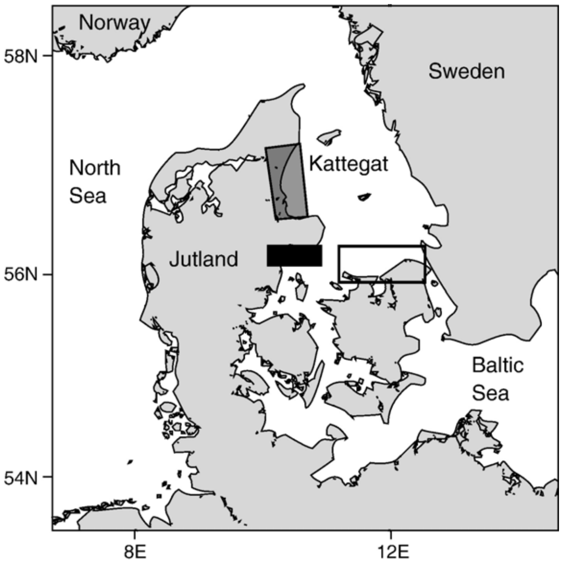

Fig. 1. Map of Denmark showing the three release sites: North Zealand (empty box), Aalborg Bay (shaded box), where multiple releases of different sizes of turbot were released during the 1990s, and Aarhus Bay (black box), where releases have been conducted since 2000. Details of the releases in the first two sites are shown in Table 1.

Table 1
Average recapture percentage and range where applicable for turbot juveniles released either in North Zealand or in Aalborg Bay (see Fig. 1) during 1991 to 1999

Year	Release Site	Total number released	Number releases	Average recaptures (%)	Range
1991	North Zealand	7581	2	4.5	4.2–4.5
1992	North Zealand	7941	1	3.6	–
1993	North Zealand	10049	1	2.7	–
1994	North Zealand	9821	1	11.4	–
1995	North Zealand	9807	5	5.7	2.5–8.3
1996	North Zealand	5579	1	1.4	–
1997	North Zealand	31479	2	1.4	1.3–1.4
1998	North Zealand	19641	1	3.7	–
1998	Aalborg Bay	33839	1	4.2	–
1999	Aalborg Bay	10707	5	2.8	0.5–13.9

Table updated 31 December 2005.

Stocking in the Baltic has not yet been attempted but a theoretical study on the potential for stocking was carried out (Støttrup et al., 2005a,b). The Baltic cod and the Baltic ecosystem are unique. This stock exists in the brackish eastern Baltic (ICES subdivisions 25-32) on the edge of its geographic distribution (Bagge et al., 1994; Nissling and Vallin, 1996). Historically, this stock spawned in the three deeper basins of the eastern Baltic: the Bornholm Basin, the Gdansk Deep and the Gotland Basin (Fig. 2). However, since the early 1990s, both the Gdansk Deep and the Gotland Basin have not provided suitable conditions for egg survival (MacKenzie et al., 1996, 2000; ICES, 2004a) i.e. a minimum salinity of 11 psu necessary for successful fertilisation (Bagge et al., 1994; Nissling, 1995) and oxygen levels >2 mg l^{-1}. The Bornholm Basin is today the major contributor to the Baltic cod reproductive volume (Jarre-Teichmann et al., 2000). The restocking study was therefore focused on ICES Subdivision 25.

The difference between the surface and bottom water salinity in the Bornholm Basin is high and a halocline separates the surface 7 psu water from the more saline (10-20 psu) bottom water. The volume of water with the optimal combination of salinity, oxygen and temperature required for successful fertilisation and survival of cod eggs was coined the ‘reproductive volume’ (Plikshs et al., 1993) and determines in effect the success of the spawning within a particular year. The reproductive volume is largely dependent on the magnitude of inflows of saline oxygenated water from the western Baltic (MacKenzie et al., 2000). Thus the egg stage is a critical stage determining cod recruitment in the eastern Baltic (Jarre-Teichmann et al., 2000; Köster et al., 2003). Jarre-Teichmann et al. (2000) found that a

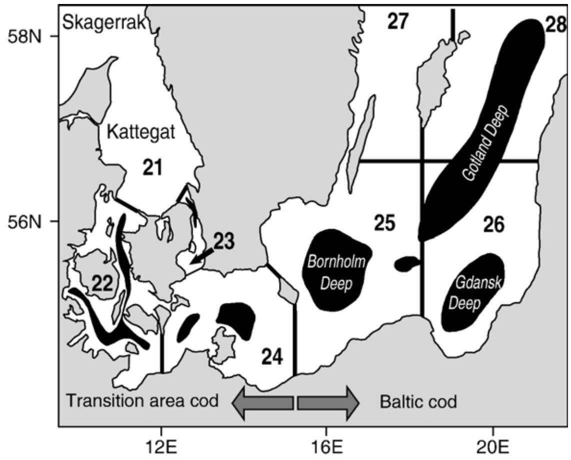

Fig. 2. Partial map of the Baltic Sea showing the three main cod spawning areas (Bornholm, Gdansk and Gotland Deep) and the nursery areas (black) in the eastern Baltic. From Bagge et al. (1994).

Ricker-type (Ricker, 1954; in Jarre-Teichmann et al., 2000) curve best described the stock-recruitment relationship for central Baltic cod (Fig. 3). The two Ricker-curves covering the two periods 1966-1980 and 1982-1994 corresponded well with the observed shift in reproductive volume level between those two periods. Thus it was shown that although environmental conditions during the egg stage are crucial in determining cod recruitment, the size of the spawning stock also plays a role (Jarre-Teichmann et al., 2000; Fig. 3). The spawning stock biomass is presently at a critically low level (ICES, 2004a), and although good environmental conditions (i.e. a high reproductive volume) may improve recruitment, this increment may be insignificant as long as the spawning stock biomass is at such a low level (Fig. 3). With a 'healthy' spawning stock biomass (eg. 400 000 t), the number of 2–y–old recruits may be doubled or tripled in years with favourable environmental conditions during the egg stage (Fig. 3). It is therefore very important to increase the spawning stock biomass as rapidly as possible as this would better enable the stock to take advantage of a year with a high reproductive volume.

To summarise this section: in many flatfish species, some roundfish species, and the exceptional eastern Baltic cod, there exists a recruitment bottleneck not primarily due to overfishing. Stocking reared individuals of these species may result in an increase in recruits to the fisheries or to the spawning stock. Considering that the highest mortalities in flatfish occur during the egg and larval stages until the stage just after settling of the metamorphosed juveniles, the size for release should be late age–0 fish or older. In the case of the Baltic cod, the recruitment bottleneck occurs during the egg and yolk–sac stage and fish larvae equal to, or larger than, first feeding larvae would be ideal for stocking. The optimal size of fish for stocking is further explored in the following two criteria for stocking.

From the literature there is evidence that stocking leads to population increases and contributes to the fisheries for a number of roundfish species. This indicates that there are other species with recruitment bottlenecks where stocking is feasible. In Japan, Kitada (1999) showed a significant contribution (54 to 74%) of released red sea bream *Pagrus major* to the commercial landings within Kagoshima Bay. Stocking that led to an increase in population size was demonstrated for striped mullet *Mugil cephalus* in Hawaii, contributing on average 13% of the commercial mullet catch in Kaneohe Bay (Leber and Arce, 1996). Also for red drum *Sciaenops ocellata* in the Gulf of Mexico (Rutledge, 1989) stocking was demonstrated to result in enhanced stocks. This has not been the case for all roundfish species examined for stocking. The Norwegian sea ranching programme conducted during 1990-1997 was discontinued because the releases were not shown to significantly increase the population size of the cod or its fishery (Svåsand et al., 2000).

3.2. Food availability (stocking criterion no. 2)

In most flatfish studies, food availability has been studied by proxy using comparisons of growth, survival and even displacement to examine this parameter. In studies with turbot releases, using alizarin marked turbot, it was shown that the released turbot had a

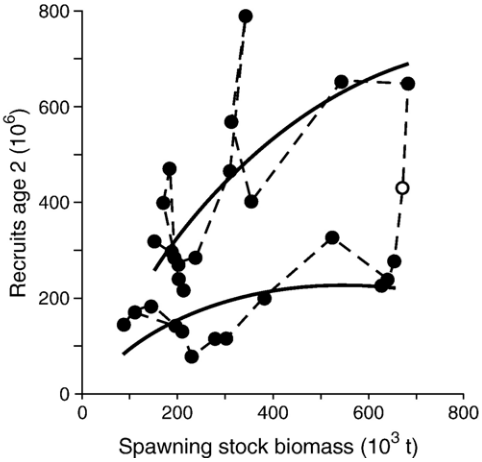

Fig. 3. Recruitment of age–2 cod in the central Baltic relative to the spawning stock biomass. (●) = data for 1966-1980 and 1982-1994; (○) = 1981. Ricker curves were fitted for the two periods separately (1966-1980 and 1982-1994). From Jarre-Teichmann et al. (2000).

higher growth rate than their wild counterparts during the first growth season after their release, but had similar growth rates the second growth season (Paulsen and Støttrup, 2004). No differences in survival rates were found and no displacement was evident from the ratio of wild and recaptured fish in the survey catches (Støttrup et al., 2002). However, during the first period after release, there may be different adaptation needs depending on the type of food available at the release site. For example, differences were observed in the time needed to adapt to the local prey when turbot were released in the exposed area of North Zealand as compared to the relatively protected Aarhus Bay (Figs. 1 and 4). The fish released in both areas were of a similar size, yet those released in Aarhus Bay began to feed on fish immediately, whereas those released in North Zealand, needed a 2-3 week adaptation period before fish became a significant part of their diet (Fig. 5). During this time the fish fed mostly on mysids, shrimps, and to a lesser extent on non-evasive prey such as snails and mussel siphons (Fig. 4). The discrepancy in initiating feeding on fish could be due to the higher presence of gobies *Pomatoschistus minutus* in Aarhus Bay, which may be more easily captured by turbot juveniles than sandeel *Ammondytes tobisus*, more commonly found in stomachs of fish caught in North Zealand. In both areas, however, there seems to be an adequate supply of suitable prey for the released fish.

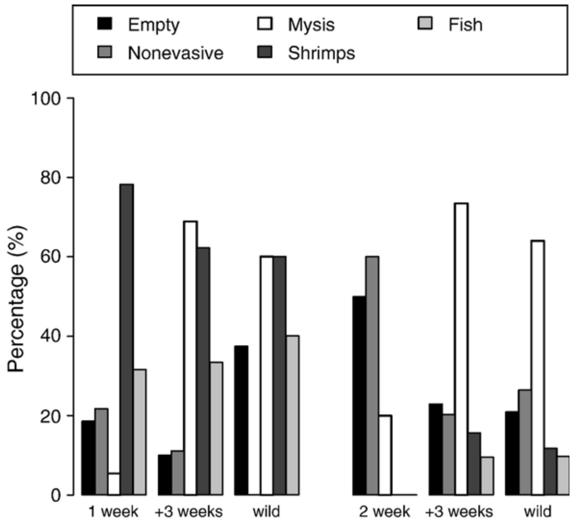

Fig. 4. (a) Occurrence of empty stomachs or of stomachs with different prey groups in turbot (15-20 cm) caught in Aarhus Bay. Numbers of observations are 113, 50 and 8 for 1 week, +3 week and wild, respectively. (b) Occurrence of empty stomachs or of stomachs with different prey groups in turbot (10-15 cm) caught near Zealand. The observation numbers are 10, 83 and 172 for 2 weeks, +3 weeks and wild, respectively. Many stomachs may have contained two or more prey groups. Data from Støttrup and Hvingel (1998), Sparrevohn et al. (2002), Sparrevohn and Støttrup (2007-this issue).

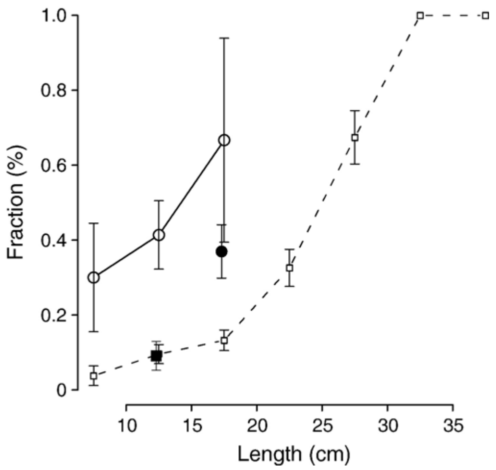

Fig. 5. Fraction of stomachs with food items containing fish. Stomachs are from turbot caught in Aarhus Bay and Zealand. (●) turbot released in Aarhus Bay, (——○——) wild turbot caught in Aarhus Bay, (■) turbot released in North Zealand, (---□---) wild turbot caught in North Zealand. Data from Støttrup and Hvingel (1998), Sparrevohn et al. (2002) and Sparrevohn and Støttrup (2007-this issue).

In Norwegian studies on stock enhancement, competition for a limited food resource is one of the main causes of the unsuccessful attempt to enhance coastal cod stocks (Svåsand et al., 2000). Density-dependant mortality was observed in cod stocked in a nearly land-locked fjord in Norway (Svåsand and Kristiansen, 1990) and food resources were fully exploited by wild stocks and their competitors in a study in Masfjorden in Norway (Smedstad et al., 1994).

In the Baltic cod case-study, the yolk–sac stage lasts 4-5 d depending on ambient temperature and the larvae swim towards surface water layers in search of food (Grønkjær and Wieland, 1997). A strong decline in the main prey item, the copepod *Pseudocalanus* sp., during the last decades became a critical factor for this species (Möllmann et al., 2000; Hinrichsen et al., 2002). In addition, a shift in the peak spawning time for the eastern Baltic cod (Wieland et al., 2000) has caused a food-limitation problem for the first-feeding cod larvae due to reduced temporal overlap of larval and prey production. The *Pseudocalanus* sp. are generally available during spring only (Möllmann et al., 2003), but because of the shift in spawning season to summer, the first-feeding cod larvae must now feed on copepods that proliferate during late summer, i.e. *Acartia* sp. and *Temora longicornis*. Therefore, the *Pseudocalanus* sp. population occurring in spring is now an unutilised food resource.

In contrast to *Pseudocalanus* sp., which occurs in the central part of Bornholm Basin, *Acartia* sp. and *T. longicornis* live in highest concentrations in shallow waters around the Bornholm Basin (Möllmann et al., 2003). Although there is ample food for the fish larvae (Jarre-Teichmann et al., 2000), it may not be readily available due to a lack of spatial overlap. This food resource may therefore not be fully exploited by the natural cod population.

The advantages of stocking first-feeding larvae of the Baltic cod include spatial and temporal utilisation of natural food resources:

- the larvae could be released during the spring *Pseudocalanus* sp. production. Since the wild Baltic cod larvae are no longer produced during springtime, there will be no competitor.
- the larvae could be released during late summer in those areas where the densities of *Acartia* sp. and *T. longicornis* are highest, thus ensuring ample food for the released larvae.
- the releases could be spread over a prolonged period of around six months, utilising both the spring and summer copepod production.

3.3. Predation pressure (stocking criterion no. 3)

For stocking to be successful, the individuals released should have reached a size-refuge from most potential predators. In the North Sea, flatfish generally have a lower predation pressure than roundfish, reflected within fisheries science as a lower natural mortality rate generally used for flatfish (0.15) compared to roundfish (0.2) in fish stock assessments (ICES WGNSSK, 2006). The difference could possibly be due to a lower frequency of cannibalism within flatfish populations and an inverse relationship between size/age and predation pressure for flatfish. The average overall mortality for the released turbot cohort over a 2–3–y period was estimated to be around 50% (Støttrup et al., 2002).

A higher post-release mortality during the first few weeks after release has been observed in several studies. For example a daily mortality of around 5 to 30% was observed for Japanese flounder juveniles released in northern or western Japan during the first 5-6 d after release (Yamashita and Yamada, 1999). After 5 d the mortality fell to around 1-5% until around 13 d after release. A similar high daily post-release mortality (14%) was observed for turbot released in a fjord on the Spanish west coast (Iglesias et al., 2003). The post-release mortality for turbot juveniles released from the shore in Aarhus Bay was estimated to be 14% d^{-1}, though limited to 3-4 d after release (Sparrevohn et al., 2002; Sparrevohn and Støttrup, 2007-this issue). The main predators identified were seagulls *Larus marinus* and *Larus argentatus*, which had quickly learnt to recognize the released, tagged turbot juveniles. Several releases were conducted in Aarhus Bay with different sizes of fish and for each release the post-release survival was estimated (Fig. 6). The resulting curve shown in Fig. 6 represents the turbot size preference of seagulls. Turbot smaller than 5 cm or larger than 16 cm were not subject to the same high predation by seagulls. In a more recent study it was shown that conditioning the fish to the environment during a predator-free period, by keeping the fish in cages for a number of days, decreased this initial mortality by around 50% (Sparrevohn and Støttrup, 2007-this issue). It is doubtful whether the fish released in North Zealand, which were released directly from a truck on board a ferry, experienced a similar post-release predation since they were released deeper (6-8 m). Some fish found their way to shallower waters and were caught near-shore at depths of around 1 m in a survey conducted about one month after the release (Støttrup et al., 2002). Thus, for near-shore releases where avian predators may be abundant, it may be necessary to release sizes less susceptible to avian predation and to adapt the fish to the environment before final release.

Much of the lack of success of the Norwegian releases of cod was attributed to the variable and numerous predators on juvenile cod both in the coastal and more exposed areas resulting in high mortalities even in age–2

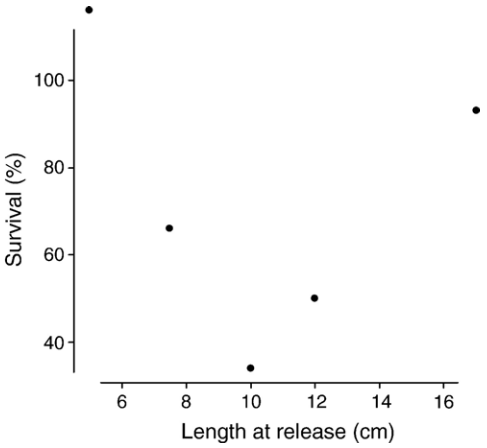

Fig. 6. The size-functional response of seagulls to released turbot derived from survival estimates for turbot juveniles during the first 3-4 days after release in Aarhus Bay. (Result >100% due to model uncertainty but indicates near to zero mortality). Data from Sparrevohn et al. (2002), and Sparrevohn and Støttrup (2007-this issue).

and age–3 cod (Otterå et al., 1999; Svåsand et al., 2000). One main predator was the cod itself, which is a highly cannibalistic species (Svåsand et al., 1998), but other species such as pollack *Pollachius pollachius*, cormorants *Phalacrocorax carbo,* shags *P. aristotelis* and possibly also mammals such as sea otters *Lutra lutra,* harbour seals *Phoca vitulina* and porpoises *Phocoena phocoena* were abundant in many of the release areas (Johansen et al., 1999; Otterå et al., 1999; Svåsand et al., 2000) and contributed to the poor yield from the releases. Salvanes et al. (1994) found that cod did not obtain a size-refuge with increasing size and it was thus better to produce cod in net pens rather than stocking. This was further supported by Johansen et al. (1999), who found that cormorants preyed mainly on the first four or five year classes of cod, preferring fish <45 cm distributed at depths within its diving range of 0-25 m.

In the case of the Baltic cod, a substantial predation on cod eggs by clupeids in the Bornholm Basin has been described (Köster and Möllmann, 2000). While sprat is the dominant predator on cod eggs in the Bornholm Basin during spring, herring prey on cod eggs during summer. A shift in the spawning season from April-June to July-August has resulted in a predator shift from sprat to herring (Köster and Möllmann, 2000; Wieland et al., 2000). The cod eggs are retained within the spawning area (Wieland, 1988). After the yolk-sac stage, which lasts around 4-5 d, the larvae swim towards surface layers in search of food (Grønkjær and Wieland, 1997) and clupeid predation decreases due to a reduced vertical overlap of prey and predator (Köster and Möllmann, 2000). Thus the combined high predation pressure on cod eggs and the limited reproductive volume are the primary driving forces for cod recruitment in the eastern Baltic (Köster et al., 2003). This again suggests that first-feeding larvae would be an optimal release size for eastern Baltic cod.

3.4. Carrying capacity

The carrying capacity is important for planning the magnitude of a release. It is defined in its broader sense as the general productivity of a given region and includes food, habitat, shelter, predators, competitors, etc. sensu Kashiwai (1995). In stocking, it is important to consider the carrying capacity for the fish of the size being released and larger sizes. Species-specific information is required for prey availability for different fish sizes, their predators and their size preference, and the bathymetry of the release area. For many flatfish species, the area available is limited by a narrow depth distribution during the juvenile stage (Gibson, 1994; Van der Veer et al., 2000). For those species well within their distribution range, abiotic factors such as temperature and salinity may be less important. However, small subtleties may define an optimal habitat. For example, a habitat with variable salinity was less suitable for growth of juvenile flounder *Pleuronectes flesus*, than one with stable high or stable low salinity (Andersen et al., 2005a).

The increase in abundance and distribution of filamentous algae due to the increased nutrient levels in coastal areas in recent decades (Isaksson and Pihl, 1992; Pihl et al., 1996, 2005) has altered the structural complexity of the habitats as well the benthic macrofauna community assemblages (Raffaelli et al., 1998). The presence of macrofauna was observed to reduce juvenile plaice abundance significantly (Wennhage and Pihl, 1994). Changes in macrofauna assemblages were found to be a less important aspect of habitat quality for flounder juveniles. This species was shown to be a robust species, exhibiting great flexibility in prey choice and habitat requirements, well adapted to the variable estuarine environment and 'more tolerant to anthropogenic changes' (Andersen et al., 2005b).

The biotic and abiotic factors contributing to the carrying capacity of the system are highly variable but very important for determining the stocking magnitude that will result in an increase in the population rather than displacement of the wild stock. This is rarely estimated in stocking programmes, and may be difficult to predict in cases where stocking aims to fill the carrying capacity when supply of juveniles fails, as was also observed for the Norwegian stocking programme (Svåsand et al., 2000). Van der Veer et al. (2000) used the population growth of juveniles expressed as total individual metabolic biomass ($W^{0.8}$) as an indicator of carrying capacity. In populations where an increase is observed throughout the growth season, the carrying capacity of the region has not been reached. The magnitude of turbot stocking in North Zealand did not increase the population to its carrying capacity (Støttrup et al., 2002). Stocking may be used to determine the carrying capacity of a system i.e. the optimal range of the release magnitude.

In the case of restocking programs, such as that of the Baltic cod, the magnitude required to restock the cod population to a level where the carrying capacity is satiated is beyond the capacity of the rearing unit designed for the stocking. The aim of this program is not to reach the carrying capacity, but to elevate the number of recruits to the fishery by 10% of an average year-class of the current recruitment within ICES Subdivision 25. An expected spin-off is the enhancement of the spawning stock biomass (SSB), which is today at a critically low level and estimated to be approximately half the level below which recruitment is impaired (ICES, 2004a). Jarre-Teichmann et al. (2000) examined the relationship between SSB and 2–y–old recruits for the eastern Baltic stock and found that a high SSB was better able to take advantage of a year with a high reproductive volume than a low SSB (Fig. 2). With the present-day SSB level, the recruitment would still be lower than the potential for recruits in the eastern Baltic system (Fig. 2). Restocking has the potential to raise SSB from its present-day critical level to a level that will be better able to profit from a year with a high reproductive volume.

3.5. Economic cost-benefit (stocking criterion no. 4)

Reports on economic cost-benefit are few, and in many cases where the stocking is aimed at improving fisheries for recreational fishermen, it may be very difficult to estimate the value of the fish recaptured. The turbot stocking programme in Denmark is funded through licences for sports fishing and recreational fishery and in several cases, the aim of stocking or restocking is to ensure a supply or restore a local fish population.

A cost-benefit analysis was conducted for the Baltic cod case study. This estimation was based on the costs of producing 474 million first-feeding cod larvae that, according to mortality rates in different life stages obtained from the literature, should result in 17 million 2–y–old recruits (Støttrup et al., 2005a). From the assessment data, the catch and spawning stock biomass generated from one cohort was estimated. The catch results were estimated using two scenarios; the fish remained within ICES 25 square or the fish dispersed within the Baltic. The economic return rate, which is the value of the returns relative to the cost of production, was 6.0 in the case of the cod dispersing within the Baltic and 9.0 for the case of cod remaining stationary within ICES square 25. The costs of release were not included and may reduce this value by up to 50%. These results will be further reduced if the released fish encounter poorer survival than expected (i.e. than the wild fish). Following the theoretical study conducted for the Baltic restocking program, a study to verify this potential has been initiated.

For recreational purposes, the economic viability is defined as the recapture rate (R) where the costs for rearing and release of one fish (Cr) match the average commercial value (Cc) of a commercial-sized fish recaptured.

$$R\% = (Cc/Cr)*100$$

For the turbot releases in North Zealand and in Aalborg Bay (Fig. 1), the turnover recapture rate should be 8%. At 8% recapture, their commercial value matched the costs for rearing and releasing the fish. A few of the turbot releases have reached this goal (Table 1). These recapture rates are minimal rates since they represent the number of tags returned only. Tags may be lost, remain unreported or the reporting may reflect the fishing effort in the different sites. Further, turbot is not a targeted species in the Kattegat but a by-catch in sole fishery. If the recaptures had been monitored at the landing sites, as described by Kitada et al. (1992), the reported recapture rates may have been higher.

For the flounder releases in Denmark, the turnover recapture rate should be 50% and these releases can never be economically viable as long as the price for flounder remains low.

4. Conclusions and perspectives

The success of stock enhancement/restocking depends on the extent of knowledge of the ecosystem dynamics and population dynamics of the species. Four criteria for stocking or restocking programmes have been highlighted and illustrated in this paper. There should be a defined recruitment bottleneck in the early life stages, ample food and space for the released fish as well as few predators or competitors. Quantitative goals and objectives need to be set, against which to test the success for the stocking or restocking. Recapture rates are the most commonly used targets, but other objectives may be defined. Models can be implemented to estimate the potential magnitude of a release, in cases where the carrying capacity may be near-satiated. Furthermore the economic cost-benefits should be examined at the onset of the releases.

Stocking should be integrated within fisheries management in long-term management, and used, where feasible, within recovery plans towards restocking severely depleted stocks (e.g. Baltic cod) or to preserve certain stocks (e.g. the European eel). Restocking may contribute to speed up recovery. Careful consideration should be given to genetic issues to maintain the genetic biodiversity, prevent genetic contamination and avoid genetic drift. Implementing stocking within fisheries management helps identify areas where information on the system dynamics is required, promotes dialogue with the end-users and furthers end-user understanding of their role within the system.

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Chapter 3

Spatial and annual variations in the abundance of age-0 turbot (Psetta maxima)and its implications for stock enhancement strategies.

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Manuscript

Spatial and annual variations in the abundance of age-0 turbot (Psetta maxima) and its implication for stock enhancement strategies

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Abstract

When stock enhancing a natural population by releasing artificially reared individuals the release strategy should be such that competition between individuals is minimized. The first step in achieving this goal is by selecting the correct release habitat with ample food and space. But even within a given habitat large variations in the natural abundance of wild juveniles might be found on both temporal and spatial scale. In the present paper the variation in the abundance of turbot age-0 cohort is examined using time series from two young fish surveys; a Danish along the Kattegat coast and a Dutch along the North Sea coast. It is found that the annual age-0 index is highly variable. No consistent spatial distribution pattern along the examined coastlines was found, indicating that within a habitat the exact release position is of minor importance. From a drift simulation performed, large variation in the transport pattern from the spawning areas was observed, with a substantial transport away from the coastal nursery areas for eggs/larvae simulated to be situated in the upper water layers. The simulation was performed for three years where a high abundance of age-0 individuals was observed in the young fish survey and three years where a low abundance was observed. For the three years with a high age-0 abundance, eggs/larvae were transported from the spawning areas and into the nursery but for two of the years with low abundance only an insignificant numbers reached the nursery. It was not possible to relate the observed age-0 index to either the commercial catches or VPA data.

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Introduction

The success of stock enhancing a marine fish stock, such as turbot Psetta maxima, with artificially reared individuals depends on several general issues and principles which have to be considered prior to the implementation. Among these is the viability of producing individuals in the aquaculture facilities, release strategy and survival after release, the carrying capacity of the environment, together with the impact from the released individuals on the wild stock (Blaxter, 2000; Støttrup and Sparrevohn, 2007). Adding more individuals into a stock can potentially result in an intra-specific competition for resources and ultimate, if the carrying capacity is reached, zero net population growth (MacCall, 1990). These aspects are not always analysed and taken into account in stock enhancement programmes. Not necessarily because it is complex, difficult and resource demanding to investigate, which it is, but because restocking and stock enhancement typically are carried out at low population levels where the saturation of the environment is not likely to be reached and hence density dependent processes are believed to be of minor importance.

Similar to most other marine fish species the overall cohort size for flatfish is believed to be mainly determined by density independent control, such as successful transport of larvae from the spawning areas to the nurseries. However, for flatfish density dependent regulation is also likely to play a role in the regulation of the cohort size. For flatfish there appears to be a relationship between the size of the area exploited by the juveniles and the size of the adult populations, a relation often referred to as the “Nursery size” hypothesis (Rijnsdorp et al., 1992; van der Veer, 2000a). It lies implicit within the “nursery size” hypothesis that the proportionality between egg production and the later recruitment is uncoupled somewhere between spawning and recruitment to the adult stock. This uncoupling is suggested to be caused by density dependent growth and/or mortality and to take place somewhere in the juvenile lifestage in which flatfish tends to concentrate in specific nurseries (Berverton, 1995; Iles and Beverton, 2000). Studies on plaice Pleuronectes platessa has shown that Crangon crangon induced density dependent mortality occurs during the first period in the nursery (van der Veer and Bergman, 1987), whereas proves of density dependent growth are more inconclusive. Some studies have shown it (Rijnsdorp and van Leeuwen, 1992; Modin and Pihl, 1994; Bolle et al., 2004) while other studies have not (van der Veer and Witte, 1993; van der Veer et al., 2000a).

For turbot it appears as if the likelihood of density dependent regulation is smaller than it is for plaice. Turbot is much less abundant and its dietary overlap with other flatfish species is restricted to the smallest individuals (Nissling et al., 2007). Turbot has a rather large increase in its available habitat during its first year of life, where its depth distribution increases from c. 1 m to c. 5 m. Finally, the size at which turbot settles is so large (Jones, 1973b; Gibson and Johnston, 1995) that a size refugee from Crangon crangon predation has been reached.

Even though, density dependent regulation seem as an unlikely mechanism in turbot cohort size regulation, it would be reasonable to apply a precautionary approach and attempt to release artificially reared fish in such a manor that that high abundances of turbot within a restricted areas is avoided and the best condition for growth and survival is provided. A first step in doing this is to select a proper release habitat, i.e. a habitat with ample space and food resources. Unfortunately, the availability of space and food resources in the marine environment is often not known on a detailed spatial scale. Instead the selection of a release area has often been based on knowledge on the distribution of the wild fish. In reality, those areas with an already existing population have typically been chosen as release habitats.

A second step in avoiding density dependent regulation is understanding the variation in age-0 abundance both on a spatial and an annual scale. With this type of knowledge at hand it would be possible to predict years with high age-0 abundance and identify areas, if any, characterized by always having a high or low abundance of age-0 individuals.

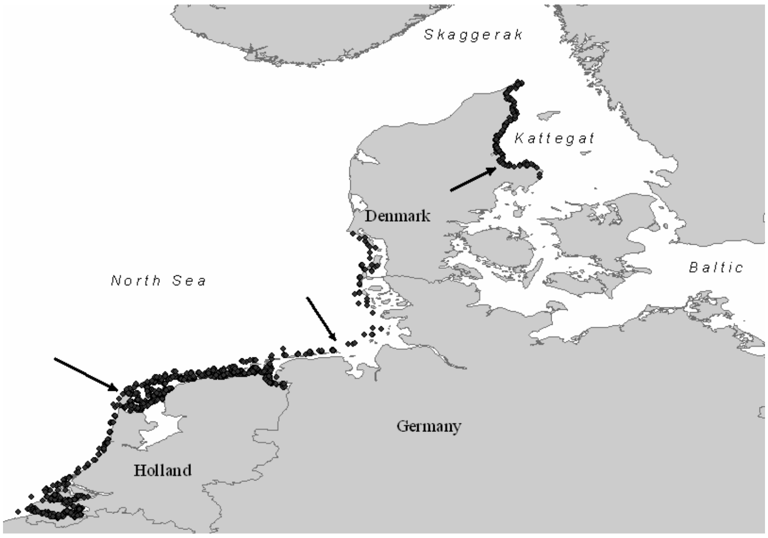

Figure 1. Map showing the areas sampled along the Dutch, German and Danish coastline. Black dots shows trawl positions. The Danish samples taken in Kattegat are the ones located to the east of Denmark and those west/south are the Dutch young fish survey samples. The arrows points to the positions used as fix points in the calculation of spatial distance. On the figure all years are shown but the spatial

By analysing time series from juvenile flatfish trawl surveys taken along the North Sea coast and the Kattegat coast, the present study investigates how the age-0 abundance varies in time and space. Based on this analysis a drift simulation experiment, where the drift pattern is mainly wind driven, is carried out for two reasons. First in order to examine whether the import of drifters from the spawning areas to the nursery differed between years characterize by high age-0 abundance and years with low. Secondly, to study if the connectivity between spawning areas and the nursery can explain whether the spatial distribution of the recruits along the coastline originated in the distribution of offshore spawning areas, or whether wind induced transport patterns of the planktonic egg and larval stages are responsible for the distribution Last the estimated age-0 cohort strength is compared to the commercial landings in the fishery and estimated population level from a VPA.

Material and Method

Survey data

Both data from Danish and Dutch juvenile flatfish sampling programs was analyzed. The Danish samples was trawl catches collected in the area between Skagen (57°43’06N, 10°41’28E) and Djursland (56°24’30N, 10°59’28E) along the Kattegat coast of Jutland, Denmark (Fig. 1). These samples were collected during two periods, the first from 1950-1971 and the second from 1985-2005. All fish caught was length measured to lowest mm and if possible divided into species. The Danish survey was carried out around July/August but the exact timing did differ from year to year. The number of hauls completed did also vary from year to year. From as low as 8 in 1987 to 90 in 1994, but in general around 60 hauls was taken each year. Years with less than 10 hauls were excluded from the further analyses. The gear used was a 4.5 m wide young fish trawl (See Støttrup et al., 2002 for further details on the gear) fished on depths between 1 m and 3 m. In general the same stations were visited annually, but since no exact geo-positions were available for the first period sampled the accuracy is unknown. The towing speed was keep steady around 1 nautical miles hour^{-1} and all trawling was parallel to the coast line. In total 1606 hauls was included from the Danish surveys and in those a total of 1784 turbot or brill was caught. Due to problems determine between brill and turbot smaller than 10 cm, the entire catch of turbot and brill of this size was pooled and termed “age-0 index”.

Figure 2. The Kattegat coast (KC) divided into the five sub-areas (1:5) used in the drift simulation. The hypothetical spawning grounds (North, Middle and South) are the shaded grey boxes.

The Dutch juvenile flatfish data was collected along the Dutch, German and Danish North Sea coast from the Belgian border (51°20’00N, 03°15’50E) to a little North of Esbjerg in Denmark (55°33’30N, 08°04’30E). These samples were collected between 1970 and 2002 during September-October. The gear was either a 3 m (estuaries) or 6 m wide shrimp trawl (coastal areas) that was towed at 3 nautical miles hour^{-1} (van Beek et al., 1989). In the Dutch samples problems separating between turbot and brill was not present hence only “true” turbot catches was included in the age-0 index. Number of hauls differed between years and years with less than 10 hauls were excluded. Since the Dutch samples program was designed to sample at somewhat deeper areas than the Danish program only hauls shallower than 5 m was included, but samples between 4 m and 5 m depth accounted for 80 % of the hauls taken. In the Dutch sampling program a total of 1773 haul were accomplished between 1970 and 2001.

In total 3 distinct areas was identified, one exposed area along the Kattegat coast (KC), one exposed along the North Sea coast (NSe) and one sheltered area also at the North Sea coast (NSs) (Fig. 1), where 400 hauls was taken in the area NSe during a 16 year period and 1347 hauls was taken in the area NSs during a 32 year period.

For both the Danish and the Dutch samples, catches was transformed into an age-0 index which equal the number of individuals caught 10.000 m^{-2} fished.

For all areas the yearly mean catch was calculated and plotted. Further the coefficient of variance (CV) was calculated from the standard deviation (sd) and the mean (Y) as:

$$CV = \frac{100 \cdot sd}{Y} \quad (1)$$

in order to produce a Taylor power plot for each of the areas.

Spatial differences between years

A Poisson family GAM model was set up to examine if the distribution of age-0 individuals along the coastline differed between years and if certain areas showed a higher age-0 index than others. Akaike information criterion (AIC) was used to evaluate the model. The smaller the AIC the better the model performed. This analysis was carried out for the two exposed areas; KC and NSe. For each area, the six year with the highest observed age-0 index was selected, whereas the rest of the years were excluded due to the low catch rate. This meant that the period 1982-1987 was analyzed for NSe and the years, 1955, 1958, 1966, 1988, 1992 and 1997 for KC. The analyses were ran seven times; first for all years combined and then for all six years separately. Dimension used in the spline smooth function were set to 5. As a measurement of the spatiality, the linear distance from a given fix point to the haul was estimated (Fig. 1). The fix point along KC was the position where the coast no longer was north-south bound but east-west. Distances north of the point were positive and distances east negative. At NSe two fix points had to be chosen in order to get a linear distance because the coastline change orientation at two locations. The southernmost fix point corresponds to a distance of zero and values south are negative.

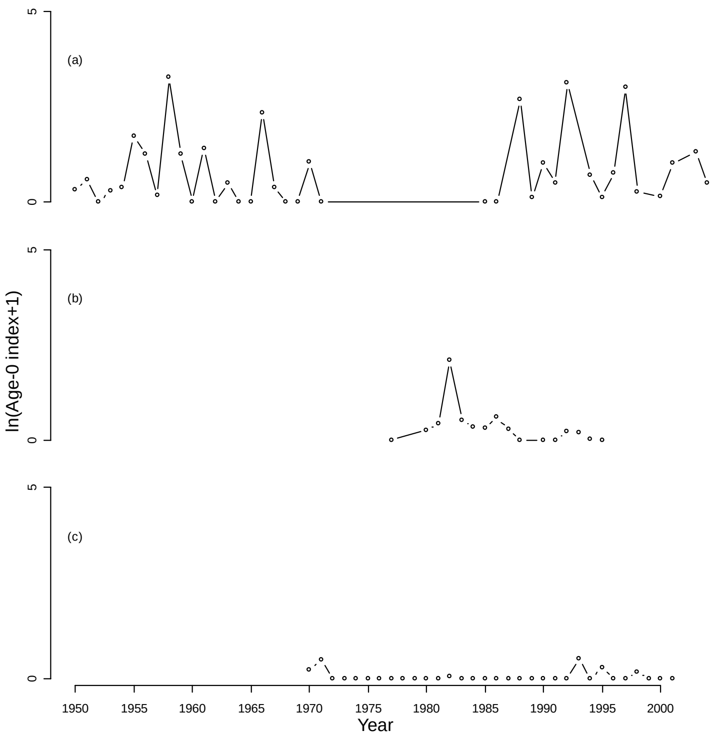

Figure 3. Age-0 index ln(x+1) transformed for each year. Panel (a) is the Kattegat Coast (KC), (b) is North Sea exposed (NSe) and (c) North Sea sheltered (NSs).

Drift simulation

For the Kattegat Coast (KC) a drift simulation was carried out based on a free surface Bryan-Cox-Semtner hydrodynamic model (Semtner, 1974; Cox, 1984). A detailed description of the equations, modifications and verifications can be found in Lehmann (1995); Hinrichsen et al., (1997) and Lehmann and Hinrichsen (2000).

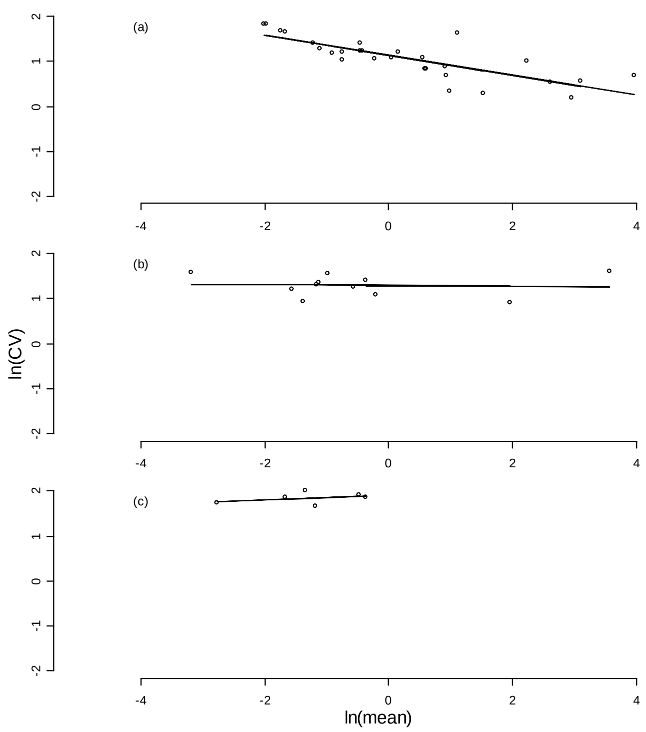

Figure 4. Taylor power plot of the ln transformed coefficient of variation (CV) for the annual age-0 index verses its mean. The CV was estimated according to eq. 1. Panel (a) is KC, (b) is NSe and (c) NSs.

A fixed number of drifters,

with no degradation were released at one of six depths: 1, 3, 5, 7, 9 and 11 m at 1st, 5th, 10th, 15th or 17th of May. These start dates was not chosen according to peak spawning, which is probably later at least for the North Sea turbot (Rae and Devlin, 1972; Jones, 1973a). Instead the start dates was estimated on basis of the observed length of turbot caught during the survey the corresponding year. The egg development time was set to 150 hours and the developmental time to 45 days [Jones (1973b) found that metamorphosis took place between 45 and 72 days, but according to the commercial hatchery Maximus it only takes 28 days (pers. Comm.)]. The size at settling was assumed to be 3 cm and subsequent growth 2 cm per month.

Drifters were released uniformly over three different hypothetical spawning areas, referred to as North, Middle and South (Fig. 2). These areas were selected on the basis of anecdotic information from fishermen. For each year, depth and date combination, 40 drifters were released at the North spawning area and 81 at the Middle and the South spawning areas. The end position of the drifter was determined together with the "realized" temperature and salinity, i.e. the temperature and salinity that the drifter had experienced from release to end. The end position was grouped into five sub-areas along the coast line (Fig. 2). Those drifters that did not end up in any of the five areas were grouped into either Kattegat or Skagerrak, where a drifter that was caught to the East of Skagen was classified as Kattegat and those to the west were classified as Skagerrak. The connectivity between the spawning areas and the coastal nurseries was evaluated for each release depth, spawning area and year and expressed as the fraction of drifters ending up in each of the end-

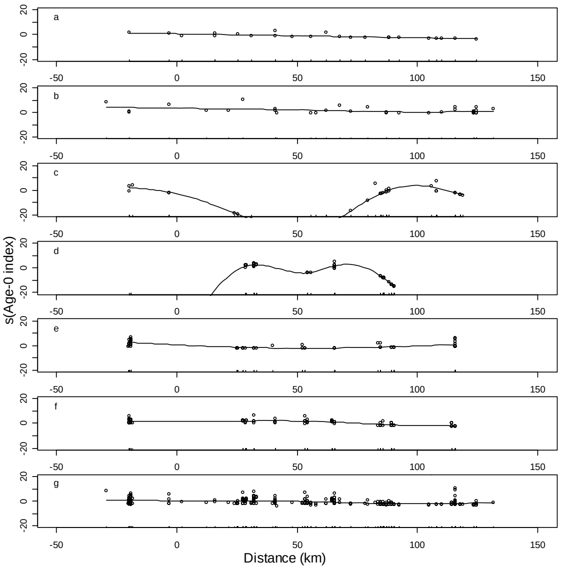

Figure 5. The GAM fitted function of the additive effect from the spatiality (distance) on the age-0 index of KC, on the scale of the linear predictor (log). The black ticks shows the distances where sampling took place and the circles are the residuals. Panel (a) to (f) is the years: 1955, 1958, 1966, 1988, 1992 and

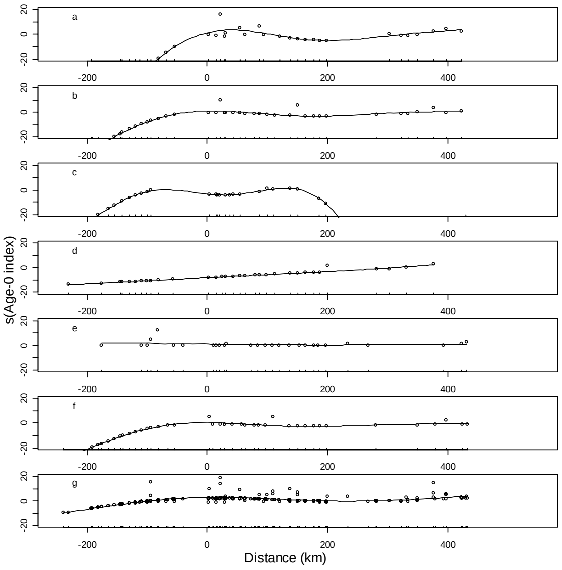

Figure 6. The GAM fitted function of the additive effect from the spatiality (distance) on the age-0 index of NSe, on the scale of the linear predictor (log). The black ticks shows the distances where sampling took place and the circles are the residuals. Panel (a) to (f) is the years: 1982 to 1987 and panel (g) is all six years combined.

positions.

In total the simulation was carried out for six years, three of the years was selected because they where characterized by a very low age-0 index (1985, 1998 and 2000) and three years were selected as they were showed a high age-0 index (1988, 1992 and 1997).

Table 1. The realized temperature (°C) for those simulated driftes that ended in one of the 5 areas investigated. Only drifters at depth 7 and 9 are included. The years 1985, 1998 and 2000 are years with high age-0 index and the other three years with low.

	Year					
Area	1985	1998	2000	1988	1992	1997
1	11.6	10.9	NA	11.7	13.2	NA
2	11.9	11.5	NA	12.9	12.7	12.0
3	12.3	11.9	12.5	13.8	14.1	11.5
4	12.5	12.1	12.8	13.0	13.3	10.3
5	12.0	12.4	11.4	13.1	NA	13.7

Table 2. The realized salinity (‰) for those simulated driftes that ended in one of the 5 areas investigated. Only drifters at depth 7 and 9 are included. The years 1985, 1998 and 2000 are years with high age-0 and the other three years with low.

	Year					
Area	1985	1998	2000	1988	1992	1997
1	25.6	26.1	NA	27.5	23.5	NA
2	25.6	25.8	NA	26.8	27.9	27.2
3	25.3	25.9	24.6	26.1	22.2	27.1
4	25.6	25.4	24.0	26.0	27.6	28.7
5	27.6	25.0	26.6	26.4	NA	20.0

Commercial data

Annual landings from Danish vessels between 1978 and 2006 were obtained from the Danish fisheries department. Catches in the North Sea was the sum of the ICES areas: IVa, IVb and IVc. All catches from Kattegat was caught within ICES area IIIas. The relationship between the estimated age-0 index and the commercial catches three years later was plotted. The reason for choosing a time lack of three years is that in the North Sea fishery very few younger non-mature individuals appeared in the catches (Rae and Devlin, 1972) and the mean size in the fishery lies around 40-44 cm (Jones, 1970). Since Weber (1979) did find that turbot recruited to the fishery already at age 2 the analyses with a time lack of two years was also tried out, but with a similar result.

For the North Sea turbot population abundance at age is estimated from VPA for the period 1981 to 1990 (Boon and Delbare, 2000). The age-0 index NSe was compared to the estimated abundance of the same cohort at age 2.

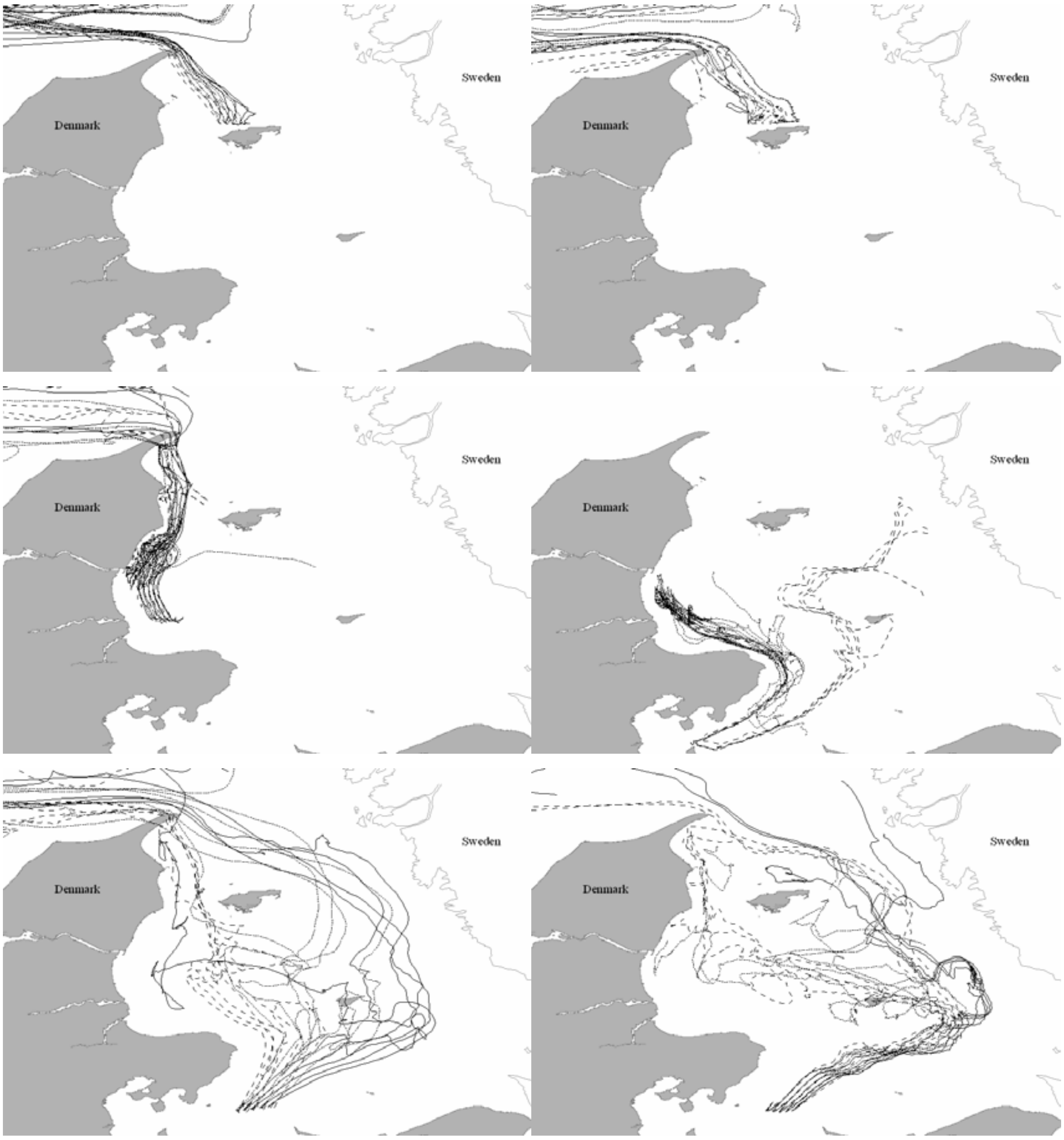

Figure 7. Each map shows drift trajectories for 5 drifters released in 1988. Top panel is drifters released at the northern spawning size, middle panel is drifters from the middle spawning site and bottom panel is drifters released at the southern spawning area. Figures in left column are drifters released at depth 1, 3 and 5 m shown by fine dashed, coerce dashed and solid line, respectively. Figures in the right column are drifters released at 7, 9 and 11 m, shown by fine dashed, coerce dashed and solid line, respectively.

Results

For the area NSs 81 % of the years sampled had no age-0 turbot in the catches, along the KC 27 % of the years had no age-0 catches and for NSe the figure was 16 % (Fig. 3). For KC the catches was highly variable and showed large annual fluctuations during the entire sampling period. Along the NSe the highest catches was observed in the period around 1980-1990. In NSs no catches was observed during this period but after 1990 turbot was caught during years where no turbot was observed in the more exposed NSe.

The coefficient of variation (CV) was for the unexposed area (NCs) higher than for the exposed areas (Fig. 4). The level of variation was the same order of magnitude for the two exposed area NCe and KC but along the KC there was a significant decrease in CV with increasing age-0 index.

Spatial variation

For the KC the model where distance was included did perform better (AIC=1924) than a model where only year was used as an expletory factor (AIC=2946). Analyzing the trend for each single year did not revile any general trend, i.e. no certain areas showed a consistent high or low abundance of age-0 individuals. (Fig. 5). For the area NSe there was a tendency for lower catches for the negative distance values, i.e. along the Dutch coast south of the southern fix-point (Fig. 6).This was supported by the AIC which increased from 909 to 1333 when distance was removed from the model. The general tendency towards lower catches in the south could be seen both for most of the years examined and when analysing all the years combined.

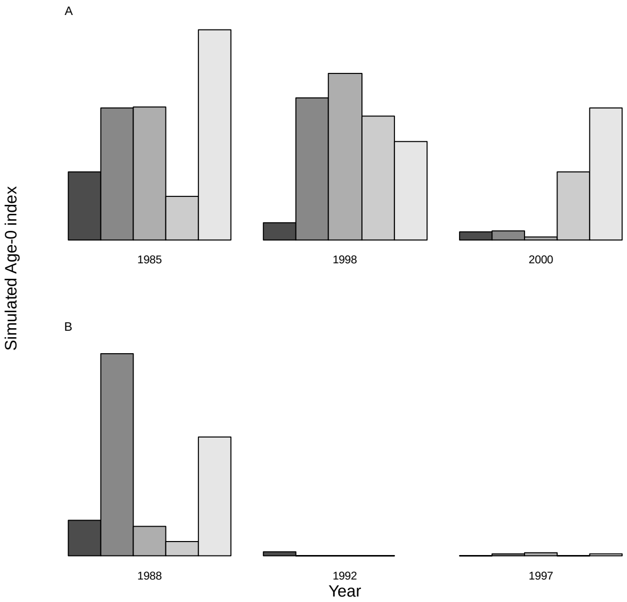

Figure 8. Barplots of the simulated age-0 density, i.e. the numbers of drifters that ended in one of the 5 sub-areas investigated. Only drifters at depth 7 and 9 are included. The 5 different areas are shown by the colors black to white; where black is area 1 and white area 5. Panel (A) is three years with an observed high abundance in the surveys and panel (B) is three years with observed low abundance.

Drift simulation

The overall picture from the drift simulated was that the transport of drifters released at 1, 3 and 5 m was in general different from those released at 7, 9 or 11 m (Fig. 7; Appendix, table A and B). It was also seen that the exact release depth did have a profound influence on the faith of the drifter. In most cases, all drifters released at 5 m depth or above were transported out of the KC area and into the Skagerrak or North Sea (Appendix, table A and B). It was clear that the drifters released at deeper water had a much higher chance of ending up in the nursery along the coast line. For the three years with an observed high age-0 index drifters were transported into all five areas for all three years, but with varying frequency (Fig. 8a). During the years with an observed low age-0 index only a minor fraction of the drifters was transported onto the coast for two of the years simulated (Fig. 8b). For the two southernmost spawning areas connectivity to all five areas was evident (Appendix, table A and B). The Northern spawning area was only able to support the two northern areas, i.e. area 4 and 5. The temperature tracked by the drifters varied between 11 and 14 degrees and the salinity varied around 25 ‰ (Table 1 and 2). The variation in temperature and salinity between years with high and low age-0 index was lower that the variation within.

Commercial data

The landing in the commercial fishery of turbot was independent of the age-0 index sampled three years earlier (Fig. 9). The same lack of relationship was observed when the age-0 index was compared to the VPA estimates from Boon and Delbare (2000).

Discussion

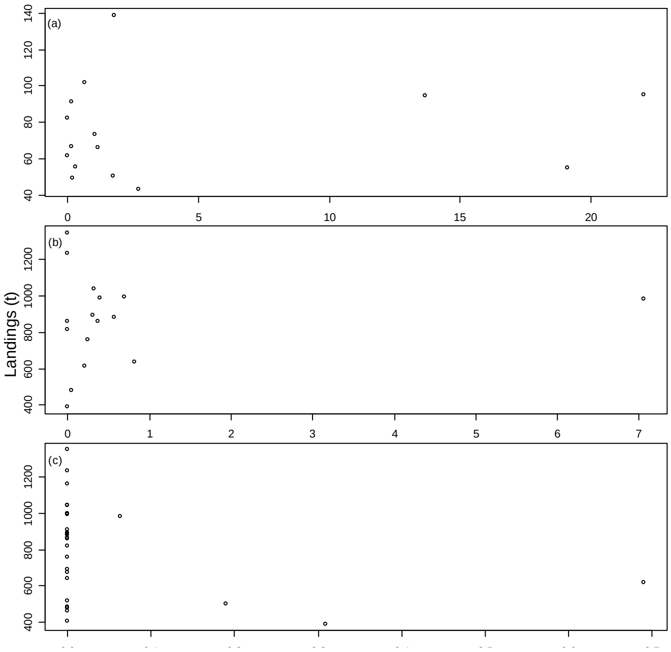

Figure 9. The relationship between the age-0 index and the catches in the Danish commercial fishery three years after the age-0 index. Panel (a) is KC, (b) is NSe and (c) NSs.

The variability in the annual age-0 index was somewhat higher for the shelter area (NSs) than the exposed. Compared to the samples taken in North Sea the Kattegat variability was depending on the mean age-0 index. A good year (i.e. years with high age-0 abundance) has a relative lower variability than a year with low abundance. This indicates that with high abundance the density of turbot will tend to even out in the spatial dimension. The mechanism behind this relationship could be one of many, such as species interactions (Kilpatrick and Ives, 2003), spatial variations in the carrying capacity (Benton and Peckerman, 2005), transport of larvae and density dependent factors within the nursery ground, but which is not possible to determine. Even though turbot is rare and varies substantially in abundance signal, a precautionary approached when releasing artificially reared individuals should be applied. The releases should be conducted in such a way that the risk of density dependent regulation of the age-0 cohort size is minimized. Unfortunately getting a thorough knowledge on when and where density dependent factors have the potential to regulate the age-0 abundance requires an intensive ecological and biological study. Since no detailed studies on the nature of density dependent processes, if any, is available for turbot, indirect measures of density dependent factors could be examined instead.These indirect measures could be altered distribution within the habitat such as a change in depth distribution or migration into less optimal areas.

Age-0 turbot is known to inhabit restricted nursery grounds as it is primarily found in the shallow surf zones of exposed areas (Gibson, 1973; Riley et al., 1981; van der Veer et al, 2000a). As predicted by MacCalls habitat basin model (1990) the result of an over saturation of these areas would be a spill over of individuals into less suitable habitat. Indication of an altered depth distribution of turbot in areas with high abundance has been observed (Sparrevohn and Støttrup, 2008). In present study no relationship between a high age-0 index in the preferred North Sea habitat (i.e. the exposed area) and the inner unexposed area (NSs) was evident. This observed de-synchronism in age-0 index between the exposed and unexposed area, could be caused by an altered transport pattern from the spawning area to the coast and that the unexposed areas could constitute an unoccupied nursery habitat. Unexposed areas that in some cases are able to provide the turbot with better feeding conditions than exposed areas (Nissling et al., 2007, Sparrevohn and Støttrup, 2008). If this is the case then stock enhancement through releases of artificially bred individuals into these areas will be prosperous, independent off the natural year class strength.

For the Kattegat coast (KC) no overall trend in the spatial distribution of recruits along the coast line was present, which showed that a high abundance of age-0 individuals was not consistently more likely to be present in certain areas. For the NS there was a slight tendency for lower age-0 index in the most southerly areas. The apparent random distribution of recruits along the KC has the consequence that when planning releases for stock enhancement they might as well be uniformly distributed along the entire coastline since there appears to be no areas with higher abundance of natural age-0 individuals than others.

A connection between wind and juvenile abundance has been established for species such as Kattegat plaice (Nielsen et al., 1998) and brown sole (Pleuronectes herzensteini) (Nakata et al., 2000), and it is plausible that the connection is even more pronounced for turbot. This is due to the fact that turbot larvae have been observed in the very upper top layer of the water-column and that Scophthalmidae has a swimbladder in contradiction to e.g. Pleuronectes (Evseenko, 1981). A relationship between onshore wind and abundance of juveniles has also been found (Riley et al., 1981).

The observed loss of those drifters located in the upper water layers could indicate that the larvae in Kattegat are located deeper in the water column than in the North Sea. Kattegat turbot will still rely on wind driven transport, which is ultimate driving force in the drift simulation, but vertical migration might be involved in increasing the likelihood of encountering a nursery. In the Kattegat the tidal amplitude is small, so it would not be expected that turbot larvae shows a selective tidal stream transport behaviour as observed for several other flatfish species (see Bailey et al., 2005 for an overview), but since it was observed that even a few meters difference in depth distribution could result in significant different counter lateral drifting pattern vertical migration of the larvae is likely.

That the transport mechanism is involved in controlling age-0 cohort strength is further supported by the fact that a higher rate of successful transport to the nurseries was seen for those simulations carried out for years with a high age-0 index compared to years with low. Differences in the temperature and salinities between years did not seem different and is hence probably not involved in creating variation in the age-0 index observed in the surveys.

Turbot is believed to spawn offshore but the exact spawning grounds for Kattegat turbot are unknown maybe due to that they are as poorly defined, as is seen for turbot in the Scottish part of the North Sea and in the German Bight (Rae and Devlin, 1972; van der Land, 1991). In present study large variation in transport pattern from the supposed spawning areas to the coast was indeed present. The two southern spawning areas were able to supply all the sub-areas along the KC with larvae. This showed that even with a restricted spawning area, which is probably not the case for turbot the variation in transport pattern is substantial and able to explain the observed random spatial distribution of the age-0 cohort.

The lack of correlation between the observed age-0 index and the later catches in the commercial fishery could either indicate that the age-0 index is not representative for the total year class strength or that the cohort strength is not established at the age-0 level. It seems likely that the explanation should be found in the fact that the surveys are insufficient in terms of sampling the nursery appropriate both in a temporal and spatial dimension. The entire coastline is not sampled, which might have severe implications for a species like turbot where large differences in the larvae transport are observed. We do not know if the areas not sampled might play a central role as nursery those years where larvae are not transported to the area covered by our surveys. Second the timing of the surveys might not ideal in order to cover the total settling period, which extend from July to end September (Jones, 1973a).

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Appendix:

Table A. The end position of drifters released at the three high age-0 index years at a given spawning area and depth. The percentage of drifters that ended up in area 1:5, Kattegat or the Norh Sea. Since the drift pattern was very alike for the drifters released at depth 1,3 and 5 m these has been pooled.

Year	Spawning Area	Depth	Area 1	Area 2	Area 3	Area 4	Area 5	Kattegat	North Sea
1985	South	1,3 and 5	2.7	8.0	4.8	2.3	3.4	37.9	40.9
		7	7.4	18.1	10.3	7.0	9.9	32.1	15.2
		9	7.0	12.8	4.1	3.3	14.4	53.5	4.9
		11	8.2	2.5		0.4		88.9	
	Middle	1,3 and 5	4.4	15.4	2.1	0.1	1.9	28.5	47.6
		7	4.1	6.2	23.9	2.9	5.8	13.2	44.0
		9	3.3	4.9	4.1	0.8	33.7	8.6	44.4
		11		10					
	North	1,3 and 5							100
		7							100
		9					6.7		93.3
		11					2	2	6
1998	South	1,3 and 5		0.3	1.1	1.4	2.1	68.4	26.7
		7	0.4	15.6	14.4	7.4	2.9	32.9	26.3
		9	4.9	16.5	7.4	2.5	7.8	47.7	13.2
		11	2.9	21.4				65.8	9.9
	Middle	1,3 and 5	0.4	1.6	3.2	2.1	1.5	57.9	33.3
		7		4.5	14.4	21.4	12.3	38.3	9.1
		9		8.6	15.2	6.2	5.3	56.0	8.6
		11	0.4	56.8			0.4	40.3	2.1
	North	1,3 and 5			0.3	0.8	1.4	11.7	85.8
		7					3.3		96.7
		9			3.3	4.2	2.5	0.8	89.2
		11					12.5	18.3	69.2
2000	South	1,3 and 5	0.1	0.3	0.3	0.8	1.4	18.4	78.7
		7		0.8		0.4	4.5	26.3	67.9
		9	1.2	0.4	0.8	1.2	2.9	46.5	46.9
		11	2.9	50.6				40.7	5.8
	Middle	1,3 and 5	0.3		0.3	1.8	2.6	9.5	85.6
		7		0.4		7.8	23.9	25.1	42.8
		9	1.2	1.2		2.5	24.7	39.1	31.3
		11	0.8	74.5	3.7			20.6	0.4
	North	1,3 and 5				0.3	18.6	1.4	79.7
		7						4.2	95.8
		9					5.0	8.3	86.7
		11					2.5	31.7	65.8

Table B. The end position of drifters released at the three low age-0 index years at a given spawning area and depth. The percentage of drifters that ended up in area 1:5, Kattegat or the North Sea. Since the drift pattern was very alike for the drifters released at depth 1,3 and 5 m these has been pooled.

Year	Spawning Area	Depth	Area 1	Area 2	Area 3	Area 4	Area 5	Kattegat	North Sea
1988	South	1,3 and 5	0.5	4.1	2.1	0.3	6.2	4.5	82.3
		7	0.4	14.8	3.3	2.1	2.5	56.8	20.2
		9	3.7	7.0	0.4	0.8		84.0	4.1
		11	5.8	7.0				79.0	8.2
	Middle	1,3 and 5	4.0	2.9	8.4	0.4	10.4	1.0	73.0
		7	1.6	12.3	3.7	0.8	14.0	28.0	39.5
		9	5.3	30.5	2.1	0.8	20.6	17.3	23.5
		11	0.8	94.2				4.9	
	North	1,3 and 5						2.8	97.2
		7					1.7	1.7	96.7
		9							10
		11				0.8	0.8	17.5	80.8
1992	South	1,3 and 5			0.8	1.1	0.8	14.3	83.0
		7					3.7	27.2	69.1
		9	0.4				9.1	21.8	68.7
		11	0.4	28.4	1.2			62.6	7.4
	Middle	1,3 and 5			0.4	0.3	0.3	6.2	92.9
		7	0.4				8.2	14.8	76.5
		9	0.4				7.8	17.3	74.5
		11		70.8	2.1			22.2	4.9
	North	1,3 and 5							10
		7					5.8	3.3	90.8
		9					7.5	11.7	80.8
		11				0.8	1.7	19.2	78.3
1997	South	1,3 and 5						0.8	99.2
		7					0.4	14.0	85.6
		9		0.4	0.4		7.4	4.9	86.8
		11	0.4	69.1	4.9		0.8	8.6	16.0
	Middle	1,3 and 5							10
		7			0.4		1.6		97.9
		9					11.5		88.5
		11		10					
	North	1,3 and 5							10
		7					3.3	1.7	95.0
		9					2.5		97.5
		11					2.5	17.5	8

Chapter 4

The use of releases of reared fish to enhance natural populations. A case study on turbot Psetta maxima (Linné, 1758).

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The use of releases of reared fish to enhance natural populations A case study on turbot *Psetta maxima* (Linné, 1758)

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Abstract

Turbot *Psetta maxima* (Linné, 1758) were used as a model species to test if flatfish populations can be enhanced through regular release of reared fish. During 1991–1998, 10,000 I-group fish (11–16 cm) and during 1993–995 around 100,000 0-group fish (4–6 cm), were released each year in the Kattegat, off the northern coast of north Zealand, the most wind and wave exposed site in the inner Danish waters. The larger fish were tagged external, numbered, T-bar tags, whereas the smaller fish were marked with alizarin complexone. The size at release of the reared fish was similar to that of their wild counterparts, although the 0-group released fish were smaller than the average wild fish. The released fish showed a much narrower length distribution due to regular size sorting in the hatchery. The growth of released fish marked with alizarin was similar to or higher than that of their wild counterparts, whereas the externally marked fish grew slower, probably as a result of the external tag. The mortality of the released fish was very variable and relatively high, but was comparable to that of the wild turbot. The releases constituted around a third of the 0-group and almost half of the I-group wild counterparts. Most of the recaptures were close to the release area. Migration of the cultured 1-year-old turbot was less than 10 km and they remained close to the shore during the first 2 years after release. This was followed by a sharp increase in migration distance with an offshore direction, possibly related to spawning behaviour. No apparent difference in depth distribution between cultured and wild turbot was evident and both groups showed the same differences in depth distribution during night- and daytime. No evidence of displacement of the wild stock was found based on the findings of similar growth, similar size distribution in the later year classes and constant ratio of reared and wild fish in the catches. The results suggest that release of reared turbot may result in an increase in fishery recruitment.

Keywords: *Psetta maxima*; Turbot; Stocking; Growth; Mortality; Migration; Tags

1. Introduction

Stocking is often the first avenue examined to solve problems with declining stocks. Since the turn of the last century, cod *Gadus morhua* eggs and newly hatched larvae have been released in millions (Solemdal et al., 1984; Shelbourne, 1964), but evidence of the beneficial effects on cod recruitment were not forthcoming. More recent trials using genetically marked cod larvae have confirmed the futility of such an exercise due to the high mortality during this stage (Kristiansen et al., 1997). In the freshwater environ-

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ment, stocking has taken place for decades with varying success (Näslund, 1998; Rasmussen and Geertz-Hansen, 1998; Saltveit, 1998). Due to the recent developments in aquaculture, marine species can be reared to different sizes and this coupled with increasing problems with sustainable management of natural stocks and drastic declines in the fisheries has rekindled interest in stocking to remedy the decline of stocks.

For stocking to succeed, the species chosen must be recruitment-limited at a stage prior to that being released, thus avoiding possible displacement problems and allowing for the potential for enhancing the natural stock. Strong evidence that the year-class strength is determined during the pelagic stage and/or very early settling-stage of 0-group in the nursery grounds was demonstrated for plaice *Pleuronectes platessa* (van der Veer et al., 1990). This was also indicated for other flatfish species such as sole *Solea solea*, dab *Limanda limanda* and flounder *Platichthys flesus* (van der Veer et al., 1991; Rijnsdorp et al., 1992; Henderson and Seaby, 1994). Heavy mortality during the first week after settlement due to predation was shown for hirame (Japanese flounder) *Paralichthys olivaceus* in a nursery ground in Japan (Tanaka et al., 1989). Experiments with transplanting larger juvenile plaice from areas of high density and low growth to other areas under-utilised by flatfish were successful on a small scale in that the fish remained and grew faster in the new site (Bagge, 1970). These findings formed the foundations for the hypothesis for stocking flatfish in our study that the supply of late 0-group juveniles to the nursery grounds was limited and that there was a suitable habitat with available food for the juvenile stage. Turbot *Psetta maxima* is not a targeted species in the Kattegat fisheries, its population is not assessed and no quotas are given for this species, neither is the population suffering from severe decline. It was chosen for this work as a model fish for flatfish, primarily because it is an important bycatch species in the Kattegat fisheries, and it is grown in aquaculture, which ensures a steady supply of juveniles for this study.

Economic appraisals of stocking species such as cod and turbot showed survival to be the most important factor influencing profitability and where survival could not be improved, costs of juvenile production needed to be reduced significantly for profitable releases (Sproul and Tominaga, 1992; Moksness and Støle, 1997). Displacement of the wild population by the released fish may also influence any economic benefit of a release (Leber, 1995), affecting the survival of the natural population. Survival rates of the released fish should be at least comparable to that of the natural population and should not affect that of the natural population. This entails the availability of suitable habitat for the released fish as well as quick and effective adaptation to the natural environment. In particular, there must be the ability to remain in a suitable habitat, to feed on natural prey items and to avoid predation.

Yamashita and Yamada (1999) proposed concentrating the release to one position in order to avoid an unnecessary loss of fish to predators. This may be an appropriate strategy for those species, or those size ranges exposed to a high predator pressure. An alternative strategy for those species, or those size ranges, which are not subject to a high predator pressure, should be to release smaller batches in different localities in order to fully exploit the available food resources in the area. Consequently, when choosing an appropriate release strategy, the nature and rate of the horizontal migration by the released fish are important parameters to monitor and also include movements related to depth distribution. The depth distribution of flatfish depends on several abiotic factors such as tidal amplitude, time of day and season (Gibson, 1973; Gibson and Robb, 1996; Gibson et al., 1996, 1998). In addition, preferred depth changes with increasing age/length and vary between species. Other biotic factors such as the distribution of potential predators and competitors for 0-group can affect their depth distribution (Gibson et al., 1998).

The primary objective of this work was to study the growth, survival and distribution of released turbot using tag-recapture experiments. In addition, the impact of the releases on the wild population was investigated. The commercial and research survey recaptures provide data for the estimation of growth and survival of the released and natural populations. They also provide information on their spatial distribution and migration patterns. On the basis of these data the basic question on whether or not released fish contributed to increasing recruitment and the stock was examined.

2. Materials and methods

2.1. Tagging and release

Each year from 1991 to 1998, around 10,000 juvenile turbot larger than 10 cm were purchased from local commercial hatcheries and tagged with numbered T-bar tags obtained from Hallprint, Australia. Around 100,000–150,000 juvenile turbot (0-group; 4–6 cm) were marked with alizarin and released during September each year from 1993 to 1995. The turbot were either reared in intensive systems on rotifers and *Artemia* nauplii, or in outdoor tanks on enhanced natural plankton supplemented with *Artemia* nauplii. The broodstock originated from the Skagerrak near the boundary to the North Sea. They were weaned onto dry feed after metamorphosis. Date, numbers, origin, average fish size and type of tag used for each release are given in Table 1.

2.2. Transport and release

The fish were collected from the rearing facilities and transported in fish-transport trucks. Transportation time varied from 8 to 12 h and the fish were provided with aeration from a bottom grid. The oxygen levels were kept at around 100–110% throughout the transport. The fish were released directly from the truck through a pipe while sailing on board a ferry. Every effort was taken to ensure similar temperatures at hatchery and release site, either by adjusting the temperature in the hatchery over a period of time, or where this was not possible, shifting the time of release until ambient temperature at the release site matched that in the hatchery.

2.3. Release site

The fish were released off the northern coast of Zealand, the most wind and wave exposed coastline in the inner Danish waters (Fig. 1). Stone reefs and hard-bottom covered with stones or gravel dominate interspaced with areas of coarse sand (Anon., 1996). This coastline is characterised by prevailing westerly winds and a broad salinity range (10–30‰) caused by mixing of bottom water flowing in from the North Sea (32–35‰) and Baltic water (8‰) (Rasmussen, 1995). The upper 10 m are not well mixed vertically, and to the west (the Belt) and east (the Sound) of the north Zealand coastline, salinity boundaries are defined by the major flow of water exchanges between the North Sea and the Baltic Sea.

The harbour at the release site is an average size harbour with around 150 vessels (Lars Brünner, pers.

Table 1
Date, number of turbot released, origin, average size and type of tag used for each release in north Zealand, Denmark

Date (code)	Numbers released	Origin (hatchery)	Average size (cm ± S.D.)	Type of tag
7 May 1991 (Spring 91)	4474	Maximus	11.4 ± 0.7	T-bar
8 August 1991 (Autumn 91)	4366	Tinfos Aqua.	11.4 ± 0.9	T-bar
1 May 1992 (Spring 92a)	4940	Thy Aqua.	11.7 ± 0.9	T-bar
1 May 1992 (Spring 92b)	3013	Morsø Aqua.	11.8 ± 1.3	T-bar
21 April 1993 (Spring 93)	9939	Maximus	10.9 ± 0.6	T-bar
6 October 1993 (Autumn 93)	80000	Maximus	05.3 ± 0.4	Alizarin
14 April 1994 (Spring 94)	9762	Thy Aqua.	13.4 ± 0.8	T-bar
12 September 1994 (Autumn 94a)	42000	Lars Back	06.0 ± 0.7	Alizarin
13 September 1994 (Autumn 94b)	111000	Maximus	04.6 ± 0.5	Alizarin
3 May 1995 (Spring 95-I)	1917	Maximus	15.0 ± 1.4	T-bar
3 May 1995 (Spring 95-II)	1973	Maximus	15.3 ± 1.1	T-bar
3 May 1995 (Spring 95-III)	1977	Maximus	14.0 ± 0.8	T-bar
3 May 1995 (Spring 95-IV)	1968	Maximus	15.0 ± 0.9	T-bar
3 May 1995 (Spring 95-V)	1972	Maximus	11.4 ± 0.3	T-bar
5 September 1995 (Autumn 95)	101100	Maximus	04.1 ± 0.3	Alizarin
19 April 1996 (Spring 96)	5579	Maximus	10.8 ± 1.1	T-bar
14 April 1997 (Spring 97)	31479	Maximus	10.6 ± 2.0	T-bar
16 April 1998 (Spring 98)	19641	Diat Aqua.	18.8 ± 2.7	T-Bar

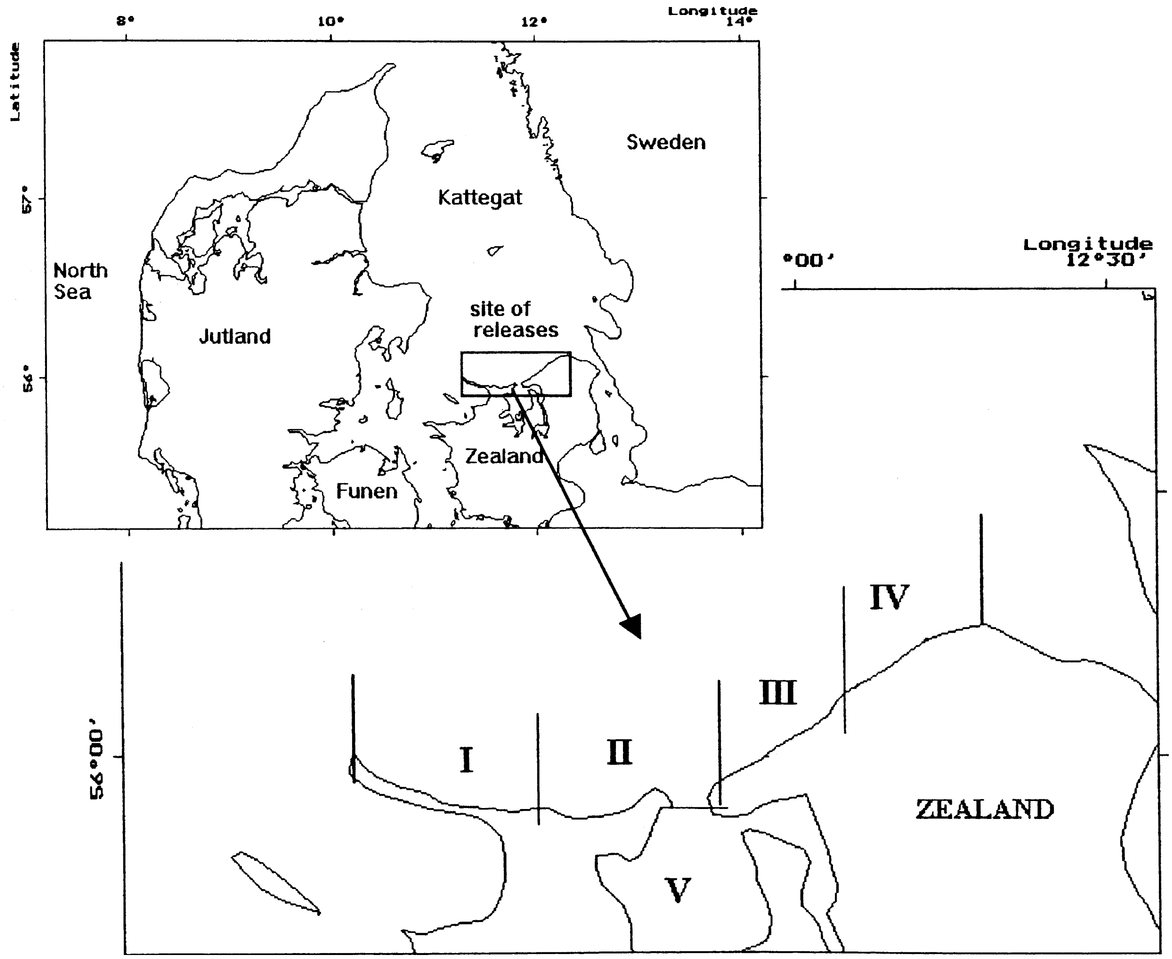

Fig. 1. The release and survey area was located in the southern Kattegat along the northern coastline of Zealand, Denmark. This area was subdivided into five, four of these along the northern coastline, the fifth being the fjord adjacent to the release site.

comm.). Gillnetters are more common than trawlers fishing sole, flounder and plaice from March to November. From around May, the gillnetters also catch turbot. Around 40% of the boats are trawlers which fish year round for cod and in season Norway lobster, sole, plaice or flounder. Trawlers catch turbot during January.

2.4. Research surveys

The survey area covered the whole of the northern coastline of Zealand from the shoreline to 20 m in depth. This was subdivided into five areas, four of these along the northern coastline, the fifth being the fjord adjacent to the release site (see Fig. 1). The releases took place in subdivision III except during 1995 where around 2000 fish were released in each of the five subdivisions (Table 1). Each year from 1994, four fishing surveys were conducted to recapture the released fish and catch wild specimens. A standard juvenile trawl was used for small fish towed for 10 min at 1 knot (40 m min^{-1}). Total length of the net is 10.8 m. The trawl is attached directly to 14 kg otter-boards measuring 85 × 50 cm separated by a 5.5 m long chain. The height of the opening is estimated at 36 cm. The body is divided into three sections with decreasing stretched mesh size of 10, 8 and 6 mm. The stretched mesh size of the cod end is 5 mm.

For the larger fish, a standard research trawl (TV3-trawl) was employed, which catches a broad size-range of different flatfish and demersal species such as turbot, plaice, sole and cod. The total length of the net is 41 m with belly and codend stretched mesh sizes of 80 and 20 mm. The 33 m long headline is fitted with floats providing a buoyancy of 38.5 kg, and the 36.5 m ground rope is fitted with rubber discs and a 20 kg wingend chain. Seventy-five meter sweeps attach the trawl to 90 kg Munkebo 60″ doors (90 × 154 cm). The trawl is towed for 15 min at 3 knots (92.6 m min^{-1}). Trawling hour was chosen to represent trawl effort. Gillnets normally used for sole (96 mm stretched mesh size, 50 m long) were also used and were deployed around sunset and tended at the latest 1 h after sunrise. Gillnet effort was estimated per length gillnet deployed. To analyse the depth distribution, the catches were divided into three depth strata: 0–2, 2–4 and >4 m.

The local fishermen were encouraged to return tags and provide data on the catch and the size and condition of the fish. This was done through posters on the releases, and the offer of a reward of approximately 4 EURO for each tag returned. To improve the quantity and quality of the information received with the returned tags, a talk was given at an annual meeting of the local fishermen, and information on the work was provided through local newspapers and fishermen's journals and annual letters to individuals who had returned tags.

2.5. Growth

Direct length measurement to the nearest lower $\frac{1}{2}$ cm of the fish at release and recapture was used to estimate individual growth rates. Recaptured alizarin-marked fish and wild specimen were aged from their otoliths for comparison of growth between wild and reared fish. The age–length key was based primarily on fish less than 20 cm as larger turbot were rarely encountered. Because of the relatively short time at liberty the comparison of growth between wild and reared turbots was best done using a linear growth model. Further, growth was divided into summer and winter periods and only growth during the summer period was estimated. The summer period represented the observed growth season for turbot as well as the commercial and survey fishery period (May–October).

2.6. Mortality

The number of annual recaptures in the commercial fishery was used to obtain a rough estimate of the mortality rate for each released batch using the simple regression of logarithm of numbers caught per year at liberty.

$$\ln(\text{numbers}) = a + b(\text{years at liberty})$$

The slope from these regressions represents the total decrease in the marked fish abundance, and can be viewed as a mortality estimate. Further, a GLM model, assuming an equal slope for each regression line was used to obtain one estimate for the mortality of the combined releases. Both approaches assume a constant fishing effort throughout the experimental period and do not account for a possible high initial mortality just after the release. Two alternative effort-independent models were also applied to the data, the Jolly and Seber model (Seber, 1973) and the Fisher and Ford model (Begon, 1979). The major difference between these two models lies in the assumptions. Fisher–Ford assumes a constant mortality throughout the experimental period, whereas the Jolly–Seber model assumes a constant mortality rate between two consecutive releases. It is also the case for these two models that they are not able to account for a possible high initial mortality just after the release. For these analyses, T-bar tagged specimen caught in the commercial fishery (T-bar C) and those caught during surveys (T-bar S) were separated into two groups. The alizarin recaptures (Alizarin) were all caught during surveys.

Natural mortality was estimated from the regression of

$$\ln(\text{numbers effort}^{-1}) = a + b(\text{age})$$

where catch data were grouped in calendar 6-month intervals and calibrated for the two different trawls used.

2.7. Replacement

The ratio of reared to wild turbot of the different age groups was examined to determine whether a shift in the ratio could be detected during the year of release as well as with the progressing age groups. This would give an indication of replacement of wild counterparts with released fish. The data was logit transformed prior to linear regression analyses.

To calculate the impact of the releases, the release area was calculated from the coastline to the 4 m-bathometer line within sub-division III (Fig. 1).

2.8. Migration

Net distance migrated was calculated for commercial recaptures in areas one to four for cultured fish released in area 3 and only for individuals where the information on recapture data was sufficiently detailed. This was estimated as the straight line between release and recapture site, using Pythagoras equation with the correction of the longitude for the curvature of the Earth. First the correction for the curvature of the earth was calculated using the following formulation:

$$k = \cos\left(\left(\frac{\text{Latitude}_{\text{release}} + \text{Latitude}_{\text{recapture}}}{2}\right) \times f\right)$$

where

$$f = \frac{180}{\pi}$$

in order to transform degrees to radians.

Kilometre migrated in the north–south direction were calculated as

$$\text{ns} = 111.111(\text{Latitude}_{\text{release}} - \text{Latitude}_{\text{recapture}})$$

Kilometre migrated in the east–west direction as

$$\text{ew} = 111.111k(\text{Longitude}_{\text{release}} - \text{Longitude}_{\text{recapture}})$$

and net km migrated utilising Pythagoras equation:

$$\text{km}_{\text{net}} = (\text{ns}^2 + \text{ew}^2)^{1/2}$$

Besides net distance migrated between the release site and recapture position, we investigated the migration pattern by separating net distance migrated (km_{net}) into an offshore migration vector ($\text{km}_{\text{offshore}}$) and an alongshore migration vector (km_{shore}). The offshore migration vector was net distance moved from release to catch position perpendicular to the coastline and the alongshore migration was net distance moved parallel to the coastline. Due to the straight-line appearance of the northern coastline of Zealand, this calculation was made simply by rotating the co-ordinate system to fit the coast. It was estimated by eye that the degree rotation necessary for the co-ordinate system to fit the coastline was approximately 35°. The following equations was used to calculate km migrated offshore:

$$\text{km}_{\text{offshore}} = \text{ns}\cos(35f^{-1}) + \text{ew}\sin(35f^{-1})$$

and alongshore:

$$\text{km}_{\text{shore}} = \text{ns}\sin(35f^{-1}) + \text{ew}\cos(35f^{-1})$$

Distances migrated were presented as bar plots with km on the *x*-axis and percent observations being the size of the bar. Observations of migrations distances above 20 km were pooled in a 20+ group. Bar plots were chosen as the best visual presentation due to the skewed nature of the data, a result of no migration less than zero. One bar plot was produced for the age groups 1, 2, 3 and 4+. Since the time at release was in May these age groups chosen corresponded to the time intervals 0–8, 9–20, 21–32 and above 32 months at liberty.

2.9. Dispersed release

Recaptures from the 1995 release (Table 1) were grouped according to release area, area of recapture and the time at liberty. These data were plotted and analysed in order to evaluate the degree of mixture between the different areas.

3. Results

3.1. Recaptures

A total of 456 alizarin-marked fish was recaptured from the surveys conducted during 1994–1997 (Table 2). The highest number of recaptures was from the second release in 1994 and constituted 0.16%.

Table 2
Recaptures for alizarin marked fish caught during surveys

Release year	Recapture year				Total recaptures
	1994	1995	1996	1997	
1993	151	19	4	0	174
1994	–	163	81	0	244
1995	–	–	7	31	38
Total recaptures	151	182	92	31	456

Table 3
Recaptures per year for T-bar tagged turbot caught during surveys (T-bar S) (no surveys conducted in 1998)

Release year	Recapture year							Total recaptures
	1991	1992	1993	1994	1995	1996	1997	
Spring 91	1	0	0	0	0	0	1	2
Autumn 91	0	1	1	0	0	0	0	2
Spring 92	–	0	12	0	0	0	0	12
Spring 93	–	–	100	9	3	0	0	112
Spring 94	–	–	–	157	5	1	0	163
Spring 95	–	–	–	–	18	1	0	19
Spring 96	–	–	–	–	–	16	3	19
Spring 97	–	–	–	–	–	–	51	51
Total recaptures	1	1	113	166	26	18	55	380

Percentage-wise the first release gave the highest recapture (0.22%).

A total of 2986 T-bar tagged turbot was recaptured until the 31 December 1998 (see Tables 3 and 4). The majority of the recaptured turbot was caught in commercial fisheries and 13% in the fishing surveys. The total recapture percentage for each release ranged from 1 to 11%.

3.2. Growth

Turbot grew primarily during the summer half-year and no or little growth was registered during the cold winter half-year (November–April) (Fig. 2). Growth estimated from the linear growth over the growth season was similar between wild and released alizarin-marked turbot although faster growth rates were observed during the first growth season after release (Fig. 2(top), Table 5). Growth differences between T-bar tagged fish (group I) and alizarin-marked fish (group I) demonstrated the effect of the external mark on fish growth (compare top and middle parts of Fig. 2; Table 5). The observed lack of growth in T-bar C fish as compared to T-bar S fish and the relatively large step-wise increase in size between season 1 and 2 in T-bar C fish suggests large inaccuracies in both the reported length and date of recapture by the fishermen. This is supported by the low fit of the regression in Fig. 2(bottom) (see Table 5). This figure illustrates the problems with using external tags and relying solely on data from the commercial (or recreational) fisheries and the need to conduct

Table 4
Recaptures per year for T-bar tagged turbot caught in the commercial fishery (T-bar C)

Release year	Recapture year								Total recaptures
	1991	1992	1993	1994	1995	1996	1997	1998	
Spring 91	29	44	26	12	0	2	2	0	115
Autumn 91	7	113	69	9	1	3	1	0	203
Spring 92	–	130	119	19	5	1	2	0	276
Spring 93	–	–	76	68	15	27	20	0	206
Spring 94	–	–	–	744	69	71	25	1	910
Spring 95	–	–	–	–	53	247	191	26	517
Spring 96	–	–	–	–	–	10	28	6	44
Spring 97	–	–	–	–	–	–	174	18	192
Spring 98	–	–	–	–	–	–	–	143	143
Total recaptures	36	287	290	852	143	361	443	194	2606

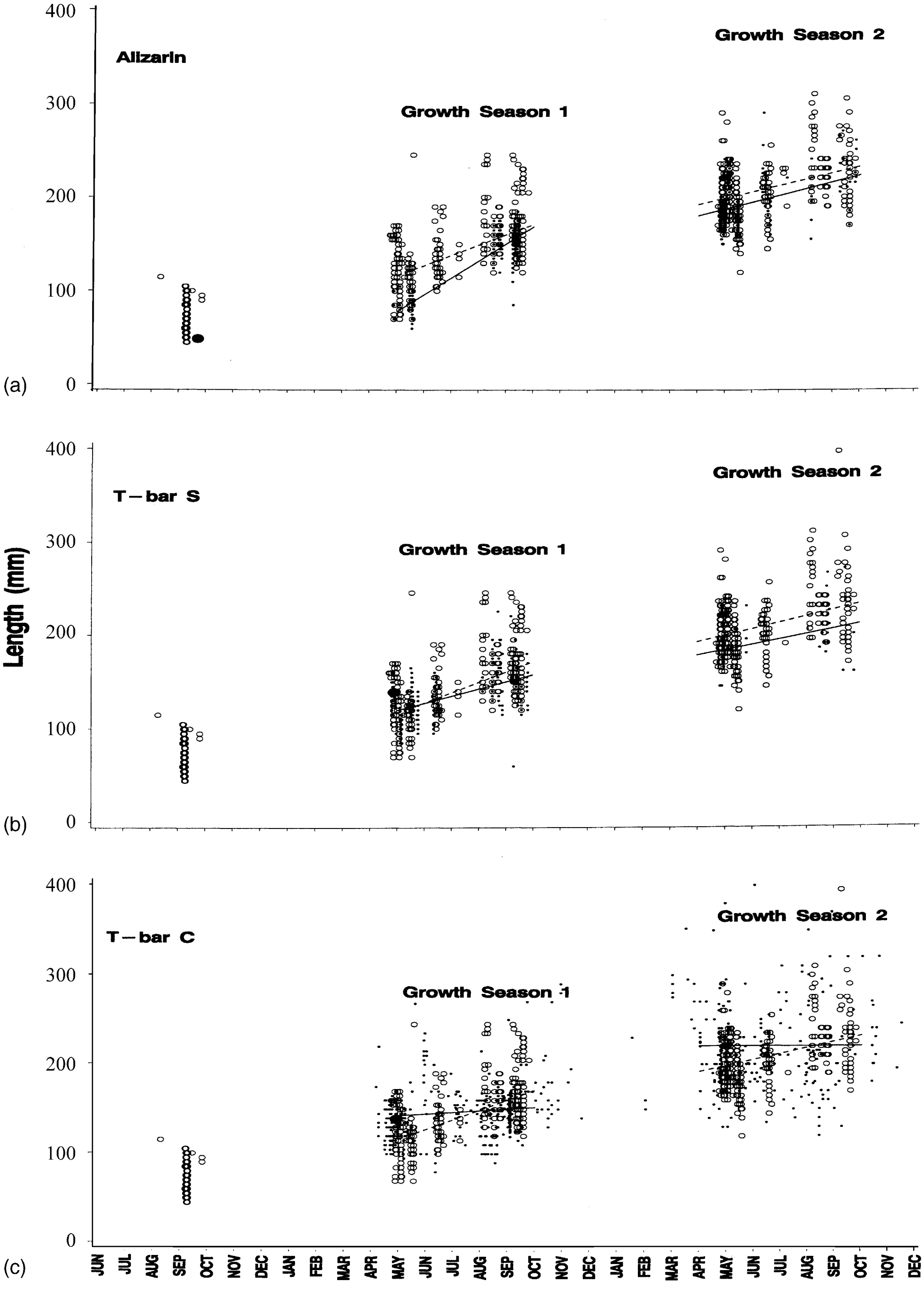

Fig. 2. Length at recapture for alizarin (a), T-bar recaptured during research fishing surveys (b; T-bar S) and T-bar recaptured by the commercial fishery (c; T-bar C) compared to length of wild turbot of the same age. Large black circle indicates average size at release of reared fish, small black circle size at recapture of individual fish and empty circle individual size of wild turbot. Dashed line is regression for data for wild fish and solid line for tagged fish.

Table 5
Growth estimates assuming linear growth during 1 and 2 growth season[a]

Type	Growth during season 1				Growth during season 2			
	mm per day	r^2	Observation	P	mm per day	r^2	Observation	P
Wild	0.36	0.32	260	<0.001	0.22	0.15	329	<0.001
Alizarin	0.59	0.75	321	<0.001	0.23	0.17	131	<0.001
T-bar S	0.25	0.27	340	<0.001	0.18	0.11	27	<0.093
T-bar C	0.06	0.01	840	<0.011	≈0	≈0	283	<0.983

[a] Wild turbot were caught during surveys and the age was determined from the otolith. Alizarin indicates alizarin-marked fish, T-bar C the commercially recaptured T-bar tagged fish, and T-bar S the T-bar tagged fish caught during fishing surveys.

research surveys for reliable data. These problems persisted despite a marked improvement in the quality of information on the returned tags when communication with the local fishermen was initiated and efforts were made to maintain a flow of information on the releases and the results. T-bar C data were, therefore, not used in the growth analysis.

The average daily growth for the alizarin-marked fish and wild turbot was 0.59 and 0.36 mm per day, respectively, during growth season 1 (age I fish) (Table 5). In comparison T-bar S fish (age I) grew 0.25 mm per day during their first growth season after release. These growth rates translate into an annual growth of around 7, 11 and 5 cm for wild, alizarin-marked and T-bar S fish, respectively, if the growth were solely during the summer half of the year. This was somewhat lower during the second growth season (age II fish), approximately 4 cm for wild and alizarin-marked turbot and 2 cm for T-bar S turbot.

3.3. Mortality

The slope from the regression of the logarithm to numbers caught in the commercial fishery per year at liberty was used to provide a rough estimate of turbot survival. This assumes a low migration to and from the area, which is supported by our recapture data and includes only data of age II+ fish. The estimate gave annual survival rates ranging from 26 to 76% (Fig. 3). Utilising a GLM model with equal slope, an overall estimate on 52% survival per year was obtained ($Z = -0.65$, $r^2 = 0.77$, $P < 0.0001$).

Survival estimates obtained using the Jolly and Seber method were highly variable ranging in mean values from 46 to 110% for T-bar tagged fish and a mean of 79% for the alizarin-marked fish (Table 6). The Fisher and Ford model provided an average yearly survival estimate of 40–55% for the externally tagged fish and 70% for the alizarin-marked fish (Table 6). Survival estimates for the different cohorts of natural turbot varied from 14 to 121% (Table 7).

3.4. Replacement

The regression on the ratio of reared to wild turbot with time at liberty showed no significant slope ($P > 0.99$, $r^2 < 0.01$) for the alizarin-marked fish

Table 6
Survival estimates of the recaptured fish derived from different mortality models (see text for more details)

Tag type	Jolly and Seber (% survival)			Fisher and Ford (% survival)
	Min.	Max.	Mean	Mean
Alizarin	44	141	79	70
T-bar S	39	56	46	40
T-bar C	40	7474	110	55

Table 7
Natural survival estimates for the different turbot year-classes derived from the regression of catch per unit effort age^{-1a}

Year-class	% Survival	Observation
1991	21	2
1992	53	3
1993	14	6
1994	63	8
1995	65	8
1996	121	5

[a] Catch data were calibrated for differences in trawl selectivity and pooled at 6-month intervals.

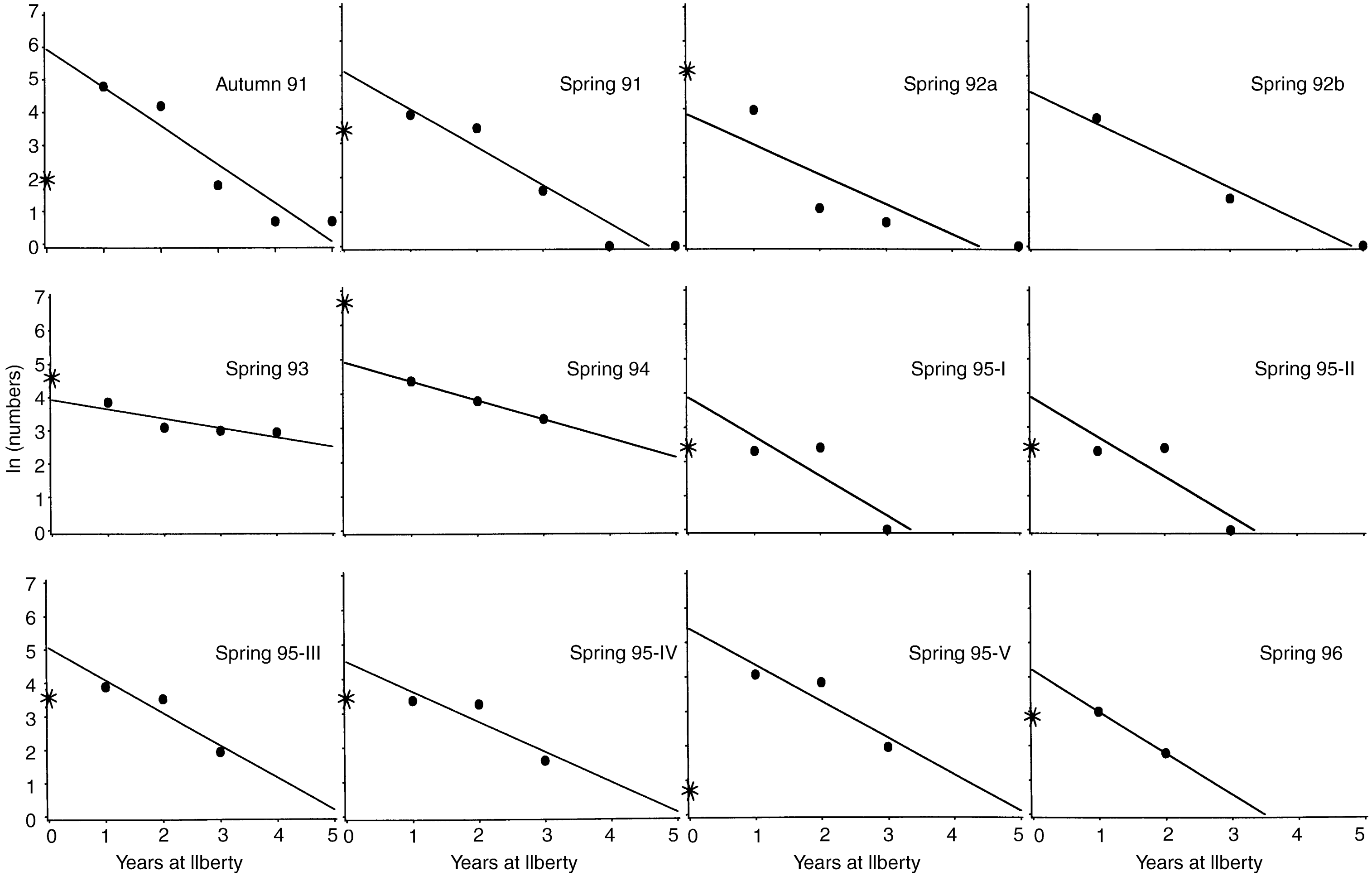

Fig. 3. Relationship between commercial recaptures in numbers and year at liberty for each release. The slope (*Z*) of the regression is used to estimate survival. Star not included in the regressions. Regressions parameters r^2 and *Z* are: Autumn 91, 0.90, −1.01; Spring 91, 0.76, −0.79; Spring 92a, 0.72, −0.87; Spring 92b, 0.98, −0.93; Spring 93, 0.73, −0.28; Spring 94, 0.99, −0.56; Spring 95-I, 0.72, −1.15; Spring 95-II, 0.83, −1.33; Spring 95-III, 0.88, −0.97; Spring 95-IV, 0.80, −0.88; Spring 95-V, 0.83, −1.06; Spring 96, 1, −1.20.

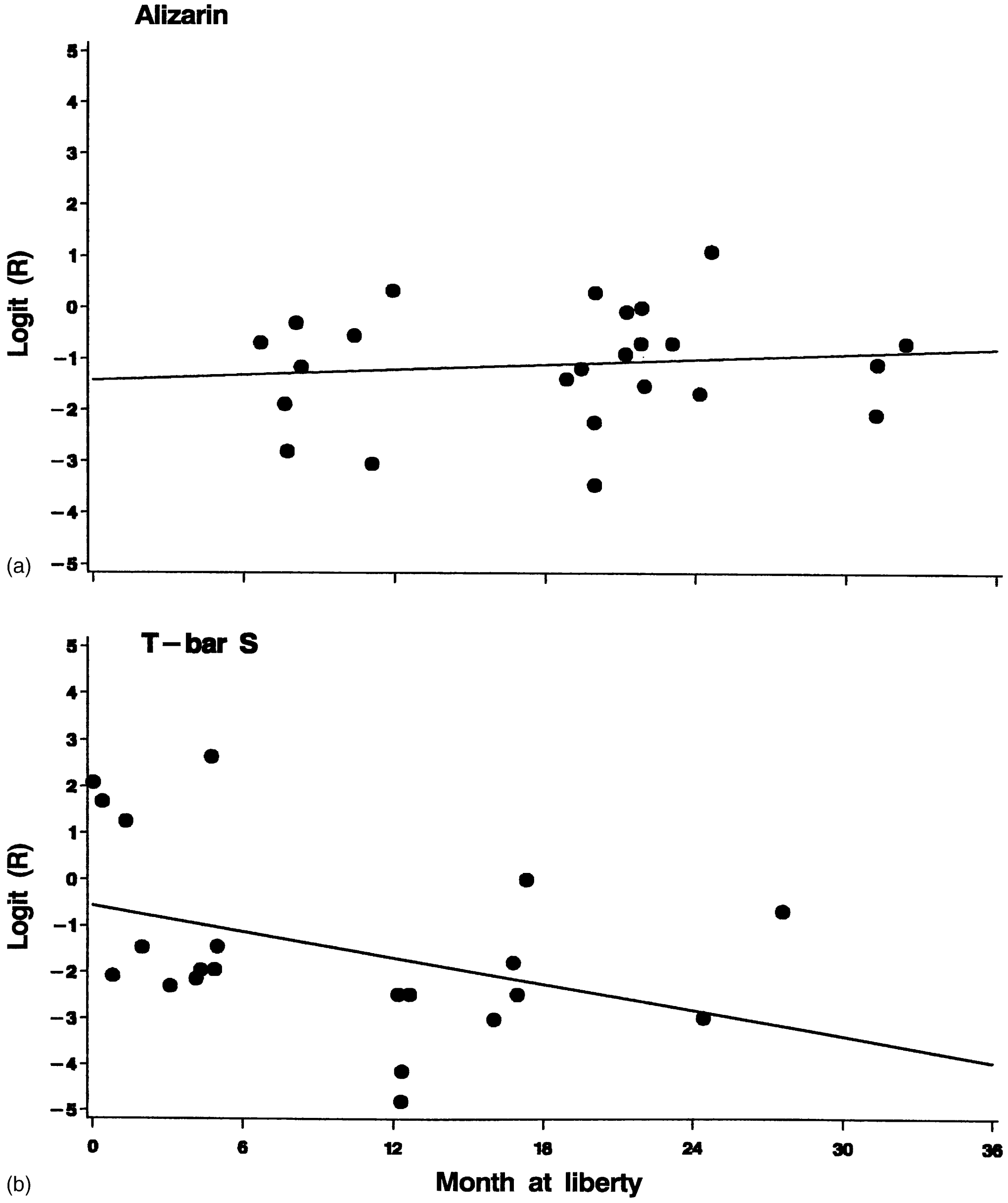

Fig. 4. The ratio between reared and wild turbot of the same age caught during each survey. (a) Ratio of alizarin-marked to wild fish; (b) ratio of T-bar S marked to wild fish.

(Fig. 4(top)) and a significant negative slope ($P < 0.05$, $r^2 = 0.2$) for the T-bar tagged fish (Fig. 4(bottom)). The releases contributed approximately 13.6–20.4 ind. 1000 m^{-2} and 1.4 ind. 1000 m^{-2} for the smaller and larger turbot, respectively.

3.5. Depth distribution

The depth distributions of the wild, alizarin-marked and T-bar tagged turbot of different age groups are given in Table 8. Only individuals caught with gillnets

Table 8
The depth distribution of the wild, alizarin and T-bar tagged turbot of different age groups for fish caught by trawl or gillnets

Depth interval (m)	Age	Trawl catches (numbers/h)			Gillnet catches (numbers/100 m)		
		Wild	Alizarin-marked	T-bar tagged	Wild	Alizarin-marked	T-bar tagged
0–2	0	13.5	0	0	0.05	0	0
	I	20.1	7.4	7.1	3.9	5.9	1.9
	II	11.1	3.2	0.7	1.2	0.1	0.05
2–4	0	27.5	0	0	0	0	0
	I	22.7	2.6	5.3	1.0	0.7	1.0
	II	67.6	23.7	0.8	0.8	0.5	0.3
>4	0	2.4	0	0	0	0	0
	I	4.5	0	1.3	0.05	0	0.9
	II	70.5	7.8	0.3	0	0.2	0.1

during night and by trawl during day are included. A total of 64 alizarin-marked, 96 T-bar tagged and 152 wild individuals were caught with gillnets. Trawl catches were 129 alizarin-marked, 47 T-bar tagged and 885 wild individuals. Forty percent of the survey trawl fishery was carried out at depths deeper than 4 m where 8% of the 0-group wild turbot were caught. Of the age 1 turbot approximately 10% of the T-bar tagged, none of the alizarin-marked and 12% of the wild fish were caught in these depths. The majority (97%) of the wild individuals caught by trawl of age group II+ were caught at depths deeper than 2 m. The gillnet catches were characterised by virtually no catches of 0-group or no catches at depths deeper than 4 m, except for the T-bar tagged fish.

3.6. Migration

For 1702 of the 3448 reported recaptures from the commercial and recreational fishery the catch position was not known, time at liberty was not known or the recapture area was in the adjacent fjord. Thus, only 1746 were used in the migration analysis. The majority (93%) of age 1 fish recaptures migrated a net distance less than 10 km from the release position (Fig. 5). Age two fish were more equally distributed in the catches with 70% within 10 km from the release position and 30% more than 10 km distance from the release position. For age 3, the percent caught within 10 km from the release position was 37% and for age 4+ 40%. The migration distance alongshore was similar to the net migration distance for ages 1 and 2, with 96 and 76%, respectively, caught within 10 km from the release site. Thereafter, there was a tendency towards longer net migration than alongshore migration. Offshore migration was somewhat different, with a very small distance migrated, less than 5 km from the release position, for the first two age groups. After that there was an abrupt increase in the distance migrated and at age 4+ 30% had migrated more than 10 km offshore.

3.7. Dispersed release

Fifty percent of the total recaptures from the 1995 release were later reported caught in area 2, whereas 34% were later caught in area 3 (Fig. 6). For the remaining three areas only few recaptures were reported. Of the recaptures in area 2, 52, 22 and 29% were fish that had been released in that area, respectively, 1, 2 and 3 or more years previously. Two years after their release, a considerable portion of the recaptures in areas 2 and 3 had been released in area 5, whereas after 3 years or more, the catches were equally distributed from the five release areas, although those from area 1 were fewer. In area 3, the percent recaptures released in area 3 were 47, 24 and 31 for, respectively, 1, 2 and 3+ years at liberty.

4. Discussion

The recaptures of up to 11% are within the expected range considering the size of fish being released

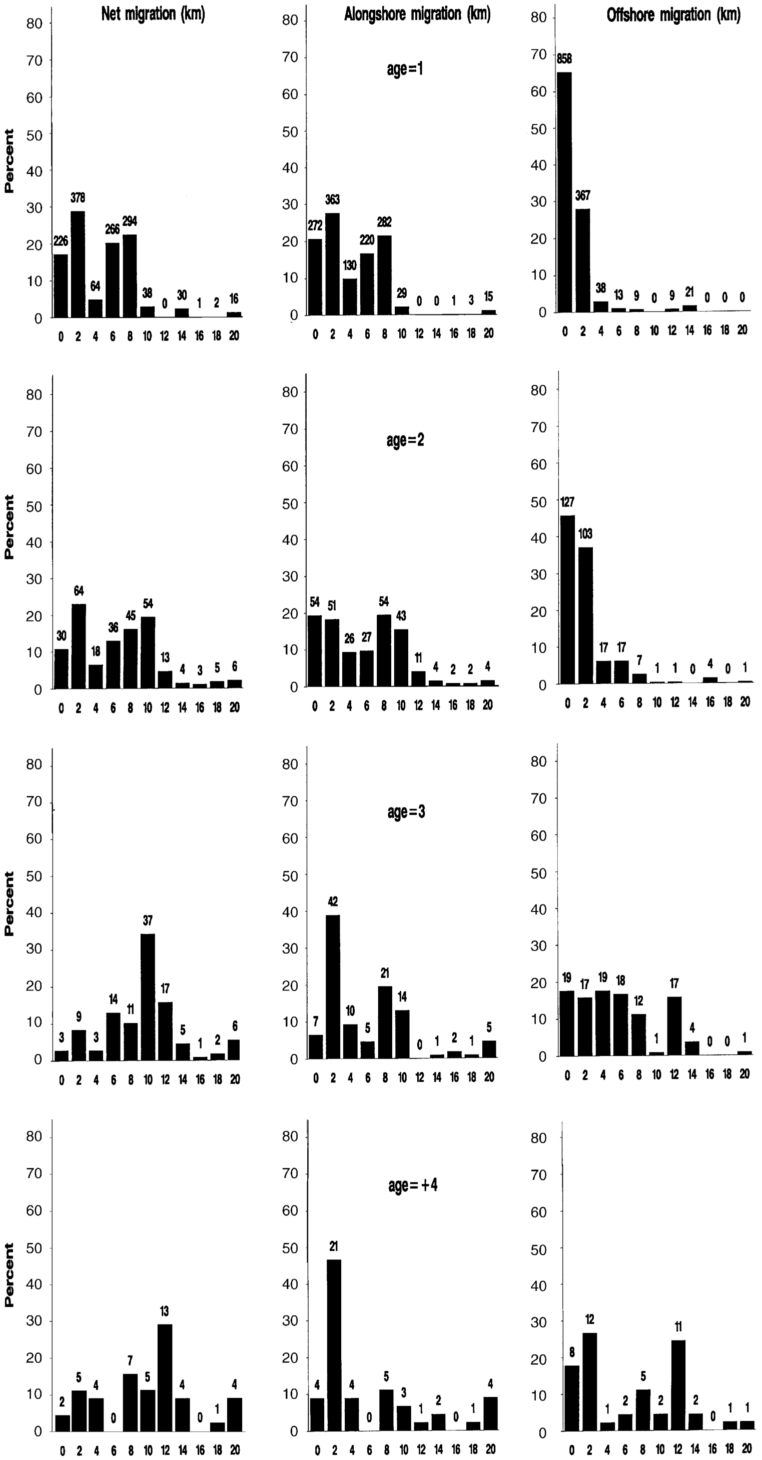

Fig. 5. Number of recaptures at different distances from the release position. Bars of each graph sum to 100 and numbers above bars are actual recapture numbers.

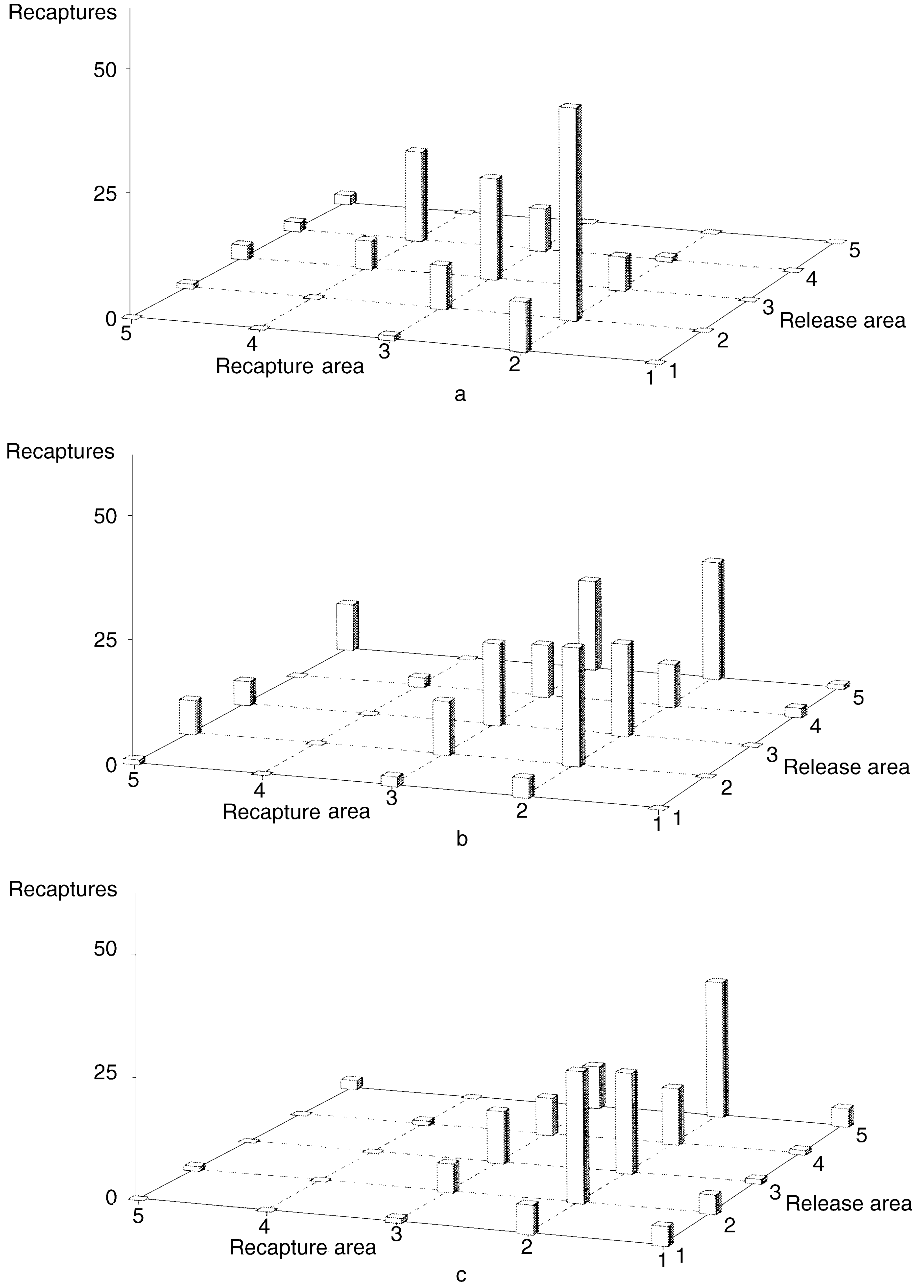

Fig. 6. Plots showing the number of recaptures within each area in relation to the initial release area. (a) Recaptures of age I fish; (b) those of age II fish, and (c) age III+ turbot recaptures.

relative to their size of recruitment to the fisheries and the exposed nature of the coastal release site. For example, Tominaga and Watanabe (1998) obtained 8.2% recaptures on Japanese flounder *P. olivaceus* around 8 cm in length released in Ishikari Bay, Japan. The commercial recaptures in this study, despite problems with lack of response or incorrect and inaccurate data are valuable, contributing to around three-quarters of the data material. The increase in number of survey recaptures during 1993 and 1994 reflect an increased effort aimed at the recaptures. In the following years, the fishing effort was more evenly distributed in the area. Dab dominated the survey catches by a 100-fold. The other flatfish species such as plaice, flounder, brill *Scophthalmus rhombus* and wild turbot occurred in similar numbers in the catches. Cod, whiting *Merlangius merlangus*, herring *Clupea harengus* and sprat *Sprattus sprattus* among pelagic fish occurred sporadically in the catches. The data collected are unusually numerous and provide a vast database with information on the biology and ecology of turbot and the impact of releases of reared turbot.

A strong size-dependent recapture rate has been observed for species such as cod (Otterå et al., 1999). Furthermore, gadoid species are highly vulnerable to predation and cannibalism even in the recruit size. Stock enhancement of cod can be successful only if they are kept in a predator-free environment until they have reached a size refuge from predators (Salvanes et al., 1994). Indeed, Kristiansen (1999) found that II+-group cod continued to encounter high natural mortality and did not seem to reach any size refuge from predation. Salvanes et al. (1994) suggested that the best yield could be gained from aquaculture rather than through releases of any size of cod. This size-dependence may be higher for roundfish species with high vulnerability to predation and cannibalism than for flatfish species. There are few known predators on turbot of the size released (10–12 cm) during springtime. An analysis of cormorant *Phalacrocorax carbo sinensis* predation on fish in the locality showed these feed primarily on cod and dab (Anon., 1995). In this analysis based on pellets from 23 different breeding colonies and two roosting sites from various parts of Denmark no turbot were identified as prey, suggesting cormorant predation on this species to be insignificant. However, there may be other predators in the area. For example, the common seal *Phoca vitulina* (Härkönen, 1987) and porpoises *Phocaena phocaena* have been observed in the area (own observations), although at least for seals, predation on turbot was insignificant. Large predatory fish such as cod (12–24 cm) have been shown to migrate inshore nocturnally to feed on smaller fishes including flatfish such as plaice (Gibson et al., 1998), but these preyed on the smaller 0-group fish. Predation of 0-group Japanese flounders by I or II-group flounders is suggested to be the major factor influencing the success of stocking this species in Japan (Furuta, 1996). Further, I-group turbot have been observed to feed on 0-group plaice and dab, but we found no accounts of flatfish predation on I-group flatfish, and particularly I-group turbot. Thus, a potential for enhancing the natural stock by releasing age 1+ juveniles exists if the following criteria are fulfilled: (1) the year-class strength is determined in the pelagic stage or early post-settlement stage, (2) the carrying capacity of the juvenile nursery grounds is not fully utilised and (3) predation mortality is very low already at age 1+.

Strong evidence that the year-class strength is determined in the early life-stages was demonstrated for plaice (van der Veer et al., 1990) and indicated for other flatfish species such as sole, dab and flounder (van der Veer et al., 1991; Rijnsdorp et al., 1992; Henderson and Seaby, 1994). Should the larval supply to the nursery grounds be sufficient to supply high densities of newly settled flatfish, they would still be within a size-range where flatfish predators are abundant. Since post-settlement predation has been shown to be the most potent regulator of densities in benthic populations during the first few weeks after settlement (Shulman and Ogden, 1987), any density-dependence may quickly be changed to density-independence within weeks of settlement. The ecological advice given by Giske and Salvanes (1999) concerning stocking included the use of species with strong recruitment limitation, low variation in food availability and with low tendencies to cannibalism. They suggested working with benthic crustaceans. In this work, a case for turbot is put foreword.

The mortality estimates, despite the large variation give an indication of the level of survival of the released fish and of the wild population. These mortality estimates do not include initial post-release mortality but are an estimate of the average mortality in the subsequent years. The average value of 52% annual survival obtained from the regressions on recaptures represents age II+ fish and includes natural and fishing mortality. Assuming a natural annual mortality of 0.2 applied for several marine flatfish species in virtual population analyses, it is suggested that the impact of the local fishery on the turbot population in the area is of the same or a slightly higher magnitude than from natural causes.

The alizarin-marked fish showed a significantly higher growth rate relative to wild turbot of the same age/size group during the first growth season after their release (Table 5). These 0-group fish were released in September, shortly before the winter period and had a narrower size-range and were similar to the smallest of the wild counterparts (Fig. 2). The reason for this higher growth may be due to the better condition of the reared fish in lieu of the imminent winter period. The size-range at the beginning of the second growth season was similar in wild and released fish as was their growth rates during the second season. The external tag was shown to effect growth in turbot (Fig. 2). The growth rate of T-bar S marked turbot during the first growth season after release was significantly lower than that of the alizarin-marked or wild fish of the same age group and may explain the higher survival rates obtained for the alizarin-marked fish regardless of the model applied. Many of the external tags returned were overgrown with mussels and algae, which renders them heavier and more cumbersome. This was not observed on any of the recaptures of similarly marked cod in an earlier study (Støttrup et al., 1994) nor mentioned in the cod literature concerning tag losses. The relatively sedentary, benthic lifestyle of turbot may encourage tag fouling.

Large differences in the depth distribution of tagged fish caught by gillnet and trawl were found in this study, especially for the age II+ group. Virtually no fish were caught at depths deeper than 4 m when fished during night with gillnets but a substantial number at depths deeper than 4 m when fished with trawl during daytime. This could be a result of the different selection in the two types of fishing gear, but the day and night differences in the fishing pattern may also have contributed to this difference. Plaice and turbot are ‘principle examples’ of species that migrate with each tidal cycle (Gibson et al., 1996). The average tidal amplitude off the coast of north Zealand is around 18 cm during springtide (Anon., 1984). We, therefore, suspect that the migration pattern is not related to tidal cycles, but is probably related to changes in light intensity triggering an inshore foraging movement. Plaice have been shown to move into shallower waters during nighttime and back to deeper waters during the daytime (Burrows et al., 1994; Gibson et al., 1998). These authors suggest that these daily rhythmical movements are related to predator avoidance during nighttime and to avoidance of high daytime temperatures. Predatory species like cod were also shown to undertake similar migrations though with slightly different triggering mechanisms; cod migration inshore seemed to be associated with foraging activity (Gibson et al., 1998). Turbot are visual feeders, active hunters predating on moving prey (Braber and De Groot, 1973). Feeding activity was observed to increase at dusk and be sporadic and low during daytime (Jones, 1973). This implies that during daytime turbot is primarily stationary, buried in the sand, whereas they are more active at dusk and in the early night hours hunting moving prey. It is possible that turbot move inshore at dusk to feed on shrimp and small fish. Likewise, we suggest that movement along the coast could not be related to tidal cycles in a microtidal area, as in our study, but may also be explained by foraging activity.

Based on our trawl hauls, 0-group turbot were caught in depth deeper than that reported for other turbot studies in European waters. Depth distribution of 0-group turbot off the coast of Wales was found to be less than 2 m (Riley et al., 1981) and less than 4 m (Jones, 1973). In Laholm Bay, a site less than 50 km from our site and with a similar bottom sediment to that in our study, Pihl (1989) reported no 0- and 1-group turbot or brill (pooled data) at depths beyond 8 m. These differences could be due to the gear used and their efficiency in catching turbot at various depths. For example, Pihl (1989) used a 2 m-beam trawl towed at a speed of 1 knot. Underestimates of juvenile densities have previously been associated with sampling gear, and inaccurate estimates of gear efficiencies have resulted in non-viable comparisons of densities between localities (Modin and Pihl, 1996; Wennhage et al., 1997). In our study, the deeper-water turbot were caught with a trawl that is designed for a wide selectivity for different species and different sizes and used in routine fish assessment monitoring in Denmark. Two scaled-up versions of this trawl design are presently used as the standard trawl for the Baltic Sea assessment of the resources.

A success criterion for stocking fish to a local stock is that the fish would contribute in numbers and biomass to the fishable stock. In this case, it would mean that they remain and grow in the area, not displace the wild stock and enhance recruitment to the local fishery. Thus, it is important that the fish reach minimum size[1] within the release area, especially

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[1] The minimum allowable size to be caught in the fishery in the area.

when the fish released are very small and several years would pass before they reach minimum size. The particular hydrographic conditions in the area serve to retain the turbot juvenile within the area of the north Zealand coastline as supported by the results from the recaptures. Cultured turbot remained close to the shore during the first years at liberty (Table 8) and within 10 km of the release site. Looking at the along- and offshore components of migration, ages 1 and 2 turbot mainly moved to the west and east along the coast, whereas the offshore component revealed mainly an offshore migration in ages 3 and 4+ fish.

For the 3- and 4-year-old fish, a second migration event took place, with a larger fraction of the turbot caught at distances further away than 10 km from the release site. This change in migration pattern is interpreted as an offshore spawning migration. There is no published information on where the turbot spawn in the Kattegat or Skagerrak but it is believed that they spawn over a broad area in the central Kattegat at depths of 10–40 m. Local fishermen have in particular referred to sandbanks southeast of the small island of Hesselø, situated 20 km north of the release site, as turbot breeding grounds (Hvingel and Støttrup, 1993) and south of Anholt, an island further to the north (Ole Bagge, pers. comm.). Bagge (1987) found a very limited migration when larger turbot were tagged and released in the central Kattegat. In our study we did get reports of recaptures of mature specimens but the numbers were too small to provide tangible conclusions. This provides however, some evidence that the released turbot are contributing to the wild spawning stock biomass.

After 32 months at liberty when the age of the released individuals was 4 years or older, a significant difference in specific growth rate between the two groups was found. The far migrating turbot were on average a 40 mm longer. A possible explanation for this may be differences in sex or maturity stage. Turbot mature at age 4–6 years depending on environmental conditions (Jones, 1974). From around the age of 3, differences in growth between sexes can be distinguished with females growing faster than males (Rae and Devlin, 1972). Further, it has been argued that the fastest growing fish should be the ones maturing first and hence starting a spawning migration first (Sterns and Koella, 1986).

In the dispersed release in 1995 the 10,000 I-group fish were released in the five areas or subdivisions along the Zealand coast, whereas in the other years all 10,000 fish were released in one area/subdivision. In terms of numbers, the 1995 release resulted in the highest number of recaptures, when disregarding a total of 555 fish caught during the first month after release in 1994 caused by an unfortunate and directed effort by local commercial fishermen. One interpretation of these results is that a dispersed release enhances the survival potential thus increasing recaptures in later years. Yamashita and Yamada (1999) argue on the contrary that concentrated releases are more effective than scattered releases as long as the numbers are within the carrying capacity. The number of prey to be eaten by a given predator is assumed fixed for a given site and thus increasing the number of sites simply increases the number of predators and thus the numbers preyed upon. However, for species or sizes that have reached a size refuge from predation, the increased exposure to food due to a scattered release may be advantageous and decrease or eliminate any potential density-dependent mortality.

The ratio of reared to wild fish was examined in the catches from the research fishery examining single cohorts and similar-aged reared fish for changes in ratio which may indicate displacement of the wild stock. The ratio of alizarin and wild fish remained unchanged with time, whereas the captures of externally marked fish relative to wild counterparts of a similar age declined with age. While this confirms the problems encountered with the external tags, the poorer growth and poorer survival suffered by the externally marked turbot due to the cumbersome tags, these results give no indication of displacement of the wild stock by the released fish.

No information on the abundance of the natural turbot population in the Kattegat is available. The magnitude of the releases contributed to the release area approximately 14–20 0-group ind. 1000 m^{-2} and 1 group-I ind. 1000 m^{-2}. The mean ratio of 0-group and I-group alizarin-marked fish to wild fish was 0.33 and 0.44, respectively. The total densities obtained with the releases did not markedly exceed those found in natural flatfish populations elsewhere, when considering different catching efficiencies of the sampling gear (Jones, 1973; 4.9 ind. 1000 m^{-2}).

While stocking may be applied to alleviate symptoms of over-fishing or habitat degradation on a local scale (Blaxter, 2000), and even when applied appropriately (Blankenship and Leber, 1995), it does not remove the symptoms. Stocking can be regarded as one of several 'tools' for resource management. Sustainable fishery, habitat restoration and environmental amelioration remain vital aspects of resource management, which should be targeted at rendering stocking redundant. Stocking should be an integrated part of resource management programs.

5. Conclusion

In conclusion, the null-hypothesis that stocking enhances the local population of turbot cannot be rejected. This is based on the results on growth, survival and ratios in the research survey catches of the released and wild fish. The released fish adapted to the natural environment and achieved growth and survival rates similar to those of their wild counterparts, and no indication of displacement of the wild population was found. It is suggested that the mechanisms underlying the potential for enhancing the local wild stock be related to specific population dynamic traits particular to the species in the area examined:

1. A size refuge from predation attained at a size smaller than that of the released fish.
2. Recruitment bottleneck at the stage prior to settling or within a short time after settling in the juvenile nursery grounds.
3. Available habitat (space and food) for the introduced individuals.

The results from this study revealed that the release site, an exposed beach composed of coarse sand sediment, was a suitable habitat for turbot juveniles. The fish spent their juvenile years here and little migration out of this area was observed. No apparent differences in depth distribution between reared and wild fish were found.

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Chapter 5

Diet, abundance and distribution as indices of turbot (Psetta maxima L.) release habitat suitability.

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Diet, Abundance, and Distribution as Indices of Turbot (*Psetta maxima* L.) Release Habitat Suitability

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Selection of a suitable release habitat is critical for stock enhancement. As part of the Danish turbot stock enhancement program, individually tagged, artificially reared juveniles were released into three different habitats. Data from the recaptures in the following year revealed a significant effect of release habitat on turbot growth. This raised the question whether such differences in growth could have been predicted before the release by comparing easily measurable characteristics of wild turbot caught in the different habitats. Three characteristics of wild turbot were examined: the diet, natural abundance, and depth distribution within the habitats. A marked difference was found among habitats in the timing of the diet change from the suboptimal exoskeleton carrying prey items such as crustaceans to fish. The habitat where the wild turbot had the lowest occurrence of fish in their diet was also the habitat with the highest natural abundance of age-0 individuals and the deepest distribution of wild turbot. This was the habitat where released turbot grew more slowly than in the other habitats, which indicate that the diet and depth distribution of wild turbot may provide good indicators for the success of turbot enhancement and restocking.

Keywords stock enhancement, releases, habitat quality, flatfish, stocking, nursery area

INTRODUCTION

During the 20th century, drastic changes in marine ecosystems have been witnessed globally. Most of their fish resources are exploited to or beyond the limit of sustainability (Hilborn and Waters, 1992). These events have initiated a whole set of fishery regulations, which have been generally unsuccessful and have resulted in a range of conflicts between fishermen and the authorities. The more proactive approach of restocking or stock enhancement through releases of artificially bred individuals has gained increasing attention during the last decades (Molony et al., 2003).

As part of the Danish stock enhancement program, turbot were released and subsequently monitored at 3 different habitats in the inner Danish waters. The largest group of juvenile turbot was released in the coastal nursery areas of North Zealand, where it was demonstrated to be a viable method for increasing the turbot stock locally (Støttrup et al., 2002). Mortality and growth after the post-release period was in the same order of magnitude for the released fish as for their natural counterparts. It was estimated that the recapture rate would need to be approximately 8% to match the cost of the releases. This was, however, only the case in some years (Støttrup and Sparrevohn, 2007). Means of improving the outcome were thus investigated with focus on growth and mortality, as these parameters are believed to be the most important factors determining the numbers of juveniles that recruit to the fishable stock (see Gibson (1994) for a review). Growth is associated with habitat quality, and therefore could be improved by selecting an optimal habitat, whereas post-release mortality was believed to be coupled to the release strategy.

Post-release mortality was examined for a Danish turbot release in Aarhus Bay and was found to be considerable (Sparrevohn et al., 2002). This result was in agreement with results obtained elsewhere for turbot (Iglesias et al., 2003) and Japanese flounder (*Paralichthys olivaceus)* (Furuta et al., 1997). Conditioning fish to their new environment before release was shown to limit post-release mortality (Sparrevohn and Støttrup, 2007), as was suggested by several authors (e.g., Kellison et al., 2000; Fairchild and Howell, 2004).

Habitat suitability is another important factor steering the success of a given stock enhancement or restocking. Besides

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larval supply, or in the case of restocking or stock enhancement, the number of fish released, prey availability, and predation pressure are the primary factors that determine the numbers of individuals that are later recruited into the fishery (Gibson, 1994). To address the concept of habitat quality, it has generally been assumed that quality and ecosystem productivity are coupled using carrying capacity as an index. This has been done independently of whether the carrying capacity is defined as the population biomass at which the per capita population growth is zero (MacCall, 1990) or as an intrinsic property of the area, e.g., its capacity for providing protection against predators (see Kashiwai, 1995). Finding the population biomass where the per capita population growth is zero is in most cases not possible, since population levels might never reach these levels, and higher population levels might result in a spill over of individuals into less favorable habitats (see MacCall's (1990) basin model). Instead, focus has been placed on estimating the individual growth typically from enclosure experiments. This has been done with some success but the method cannot account for any ontogenetic effect attributed to diet or growth during such short-duration experiments (e.g., Manderson et al., 2002; Andersen et al., 2005; Fairchild et al., 2005).

Essential fish habitats (EFH) have been used to characterize habitat suitability; assuming that the number of individuals present in a given habitat is a measurement of its quality, but as pointed out by Stoner (2003), the recruitment of larvae or post-settled individuals to the area also needs to be taken into account. Therefore, Stoner (2003) proposed a combination of high recruitment and high survivorship to be used as an index for habitat suitability. In a stock enhancement context this thought is attractive, since an area that provides high survivorship but has low recruitment will be an area with a high stock enhancement potential.

In this article we propose a simple, practical, and economically feasible method to evaluate the suitability of a given habitat as a release area. We examined the stomach content and total abundance of the existing wild population in the habitat together with their depth distribution and compared this with growth in reared, tagged turbot released in the same habitats. Since juvenile turbot have been found to have a limited depth distribution in the very shallow near-shore areas (Jones, 1973; Iglesias, 1981; Riley et al., 1981), a broader depth distribution is used as an indication of spillover of fish into less favorable habitats as predicted by MacCall's (1990) habitat basin model. We hypothesize that areas with high feeding potential, low natural population abundance, and a narrow depth distribution will provide the best conditions for the reared individuals released.

STUDY AREA AND METHODS

Study Habitats

Aalborg Bay (AB) has a north–south oriented long stretch of straight coastline located in East Jutland (Figure 1). Even though sheltered from the westerly winds, the fetch is large if the wind is easterly. Tagged turbot were released at 5 different locations in 2

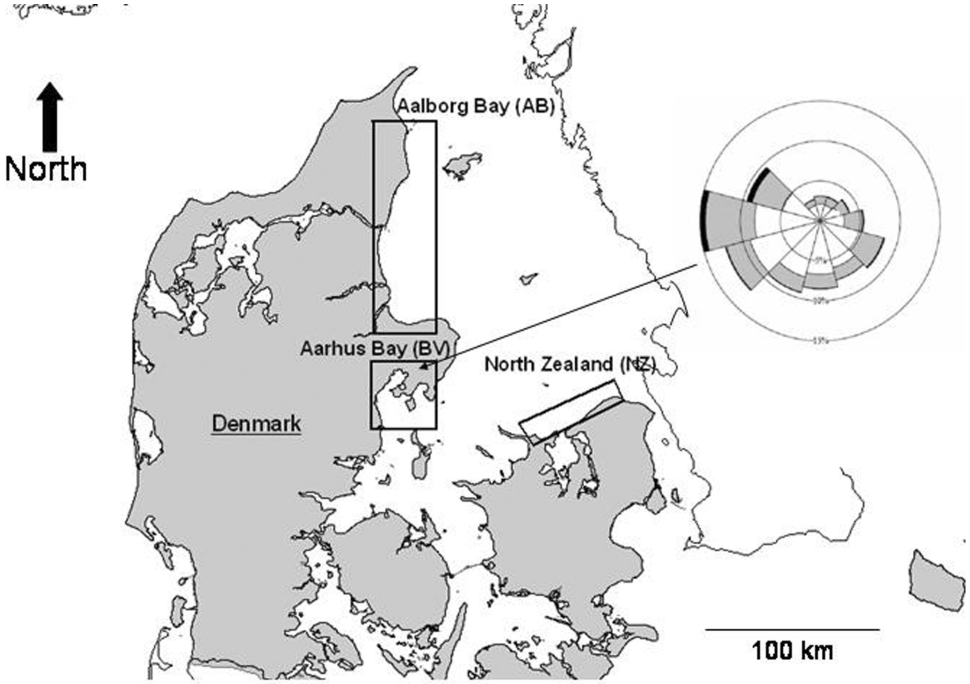

Figure 1 Map showing the 3 habitats, Aalborg Bay (AB), Aarhus Bay (BV), and North Zealand (NZ), where turbot have been released and wild turbot caught. The area within the black boxes is the area used in the estimation of total abundance. The wind rose shows the distribution of wind in the period 1971–2000 measured at the position shown by the arrow (from Cappelen, 2002). The wind direction is divided into 12 sectors, each representing 30 degrees. The wind speed is divided into 3 categories shown by white, grey, and black color. White represents speeds between 0.3–5.4 m/sec, grey speeds between 5.5–10.7 m/sec, and black speeds higher than 10.8 m/sec. The inner orbit represents 5%, the middle 10%, and the outer 15%.

Table 1 Characteristics for the three habitats where releases were conducted and wild individuals sampled

Season	Depth	Parameter	$AalborgBay(AB)$	$AarhusBay(BV)$	$NorthZealand(NZ)$
Summer	0–1 m	T	17.2 (11.4–22.4)	16.9 (12.2–22.4)	17.5 (13.5–22.3)
	0–1 m	S	22.2 (15.3–29.8)	21.3 (12.6–26.9)	16.9 (13–21.1)
	4–5 m	T	16.2 (9.5–21.3)	16.7 (12.2–22.5)	17.3 (13.5–20.7)
	4–5 m	S	23.1 (19.2–26.8)	21.7 (12.8–27.3)	17.4 (13.7–21.1)
Winter	0–1 m	T	2.8 (–0.7; 5.1)	2.8 (0.0–6.1)	2.1 (0.1–4.4)
	0–1 m	S	25.4 (19.5–29)	23.1 (15.7–30.42)	22.1 (15.7–26.1)
	4–5 m	T	2.9 (−0.6–5.8)	2.9 (0.1–7.2)	2.3 (0.2–7.1)
	4–5 m	S	26.1 (21.8–29.3)	23.6 (15.7–30.4)	20.2 (12.5–26.2)

Summer is the months June, July, and August; winter January and February. T is temperature in °C, and S is salinity in ‰. Numbers in brackets are the range. All data are from The National Environmental Research Institute homepage: http://www.dmu.dk/ International/Water/Monitoring+of+the+Marine+Environment/MADS/. Only data gathered after 1990 are included. AB is station 4,410 where the depth was 11 m, BV station 170,006 where the depth was 16.6 m, and NZ station 1,937 where the depth was 11 m.

different years—1998 and 1999. Four surveys were carried out in this area; 2 in 1998 (May and June) and 2 in 1999 (June and late August). The bottom sediment consists primarily of sand with stones and scattered patches of vegetation.

Aarhus Bay (BV) is a complex of bays and inlets (Figure 1). The releases were at 5 different locations, but the majority of fish were released in Begtrup Vig. Begtrup Vig faces the south and the coastline is east–west oriented. All wild turbot came from this location and were caught in 8 surveys between 2001 and 2006 (6 in May, 1 in June, and 1 in September). The degree of exposure in Aarhus Bay varies from place to place, but Begtrup Vig is a wind-protected, semi-enclosed bay. The bottom sediment is mostly pure sand with some eel-grass (*Zostera marina*) and stones. The reported recaptures of released turbot were distributed throughout the entire habitat of Aarhus Bay.

The northern part of Zealand (NZ) is an east–west orientated coastline, and the most wave-exposed coastline in the inner Danish Waters (Rasmussen, 1995). The bottom consists of sand with few stones and limited vegetation. Turbot were released at 6 different locations throughout the coastline. In total, 15 surveys were conducted in this area (10 in April/May, 3 in June, and 3 in September). For more detailed information on the area and the releases, see Støttrup et al. (2002).

The principal difference between the 3 release habitats was the orientation of the coastline and hence the degree of exposure to the dominant westerly winds. Wind from the southwest was the second most frequently observed during the years 1971–2000, but when looking at winds stronger than 10.8 m/sec, these were mainly from the west or northwest. (Figure 1). The salinity also differed at both 0–1 m and 4–5 m depth. The range of salinities observed was much higher in BV and NZ than AB, and the mean salinity was somewhat lower at NZ (Table 1). No noticeable differences in temperature were seen between the 3 release habitats.

Hatchery Fish and Releases

All released turbot originated from commercial Danish hatcheries and were reared in extensive systems. The turbot released at the Northern part of Zealand were from 3 different hatcheries, whereas all fish released at Aarhus Bay and Aalborg Bay originated from a single hatchery. The hatcheries obtain turbot eggs or larvae from a Norwegian hatchery, whose broodstock originates from the Kattegat/Skagerrak area, i.e., the area North of Denmark between Sweden and Norway.

After metamorphosis the turbot were transferred to indoor glass fiber tanks and fed commercial dry feed. One to two weeks before the turbot were transported to the release site, the 1-year-old fish were tagged on the eye side close to the tail and near the dorsal fin with an external individual identifiable T-bar tag (Hallprint, Victor Harbor, Australia). The total length of all fish was measured during tagging to the lowest 0.5 cm. The number of fish released at one time ranged from less than a 1,000 to as many as 30,000. The mean length and standard deviation of turbot released was 13.6 ± 2.8 cm at NZ, 14.2 ± 3.5 cm at BV, and 14.7 ± 3.6 cm at AB.

The fish were transported directly from the hatchery to the release site by truck. From the truck the fish were either carried the last distance to the sea in baskets or the truck was taken on board a chartered ferry and the fish were released through a pipe from the truck directly into the sea.

Growth of Released Turbot

All reported recaptures from the commercial or recreational fishery as well as recaptures from surveys were included in the growth analysis. Data received from commercial or recreational fishermen were thoroughly scrutinized to confirm the reported time of recapture and the length at recapture. Incomplete reports (e.g., exact size or recapture date lacking) were ignored. The increase in length from the year of release to the year of recapture was estimated and tested with a student's t-test. The Specific Growth Rate (SGR) was calculated as:

$$SGR = 100 \cdot \left(\exp(\frac{\ln(L_t) - \ln(L_0)}{DAL}) - 1 \right) \qquad (1)$$

where L is the length at recapture (t) or release (0). DAL is the days at liberty experienced during the growth period, i.e., between April and November.

Estimating Abundance of Wild Turbot

The trawl used was a standard 4.5 m wide and 36 cm high, young-fish trawl (see Støttrup et al., 2002 for further details on the gear). Sampling in all 3 areas was stratified by depth to cover the entire depth distribution of the age-0 turbot. Only data from fall surveys were included to ensure that the peak settling had occurred. A total of 40, 34, and 30 hauls were made in September in the areas North Zealand and Aarhus Bay and in late August in Aalborg Bay, respectively. The hauls were made at a specific depth with 10-min trawling duration at a speed of 1 knot. The swept area for a single haul of 10 min was about 1800 m^2. The depth stratified area in km^2 within each of the habitats and the total length of the coastline were determined using GIS.

According to the length-age key from Støttrup et al. (2002), all fish smaller than or equal to 10 cm were assumed to be age-0 individuals.

To convert trawl catch data into real abundance data, the catchabililty (efficiency) of the trawl when catching turbot of different sizes had to be known. To find this, a preliminary experiment with releases of a known number of hatchery-reared turbot was conducted. Two different length classes: 4.5 cm and 11 cm were released and combined with results from an earlier experiment where 17-cm large turbot were released (Sparrevohn and Støttrup, 2007). After release, turbot were sampled daily using the young fish trawl and a sampling scheme where the spatial dynamics of the fish was included, i.e., the dispersal away from the release position were taken into account. See Sparrevohn et al. (2002) for a thorough description of the model and the sampling strategy. The fraction of the number released that is estimated from the trawl data is called the recatchable part (q_t), which is linked to the mortality (Z) and catchability (ρ) according to:

$$q_t = \rho \cdot \exp(-Z \cdot t) \qquad (2)$$

Estimates on Z and ρ can be obtained from Equation (2) by a log-transformation and least-square regression. Only the first 3 days of sampling were included in this regression since the impact from the post-release mortality is known to be limited to these days (Sparrevohn and Støttrup, 2007).

Stomach Contents of Wild Turbot

All sampling took place in the daytime, and all turbot caught were kept on ice on board the ship for later freezing on land. During ice storage, no signs of disgorged stomach contents were evident. The stomachs were later thawed and examined in the laboratory. All prey items were identified to species where possible, or alternatively to classes. A total of 1,150 stomachs from wild turbot were available, where 150 were from AB, 193 from BV, and 807 from NZ. The stomachs were divided according to fish total length into 3 size classes ($<$10 cm, 10–20 cm, and $>$20 cm).

The first analysis was on whether the occurrence of empty stomachs found in wild turbot was dependent on the area and the length of the turbot. This was analyzed using a logistic GLM, where the stomach (E) can be empty (0) or containing food (1) and is binomially distributed, i.e., $E \sim \mathrm{b}(1, p_E)$, where p_E can depend on the size of the turbot (Lgd) and the area (a). The crossed effect between area and fish size was not added to the model, i.e., the model with the constants α, λ, and β is:

$$Logit(p_E) = (\alpha + \lambda_a) + \beta \cdot Lgd \qquad (3)$$

The next model runs were set up to analyze whether there were differences in the occurrence of fish in the diet of the wild turbot from the 3 different areas, and if this was dependent on the size of the fish. Again, the dependent variable was occurrence of fish in the stomachs (F), which is binomially distributed $F \sim \mathrm{b}(1, p_F)$. If fish were present F was 1, otherwise 0. In this analysis, only those stomachs containing food items were included, hence the number of stomachs was reduced to 100 in AB, 76 in BV, and 638 in NZ. Again a logistic GLM was used, including area and fish size, and where α, λ, and β are constants.

$$Logit(p_F) = (\alpha + \lambda_a) + \beta \cdot Lgd \qquad (4)$$

For the wild age-0 turbot caught at NZ, the stomach content was weighed (wet weight) and from this a stomach fullness index (*SI*) was estimated as:

$$SI = 100 \cdot \frac{Stomach\ weight}{Fish\ weight} \qquad (5)$$

To examine any effect from depth, *SI* from the different depth intervals: 1.5–2.5 m, 2.5–3.5 m, and deeper than 3.5 m, was compared using a Students t-test. Fish with empty stomachs were set to have a stomach weight of 0.

All statistical tests were done using freeware R 2.2.1, downloaded at www.r-project.org, except for the area estimation which was done using the software ArcMap (© 1999-2006 ESRI Inc., USA).

RESULTS

Growth of the Reared Released Turbot

The average increase in length during the first year after release was not significantly different between the areas AB and BV. The average length increment was 9.7 and 10.8 cm (t-test, $p = 0.17$) for AB and BV, respectively (Figure 2). These two habitats differed significantly from NZ where the average length increment one year after release was only 8.6 cm (t-test, $p < 0.01$). This pattern continued throughout the second and third year after release, and the length increase in BV continued to be significantly higher than in NZ (t-test, $p < 0.01$ for both years). The specific growth rate was calculated, assuming that all growth occurred from April–November (Støttrup et al., 2002), and was estimated as 0.21, 0.21, 0.17 %/day for AB, BV, and NZ, respectively.

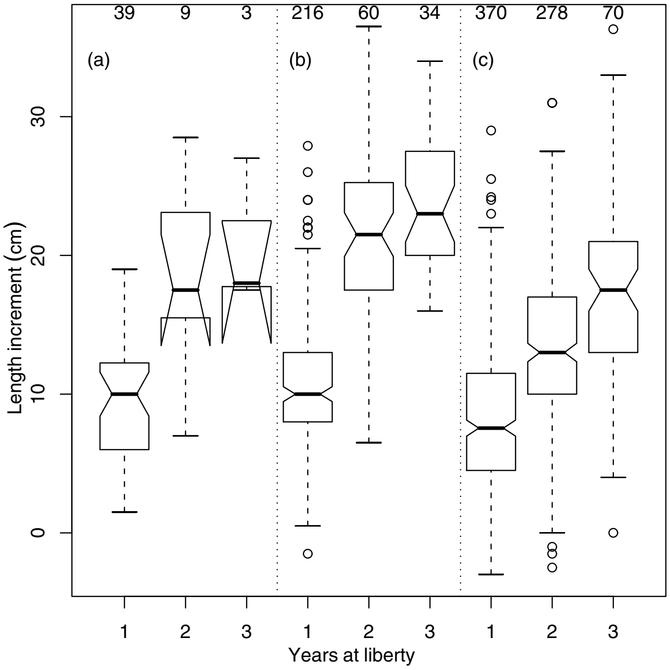

Figure 2 The length increment from year at liberty to year 1, 2, and 3 after release, drawn as box-plots. Box-plots in panel (a) represents Aalborg Bay (AB), panel (b) Aarhus Bay (BV), and panel (c) North Zealand (NZ). Numbers above each box shows number of observations. The features are: solid thick line is the median, the first and third quartiles are the upper and lower limit of the box, i.e., the inter-quartile range (IQR). The extreme values (within 1.5 times the IQR from the upper or lower quartile) are the ends of the dotted lines extending from the IQR. Points at a greater distance, i.e., outliers, are indicated with circles. The notch in the box around the median is the 95% confidence interval of the median. This can be interpreted as if the notches of 2 plots do not overlap; this is a strong indication that the 2 medians differs.

Abundance and Depth Distribution of Wild Individuals

No age-0 turbot were caught during the late August surveys in AB, even though 30 hauls were made at 5 different locations at depths between 1.2 and 3 m. In the same surveys, older turbot were caught using a larger trawl. During the September surveys at NZ, 128 age-0 turbot were caught. Three surveys were done in 3 different years, and age-0 turbot were only caught during 2 of these surveys. In BV, 88 age-0 turbot were caught during the September surveys.

The depth distribution of the turbot caught at NZ was centered at 3 m depth, but age-0 turbot were caught at depths to 8 m. This depth distribution of turbot at NZ was very different to that found at BV. At BV, the occurrence was highest at 1–2 m depth and none of the age-0 turbot were caught below 4 m (Figure 3).

One of the critical elements in trying to estimate the total abundance from catch data is that the catchability (efficiency) of the gear used is most often unknown. From the preliminary experiment, with releases of a known number of reared turbot, the catchability was estimated for the 3 sizes of turbot: 4.5, 11, 17 cm to be 40, 26, and 11%, respectively, when caught with a young-fish trawl (Figure 4).

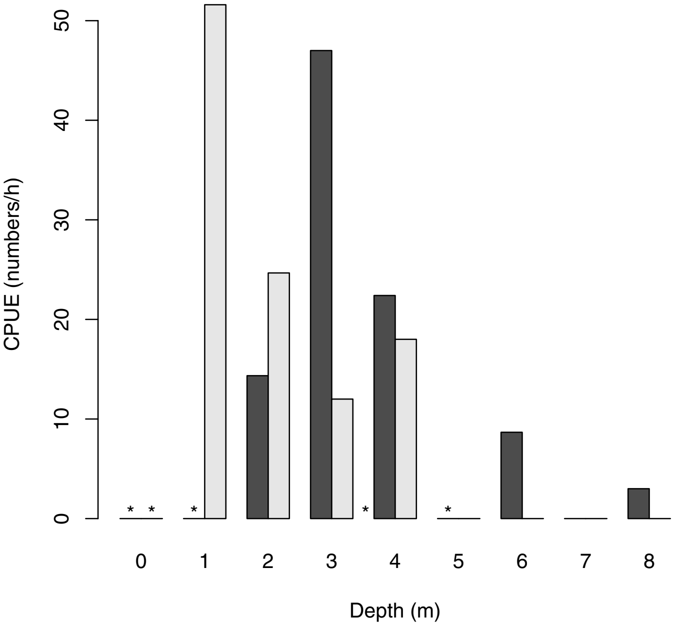

Figure 3 Depth stratified catch per unit effort (CPUE) in number individuals caught per hour trawling for Aarhus Bay (BV, white bars) and North Zealand (NZ, solid bars). Asterisks indicate absence of sampling.

The total abundance of juvenile turbot was estimated for the 3 habitats (Figure 1; Table 2). In NZ, the total number of age-0 turbot was estimated to be approximately 360,000 individuals, and in BV the total number was found to be 478,000. Excluding the catches of fish at 8 m depth in NZ did not change the results dramatically, since these catches only summed up to 15% of the total catch. In AB not a single age-0 turbot was caught. Knowing the coastline length, it was possible to estimate the total abundance of juvenile turbot/mcoastline. In NZ it was estimated to be 6, BV 3, and 0 turbot/m coastline in AB.

Stomach Content of Wild Individuals

The distribution of wild turbot with empty stomachs did not show any habitat dependency (GLM, $p = 0.3$), but differed with fish size (GLM, $p < 0.01$) (Figure 5). The trend was a decrease in the numbers of stomachs containing food with increasing fish size.

The occurrence of fish in the diet depended on turbot size (GLM, $p < 0.01$) and on the release habitat (GLM, $p < 0.01$). The length at which 50% of those stomachs containing food items had one or more fish included in the diet was 15.0 cm for BV, 19.2 cm AB, and 26.4 cm for NZ (Figure 6). The other dominant food items for turbot were mysids and shrimp (Table 3). The dominating prey fish species was the sand goby (*Pomatoschistus minutus* (Pallas)) which was found in 59% of the 279 stomachs containing fish. In the age-0 turbot, i.e., turbot smaller than 10 cm, sand gobies were the major fish prey item in both BV and NZ, where it was present in 97% and 90% of those stomachs containing fish. But in total, only 13% had eaten fish in NZ compared to 36% in BV. For the larger size-group

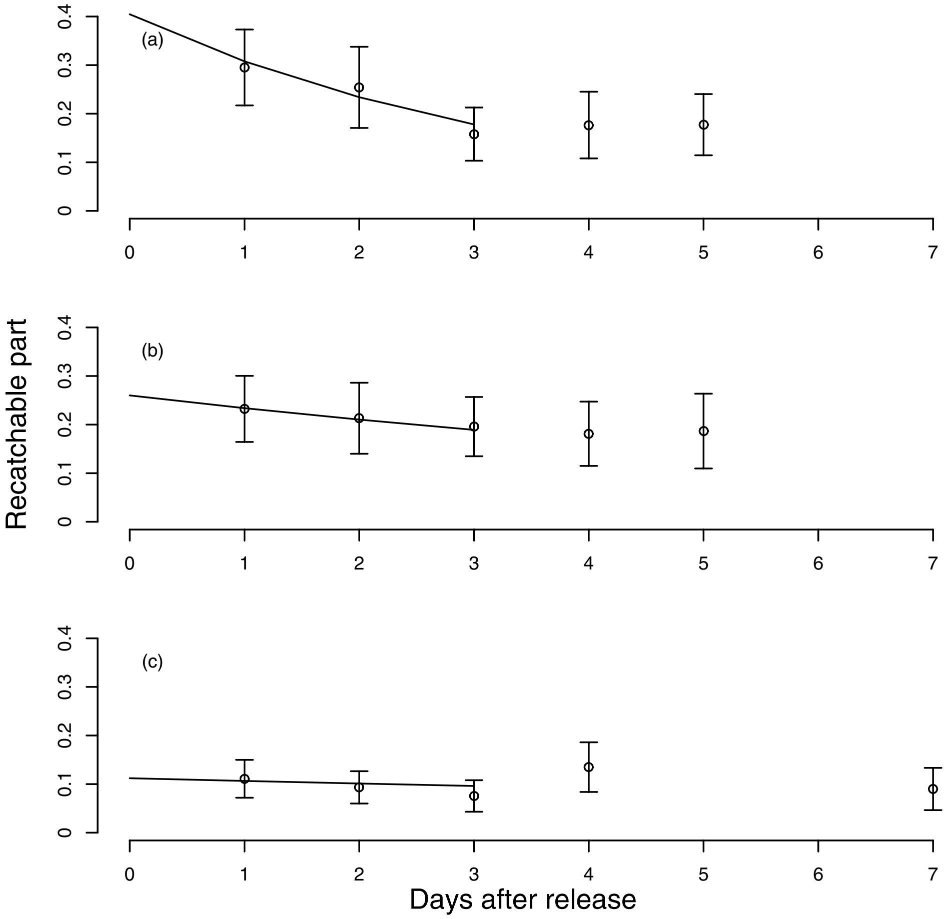

Figure 4 The recatchable part for turbot released at BV. Panel (a) shows turbot of size 4.5 cm, panel (b) 11.0 cm, and panel (c) 17.0 cm. Bars represent the 95% confidence interval. The catchability is estimated by extrapolating the solid line onto the y-axis, i.e., the catchability at time of release. For those days where no estimate is shown, the catches were either too small to produce a reliable result or no fishing took place.

(10–20 cm), sand gobies continued to be the most important prey species and were found in 90, 92, and 77% of those stomachs containing fish in AB, BV, and NZ, respectively. In NZ fish only 15% of the stomachs were found to contain food items, compared to 40% in AB and 50% in BV. Hence, the sand goby was the first fish species observed to be eaten by turbot and continued to be the most important fish prey until the turbot had reached a size of at least 20 cm.

Table 2 The estimated total abundance of age-0 turbot per 1 km coastline and the values used in the calculation, the total catch per area, depth stratified areas, and the length of the coastline

	Aalborg Bay (AB)	Aarhus Bay (BV)	North Zealan (NZ)
Catch	0	88	128
Number hauls	30	34	40
Area (km^2)			
0–1 m	60	23	4
1–2 m	32	13	4
2–3 m	38	15	5
3–4 m	84	22	8
4–5 m	145	28	14
5–6 m	159	31	17
6–7 m	266	27	21
7–8 m	310	27	21
Coastline (km)	147	163	62
Total Numbers	0	≈478,000	≈360,000
Numbers/m coastline	0	≈3	≈6

The average stomach index *SI* did not differ significantly between depth intervals (t-test, all $p > 0.4$). The values ±SD were 1.2 ± 1 ($n = 65$), 1.4 ± 2 ($n = 49$), and 1.3 ± 2 ($n = 55$) for the depth intervals 1.5–2.5 m, 2.5–3.5 m, and deeper than 3.5 m, respectively.

DISCUSSION

Growth of Reared Released Individuals as Habitat Suitability Indicator

Growth is one of the easiest measurements of an individual's "health" and has been routinely used to assess the success of releases of artificially bred fish into a given habitat. High growth rates are generally assumed to indicate suitable habitats for stock enhancement or restocking. One downside of using growth is that it is a post-release measurement of habitat suitability and not a predictive one.

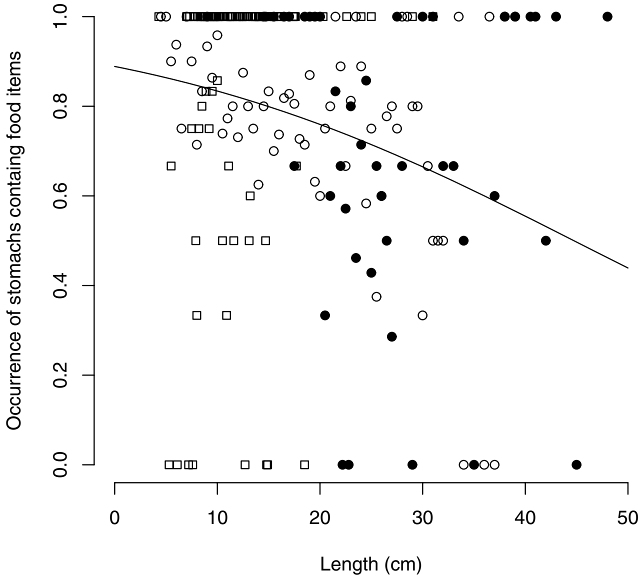

Figure 5 The occurrence of stomachs containing food items against the total length of the wild turbot caught at the 3 different release habitats. Each symbol represents the occurrence per 0.5 cm length. Solid circles are Aalborg Bay (AB), squares represents Aarhus Bay (BV), and circles North Zealand (NZ). The solid line is the predicted relationship, and, since habitat influence was non-significant, the line applies for all habitats.

The specific growth rate is influenced by temperature and salinity, and the optimum temperature for turbot growth decreases with increasing ontogenetic stages of turbot (Imsland et al., 1996; Imsland et al., 2001). In two of the habitats in the present study, we found a yearly increase from age 1 to age 2 of approximately 10 cm, which was similar to the growth estimated in field studies of wild individuals (e.g., Jones, 1970). In the NZ site, growth was significantly lower, and, although the salinity and temperature of the 3 habitats examined varied slightly, these differences cannot explain the inferior growth observed in NZ (Table 1, Figure 2). Although NZ had the lowest mean salinity, these salinities were comparable to those at BV, where the fastest growth was recorded. Furthermore, intermediate salinities (18â), i.e., similar to those at NZ, provided the best growth and food conversion in laboratory studies of juvenile turbot (Imsland et al., 1996). In laboratory studies, the specific growth rate in length was found to be 0.28, 0.41, 0.52, and 0.52 %/day at temperatures of 10, 13, 16, and 19°C (calculated from Table 2 in Imsland et al., 2006), respectively. These laboratory values are higher than those found in the present study, but the temperature in the Danish waters can also be lower than 10°C during the growth period, depending on the time of the year and water depth. Temperature was relatively similar in the 3 habitats, so neither temperature nor salinity is likely to be a proper explanation for the marked differences in growth observed between habitats.

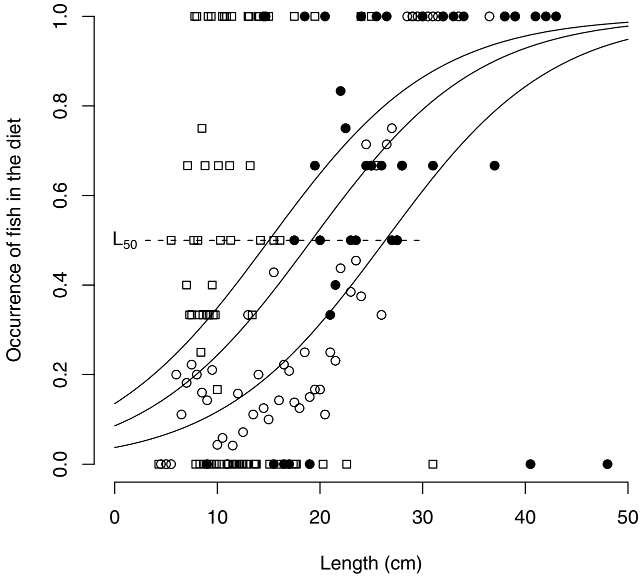

Figure 6 The occurrence of fish as prey in the diet of those wild turbot with stomachs that were not empty. Each symbol represents the occurrence per 0.5 cm length group. Solid circles are Aalborg Bay (AB), squares represents Aarhus Bay (BV), and circles North Zealand (NZ). The lines are the predicted relationship, and the line on top represents BV, the middle line AB, and the lower NZ. L_{50} is shown by the vertical dotted line and is the length at which 50% of the stomachs contain fish as prey. L_{50} was 19.2, 15.0, and 26.4 cm for AB, BV, and NZ, respectively.

Wild Fish Characteristics to Determine Suitable Release Habitat

Abundance and Depth Distribution of Wild Individuals as Indicators. The distribution of juvenile turbot at NZ differed to that at BV and to those recorded in a number of other studies. Riley et al. (1981) found no individuals deeper than 2 m, and Jones (1973) found none below 4 m. MacCall's (1990) habitat basin model predicts a trade-off between density-dependent and density-independent factors affecting the overall fitness of an individual. The marked change in depth distribution may be a result of turbot choosing a less favorable depth to avoid competition with other individuals or to seek a greater supply of food. This may be an important aspect and should be considered as a criterion for choosing release habitats within restocking or stock enhancement programs.

The catchability found in the preliminary experiment differs to some degree from earlier studies where the catchability of turbot between sizes 7.8 and 12 cm was estimated to be around 45% (Sparrevohn and Støttrup, 2007). The reason for this discrepancy may be due to differences in post-release mortalities observed (see Støttrup and Sparrevohn, 2007, for further information). In the present study, the post-release mortality was minor, whereas in the study by Sparrevohn and Støttrup (2007) mortalities up to 66%/day were estimated. The lower mortality in this study made the extrapolation to the time of release more robust than in the case where a large decline in the numbers of fish present in the release area has been witnessed after release. For other flatfish species, similar catchabilities have been observed, e.g., 15–60% for juvenile flounder and dab (*Limanda limanda*) (Weenhagen et al., 1997), 75–100% for plaice <7 cm long, decreasing to 15–30% plaice >15 cm (Kuipers, 1975).

Table 3 The number of stomachs examined and the number of stomachs containing food together with the occurrence of prey species in the stomachs of different size groups of turbot

	Aalborg Bay (AB)			Aarhus Bay (BV)			North Zealand (NZ)		
	<10 cm	10–20 cm	>20 cm	<10 cm	10–20 cm	>20 cm	<10 cm	10–20 cm	>20 cm
Stomach examined	1	21	128	106	81	6	176	434	197
Stomachs with food	1 (100)	20 (95)	79 (62)	91 (85)	66 (11)	6 (100)	156 (88)	331 (76)	150 (76)
Crangon.	1 (100)	9 (45)	23 (29)	18 (20)	27 (41)	3 (50)	24 (15)	75 (23)	46 (31)
Mysidacea.	1 (100)	4 (20)	2 (3)	41 (45)	18 (27)	2 (33)	123 (70)	232 (70)	68 (45)
Pisces	0 (0)	10 (50)	55 (70)	33 (36)	26 (40)	3 (50)	21 (13)	52 (15)	79 (53)
Pisces in detail									
Pomatoschistu minutus	0 (0)	9 (90)	13 (24)	32 (97)	24 (92)	3 (100)	19 (90)	40 (77)	22 (28)
Ammodytidae spp.	0 (0)	0 (0)	7 (13)	0 (0)	0 (0)	1 (33)	0 (0)	8 (15)	24 (30)
Flatfish (Misc.)	0 (0)	1 (10)	21 (40)	0 (0)	0 (0)	0 (0)	0 (0)	1 (2)	1 (1)
Roundfish (Misc.)	0 (0)	1 (10)	25 (45)	1 (3)	1 (4)	1 (33)	0 (0)	2 (4)	34 (43)
Unidentified fish	0 (0)	0 (0)	5 (9)	0 (0)	2 (8)	0 (0)	7 (33)	3 (6)	3 (4)

All numbers in brackets are percentages. For stomach with food, the percentages are of total number of stomachs examined, for *Crangon, Mysidacea*, and *Pisces*, the percentages are of number stomachs with food, and for categories of fish, they are the percentages are of *Pisces*.

Since both the depth distribution was observed and the catchability estimated, the total number of individuals present could be estimated, and it was found that the density of turbot/m of coastline was twice as high at NZ compared to BV (Table 2).

From 1993–1995 a total of 80,000, 153,000, and 101,000 alizarin tagged age-0 turbot were released in NZ during the fall (Støttrup et al., 2002). Assuming a constant carrying capacity over these years, 18, 30, and 22% of the following year's catches of that cohort are predicted to be released fish with an alizarin mark. This compares with an overall percentage of 25% (Støttrup et al., 2002), indicating that the predicted figures and overall estimated abundance of wild age-0 population are reasonable.

Stomach Content of Wild Individuals as Indicators. For the turbot sizes examined in this experiment, the occurrence of empty stomachs could not be used as an indicator describing the 3 different release habitats.

The diet of turbot in the current study (Table 3) was similar to that described in other studies, with fish, mysids, and shrimp as the major prey items (e.g., Braber and De Groot 1973; Jones, 1973; Aarnio et al., 1996) and for smaller individuals, occasionally polychaeta (Jones, 1973). Sand gobies were also observed to be important prey items for juvenile turbot as small as 3 cm within the Swedish Åland archipelago located in the Northern Baltic Sea (Aarnio et al., 1996). At sizes between 3 and 5 cm, 40% of the turbot stomachs examined contained sand gobies. In a coastal area in Wales, *P. minutus* was observed in the stomachs of 2 age-classes of juvenile turbot, although a limited number were found in turbot smaller than 15 cm (Jones, 1973). In a study at an exposed beach in Spain, the inclusion of fish in the diet of turbot juveniles occurred at sizes between 6 and 15 cm, and the main prey fish species here was *Ammodytes tobianus* L., another fish species of a suitable size range as prey for juvenile turbot. The relationship between turbot mouth size and fish length in the diet has been described, and the largest age-0 turbot measuring 10 cm was calculated to have a mouth gape of 1.5 cm (Irwin et al., 2002), large enough to swallow a sand goby or a small *Ammodytes tobianus* L., but probably unable to swallow larger fish, such as gadoids and flatfish. Thus, in the absence of suitably sized fish prey items, the juvenile turbot continue to eat less favorable prey, e.g., shrimps and mysids. In NZ, fewer fish were found in the turbot diet, and they were also first found in the diet of larger turbot than in the other 2 areas, which could account for the slower growth recorded at NZ.

Changing the diet from mainly crustacean prey items with exoskeletons to vertebrate fish is an important ontogenetic shift, considered beneficial for turbot, since the evacuation rate of fish is higher (Andersen, 2001). This would result in a higher energy intake rate and consequently an improvement in the potential growth rate. Adult turbot are also found to feed almost exclusively on fish, and prey size has been observed to increase with increasing fish size (Braber and De Groot, 1973; Jones, 1973).

Throughout the Baltic, *P. minutus* is very common, and in shallow areas it can reach abundances up to 11.2 individuals/m^2 (Aarnio and Bonsdorff, 1993). Its presence is generally associated with soft sediment and wind- and wave-protected areas rather than habitats with high wave exposure and coarser sediment. These highly exposed areas therefore may not provide a sufficient number of small fish prey for the age-0 turbot to shift to a diet consisting of fish at an early stage, resulting in slower turbot growth. This contradicts the general impression that turbot is a species associated with highly exposed beaches, prefers the surf zone, and that their generally low abundances are associated with a highly restricted nursery habitat (Van der Veer et al., 2000). Their occurrence in such habitats may be related to larval transport processes rather than habitat preference or suitability. This is supported by evidence of correlations between year-class strength and onshore wind (Van der Veer et al., 2000).

SUMMARY AND CONCLUSION

The objective in the present paper was to evaluate if information gathered on the wild population could be used to assess the suitability of a given habitat for stock enhancement.

The highest number of turbot/m of shore line was found in NZ, where the fish were distributed in deeper waters and over a broader range of depths than in the other 2 areas. This unusual depth distribution indicates a spillover to less favorable depths. It was not possible to find correlations between the depth at which the turbot were caught and the amount of prey found in the stomach. The stomach analyses further revealed that the turbot at NZ were forced to maintain a diet of shrimp and mysids to a much larger size than at AB and BV, resulting in significantly slower growth rate for released fish at NZ than in the other 2 habitats. It is therefore possible to use information on turbot abundance, depth distribution, and diet to evaluate habitat suitability for releases. This information is also useful in assessing the quality of juvenile nursery grounds for turbot in different areas.

The search for methods to evaluate ideal juvenile nursery grounds is not restricted to stocking experiments. With the increasing pressures on the coastal zone, conflicts between resource exploitation and resource protection create higher demands for knowledge-based integrated management. The kind of information generated from this study is useful in both fisheries management and ecosystem-based management. There is a need for methods to help identify EFH, functional Marine Protected Areas (MPAs) or no-fish zones. The method described in this article is applicable for all those purposes and can be achieved with reasonable costs, but it is restricted to one species of fish.

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Chapter 6

Diffusion of fish from a single release point.

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Diffusion of fish from a single release point

Claus R. Sparrevohn, Anders Nielsen, and Josianne G. Støttrup

Abstract: In a field experiment, 3529 turbot (*Psetta maxima*) were released in order to estimate and describe the movements of hatchery-reared fish by applying diffusion theory. After liberation, the development of the population density was estimated during the following 9 days, and from that, the rate of diffusion and the advection were determined. Two approaches were followed to describe the data: a normal distribution approximation (NDA) model and a partial differential equation (PDE) model. In the latter, it was possible to include the effect of sampling. The two models gave similar results, indicating that the sampling of fish during the experiment did not have any detectable effect on the population density. The activity of the released turbot resulted in an individual daily displacement of 151 m·day^{-1}, except for the first 2 days at liberty, where the displacement was estimated to be considerably lower. Advection was significant and was related to the displacement of the water body. Further, it was possible to estimate the postrelease mortality as 14%·day^{-1} and the catchability of the turbot when caught with a young fish trawl as 28%.

Résumé : Dans une expérience sur le terrain, 3529 turbots (*Psetta maxima*) ont été relâchés dans le but d'estimer et de décrire les déplacements de poissons élevés en pisciculture d'après la théorie de la diffusion. Après la libération, l'évolution de la densité de la population a été suivie pendant 9 jours; par la suite, le taux de diffusion et l'advection ont été déterminés. Deux approches ont été utilisées pour décrire les données, un modèle d'approximation de la distribution normale (NDA) et un modèle d'équation différentielle partielle (PDE); il a été possible d'inclure dans ce second modèle les effets de l'échantillonnage. Les deux modèles donnent des résultats similaires et indiquent que l'échantillonnage des poissons durant l'expérience est resté sans effet décelable sur la densité de la population. L'activité des turbots relâchés a produit un déplacement journalier individuel de 151 m·jour^{-1}, sauf pendant les deux premiers jours de liberté où le déplacement estimé a été beaucoup moindre. L'advection était importante et variait en fonction du déplacement de la masse d'eau. De plus, il a été possible d'évaluer la mortalité après la libération à 14 %·jour^{-1} et la capturabilité des turbots par un chalut pour jeunes poissons à 28 %.

[Traduit par la Rédaction]

Introduction

When releasing cultured fish into a natural habitat, it is crucial to analyze the speed and direction at which these newly released individuals colonize the habitat. This is important because the dispersal into the area will influence the density as well as the numbers of prey and predators that the introduced fish will encounter. In addition, one might want to know which factors (i.e., the hydrographic environment or migratory behavior) influence advection.

One very successful way of modeling movements of living organisms has been to apply diffusion theory. A central parameter in diffusion models is the rate at which the population diffuses into the environment (D), which can be interpreted as a result of movements made by each single organism following a Brownian motion. One way of deriving the Brownian motion is as the limit of a random walk. Let τ be the time between two steps and δ be the length of each step in a random walk. If we let $\tau,\delta \rightarrow 0$ in such a way that $(\delta^2/\tau) \rightarrow (\sigma^2/4)$, then we get a Brownian motion with variance parameter σ^2. The resulting diffusion model at population level will have a diffusion coefficient of $D = \sigma^2/2$. If the probability of stepping in one direction is ε greater than the probability of stepping in the other direction and $\lim_{\delta,\tau,\varepsilon\rightarrow 0} \varepsilon\delta/\tau = \alpha$, then we get a Brownian motion with advection α. The assumption that each individual organism follows a Brownian motion can be relaxed in several ways without losing the application of the diffusion model at the population level (Okubo 1980). For instance, whether the steps of each individual are correlated in short time intervals is of minor importance, the key assumption is that the individuals move independently of each other.

When analyzing movement of individuals and applying diffusion models, it is crucial to address the problem of spatial scaling (Levin 1992). One can view the movement on a small spatial scale and analyze the nature and dispersal range of individual organisms (e.g., Kareiva and Shigesada 1983; Viswanathan et al. 1996). Another approach is to look at a larger spatial scale and analyze the diffusion of populations (Kareiva 1983; Andow et al. 1990; Sibert et al. 1999), where a major part of the work on the application of diffusion theory to natural events has been to analyze the speed at which invading animals colonize new habitats (e.g., Skellam 1951; Lubina and Levin 1988).

In fisheries biology, the main interest concerning move-

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ments of marine fish has been on a large scale, where the focus has been on migrating species and the mobility of exploited stocks. Much effort has been devoted to a descriptive approach of evaluating the migratory behavior of fish and fish stocks in order to identify spawning, nursery, and feeding areas. Some studies, though, have been dealing with complex models, such as the advection–diffusion–reaction model applied to data on tagged skipjack tuna (*Katsuwounus pelamis*) (Sibert et al. 1999). Further, most studies have been based on data from traditional capture–recapture experiments, but in recent years experiments have also been based on data gathered from data storage tags (DST) (e.g., Metcalfe and Arnold 1997).

Most work focusing on large scale movements of fish and fish stocks has been based on capture–recapture experiments where the time and distance between release and recapture typically is big. As a consequence of that, although known to be an important factor in the coexistence of species (Levin et al. 1984) and the interactions between fish stocks (Rose and Leggett 1990; Neuenfeldt 2002), small scale movement has been neglected.

In this study we present an investigation on small scale diffusion in a natural environment. In mid-May 2001, a total of 3529 turbot (*Psetta maxima*) between 7 and 8 cm in length were released in a homogeneous coastal area. For the following 9 days, the released turbot were recaptured in order to estimate the resulting population density. We decided to sample and analyze our data in one dimension only, i.e., only the distance parallel to the shore was considered. This unique dataset carried the foundation for present analysis, where the primary objective was to estimate the rate at which the released turbot dispersed into the habitat in addition to analyzing the interaction between hydrographic properties and advection. Further, as a result of the experimental design, we were able to estimate the mortality and in addition the catchability of the released turbot when caught with a young fish trawl. Two models were applied to describe the data: an easily implemented normal distribution approximation (NDA) model and a more complex partial differential equation (PDE) model. With the latter, it was possible to include any effect from sampling on the distribution.

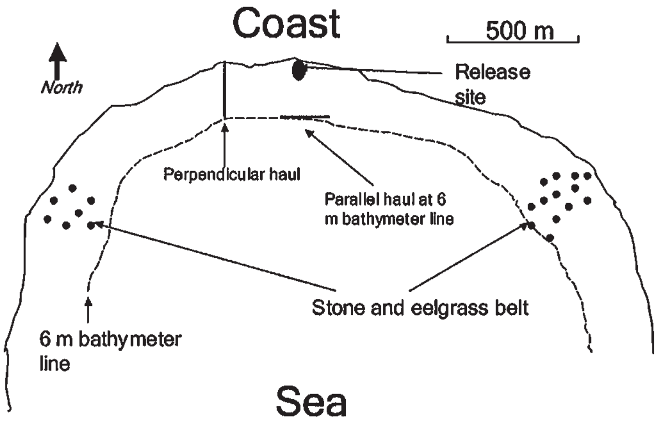
Materials and methods

Location and experimental design

Begtrup Vig, a small bay located near Århus, Denmark, was the chosen site for this experiment. This bay was found to be suitable because the bottom was exclusively sand to a depth of approximately 4 m, which corresponded to 400 m from the shoreline, and therefore it was easy to fish with a young fish trawl. Further, the bay was a natural habitat for turbot with a small wild population. The release position was central in the bay (Fig. 1). In the western direction, the sand area stretched to 1300 m from the release point. Beyond this point, a large eelgrass (*Zostera marina*) belt made it impossible to fish. In the eastern direction, larger stones at a distance approximately 1100 m from the release site delimited the survey area.

Turbot of an average size between 7 and 8 cm were purchased from a commercial fish farm. Fifteen days before liberation, turbot were sorted at the fish farm to ensure as narrow a length distribution as possible and were tagged with external individually identifiable T-bar tags. They were not fed for 2 days before release to ensure empty stomachs. The turbot were transported at 11.5°C from the fish farm to the release site by truck. At the time of release the temperature in Begtrup Vig was 17°C. A total of $N_{0,0}$ = 3529 was released at 18:00 (t = 0) at 0.5 m depth. Fishing for the released turbot started the next morning and continued for the next 9 days with a varying number of hauls per day. Every fishing day started with one haul parallel to the coast at the 6 m bathometer line. The duration of these parallel hauls was 10 min with equal time devoted east and west of the release site. The purpose of this haul was to ensure that it was appropriate to end the following hauls, which were perpendicular to the coast at a depth of 6 m. For the rest of the day, only hauls perpendicular to the coast were conducted. These hauls all started at the shore or as close to the shore as possible and were towed to a depth of 6 m. The intention was to maintain a towing speed of 0.8 knots, but problems with maintaining the direction were encountered when the wind was stronger than 5 $m \cdot s^{-1}$, from either the east or the west. Thus, on a few occasions a compromise was made between increasing the speed to 1 knot and deviating from a 90° angle from the coastline. This was only a problem towards the end of the survey, i.e., days 8 and 9. The trawl used was a young fish trawl with a total opening of 4.5 m. For a more detailed description see Støttrup et al. (2002).

Fig. 1. A schematic representation of the investigation area. As no turbot were caught in the perpendicular hauls at the 6 m depth, they were mainly assured to spread out parallel to the coast. The data used in the analysis were collected with the perpendicular hauls. The investigation area was delimited by stone and eelgrass belts in the eastern and western direction.



The distance of the haul from the release position was not chosen at random but was fixed to sampling distances, about 0, 1, and 2 times the predicted standard deviation of the population density. This strategy was chosen to optimize the information about the population density with a limited number of hauls (see Appendix A). Additional hauls were chosen at random but within the area where 90% of the released turbot were expected.

Stomach analysis

A subsample of the total catch of tagged turbot was taken for later stomach analysis in the laboratory. The remaining fish were liberated at a depth of 1 m in the middle of the trawl track. Towards the end of the survey the entire catch was sampled because of low catches. In the laboratory, stomachs were analyzed to determine if the fish had begun feeding on natural prey. All fish with traces of food items in their stomach were defined as fish that had started feeding.

Model and data handling

Let $x_t^{(i)}$ denote the x position of the ith fish at time $t > 0$. Assuming that the fish are independent and that the movement of each fish can be approximated by a biased Brownian motion, where $B_t^{(i)}$ is a normalized Brownian motion, then

$$(1) \qquad x_0^{(i)} = 0 \text{ and } \mathrm{d}x_t^{(i)} = \alpha \mathrm{d}t + \sigma \mathrm{d}B_t^{(i)}$$

The key assumption of independent movement is difficult to confirm, but to our knowledge, social behavior, schooling, or synchronization in the swimming activity of turbot has never been observed or reported except during the spawning season.

Normal distribution approximation

Assuming that the effect of fishing is negligible, the density of the stock at some time $t > 0$ can be described as the density of a normal distribution $\varphi_{\alpha t,\sigma^2 t}$ with mean αt and variance $\sigma^2 t$. The expected number of tagged fish in a trawl width w around a position p at time $t > 0$ is denoted as follows:

$$(2) \qquad \begin{aligned} \bar{N}_{w,p,t} &= E(N_{w,p,t}) \\ &= N_{0,0}\int_{p-w/2}^{p+w/2} \varphi_{\alpha t,\sigma^2 t}(u)\mathrm{d}u \\ &= N_{0,0}\left(\Phi\left(\frac{p+w/2-\alpha t}{\sqrt{\sigma^2 t}}\right) - \Phi\left(\frac{p-w/2-\alpha t}{\sqrt{\sigma^2 t}}\right)\right) \end{aligned}$$

where Φ is the distribution function of a normal distribution and $N_{0,0}$ is the number of fish initially released. The expected catch ($\bar{C}$) is the fraction $q \in (0,1)$ of the expected number of fish that has survived to time t that can be caught:

$$(3) \qquad \bar{C}_{w,p,t} = q\bar{N}_{w,p,t}$$

If the standard deviation of the distribution of the tagged fish $\sqrt{\sigma^2 t}$ is large compared to the trawl width, then we can assume that the number of caught fish follow a Poisson distribution:

$$(4) \qquad C_{p,t} \sim \mathrm{Pois}(q\bar{N}_{w,p,t}(\alpha,\sigma))$$

Another approximation that is also valid if the standard deviation is large compared to the trawl width is

$$(5) \qquad \bar{N}_{w,p,t} \approx N_{0,0} w \varphi_{\alpha t,\sigma^2 t}(p)$$

This can be useful if it is too time consuming to evaluate Φ.

The negative log likelihood function of the observed catches (c) given the parameter values is given by

$$(6) \qquad \begin{aligned} l(\underline{c};q,\alpha,\sigma) &= \sum_{(p,t)} (\log(c_{p,t}!) + q\bar{N}_{w,p,t}(\alpha,\sigma) \\ &\qquad - c_{p,t}\log(q\bar{N}_{w,p,t}(\alpha,\sigma))) \\ &\propto \sum_{(p,t)} (q\bar{N}_{w,p,t}(\alpha,\sigma) - c_{p,t}\log(q\bar{N}_{w,p,t}(\alpha,\sigma))) \end{aligned}$$

Partial differential equation

Let us again assume the x position of each fish to follow eq. 1 and to be independent. The development of the stock density can be described by a partial differential equation (Okubo 1980):

$$(7) \qquad \frac{\partial}{\partial t} N_{x,t} = -\alpha \frac{\partial}{\partial x} N_{x,t} + \frac{\sigma^2}{2}\frac{\partial^2}{\partial x^2} N_{x,t}$$

and $N_{\cdot,0} = 1_{\{0\}} N_{0,0}$. This model is exactly the same as the NDA model if we simply solve the equation.

Besides solving the PDE model analytically where the solution is the NDA model, an equation like eq. 7 can be solved numerically by iterating forward in time from the initial condition $N_{\cdot,0} = 1_{\{0\}} N_{0,0}$. This way of solving a PDE model can be used to incorporate the effect of fishing into the solution. Each time the solution scheme passes a time point where catch–release takes place, we simply update the solution accordingly. If a large fraction of the total number of fish are caught each day, we should include this information in the model, even though we re-release the fish we catch at the same position. From the solution of eq. 7, the expected number of tagged fish in a trawl width w around a position p at time $t > 0$ can be estimated. This number is denoted $\tilde{N}_{w,p,t}$.

The negative log likelihood is derived as before:

$$(8) \qquad l(\underline{c};q,\alpha,\sigma) \propto \sum_{(p,t)} (q\tilde{N}_{w,p,t}(\alpha,\sigma) - c_{p,t}\log(q\tilde{N}_{w,p,t}(\alpha,\sigma)))$$

Numerical solution of the PDE model

Because the numerical solution scheme is needed as part of an optimization routine, it is very important that it is efficient. It may be necessary to evaluate the solution hundreds of times. A relatively fine spatial resolution of $\Delta x = 1$ m was chosen because the trawl is only 4.5 m wide. The time resolution was chosen to be 1 min.

Finite-difference schemes are frequently used to solve differential equations like eq. 7 (e.g., Sibert et al. 1999) and are efficient if the (approximate) solution is needed for every grid point. Several finite-difference schemes were implemented, but it became evident that it was too time consuming with the desired resolution. Fortunately, the solution in every grid point is not necessary. To optimize the likelihood, it is sufficient to know the solution in catch points at catch times. This is used in the following solution scheme.

The solution scheme needs to keep track of every single discrete impact to the system, denoted as impulses. An impulse is a set of three parameters $\mathcal{I} = \{n,p,t\}$, where n is the number of fish added to the system (catches are negative), p is the position, and t is the time. The first impulse is the release of the $N_{0,0}$ tagged fish at position $p = 0$ at time $t = 0$, or in other words $\mathcal{I}_0 = \{N_{0,0},0,0\}$. If this impulse was the only one, we could calculate the solution in every future point from formula 2. This is not the case in our experiment because the catches are additional impacts on the system. The first catch results in a number of impulses equal to the number of spatial grid points covered by the trawl. Each of these impulses is a fraction of the catch proportional to a fraction of the trawl width, which covers the interval multiplied by the population density, known from previous impulses. This implies that the impulses can only be calculated forward in time. After the impulses from the first catch follow the impulses from the first re-release, and so on.

Each of these impulses contributes to the total solution, in any future points, in exactly the same way as the first impulse. The total solution is found as the sum of the contributions from each of the previous impulses. Given the set of impulses $\mathcal{I}_0$, $\mathcal{I}_1$,..., $\mathcal{I}_I$ we can calculate the numerical solution in any grid point (p,t) from

$$(9) \qquad \tilde{N}_{\Delta x,p,t} = \sum_{\{i:t>t_i\}} n_i \left(\Phi\left(\frac{(p+\Delta x/2) - p_i + \alpha(t-t_i)}{\sqrt{\sigma^2(t-t_i)}} \right) - \Phi\left(\frac{(p-\Delta x/2) - p_i + \alpha(t-t_i)}{\sqrt{\sigma^2(t-t_i)}} \right) \right)$$

This solution scheme dramatically reduces the calculation time in this example, and the gain will be even greater if the spatial dimension was 2 or higher. The only drawback is that a bit more bookkeeping is required.

Parameterization

For simplicity, in the previous presentation of the models the parameters q,α,σ are assumed to be constant during the 9-day sampling period. This is not a realistic assumption because the hydrographic parameters change during the experimental period and the released turbot adapt to their new environment.

Therefore, to allow changes in these parameters, an NDA model where each of the three parameters is assumed constant during 24-h intervals (counting from release time) was fitted to the data. Hence q_t, α_t, and σ_t are estimated, where $t = 1,...,9$ equals days at liberty. The resulting model, called the full model, corresponds to estimating one normal distribution from each of the 9 days' catches, which produces a total estimation of 27 parameters.

From this full model the goal was to find another model with fewer parameters needed to describe the density distributions. This reduced model was found by testing the hypotheses that advection was zero ($\alpha_t = 0$) and that the variance was the same all (or some) days ($\sigma_1 = \cdots = \sigma_9$). The recaptured part ($q_t$) being connected to the trawl catchability (ρ) and the total mortality (Z) as

$$(10) \qquad q_t = \rho e^{-Zt}$$

was also analyzed, where it was assumed that mortality and catchability are constant. All hypotheses were tested by standard likelihood ratio tests.

Normal distribution approximation vs. partial differential equation

To evaluate if the two models gave identical results, the parameter estimates were compared. This comparison was done only for the reduced model but for all parameters (α_t, σ_t, ρ_t, and Z_t).

Because the NDA model is the solution to the PDE, the differences between these two models does not lie in the basic assumption about diffusion. The main difference is that the PDE model incorporates our interference with the population density. To make the NDA model even simpler, we assumed that the population density does not change between catches taken on the same day. This assumption was not necessary to make the NDA model work, but it made the model very simple and intuitive. Unfortunately, this assumption makes it difficult to compare the estimates from the two models because the population density (and the resulting parameters) estimated from the NDA actually represents an average of several population densities. Therefore, to facilitate a comparison, we chose simply to compare the daily population estimates from the NDA to the population estimates from the PDE at 18:00 each day.

Wind data

Wind data, consisting of eight measurements per day, were purchased from the Danish Institute of Metrology, and from those, the water body displacement (WBD$_t$) in the east–west direction parallel to this coast was calculated. Because the thickness of the Ekman layer was much larger than the depth at the location, Coriolis forces could be excluded. Hence WBD$_t$ could be calculated as the steady state balance between wind stress and bottom friction with the surface and bottom drag coefficients set equal:

$$(11) \qquad \mathrm{WBD}_t = \int_0^t \lambda \sqrt{v^2(s) \cdot |\sin(u(s))| \cdot \rho_a / \rho_w}\, \mathrm{d}s$$

Where $\lambda = -1$ or 1 for western and eastern wind, respectively, ρ_a and ρ_w represent the density of the air and water, 1.22 $\mathrm{kg \cdot m^{-3}}$ and 1028 $\mathrm{kg \cdot m^{-3}}$, respectively. Wind velocity is v, and wind direction is u. Each wind measurement is denoted by s. The integral was estimated by summing the average between two subsequent wind measurements. Two different estimates of water body displacements were calculated: one using the wind data from the entire day and one using only the wind in the period from 21:00 to 06:00, i.e., during the night. These data were compared with the advection estimates found in the NDA.

Results

No released turbot were caught in any of the hauls towed parallel to the coast at the 6-m depth. During the sampling period, 332 catches were accomplished distributed on 105 hauls perpendicular to the coastline. Fewer than 10 wild turbot of the same length class were caught, which were easily recognized by their darker pigmentation, aside from the lack of a T-bar tag. Out of the total recaptures, 136 were frozen for stomach content analysis in the laboratory. One haul on day 7 where two turbot were recaptured 1030 m west of the release position was excluded in the data analysis. The maximum catch was obtained on the first day, when more than

Fig. 2. Recaptured turbot per day (○) with the density distribution estimated from the full NDA model (solid line). Solid vertical line is the release position. Distance between small broken vertical lines represents 100 m, whereas distance between large broken lines represents 1 km. Day is days at liberty.

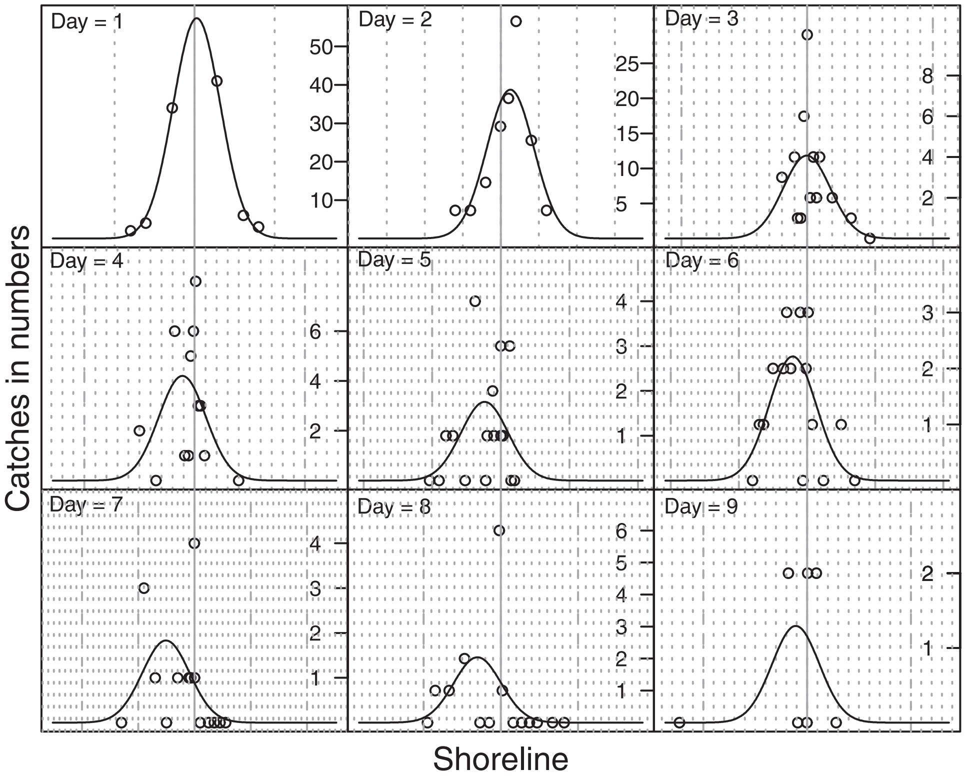


Fig. 3. Estimated values and 95% confidence limits for the parameters describing the normal distribution curves seen in Figs. 2 and 4. The parameters are (*a*) the cumulated standard deviation (σ_t), (*b*) the advection (α_t), and (*c*) the recaptured part (q_t). In the full model, parameters describing one normal distribution curve for each single day were estimated. In the reduced model, σ_t and q_t were restricted as described in the text.

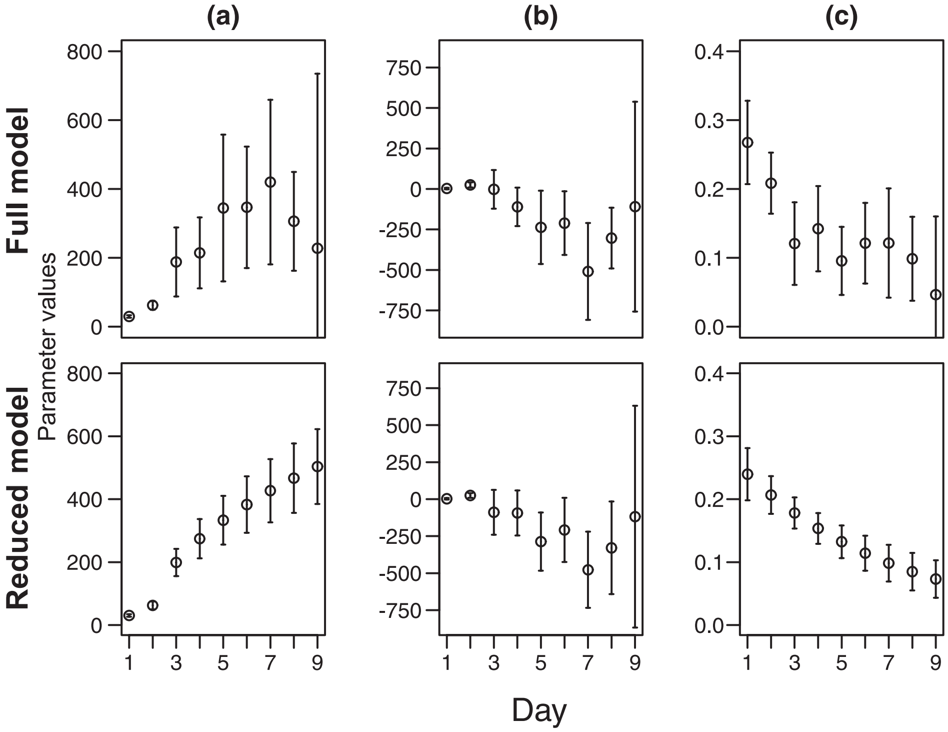
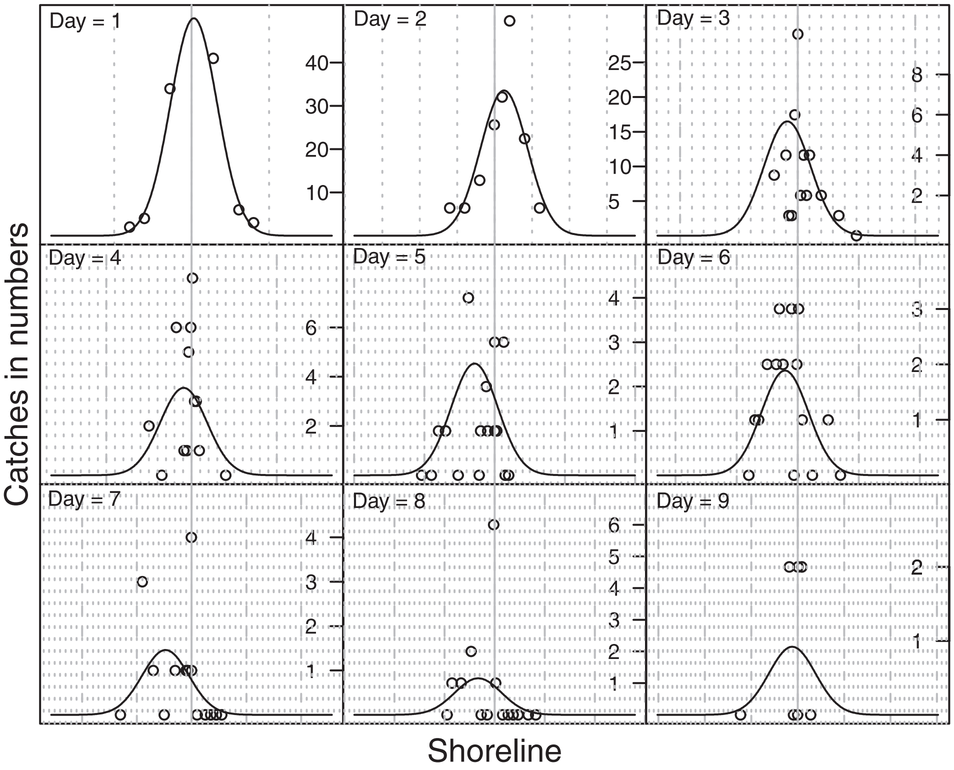


Fig. 4. Recaptured turbot per day (○) with the density distribution estimated from the reduced NDA model (solid line). Solid vertical line is the release position. Distance between small broken vertical lines represents 100 m, whereas distance between large broken lines represents 1 km. Day is days at liberty.



40 individuals were caught in a single haul. During the following period, the daily catches gradually decreased to a minimum on day 9.

The first attempt to analyze the catch data was to fit a full NDA model, meaning that one normal distribution curve was fitted to the recaptures from each day and thus for each day one set of parameters describing a normal distribution curve was estimated (Fig. 2). These parameters are σ_t (m·day$^{-½}$), α_t (m·day^{-1}), and q_t (as a fraction) (Fig. 3).

The full model (Fig. 4) was reduced to a model with fewer parameters where the fit was not significantly reduced (likelihood ratio test with p value = 47%). It was possible to describe the spreading of the released turbot using one single σ value for each day from days 3 to 9 (Table 1). It was reasonable to describe q_t with one constant mortality (Z) and one constant catchability (ρ). The catchability was found to be 28%, indicating that 72% had escaped a direct contact with the trawl. The mortality was estimated to be 14%·day^{-1}, which means that at the end of the experimental period only 900 individuals of the initial 3529 would still be alive.

In Table 1, the parameter estimates from both the reduced NDA and PDE are shown. The estimates for mortality (Z) and catchability (ρ) derived from the two models were similar. Further, these two estimates are also determined with the same precision and the two models produced identical values for the standard deviation (σ_t). For the advection estimated, minor differences were found between the two models, but it should be noted that the precision at which this parameter is estimated is quite low and that it is mainly during the last day of sampling that differences are present.

From the model, we estimated the daily average movement for the released turbot (see Appendix B). The average distance moved was estimated to be 24 m·day^{-1} on the first day, 44 m·day^{-1} on the second day, and 151 m·day^{-1} in the remaining days. These values correspond to 320, 587, and 2013 body lengths·day^{-1}, respectively.

The proportion of fish that had started to feed was constant around 22% during the first 2 days at liberty (Fig. 5). After day 2 the percentage that had started to feed increased abruptly to approximately 95% and remained constant during the following days, except during day 8 when only 75% of the recaptured fish had traces of food in their stomachs.

It appears that displacement calculated using night wind only agrees better with the advection found in the reduced NDA model than when displacement is calculated using wind data from the entire day (Fig. 6). However, one should note that the difference between the two estimated WBD$_t$ is a result of an eastern wind during the 2 first days; after that, the trend is similar, independent of whether wind data was taken all day or only during night for the calculation of WBD$_t$.

Discussion

No released turbot were caught in any of the hauls towed parallel to the coast at the 6 m depth. During the first period after release, liberated turbot are known to remain in shallow waters (Støttrup et al. 2002) and natural turbot of this small size group have only been observed at depths shallower than 2 m (Gibson 1973). Thus, the experimental design with fishing to the 6 m depth bathometer line is considered sufficient to cover the entire depth distribution of the released turbot

Table 1. Daily standard deviation (σ_t), advection (α_t), mortality (Z), and catchability (ρ) estimates from both the normal distribution approximation (NDA) and the partial differential equation (PDE) models.

Parameter name	NDA estimate (95% CI)	PDE estimate (95% CI)
ρ	0.28 (0.22; 0.34)	0.26 (0.2; 0.31)
Z	0.15 (0.09; 0.21)	0.15 (0.08; 0.22)
σ_1	30.20 (26.26; 34.15)	37.04 (32.37; 41.71)
σ_2	54.66 (39.84; 69.47)	59.22 (39.18; 79.26)
$\sigma_3 = \cdots = \sigma_9$	188.85 (143.49; 234.21)	192.03 (107.15; 276.91)
α_1	2.86 (–2.27; 8.0)	5.95 (–1.8; 13.7)
$\alpha_1 + \alpha_2$	25.04 (9.39; 40.69)	30.96 (8.26; 53.66)
$\alpha_1 + \cdots + \alpha_3$	–88.67 (–239.73; 62.38)	–41.49 (–976.45; 893.47)
$\alpha_1 + \cdots + \alpha_4$	–93.44 (–245.44; 58.55)	–127.61 (–509.05; 253.83)
$\alpha_1 + \cdots + \alpha_5$	–286.51 (–482.47; –90.55)	–336.89 (–630.45; –43.33)
$\alpha_1 + \cdots + \alpha_6$	–208.04 (–424.78; 8.7)	–171.57 (–465.85; 122.71)
$\alpha_1 + \cdots + \alpha_7$	–476.91 (–734.45; –219.37)	–571.48 (–981.7; –161.26)
$\alpha_1 + \cdots + \alpha_8$	–329.00 (–641.86; –16.14)	–193.37 (–765.07; 378.33)
$\alpha_1 + \cdots + \alpha_9$	–118.04 (–866.46; 630.38)	–47.29 (–1331.89; 1237.31)

Note: The 95% confidence intervals (CI) are given in parentheses.

Fig. 5. The percentage of turbot with food or traces of food items in their stomach. Day is days after release, and all catches during the day are pooled.

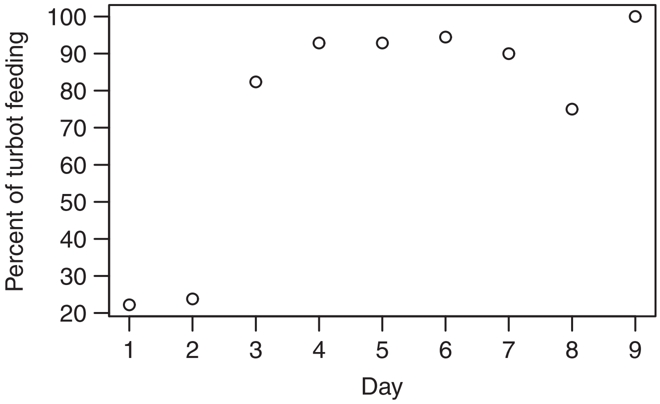
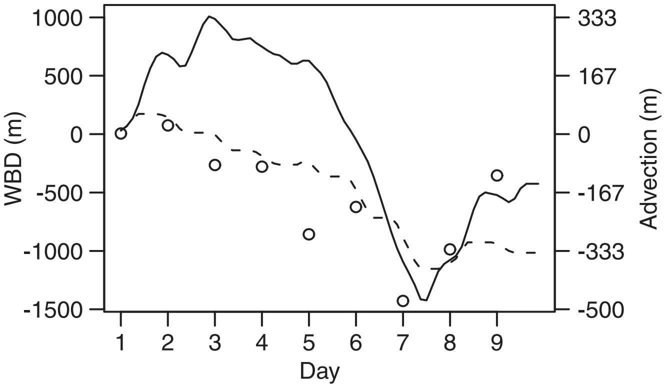


Fig. 6. Water body displacement (WBD) was calculated from wind data. The solid line indicates the displacement when only night wind was included in the calculation and the broken line indicates displacement calculated from the wind for the entire day. Open circles are the advection (α) estimated from the normal approximation model.



and provides the opportunity to analyze dispersal in one dimension only.

One single haul was treated as an outlier and was excluded from the data analysis. This was a haul from day 7, where two tagged turbot were caught 1030 m west of the release position. A large eelgrass belt located 1300 m from the release position limited the investigation area in that direction and the high catch may have been the result of an accumulation of turbot at the boundary of the sand area.

During the first days after liberation, it was clear that there was a good and highly significant agreement between the normal distribution curve estimated by the full NDA model and the observed data. As time at liberty increased, the visual presentation could give the impression of a decreasing fit of the model, but this was a result of the fact that only integer number of turbot could be caught. The model still described the low catches well.

The reduced model was not significantly worsened compared with the full model, as seen from the likelihood ratio test, but the number of parameters estimated was reduced from 27 to 14. This model revealed a catchability of turbot of 28% when using a young fish trawl. However, the last column on Fig. 3 indicates that the reduced model overestimates the mortality during the last days and underestimates the mortality during the first days.

In this experiment the daily mortality was estimated to be $14\%\cdot\text{day}^{-1}$, which would result in no fish surviving beyond a year. That released turbot do survive beyond a year and can be recaptured in subsequent years has been demonstrated in a previous study (Støttrup et al. 2002). In that study, the mortality estimated from the year following the release and over the subsequent years was $0.15\%\cdot\text{day}^{-1}$. Although the study by Støttrup et al. (2002) was conducted on slightly larger fish, i.e., 15 cm compared with 7–8 cm in this study and size-at-release has been demonstrated to be important for postrelease mortality (Yamashita et al. 1994), the size difference does not account for the large differences in the estimated mortality. These results suggest that there may be an initial "adaptation" period when the released fish are highly vulnerable and suffer high mortality rates. This is supported by the study of Furuta et al. (1997), who estimated mortality rates of approximately 10%·day^{-1} for juvenile Japanese flounder (*Paralichthys olivaceus*) within the first week after release. Thus, measures to improve survival immediately following the release may help improve the outcome of fish releases.

It appears from this study that the mortality provided by the model is overestimated during the last 6 days at liberty and underestimated during the first 3 days. Apart from this apparent repetitive change in mortality rate with days at liberty, there were other indications that pointed towards the possibility that what was actually observed was a mixture of two different activity levels and hence two different diffusion patterns. This was indicated by the fact that the model was not able to describe the diffusion using one single estimate on σ, but could only reduce the model down to having the same σ from day 3. One other indication of a switch in behavior and diffusion pattern was the sudden increase in the percentage of turbot that had started to feed between the 2nd and the 3rd days of liberty. At this time, a change to a steady diffusion pattern is observed, which could be described by one σ. The event of feeding, the mortality, and the diffusion rate are not necessarily connected but they seem to occur simultaneously.

Advection estimated from the reduced NDA was three times lower than the estimated displacement of the water body. Turbot, being a flatfish, spends a large proportion of its time inactive at the bottom, and during that inactive period, the current will not have any effect on the position of the fish. Hence if the advection of the released fish is a result of the current, it would mean that the fish is only present in the water column one-third of the day. Whether the better fit using the night wind alone to describe the WBD is a result of the turbot being more active during night or a result of a lower activity level during the first 2 days is difficult to tell. It is known that other flatfish species increase their activity level during dusk and dawn (Gibson et al. 1998), but the difference might well be a result of lower postrelease activity caused by stress. The constant speed at which the turbot dispersed after day 3 would, under the assumption that they were active one-third of the day, be 0.07 body lengths·s^{-1} if they had moved in a straight line between release and recapture position. This is not a realistic swimming speed, because flatfish are negatively buoyant and the energy needed to lift the body from the bottom results in uneconomical swimming speeds below 0.6 body lengths·s^{-1} (Priede and Holliday 1980). Further, Priede and Holliday (1980) estimated the optimal swimming speed to be around 1.2 and 1.6 body lengths·s^{-1} at 5 and 15°C, respectively. Hence, assuming a swimming speed of 1 body length·s^{-1} and that turbot move in a straight line, the resulting daily time spent in the water column from day 3 would be approximately 35 min. Juvenile Japanese flounder of the same size class as the turbot used in this experiment fed on mysis, which was also the main diet for turbot in our release. They were observed to increase their swimming activity as the level of hunger increased by swimming for a longer period in the water column after an attack on a prey (Miyazaki et al. 2000).

There were only minor differences between the ρ and Z values estimated from the NDA and the PDE models. So even though approximately 10% of the released turbot were caught within a 9-day period, this relatively high recapture rate did not result in any detectable effect on the distribution of the released turbot.

This study has shown that applying diffusion theory is a very successful method for modeling movements of living organisms even when applied to small-scale migration experiments. Further, it has been shown that even though the sampling intensity in this experiment was fairly high, it was sufficient to fit an NDA model instead of using the more complex PDE model. It seems as if the dispersal took place in two steps and that the change from one dispersal rate to another happened simultaneous to a change in mortality and to the event of feeding. The current is one factor that may have determined the direction of turbot displacement. These results provide more information needed to ensure a successful stocking of marine fish species. In addition, this type of experiment provides knowledge on postrelease mortality and the catchability of the implemented gear. In the near future, improvements in the capability of data storage tags may provide us with valuable additional knowledge that could be prosperous when combined with data obtained from studies similar to this.

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Appendix A

Optimizing the fishing effort

The obvious question is where should we trawl to get most information about the model parameters? In other words, we wish to estimate (q,σ) and need to decide on a number of positions $p_1,\ldots,p_m$.

Frequentist approach

We start by assuming that we know the true parameter values (q_0,σ_0). This may seem unreasonable, but as the experiment progresses we will improve our knowledge about the true parameter values.

To make calculations simple, we used the following approximation to the log likelihood for some fixed time point t_0:

$$\log L(\underline{c};q,\sigma) \overset{\text{app.}}{\propto} \sum_p \left(c_{p,t_0} \log(q\varphi_{0,\sigma^2 t_0}(p)) - qN_{0,0}w\varphi_{0,\sigma^2 t_0}(p)\right)$$

We calculate the Fisher information I by

$$I = -E_{q_0,\sigma_0}(D^2_{q,\sigma} \log L(\underline{c};\theta,p)) = -\sum_p E_{q_0,\sigma_0}\begin{pmatrix} \dfrac{c_{p,t_0}}{q^2} & N_{0,0}w\varphi'_{0,\sigma^2 t_0}(p) \\ \bigstar & \dfrac{c_{p,t_0}(\varphi'_{0,\sigma^2 t_0}(p))^2}{(\varphi_{0,\sigma^2 t_0}(p))^2} + qN_{0,0}w\varphi''_{0,\sigma^2 t_0}(p) - \dfrac{c_{p,t_0}\varphi''_{0,\sigma^2 t_0}(p)}{\varphi_{0,\sigma^2 t_0}(p)} \end{pmatrix}$$

In this case, it is simple to evaluate the mean because I is a linear function of c. We get

$$I = -\sum_p \begin{pmatrix} \dfrac{N_{0,0}w\varphi_{0,\sigma^2 t_0}(p)}{q} & N_{0,0}w\varphi'_{0,\sigma^2 t_0}(p) \\ \bigstar & qN_{0,0}w\dfrac{(\varphi'_{0,\sigma^2 t_0}(p))^2}{\varphi_{0,\sigma^2 t_0}(p)} \end{pmatrix}$$

The covariance V of the parameter estimate is estimated by the inverse of the Fisher information $V = I^{-1}$. Hence we should choose the positions $p_1,\ldots,p_m$ that minimize (some scalar extracts of) V. For instance, if we want to get the most precise estimate of σ, we should choose the points that minimize $V_{2,2}$. For overall optimization, it is often chosen to minimize $|V|$.

Bayesian approach

As seen above, the covariance V is a function of the positions and the parameter values. In the frequentist approach, we simply assumed to know the true parameter values (q_0,σ_0) and then minimized V with respect to the positions.

In the Bayesian approach, we try to express our knowledge (uncertainty) about the parameters in terms of a prior distribution and then minimize the expected variance

$$E_{\text{prior}}\{V\ (\underline{p};\ (\mathrm{q},\sigma))\}$$

with respect to the positions.

As we do not really know the true values of the parameters, this approach may seem more reasonable, but we must keep in mind that we do not know the true distribution of our knowledge either. A more pragmatic view is that the frequentist approach is the special case of the Bayesian approach where the variance of the prior distribution is (close to) zero.

Parameterization

If we try to minimize $|V|$ without any restrictions on $\underline{p}$ we will not be able to find a unique minimum, as any permutation of the elements in $\underline{p}$ will result in the same value of $|V|$. We have to find a different parameterization of the problem.

To further simplify the problem, we will only consider symmetric designs containing the point zero. We choose the following parameterization:

$$p_{\lceil m/2 \rceil} = 0,\ p_{\lceil m/2 \rceil+1} = \tilde{p}_1,\ p_{\lceil m/2 \rceil+2} = \tilde{p}_1 + \tilde{p}_2, \ldots, p_m = \sum_{i=1}^{\lfloor m/2 \rfloor} \tilde{p}_i$$

where $\tilde{p}_i > 0$ and $p_{\lceil m/2 \rceil+i} = -p_{\lceil m/2 \rceil-i}$

Appendix B

Calculation of average daily movement

The daily average movement is calculated from the daily standard deviation σ_t under the assumption that the daily advection α_t is zero. Biologically this assumption means that any advection, if present, is caused by passive movement, hence the average movement that we calculate equals the movement caused by active swimming.

The daily average movement is calculated as the mean of absolute distance from the center of the normal distribution with standard deviation equal to the daily standard deviation. In other words, the daily average movement (in metres) is calculated as

$$\int_{-\infty}^{\infty} |x| \varphi_{0,\sigma_t^2\cdot 1\text{day}}(x)\mathrm{d}x = \sqrt{2/\pi}\,\sigma_t \approx 0.8\sigma_t$$

Chapter 7

Post-release survival and feeding in reared turbot.

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Post-release survival and feeding in reared turbot

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Abstract

As part of the Danish restocking program, an experiment was carried out with four groups of turbot *Psetta maxima* released on two different occasions at the same location in Århus Bay, Denmark. One objective was to analyse the duration of post-release mortality and the magnitude of this mortality. In 2003 a group called Large turbot (17.1 cm total length (L_T)) and a group called Intermediate ($L_T = 11.8$ cm) were released, and in 2004 two similar-sized groups called Naive and Conditioned ($L_T = 9.8$ cm) were released. The Conditioned differed from the Naive turbot by being transferred to enclosures at the release location six days prior to the actual release. This experiment was performed to investigate whether such a conditioning period had a positive effect on the survival and hence the success of the stocking. All the groups released were monitored daily until day 8, using a juvenile flatfish-trawl to recapture the fish. The catches were analyzed on the basis of a normal distribution approximation method, founded in diffusion theory, from which daily abundance of the released fish and hence post-release mortality could be estimated. The group of Large turbot suffered negligible post-release mortality, but for the Conditioned, Naive and Intermediate groups the loss varied between 34 and 66% d^{-1}. The mortality for the Conditioned group was found to be half that of the Naive turbot released simultaneously. The period of high post-release mortality was estimated to be restricted to three days after release. The only active predators observed in the area were birds. Besides estimating mortality the diffusion model provides an estimate on the catchability of the released turbot when fished with a juvenile flatfish-trawl. Catchabilities varied between 38 and 52% for all releases except for the 17 cm sized turbot released, where catchability was only 12%. The feeding performance of the released fish was also analysed and compared with that of wild fish caught at the same location. These results showed that the proportion of stomachs containing food increased not only with time after release, but also with the size of the turbot. However, whether or not fish was included in the diet was not related to size but to time after release and to whether they had been conditioned or not.

Keywords: Stocking; Post-release mortality; Catchability; Conditioning; Bird predation; Burying behaviour

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1. Introduction

As witnessed in other marine ecosystems, several of the most important fish species in the inner Danish waters have been subject to drastic declines during the last decades (Hoffmann, 2000; Munch-Pedersen, 2005). Consequently, severely reduced catches have been observed in both commercial and recreational fisheries. In an attempt to reverse this trend, a Danish fish stocking program was initiated in 1989 to restore fish stocks in both inland and marine waters (Rasmussen and Geertz-Hansen, 2001; Støttrup, 2004). One strategy for marine waters was to examine the potential for stocking through multiple releases of artificially bred juveniles. Turbot *Psetta maxima* was used as a model species and a large-

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scale tagging/recapture program was carried out between 1991 and 1997. The results showed the same mortality and growth in wild and reared turbot, when the post-release period was not taken into account (Støttrup et al., 2002). This research led to the conclusion that restocking flatfish such as turbot through releases is a viable option and that future work should focus on optimizing such releases in terms of finding ideal habitats, reducing the hatchery costs and improving post-release survival of the released individuals.

Recent studies have shown increased mortality of reared turbot just after release, a phenomenon referred to as the post-release mortality (Sparrevohn et al., 2002; Iglesias et al., 2003). Similar results have been reported for stocking experiments with other species, e.g. Japanese flounder *Paralichthys olivaceus* (Furuta et al., 1997) and Atlantic salmon *Salmo salar* (Henderson and Letcher, 2003). A link between post-release mortality and increased vulnerability to predators has been demonstrated in laboratory studies (e.g. Kellison et al., 2000; Hossain et al., 2002; Fairchild and Howell, 2004). This was suggested to be due to a lack in behavioural skills of the reared individuals compared to their wild counterparts. In order to limit the loss during the critical post-release period, it has been proposed that hatchery-reared fish should experience a period of conditioning before release (Howell, 1994; Kellison et al., 2000). Ways of improving natural skills in flatfish can be to introduce them to sediment that resembles the sediment found in their natural environment, either at the hatchery or alternatively keeping the fish encaged and protected from predators in the release area for a period before the actual release. Another option is to rear the fish to a size where they have reached a refuge from most predators (Leber, 1995), a strategy that might not be viable for economic reasons.

Reported post-release mortality rates are high, and if they were to remain at that level for a prolonged period, there would very soon be practically no survivors. On the other hand, results from several tag-recapture studies have shown this could not be the case as recaptures were made up to a number of years after their release (e.g. Leber and Arce, 1996; Støttrup et al., 2002). Therefore, post-release mortality seemed to be restricted to a limited period, and hence not only the intrinsic mortality should be investigated and minimized, but also the length of period during which high post-release mortality rates are observed.

Estimating mortality and growth of released individuals can be expensive and time consuming. Instead, stomach content and proportion of empty stomachs can serve as proxies for how well the released fish have adapted to their new environment. These measurements can easily be obtained and compared to data from wild individuals in the area. For Japanese flounder, one study has shown that feeding behaviour differs between reared and wild individuals, where the latter spend less time off-bottom (Furuta, 1996). Another study has shown that the time spent off-bottom increases with starvation (Miyazaki et al., 2000). So stomach content is not only a direct measurement for the feeding performance of released individuals, but may also indirectly provide information on related behavioural traits that may affect their predation risk.

In the present study, both the duration of the post-release mortality period and its impact on the numbers of individuals surviving were determined for four groups of released turbot. The total length of the fish released ranged from 10 to 17 cm. One group was kept encaged at the release position in order to condition them to the environment before release. These results were compared with a previous study on released turbot at the same location (Sparrevohn et al., 2002). Besides estimating the mortality for each group, stomachs were analyzed in order to establish how size and conditioning affected initial post-release feeding performance.

2. Materials and methods

2.1. Study area

Begtrup Vig (56°10′30 N, 10°28′00 E) is a small bay in the eastern part of Jutland, Denmark. It has a homogenous sandy bottom and limited exposure to the dominant westerly wind, two features that make it suitable as study area.

2.2. Fish and tagging

All turbot released in this experiment came from one commercial hatchery and the same Skagerrak brood stock. The fish were reared in outdoor ponds on natural zooplankton during the larval stage and transferred to indoor tanks after metamorphosis, where they were weaned to a dry diet. Two weeks prior to release, total length (L_T) was measured and each turbot was tagged with an individually identifiable external T-bar tag, obtained from Hallprint, Australia. In 2003, a total of 5000 large-sized turbot (Large; $L_T \pm SD = 17.1 \pm 1.7$ cm) and 5000 intermediate-sized (Intermediate; 11.8 ± 0.9 cm) turbot were released. In 2004, 5000 turbot (9.8 ± 0.9 cm) were divided equally into two groups called Naive and Conditioned. The term ‘conditioning’ in this paper describes the period when the turbot were confined to cages placed in their natural environment. The term ‘naive’ is used to describe those turbot that were transferred from the hatchery directly to the release site. Besides data collected in 2003 and 2004, data from a similar experiment conducted in 2001 with smaller turbot released directly from the hatchery (Small, 7.5±0.6 cm) were analysed (Sparrevohn et al., 2002).

2.3. Releases and conditioning

All fish were transported from the hatchery to the release site by truck and carried in buckets the last distance from the road to the sea and released or encaged. In 2003 the depth at release for Large and Intermediate turbot was 70 cm and the two groups were released simultaneously at 14:00 h on 3 June. Wave height was less than 10 cm. The Conditioned turbot were transported to the release area 6 days before the actual release and kept encaged in five 2 m^2 cages at a depth between 20 and 100 cm, depending on the water level. The cages had no bottom, allowing the fish direct contact with the natural sediment. The cages were constructed of an aluminium frame mounted with a 6 mm mesh sized net on all four sides and a coarser net on top to prevent avian predation. The cages were checked twice daily to make sure that they remained stable, that no fish could escape and to remove any dead fish. The fish were offered the same food pellets as in the hatchery. For a 1–min period after the pellets were offered, the fish were observed in order to detect any feeding activity. At 16:00 h on the release day (4 May 2004), the Conditioned fish were set free by removing the cages at exactly the same moment and place as the Naive group was released. The depth at the release position was 70 cm, weather conditions fine with no wind or waves.

In order to assess whether there was an effect of the individual cages on the outcome of the conditioning experiment, the contribution that each cage had on the catches of Conditioned turbot was analyzed using a χ^2 test. Both the total catch during the experiment and the daily catches were tested. If the daily catch of Conditioned turbot was less than 25, the catches from two consecutive days were pooled, in order to avoid the expected frequency from each cage being less than 5 (Sokal and Rohlf, 1981).

2.4. Sampling

After release, the area was fished daily with a 4.5 m wide juvenile flatfish-trawl (see Støttrup et al., 2002 for further details on the gear). The area was not sampled at random. Both the coverage and the actual number of hauls taken were increased with time, since the released fish are initially concentrated close to the release position, then move and gradually spread over a larger area (Sparrevohn et al., 2002). Each sampling day started with a single 10 min haul parallel to the coastline at 6 m depth to ensure that no turbot was found at that depth, i.e. all turbot, as expected, were located between the shore and this depth. Subsequently, a number of hauls were taken perpendicular to the coast from the shoreline to 6 m depth. From these perpendicular hauls the catch rates of released turbot at a given distance from the release position were obtained. Since the hauls are perpendicular to the coast the distance was measured along the coast. The towing speed for all hauls was kept around 0.8-1 knot, but was increased to a maximum of 1.5 knot on several occasions because of problems with keeping the course due to strong wind parallel to the coast. All sampling was started around 9 am and ended at 6 pm. For a more detailed description of the sampling strategy see Sparrevohn et al. (2002).

2.5. Post-release mortality and catchability

A way of describing the spreading of released fish from a given position is as an advection/diffusion process. One feature of this spreading pattern is that the density distribution of the released fish will be normally distributed and that the displacements of the individuals are proportional to the square-root of time. Since the density distribution is a normal distribution, the catch rate distribution found when fishing perpendicular to the coast at a given distance from the release point will also be a normal distribution with a variance that increases with time (Sparrevohn et al., 2002). Hence, the expected catch rate of N_0 released fish, caught with a trawl of width w, at time t, and position p can be approximated as:

$$\bar{C}_{p,t} = w \cdot N_0 \cdot q_t \cdot \varphi_{\alpha t, \sqrt{\sigma^2 t}}(p) \qquad (1)$$

where φ is the normal density distribution with mean αt and variance $\sigma^2 t$. The parameter q_t (the re-catchable part) is a combination of two important factors that determine the catch rate, namely the mortality (Z) and the catchability (ρ) of the fish released. The daily catch rates were fitted to Eq. (1) using maximum likelihood with the assumption that the error of the catch is Poisson distributed. The re-catchable part can be interpreted as the proportion of estimated individuals to the actual number of turbot released. The catchability is, in this work, defined as the proportion of fish lying in the trawl-path between the doors that is eventually found in the catch. The mortality and the catchability cannot be distinguished if the catch rate is simply estimated from one single point in time since they are related according to:

$$q_t = \rho \cdot \exp(-Z \cdot t) \tag{2}$$

Estimates on Z and ρ were obtained from Eq. (2) by a log-transformation and least-square regression. The regression was weighted with the inverse of the variance of q_t. Since the post-release mortality is expected to be limited to a certain period, only the days on which the released fish are affected by the post-release mortality should be included in the regression, i.e. a cut-off point where the post-release mortality has levelled out had to be chosen. A statistical test for locating the cut-off point where mortality rate levelled out was considered, but could not be applied for two reasons. Choosing a common cut-off point facilitated comparison between the four groups and no sample was taken on day 3 during the 2004 experiment. Therefore this cut-off point was visually determined. Besides the visual method, the duration of the period with high post-release mortality was further investigated for the release in 2004 when the proportion of fish caught that originated from the Naive group was estimated daily during the entire 8 d period after release. The standard deviation was calculated as: $\sqrt{(1-P) \cdot P/n}$, where P is the proportion and n is the number of fish used in the proportion calculation. Estimating the proportion would make little sense if the spatial distribution between the two groups of turbot differed, and therefore it was not estimated for the Large/Intermediate released in

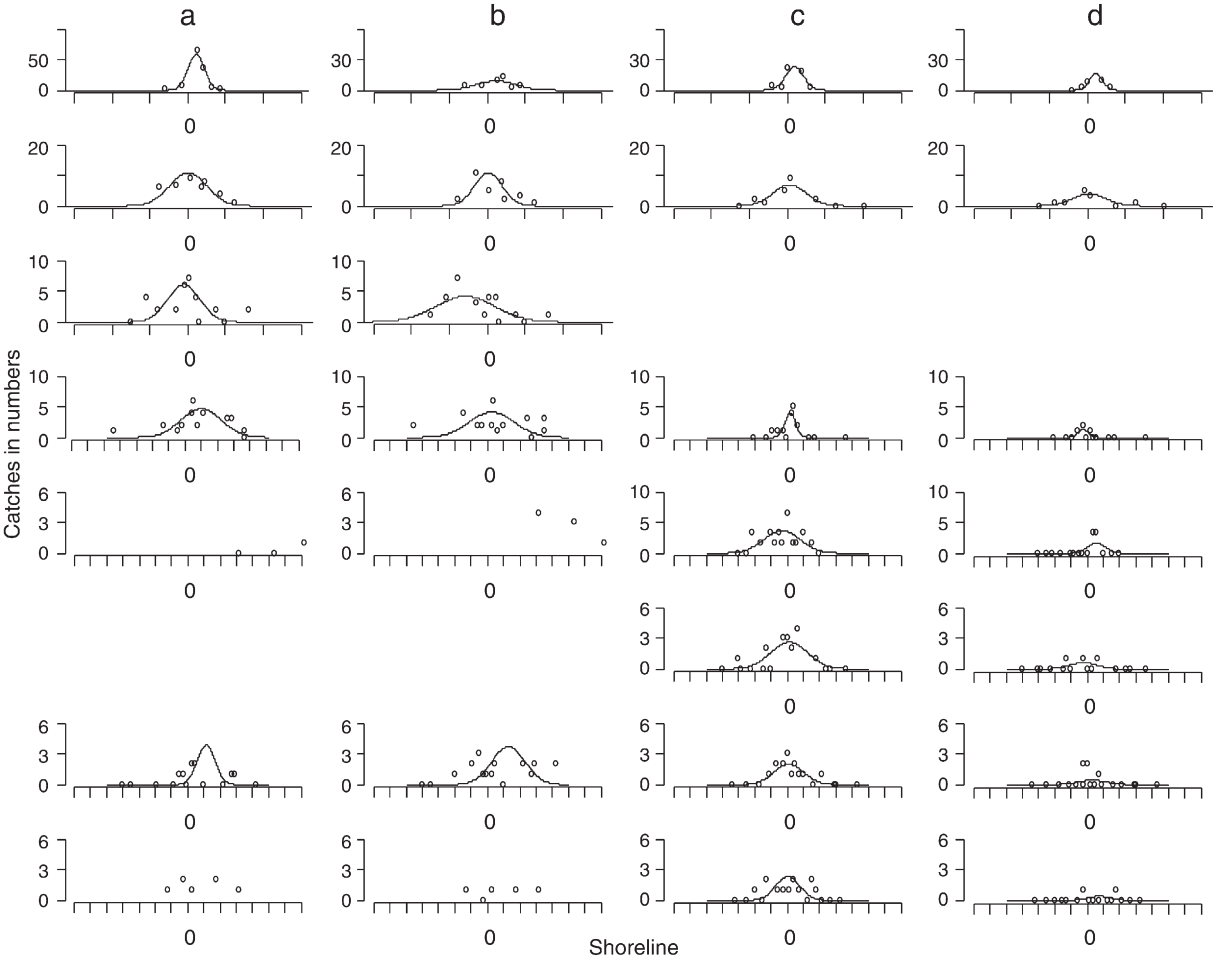

Fig. 1. Distribution of turbot (open circles) after release in 2003 and 2004 in relation to distance from release position and time after release, together with estimated normal distribution (solid line). (a) Intermediate fish in 2003; (b) Large fish in 2003; (c) Conditioned fish in 2004; (d) Naïve fish in 2004. Top panels show data from the first day after release; those below show data from the consecutive days after release. No figures indicate days without fishing. The distance between tick marks equals 200 m and '0' is the release position. No normal distribution curve was drawn in figures where the likelihood function would not converge to the catches from that day.

2003, where it was evident that the Large group had a higher dispersal than the Intermediate. For the Conditioned/Naive the assumption of equal distribution was tested using an Exact Binomial Test, where the catch (C) of type *d* fish (i.e. Naive or Conditioned) for each single haul (*j*) on day *i* was assumed to be distributed with a probability calculated from the overall catch that day (C_{di}/C_i), i.e. the null hypotheses was $C_{dji}/C_{ji}=C_{di}/C_i$.

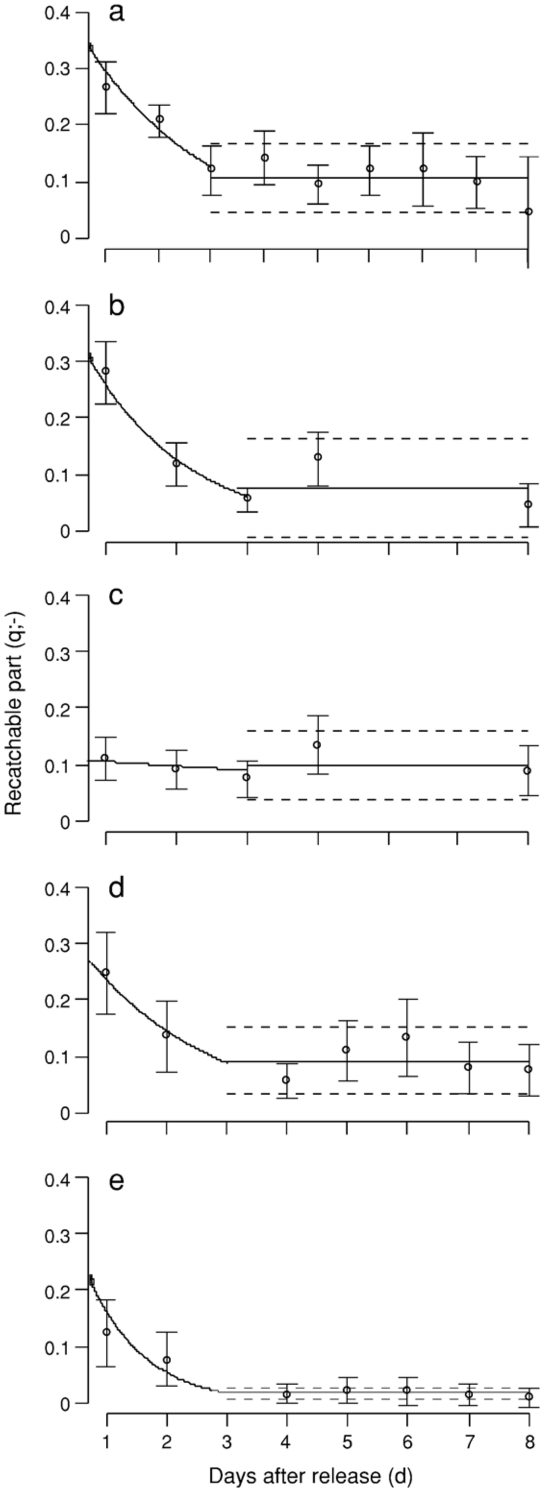

Fig. 2. Recatchable part (q;–) of turbot together with 95% confidence intervals in relation to days after release. Between brackets: year of release. (a) Small turbot (2001), recalculated from Sparrevohn et al. (2002); (b) Intermediate (2003); (c) Large turbot (2003); (d) Conditioned (2004); (e) Naive turbot (2004). The solid line until day 3 shows the decrease in numbers and the slope is the post-release mortality with the intercept at the y-axis being the catchability. The horizontal lines indicate the average recatchable part (solid) and 95% confidence limit (dashed) from day 3 onwards.

Since all turbot released carried an external visible T-bar tag, fishermen in the area were encouraged to report any catches to the Danish Institute of Fisheries Research together with the tag and if possible information on size, recapture position and time of recapture. From these data the proportion of Naive fish caught after the end of the experiment was calculated.

2.6. Feeding

All turbot caught were kept on ice on the boat and frozen on land for analysis of the stomach contents in the laboratory. All stomachs were classified into one of three classes: empty stomachs (E) with no sign of food items, stomachs which contained food items (F) and stomachs containing fish (P). The proportion of turbot that had commenced feeding was estimated as: $R_F=F/(E+F)$ and the proportion of those feeding that were feeding on fish was calculated as: $R_P=P/F$. The standard deviation was estimated as: $\sqrt{(1-R)\cdot R/n}$, where n is the numbers of stomachs used in the proportion calculation. Stomach content was compared to bottom water temperature in the bay, which was monitored using HOBO water Temp Pro loggers, set to register and store the temperature every 20 min. In 2003 the temperature logger was placed at 2 m depth and in 2004 at 3 m depth; this disagreement in depth between years was not intentional.

All statistical tests, calculations and graphic presentations were done using freeware R 2.2.1, downloaded at www.r-project.org.

3. Results

3.1. Study area

In the area of release, great black-backed gull *Larus marinus* and herring gull *Larus argentatus* were observed to search, catch and eat the released turbot. No other potential predators such as harbour porpoise *Phocoena phocoena* or cormorant *Phalacrocorax carbo* were observed hunting in the area.

3.2. Fish and tagging

Besides dissimilarity in size, the Large and Intermediate turbot groups released in 2003 behaved differently and had different pigmentation. In the hatchery, the Large turbot were sedentary on the bottom and had a dark brown to black pigmentation. The Intermediate turbot were light grey and more actively swimming in the water column. There was no indication of feeding in the group of Conditioned turbot during their confinement in the cages (pers. obs.). Pigmentation was observed daily but no change in colour was visually apparent, hence the pigmentation did not differ markedly between the Condition and the Naive at the time of release.

3.3. Releases and conditioning

For all groups no mortality during transport was observed, and less than 10 of the Conditioned individuals were found dead during the 6 days spent in the cages.

The total number of Conditioned fish caught from the different cages was: 31, 37, 31, 42 and 23, which is not significantly different from random ($p=0.18$). If the catches from the first day are ignored, the contribution from each cage to the total catch is even more homogenous (25, 21, 22, 26 and 21) and still not significantly different from random ($p=0.91$). The first day after release the contribution from each single cage to the total catch was significantly different from random ($p<0.01$). The catches on that day were: 6, 16, 9, 16 and 2. The catches the following days were pooled into day 2+3, 3+4, 5+6, 7+8 and for none of these groups were the contribution from the different cages significantly different from random.

Table 1
Estimated post-release mortalities and catchabilities with the statistical output for the four groups of turbot examined in the present study together with the recalculated values for Small turbot from Sparrevohn et al. (2002)

Group	R^2; p-value	Mortality (% d^{-1})	Catchability (%)
Small	0.87; >0.1	34 (−32;67)	45 (11;182)
Intermediate	0.95; >0.1	50 (−2;76)	52 (12;212)
Large	0.46; >0.1	7 (−33;36)	12 (6;23)
Conditioned	0.96; >0.1	38 (19;53)	38 (20;72)
Naive	0.98; <0.1	66 (11;87)	48 (2;770)

Numbers in brackets are standard errors.

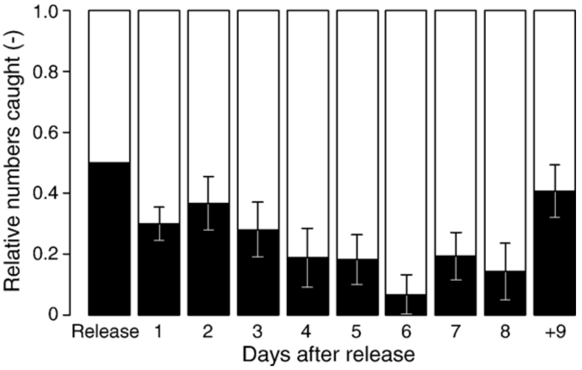

Fig. 3. Relative share (–) of Naive fish (black bar) and Conditioned fish (white bar with standard deviation) in the total catch constituted by. The +9 group is calculated on the basis on turbot caught after the survey by recreational fishermen in the area.

3.4. Post-release mortality and catchability

Number of hauls taken the first day after release was 6 in 2003 and 5 in 2004 and increased with days after release to a maximum of 20 hauls per day. In both 2003 and 2004 fishing was abandoned one day due to wind conditions. In 2003 this happened on day 6 and in 2004 on day 3, when it was only possible to fish parallel to the coast.

A normal distribution curve was fitted to the daily catches (Fig. 1). In addition to the days with no sampling, the catches on two other days in 2003 were so small that it was not possible to get convergence in the maximum likelihood optimization and hence the normal distribution parameters were not estimated. For those days on which the catches were sufficient to estimate the recatchable part (q_t), this was plotted against days after release together with the data from 2002 (Fig. 2). For the group of Large turbot no obvious trend in q_t was seen, i.e. no or only a negligible post-release mortality was evident. The catchability was estimated to be 12%, meaning that 12 out of 100 fish lying in the path of the trawl were actually caught. For Small and Intermediate turbot there was a drastic decline in q_t from day 1 to 3, hereafter q_t was stabilized. For Naive and Conditioned a decline in q_t was evident until day 4 but one should notice that no observation was available for day 3 due to too much wind that day. It was visually decided that day 3 was the cut-off point, so the regression performed in order to estimate mortality (Z) and catchability (ρ) was done on data from day 1, day 2 and the average of day 3 and onwards (Table 1). The post-release mortality was estimated to be

52% d^{-1} and the catchability 50% for Intermediate sized turbot. For Conditioned turbot the post-release mortality was found to be 45% d^{-1} and the catchability was 34% (Table 1). For the Small group of turbot released in 2001, Sparrevohn et al. (2002) found a post-release mortality of 15% d^{-1} averaged over the first nine days after release. Recalculating this for a 3 d effective post-release period gave a catchability of 46% and a mortality of 36% d^{-1}.

In 2003 the daily proportion of Naive fish in the catch was calculated. These data are shown together with the proportion calculated from recreational fishermen's reports (Fig. 3). From the day the survey ended until 1 October 2005, a total of 22 recaptures were reported by recreational fishermen in the area. Of these, 40% of the recaptures from the 2004 release were Naive and 60% Conditioned turbot. The decline in the proportion of the Naive turbot lasted until day 4. At the end of the period, only 2 out of each 10 released turbot recaptured were Naive. The method of calculating proportion seemed appropriate since none of the Exact Binomial Test performed rejected the null hypotheses.

3.5. Feeding

For the Large turbot the proportion of stomachs containing food items (R_F) was constant at 0.85 from day 1 onwards and similar to that found in the wild turbot caught during the same survey (Fig. 4). For the Intermediate, Conditioned and Naive groups it took approximately 4 days to reach the same level of feeding as observed for the wild counterparts. The proportion of stomachs from wild turbot with food present was 0.82 ($n=11$; $L_T=14$ cm) in 2003 and 0.93 ($n=42$; $L_T=12$ cm) in 2004. In both 2003 and 2004, the proportion of wild fish

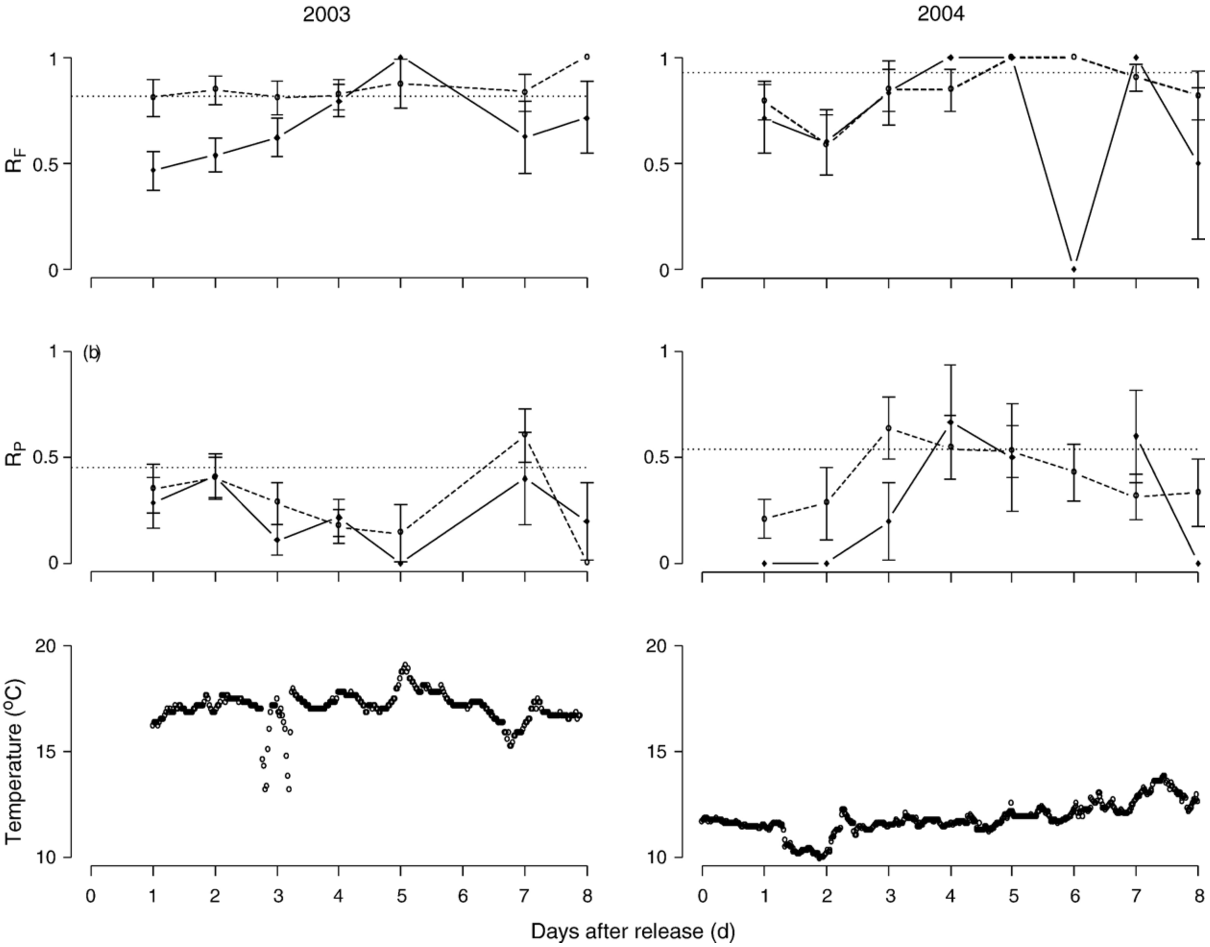

Fig. 4. Stomach content analysis of released (symbols) and wild turbot (horizontal dotted line) in 2003 (left column) and 2004 (right column). Top panels: proportion of stomachs of Large turbot (circles) and Intermediate turbots (dots) containing food items (R_F). Middle panels: the proportion of non-empty stomachs of Conditioned turbots (circles) and Naive turbots (dots) containing fish prey (R_P). Lower panels: the temperature at the release position.

caught that had eaten fish (R_P) was 0.55. In 2004, fish that had been conditioned to their new environment showed a higher proportion of fish in their diet during the first three days after release than did the Naive. From day 4 and onwards, the proportion with fish in the diet was similar for wild, Conditioned and Naive turbot. The temperature in the area was around 16 °C in 2003. In 2004, the temperature was approximately 12 °C during the entire period except on day 2 when it declined to 10 °C.

4. Discussion

4.1. Sampling and data analysis

The aim of this study was to estimate the daily abundance of four groups of reared turbot throughout the first 8 days after release and not the analysis of the actual process of how released individuals invade an area. The daily abundance was later used to estimate mortality together with catchability, where the catchability can be separated from the mortality in this type of experiment since it is known how many fish were initially released (Sparrevohn et al., 2002). To estimate the abundance, one should take into account how the individuals are distributed in order to have a well-defined statistical population (Krebs, 1999). It would be inappropriate to assume that the released fish have a distribution covering the entire bay during the first days after release, whereas this assumption might be appropriate several weeks after the release. The method used to estimate the abundance from this temporal/spatial dynamic distribution on such a short time scale is founded in the work of Skellam (1951), showing that the spreading of an invading organism can be described as a diffusion process. This pioneer work has led to a whole range of spatial distributions for a variety of other species to be analyzed as diffusion processes (e.g. Kareiva, 1983; Sibert et al., 1999). Also turbot has been analyzed in this framework: it was shown that the spreading parallel to the coast after release followed a diffusion process and hence their density distribution could be described as a normal distribution where the variance increases linearly with time (Sparrevohn et al., 2002). In the present study, the agreement between the observed catches and the estimated normal distribution curve differed from day to day, but even in the cases where the fit was poor, the daily estimated abundance will be based on prior knowledge on the distribution of the fish located in the area and not on an unrealistic assumption, for instance that the fish are evenly distributed in the bay.

The experimental set-up in the present study suffers in that it is difficult to incorporate treatment variability. The 2500 turbot that were conditioned during the experiment in 2004 were placed in five different cages, but analysing catches from each single cage using the diffusion approach was not possible since the catches would be too low to produce a reliable result. Instead the treatment variability was evaluated by analysing the contribution that each cage had on the total catch. The underlying hypothesis for this approach is that if each cage contributes to the total catch equally, the treatment variability is of minor importance. There were no significant differences in the individual cage contribution to the total catch as a whole with the exception of the first day after release. The cages were positioned parallel to the coast with approximately 20 m between the start of the first cage and the end of the last. Since the dispersal is still limited during the first day, the mixing of fish from the five cages might not have been complete so the actual position of the cage relative to the sampling position might have had a large effect on how the different cages contributed to the catch on that day.

4.2. Post-release mortality

The post-release mortality found in this experiment ranged from negligible for Large turbot to 66% d^{-1} for Naive turbot released in 2004. In a similar experiment with releases of reared 4-6 cm large turbot in Spain, a high loss of reared turbot was also observed and credited to post-release mortality (Iglesias et al., 2003). High post-release mortalities have also been observed for Japanese flounder (Furuta et al., 1997). In a large-scale experiment Støttrup et al. (2002) found that the mortality for wild and released turbot was equal for the years following the release. In that experiment, where post-release mortality was not accounted for, the general daily mortality rate was found to be 0.15% d^{-1}. In the present experiment, the duration of the period with high post-release mortality was visually determined to be around 3 d. Since no hauls perpendicular to the coast were taken on day 3 in 2004 it is difficult to validate this choice. Nevertheless the results showed that the post-release mortality connected with the transition of artificially reared turbot from the hatchery to a natural environment is within this time-frame. Hence future studies designed to optimize the outcome of a release should pay special attention to these first few days. That the post-release period is limited to 3 d has the detrimental consequence that estimating the actual mortality is based on three abundance estimates. Consequently, the confidence limits are enormous and the significance level makes little sense. For example the interpretation that a non-significant slope indicates no post-release mortality is misleading (see Fig. 2 and compare with the statistics found in Table 1). Another bias arises from the fact that the mortalities estimated for the three different years are difficult to compare, due to our lack of knowledge on yearly differences in predator pressure. Even within a year, a major bias in the estimate arises from the experimental design, where the easily detectable prey (i.e. the Naive fish) may attract predators to the area that will also prey on the Conditioned turbot released simultaneously. Therefore, the post-release mortality of 38% d^{-1} found for the Conditioned turbot released in 2004 would most likely have been much lower had the Naive fish not been released together with them. The effect of the conditioning period was seen as a reduction in the mortality rate but the duration of the period of high mortality seems less affected. This might be due to an unusually large number of predators attracted by the Naive fish. If the estimated mortalities for the 2004 groups are correct, the proportion of Naive would be 0.16 after the period with post-release mortality. This is in agreement with the proportion found during the survey but diverge from the values based on recreational fishermen's recaptures, where the estimated proportion was 0.4. This disagreement could be due to misreports from the fishermen or because some of the tags reported had been gathered on shore from bird excrement and did not represent turbot actually caught.

Part of the post-release mortality can be due to damage from physical handling involved in the transport and release, or to the fish being released into a non-suitable habitat (Leber and Arce, 1996). Further, it as has been demonstrated in laboratory studies that hatchery-reared individuals exhibit poor behavioural skills compared with their wild counterparts and are therefore more likely to be vulnerable to predation (e.g. Kellison et al., 2000; Hossain et al., 2002; Fairchild and Howell, 2004). In an earlier Danish study, the transport and release mortality of turbot was found to be negligible (Paulsen and Støttrup, 2004). In the present study, the mortality of the turbot during their confinement in the cages at the release location was also negligible, indicating that the high mortality was not caused by stress or by the T-bar tag. During the following experimental fishery, a total of 53 wild juvenile turbot were caught, indicating that the release area served as a natural nursery habitat for turbot, and hence the high post-release mortality found could not be explained by an unsuitable habitat. It is more likely that the observed elevated mortality was a result of increased predation pressure. In the study area, high gull activity was observed in both 2003 and 2004: gulls were observed to dive, catch and eat the released turbot (pers. obs.). The dominant species were the great black-backed gull and the herring gull, the same species as observed to be the main avian predators on 5.3 cm cultured juvenile winter flounder *Pseudopleuronectes americanus* in an enclosure field experiment (Fairchild and Howell, 2004). That gulls might be responsible for the high post-release mortality is further supported by the fact that no post-release mortality was evident for the 17 cm large turbot released in 2003, a size that the gulls were have problems handling and swallowing (pers. obs.). The same year, Intermediate turbot of 11.8 cm size suffered a post-release mortality estimated to be 50% d^{-1}. Besides the different sizes, the higher mortality found for the Intermediate-sized turbot could have been caused by different pigmentation and behaviour. In the hatchery, the Larger fish had a darker pigmentation and lay more on the bottom, whereas the Intermediate turbot were observed to spend more time actively swimming in the fish tanks. For Japanese flounder an increased off-bottom activity has been observed for reared individuals compared to wild ones (Furuta, 1996).

At least two characteristics could be involved in predator avoidance and hence explain the lower mortality observed for the Conditioned compared to the Naive turbot. First, juvenile turbot can escape by burst swimming during an attack. However, the time that the Conditioned turbot spent in cages is unlikely to affect their swimming performance. Second, predation can be prevented either by changing coloration or by burying in the sediment. The colour did not change markedly during the time the fish spent encaged so at the time of release there was no visual difference between the Conditioned and the Naive groups. The ability to bury in the sediment is one of the key characteristics of flatfish behaviour (Ellis et al., 1997) and laboratory studies have shown that development of burying behaviour occurs within days (Fairchild and Howell, 2004). The Conditioned turbot were observed to develop burying behaviour during the time spent in cages so this seems to at least partially explain the lower mortality observed for this group.

4.3. Catchability

A decrease in catchability with size has been found for plaice, using a 2 m beam-trawl (Kuipers, 1975), a trend confirmed in this study where the catchabillity for the 17 cm long turbot was 12% and between 38 and 52% for 8-12 cm sized turbot. We do not know how the turbot escape the trawl but plaice have been observed to escape either underneath the trawl if the trawl is lifted from the sediment, or through forward and lateral movements (Edwards and Steel, 1968). In another experiment with flatfish (mainly rocksole, *Lepidopsetta bilineata*) two distinct behaviour patterns were observed, and described as 'avoidance' behaviour where the fish after a herding period are eventually scooped into the trawl, and 'escape' behaviour where the fish after herding rise from the bottom, turn 180 degrees and swim actively into the trawl (Bublitz, 1996). During the survey in 2004, one of the hauls was excluded because a 20 × 20 × 40 cm concrete building block was caught with the chains in front of the trawl. In this particular haul, taken on day 7 at 40 m west of the release point, eight turbot were caught, whereas the expected catch rate was less than three. This might indicate that the efficiency of the haul is increased with increasing sediment disturbance and that the catchability of the released turbot is dependent on their burying behaviour. This result is supported by the findings that the efficiency of a beam-trawl is increased if it is mounted with heavy spiked chains instead of a normal chain (Rogers and Lockwood, 1989). Further for the Conditioned group, catchability was estimated to be 38% compared to 48% for the Naive released simultaneously. Even though these estimates should be evaluated with caution, they indicate that catchability could decrease with increasing time at liberty, thereby creating a bias in the mortality estimate.

4.4. Feeding

In order to analyze the feeding performance of the released turbot two different approaches were tried. First, the fraction of empty stomachs found in the released turbot was compared with what was found for the wild turbot caught during the same survey. In 2003 this fraction was identical for the group of Large turbot from day 1. This indicates a prompt response to environmental cues for this size group and that the need for acclimating with respect to feeding might be small. This result differs from what has been found in laboratory experiments for smaller reared turbot feeding on shrimp *Crangon crangon* in comparison to similar-sized wild turbot (Ellis et al., 2002). The pattern was also different from what was found for the Intermediate group released in 2003 and the Conditioned and Naive released in 2004. Here a period of 3–4 d was needed before the same level of empty stomachs was seen.

Another way to analyse the feeding performance is to look at the fraction of stomachs with food that contained fish items. This fraction was the same for Large and Intermediate-sized turbot, both showing a decrease from day 2. In 2003, 10 000 turbot were released summing up to a biomass of around 800 kg turbot whereas in 2004 the released biomass was only 125 kg. The large amount of fish released in 2003 might explain the lower percentage containing fish in their stomachs after release during that year. A similar effect was observed in Japanese flounder released in high numbers in a coastal area (Tanaka et al., 2005). Predators affect their prey not only by eating them, but also induce significant behavioural changes in their prey through for example intimidation (Nilsson et al., 1995; Lauridsen et al., 2001; Preisser et al., 2005). A well-documented effect of a predator on its prey is the induction of defensive tactics aimed to decrease the vulnerability of the prey (Rönn et al., 1988; Linden et al., 2003). The sudden high number of predators within a small area may have resulted in temporary density–dependent food intake leading to prey depression, not by decreasing their numbers but by inducing more effective predator avoidance responses in their prey.

In 2004, the Conditioned group had a higher fraction of fish in stomachs with food than was found for the Naive group. Turbot are visual hunters, lying in or on the bottom sediment, waiting for suitable, unsuspecting prey to pass by (De Groot, 1969), indicating that burying behaviour is an important factor in fish prey capture. This indicates that conditioning the turbot for a period before release not only improves survival of the released turbot but also their ability to feed, and that it is in particular the burying behaviour that is improved.

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CHAPTER 8:

General discussion

1 General discussion

The overall aim of present thesis is to analyze, evaluate and optimize the release of artificially reared turbot in order to increase the likelihood that the release will increase the stock size. Further, it is the objective to illustrate how stock enhancement should combine ecological and biological knowledge, from stock-recruitment theories to information on individual behaviour. In this chapter, I synthesize the result from previous chapters into an overall discussion and will present results not included in any of the previous chapters. The discussion is structured according to the objectives set up in the section *Scopes and objectives* in chapter 1.

Objective 1: To discuss criteria for stocking with special reference to flatfish

In chapter 1 and 2 it is discussed how an understanding of the ecological processes, such as density-dependent growth and mortality is needed in order to assess whether there is a potential for increasing the cohort size by adding new individuals. I argue that for a flatfish species like turbot (*Psetta maxima*) there is most likely potential for stock enhancement because: 1) It seems that cohort size is controlled through density independent transport of larvae from the spawning areas to the nursery areas; 2) Density dependent growth and mortality may occur under certain conditions for flatfish but is restricted to the early post-settled stages (van der Veer and Bergman, 1987; Beverton, 1995, Iles and Beverton, 2000, van der Veer et al., 2000) and fish for stock enhancement will typically be released at a larger size; 3) Turbot is much less abundant than plaice and has a diet that does not show much overlap with other flatfish in the nursery (Nissling et al., 2007); 4) Turbot experiences a large increase in its available habitat during the first year of life since the preferred depth is increased from 1 m to 5 m; 5) Turbot settles at a size where they are not likely to be affected by the density dependent mortality induced by *Crangon crangon* predation.

Objective 2: To analyze spatial and temporal variation in age-0 turbot cohort size

In order to maximize the likelihood of a successful stock enhancement, survival and growth of the released individuals should be as high as possible. A step towards achieving this is to select a correct release habitat with sufficient food and space. This is not an easy decision since it is complicated by the fact that large variations in the abundance of natural turbot can be observed both on a temporal and a spatial scale. The objective in chapter 3 was to analyze the variation in the age-0 cohort size using two time series of flatfish samples taken along two different coastlines. This study showed that the abundance of age-0 turbot is highly variable between years. This variance is probably connected to the transport of the larvae into the nursery, which has been shown earlier for turbot (Riley et al., 1981), Kattegat plaice (*Pleuronectes* *platessa*) (Nielsen et al., 1998) and brown sole (*Pleuronectes herzensteini*) (Nakata et al., 2000). Simulating the drift trajectories, from the spawning area to the costal nursery, showed that the year to year variation was high and could explain the lack of recruits during some years, i.e. indicating that for some years a limiting factor for recruits in the nursery is the import of larvae to the nurseries. If these years could be identified at an early stage it could greatly improve the chances of a successful stock enhancement.

Objective 3: To evaluate a large scale stock enhancement experiment using recapture data

In chapter 2 it is argued that quantitative targets evaluating the success of stock enhancement should be set and tested, e.g. recapture rate, growth performance, mortality level or economic viability. This is the objective of chapter 4, where results from the first large turbot release project along the Danish coast is analyzed. Here it is shown that the growth of released fish was similar to or higher than that of their wild counterparts. The mortality of the released fish was highly variable but comparable to what was found for wild turbot. Finally, no indication of a replacement of the wild by the released individuals was found. From this it was concluded that it is possible to increase the Kattegat turbot stock by releasing artificially reared individuals.

This leads to the question whether it is possible to assess the increase in the commercial fishery catches. Several approaches can be explored to detect a signal from the stock enhancement in the fishery. If the released individuals can be identified from the wild a direct measurement of the quantity of hatchery reared fish caught in the fishery can be taken at harbours or at the auctions. This type of validation has been applied with success for the Japanese flounder (*Paralichthys olivaceus*) stocking program (Kitada et al., 1992) and the Hawaiian Stripet mullet (*Mugil cephalus)* program (Leber and Arce 1996). This method was not applied in the Danish turbot stock enhancement program since the major co-operation was with the recreational fishermen and a sampling of those catches would require a major effort as the catches are not processed centrally.

For turbot in the Kattegat the detection of an increase in the stock size is further complicated by the lack of any kind of population assessment. Instead the chosen option was to correlate the number of released juveniles with the total commercial landing and the Catch Per Unit Effort (CPUE) in the commercial fishery. No clear relationship was present between numbers released and the total landings of turbot in the adjacent harbours (Fig. 1A). However there was a tendency for an increase in the commercial CPUE (Fig. 1B) but it should be noted that no data was available before 1995.

Objective 4: To evaluate habitat suitability by analyzing stomach content of the wild population

The theoretical considerations on factors regulating the turbot cohort size combined with the result found in chapter 4, led to the conclusion that releases of artificially reared individuals into a local flatfish population were a viable option in order to enhance the stock size. Thus, the focus was subsequently moved onto ways of improving these releases, either by finding the optimal release habitat in terms of providing the released individuals with good conditions for growth or by increasing the post-release survival by releasing fish of a proper size or applying a conditioning experiment prior to the release.

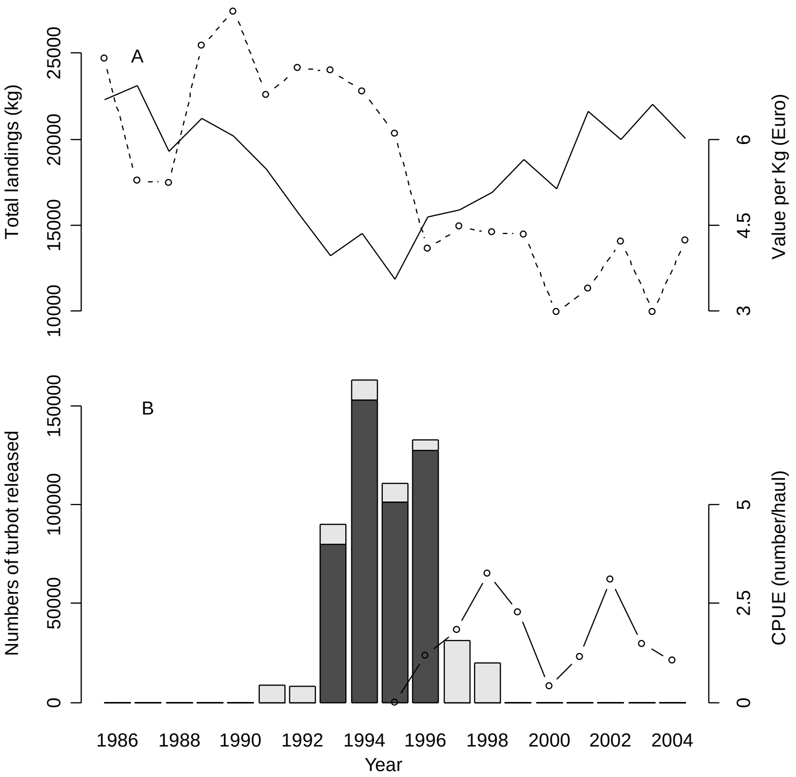

Figure 1. Dotted line in panel A: the total commercial landings of Kattegat turbot at harbours on the Northern part of Zealand. Solid line in panel A: the average price kg^{-1} for turbot sold at the marked. Bars in panel B: total numbers of released turbot. Black are age 0 released and white are age 1. Dotted line in panel B: CPUE (individual haul^{-1}) in the commercial trawl fishery. Data from the Danish monitoring program.

In chapter 5, data from three releases carried out at different locations in the Kattegat area are used together with samples of wild individuals to evaluate the suitability of the habitat. Here it was shown that the growth performance of the released artificially reared turbot differed significantly between release habitats. The three habitats differed in they degree of wind exposure, where the one with the highest exposure was believed to be the best habitat for turbot (Gibson, 1973; Riley et al., 1981). As predicted, the area with highest degree of exposure had the highest abundance of wild turbot, but surprisingly the released turbot showed an inferior growth compared to fish from the more wind protected areas. The diet of the wild turbot in the three areas was analyzed and it was found that in the exposed areas the fish switched from exoskeleton carrying prey items such as crustaceans to fish (e.g. sand gobies, *Pomatoschistus minutus*) much later than in the more sheltered areas. Since the evacuation rate and hence the energy assimilation is more efficient for fish as prey than crustaceans (Andersen, 2001), this may result in low growth in those areas. In this chapter it was demonstrated that a relative easy achievable and cost-efficient measurement such as the diet of the wild individuals has the potential to be used as predictor for habitat suitability. However it was also shown that releasing fish according to where the largest natural abundance is found might not always give the best result.

This result indicates that there appears a potential in releasing artificially reared individuals into other areas that are suitable as nurseries but with a limited population due to a lack of larvae transport.

Objective 5: To provide a methodology for estimating post-release mortality and spreading of released turbot applying a diffusion model

In chapter 6 a model was developed to describe the spreading of the released fish and to estimate the post-release mortality and in chapter 7 ways of limiting the loss of fish during the post-released period, either by manipulating the size of fish released and/or by applying a condition period, was presented.

The model developed in chapter 6, a diffusion/advection model, was not arbitrarily chosen but originates from the pioneer work by Skellam who in 1951 applied a diffusion model to the spreading of an invading organism, the muskrat (*Ondatra zibethica*). This type of model has later successfully been applied to various organisms such as insects (Kareiva, 1983) and fish (Sibert et al., 1999). Two methods, a Partial Differential Equation (PDE) and a Normal Distribution Approximation (NDA) were used to parameterize this diffusion/advection model. In here I will shortly go through the difference between these two, since they both had strengths and weaknesses that did influence the parameter estimation in the experiments to come.

In the NDA all samples from one given day were treated as if they were sampled at the same time, i.e. day 1, 2…n. By doing so, one could assume that the resulting density distribution for a single day would be Normal around the mean position in the area, where the mean position in the area is the release position ± advection. This implies that dispersal during the time span between the first and last sample of the day was not taken into consideration. Further, this model suffers from the fact that the removal of some of the captured fish (for stomach analyze) is not accounted for, even though this ultimately will flaw the normal density distribution. To estimate whether these two drawbacks did have an effect on the estimation of parameters the NDA was compared to the PDE in which it is possible to take both the removal of fish and the exact catchtime into consideration. The down side of these PDE's is that they are very heavy in calculation (which was solved by Anders Nielsen, DIFRES) and complicated to program. So without good programming and statistical skills this type of modelling will be difficult to apply in practice. Fortunately, the conclusion was that there was no significant difference between the estimates from the two approaches, meaning that estimating the numbers of fish from a NDA gave the same mortality, diffusion and advection estimates as the PDE.

It should be mentioned that the model is not generic and can only be applied to certain species, mainly because two assumptions had to be satisfied. First, the released individuals should move independently of each other. This assumption will likely be fulfilled in the case of turbot in contrast to a schooling species like herring (*Clupea harengus*). The second assumption is that the distances moved by each single fish within a given time applies to the central limit theorem. This means that the distance moved must not be infinite and that each single fish should have the same distribution of movements (directions and distances) at which it can chose at random. If two or more types of dispersal strategies are present in the population the resulting density distribution of fish in the area will not be normal but leptokurtic, a result found for some fish species, which appears to be related to their individual boldness (Fraser et al., 2001).

Objective 6: To manipulate size of the turbot released and apply a method for conditioning prior to release in order to minimize post-release mortality

Plotting the recatchable part for the 7.5 cm turbot released in the first experiment in 2001 revealed a decline from the day of release to the last day of sampling (Fig. 2a). The decline corresponded to a 14 % day^{-1} mortality during the period examined. This high mortality was believed to be restricted to a limited period after the release, the *post-release* period. Thus the decline in recatchable part was interpreted as a mixture of an extremely high initial mortality risk during the first days at liberty followed by a gradual decrease in mortality risk until a natural level was reached. This meant that in future experiments it was no longer enough to quantify the mortality but also the duration of the post-released period should also be considered as an important parameter determining the survival of the released fish. The experiment was repeated the following year to verify that the loss of fish was as high as estimated, but this release failed since it was not possible to catch enough released fish to obtain reliable results, probably due to an even higher mortality than previously seen. During this later release a high seagull [great black-backed gull (*Larus marinus)* and herring gull (*Larus argentatus)*] activity was witnessed and on several occasions the gulls were observed to capture released turbot. The experiment was terminated after 3 days and during this period more than 500 tags was found lying at the beach, also pointing towards a high predation rate by gulls.

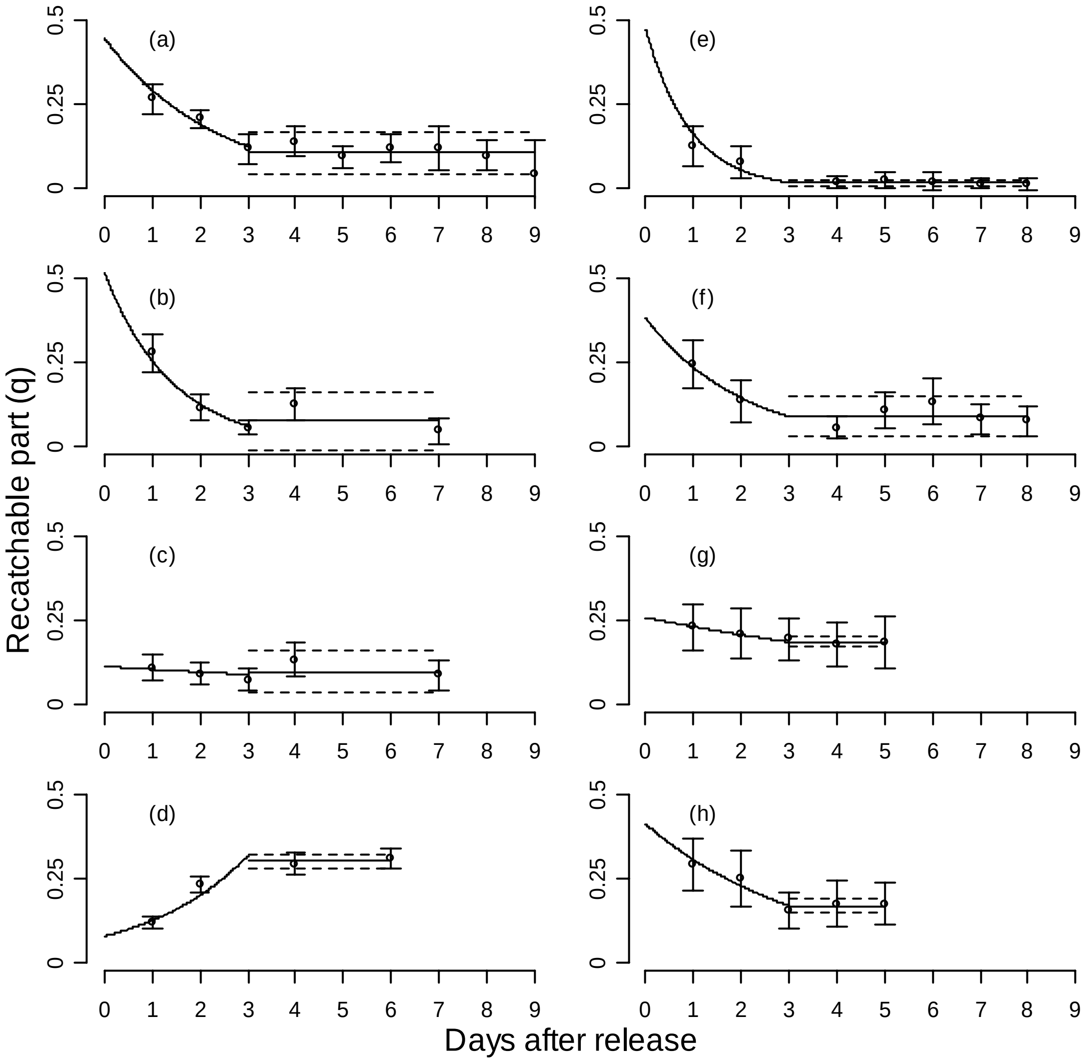

Figure 2. Recatchable part (q;–) of turbot together with 95% confidence intervals relative to days after release. (a) 7.5 cm naïve turbot released in 2001; (b) 11.8 cm naïve turbot released in 2003; (c) 17.1 cm naive turbot released in 2003; (d) is a mixture of conditioned and naïve turbot of size 3-5 cm released 2004; (e) 9.8 cm naive turbot released in 2004 released simultaneous with the 9.8 cm conditioned released in 2004 shown in figure (f); (g) 11 cm conditioned turbot released in 2006; (h) 4-5 cm conditioned turbot released in 2006. The solid line until day 3 shows the decrease in numbers and the slope is the post-release mortality with the intercept at the y-axis being the catchability. The horizontal lines indicate the average recatchable part of the released fish (solid) and 95% confidence limit (dashed) from day 3 onwards.

To circumvent the high initial mortality of the released fish, a series of experiments was performed in order to analyze and improve the survival in future releases. Most of these experiments are presented in chapter 7 but not all. Two different approaches were taken: 1) to increase the size-at-release of the fish from 3 cm to 17 cm; 2) to condition the fish prior to the release. Table 1 gives an overview of the different releases conducted in Begtrup Vig in Århus bay.

Table 1. The various experiments which provide the results for the investigation of the post-release period and mortality. *Naïve* fish are fish that were brought directly from the hatchery and released whereas *conditioned* fish had experience a period encages at the released location prior to the actual release.

Year	Size (cm±sd)	No. released	Type	Days monitored	Release date
2001	7.5± 0.6	3529	Naïve	9	14 May
2002	10.5	10649	Naive	3*	10 May
2003	11.8±0.9	5000	Naïve	7	3 June
2003	17.1±1.7	5000	Naïve	7	3 June
2004	9.8±0.9	2500	Naïve	8	4 May
2004	9.8±0.9	2500	Conditioned	8	4 May
2005	3-5	10.000	Naïve**	6	10 June
2005	3-5	10.000	Conditioned**	6	10 June
2006	4-5	2500	Conditioned	5	5 May
2006	11±1.0	2500	Conditioned	5	5 May

*Sampling was ended since the recaptures was very small. During the 2 days 507 tags was found lying on the beach.

**Due to complications in detection of the alizarin marked otoliths of the naïve fish they could not be separated from the conditioned turbot.

In 2003 two size groups (11.8 and 17.1 cm) which were larger than the fish released in 2001 and 2002, were released. Here a high mortality for the size group 11.8 cm was observed whereas no mortality was observed for the 17.1 cm fish (Fig. 2b and c, respectively). Presumable the largest fish were too large to be eaten by the gulls. This assumption was supported by personal observations of a gull having caught a turbot without being able to handle and swallow it. Hence these releases demonstrated that the mortality can be brought to a minimum by releasing fish of a proper size, however, it may not always be economical feasible as the price of turbot increases with size.

Figure 3. Cages designed for keeping the turbot encaged at the location prior to the actual release. The cages have no bottom thus leaving the turbot in direct contact with the bottom sediment. A coarse net is mounted on top to avoid bird predation.

The second approach to lower the loss of fish during the post-release period involved a conditioning experiment. This aimed at improving the behavioural skill of turbot released and thereby increasing their survival (Howell, 1994; Hossian at al., 2002). The actual conditioning procedure was rather simple. Turbot intended for release was kept in cages in their release habitat for a period (3-6 days) prior to release (Fig. 3). Depending on size of the individual fish, between 250 and 2500 fish were kept in each cage. Fish that had experienced this conditioning period was termed *conditioned* whereas fish brought directly from the hatchery and released are referred to as *naïve.*

During the first experiment with encaged fish it was decided to release a control group of naïve fish together with the conditioned individuals (Fig. 2 e and f). The experiment was designed such that the naïve and conditioned fish were released simultaneously. The naïve fish were carried in baskets from the truck, in which they had been brought from the hatchery to the release position, and into the sea, after releasing a basket of naïve fish, but before going back to the shore, one cage was lifted from the bottom hence releasing the conditioned individuals. This first experiment showed that the mortality was almost twice as high for the naïve compared to the conditioned turbot. Thus, conditioning limited the mortality though it was not brought to a minimum as expected. Presumably the naïve fish attracted an abnormally high number of predators thereby increasing the mortality of the conditioned turbot to a level beyond what would have been observed if the conditioned turbot had been released alone. In 2006 this hypothesis was confirmed by a release of only conditioned fish where only a minor decrease in the recatchable part was seen, indicating limited mortality (Fig. 2 g).

In 2005 and 2006 the turbot released was as small as *c.* 4 cm (Fig. 2 d and n). The very first experiment with this size group involved both groups and indicated a “positive mortality”. This particular experiment was however flawed by difficulties of identifying the conditioned turbot from the naïve (Fig. 2 d). Some bird activity was witnessed but it seemed that the sea-gulls did not continue to search the area for released turbot, maybe because it was not worth spending time searching for such a small fish or other and better sources of food were available in the area.

Later the experiment was repeated in an experiment where all individuals were conditioned prior to the release and released simultaneous with 11 cm turbot. This experiment showed that the morality for the 4 cm fish was higher than for the 11 cm conditioned turbot (Fig. 2 h and g respectively). Again little bird activity was observed indicating the other sources of mortality might be responsible for the decrease of fish.

So what mechanism lies behind the success of conditioning? Is it the burying behaviour or other physiological aspects such as swimming performance or changes in colour and appearance? The swimming performance of wild juvenile turbot is found to be superior to hatchery reared turbot, at least until 2 weeks after the wild had been captured and brought to the laboratory (Gibson and Johnston, 1995). But since the conditioning did seem to have a very pronounced effect even when kept encaged for only 3-4 days the swimming speed is considered to be an unlikely explanation.

In 2004 the pigmentation was visually observed and pictures were taken of turbot daily for the first 10 days after the turbot had been brought from the hatchery to the release location. It was obvious that no visual difference in the colour or pigmentation was found during the period examined.

In May 2006 the actual burying behaviour of the turbot being encaged at the releases location was monitored. Eight cages were mounted at the release location and 312 turbot were released into each cage. The number of visible turbot was counted using a hydroscope at different time after the release. A clear tendency toward fewer fish being visible in the cages as time proceeded was apparent (Fig. 4). Unfortunately the experiment was ended 3 days after start, where the numbers of visible fish seemed to have reached a minimum level, but since the fish had to be released at that day it could not be verified whether this was a constant low level or not.

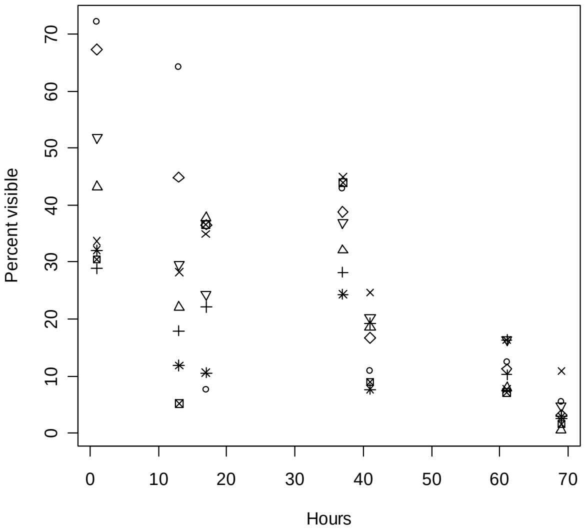

Figure 4. The percentage of the 312 juvenile turbot of size 11.5 cm kept in each of the 8 cages that were visible. Hours are the time since they we put in the cage. The different symbols used correspond to each different cage.

The conclusion of these experiments was that the post-release mortality could be very high and a serious problem in stock enhancement. At least two strategies were recognized being able to limit the mortality: 1) releasing turbot of a larger size or 2) applying a conditioning period prior to the actual release. Increasing the size increased the survival since the main predators was not able to handle and/or swallow the turbot, whereas the condition trial gave the turbot a chance to develop cryptic behaviour such as the ability to bury thereby increasing the survival probably due to a lower detection rate by predator.

1.1 Perspective

With the increasing pressure witnessed on the world's natural marine resources, new proactive management strategies, such as stock enhancement by releasing artificially reared individuals, are likely to become more important in the future. Aquaculture is already capable of producing large numbers of juveniles at a reasonable price, so research should be focused on improving the survival and growth of the released animals in order to increase the likelihood of success.

First a solid theoretical basis should provide the arguments for the concept that adding a number of fish to a stock will increase the stock size and will not lead to an increased mortality and/or reduced growth due to density dependent regulation. Further, the switch from a homogenous predator free environment experienced in the aquaculture to a heterogonous release locality with waves bottom sediment and predators should be given special attention since this period can be accompanied by a highly elevated mortality. Consequently, ways of conditioning the artificially reared individuals should be considered and tested. When and where to release the artificially reared individuals should also be a subject for future research. It appears that the transport of larvae is a limiting factor in some areas that otherwise could serve as nurseries. This could be areas where human constructions acts as an artificial barrier between the spawning grounds and nurseries or enclosed bays and fjords where limited water transport from the adjacent waters restricts the import of larvae. If individuals are to be released into these habitats where they do not occur naturally, monitoring is necessary in order to secure that unforeseen negative interactions e.g. with other species does not occur. The cohort size varies considerable from year to year, not only for turbot but for most other marine fish species. Therefore, if years with undersized age-0 cohorts could be identified, stock enhancement could be concentrated to those years. This is an appealing thought but tuning the aquaculture facilities to such a system might be difficult. It will require an ability to predict the cohort strength at a very early stage, which at present is not possible for most species. Further, it might be a dangerous strategy if the absence of age-0 individuals is not due to lack of larvae transport into the nursery but to predation or starvation within the nursery. The genetic composition of the fish released should in addition be considered. I have not included any thoughts on this subject in present thesis but this does not mean that it should not be taken into account. Especially for stock enhancement carried out in areas such as the inner Danish waters where different genetic strains occur geographical quite close to each others. Whether mixing of genetic strains in the hatchery, or releasing fish from one genetic defined area into another, will have a negative effect on the outcome of a stock enhancement has, for marine fish species, yet to be proven. But until research has been devoted to this subject, a precautionary approach should be taken, securing that genetic strains are not released outside their geographical area.

This thesis has provided methods for optimizing and analyzing releases of artificially reared individuals, but the decision makers are likely to ask one question before launching any kind of initiative for a stock enhancement, namely: *is it economical viable*? In previous chapters this question has only briefly been touched even though it is the most frequent question asked. Therefore I would like to end this thesis devoting the last paragraphs to this question.

It is straight forward to estimate the cost of releasing one fish. However, to set the value of the released fish when caught again is more complicated because it is not known how many of the released fish that is later caught in the fishery. Relying on the reported recaptures as done in chapter 2 is problematic due to the uncertainty in the reporting rate and shedding of tags. This can be illustrated using the reports received for the turbot released at the Northern part of Zealand. Here more than a 100 out of the total 2600 reported recaptures come from the fish auction; hence not all fishermen had detected the tag. Secondly, the value of a turbot caught is difficult to find. It can be obtained from the first sale value when sold at the fish auctions but the value of a turbot caught in the recreational fishery may represent different value, which is difficult to compare.

Despite these uncertainties, the profits can be guessed using the growth and mortality estimates found in chapter 4. Assuming a length increase from 10 cm to 26 cm during the first two growth seasons, the individual weight at the end of the second growth season is *c.* 300 g, representing a commercial value of 3 €. The survival during these two first years after release was estimated to be *c.* 70 % per year and hence the average value will be down to 1.5 €. As the price for one turbot released is *c.* 1.5-2 €, including transport, labour and release, it hence almost breaks even. It is important though, to be aware that the survival is accompanied by large uncertainties and that it does not include any loss of fish during the post released period. Nevertheless, the calculation shows that there is a potential for stock enhancement of natural flatfish stocks with releases of artificially reared juveniles, if done properly and thoughtful.

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Summary

The overall objective of this thesis is to evaluate and optimize a stock enhancement program of natural population of flatfish in which artificially reared fish are released in coastal areas using turbot (*Psetta maxima*) as model. Biological and ecological criteria are developed to evaluate the likelihood for success, i.e. increasing the stock size, based on ecological knowledge. Special reference is given to processes involved in the regulation of the natural population, such as density-dependent and density-independent mortality and growth. Field data on the temporal and spatial variation in the abundance of age-0 turbot is analyzed and implications for stock enhancement are discussed. It is concluded that there is a solid theoretical background indicating that stock enhancement through releases of artificially reared juvenile individuals is a viable option for the turbot stock.

Support for the hypothesis that stock enhancement is a viable option is provided by the results of a series of filed experiments conducted under a stock enhancement program in the southern part of Denmark. The focus of these experiments was on the growth and mortality of released fish in comparison to wild fish, and the importance of the characteristics of the release habitat. The growth of the released fish was similar to, or higher than, that of their wild counterparts, and the mortality, even though highly variable, was on a comparable level. No indication of replacement of the wild individuals with released ones was found. The importance of the release habitat was investigated by releasing turbot into three areas that differed in wind exposure. The area with the highest degree of wind-exposure was, as predicted, the area where the highest abundance of wild juvenile turbot was found. The highest growth of released individuals was not found in this area but was found in the one characterized by the lowest degree of wind-exposure, an atypical nursery ground for turbot. The effect of the release habitat on the growth could be related to the quality of the prey items observed in the stomachs of wild turbot sampled in the three areas. Besides the choice of a suitable release habitat, the release size of the fish and the conditioning to the release habitat was shown to be critical for survival of released fish. In order to study the mortality of the released fish, a methodology applying diffusion theory was developed and tested. Using this method the post-release mortality was found to be as high as 14%•day^{-1} for the 9 day period examined in 7.5 cm sized fish. Mortality decreased with increasing release size and became negligible at a release size of 17cm. After conditioning reared fish to the release environment allowing fish to develop their natural burrowing behavior prior to release, the post-release mortality was found to be insignificant.

Since it was possible to enhance the turbot stock through releases of artificially breed individuals, stock enhancement may be considered as a supplement to traditional stock management. It can be applied in species with a

turbot like life cycle where density-dependent regulation occurs early in life, and where the cost of production young fish is less than the gain in fisheries yield. As long as the artificially reared juveniles are added to the population after the stage where density-dependent regulation occurs, it can be expected that the released fish will contribute to the natural stock. Further, in order to optimize the outcome when stock enhancing, two aspects should be given special attention, 1) finding a proper release habitat where not only the food quantity but also its quality provides optimal growth conditions and 2) the risk of a server loss of fish during the post release period which can be avoided either by manipulating the size of the individuals released or by applying a conditioning period prior to the release.

Samenvatting

Dit proefschrift heeft tot doel om een onderzoeksprogramma te evalueren en te optimaliseren waarbij jonge kustmatig opgekweekte vissen in hun natuurlijke leefomgeving worden uitgezet ter vergroting van de bestandsgrootte (‘stock enhancement’ ofwel bestandsvermeerdering) van een natuurlijke populatie van tarbot (Psetta maxima) in de wateren van zuid Denemarken. Op basis van ecologische kennis werden biologische en ecologische criteria ontwikkeld om de kans op succes te evalueren. Hierbij werd speciaal aandacht geschonken aan de processen die ten grondslag liggen aan de aantalsregulatie van natuurlijke populaties, zoals dichtheidafhankelijke en -onafhankelijke sterfte en groei. Veldwaarnemingen over de ruimtelijke en seizoensmatige veranderingen in de verspreiding van 0-jarige tarbot werden geanalyseerd en de implicaties voor de bestandsvermeerdering werden besproken. Er werd geconcludeerd dat de ecologische kennis een stevige basis biedt voor bestandsvermeerdering door het loslaten van kunstmatig opgekweekte jonge tarbot.

Ondersteuning voor de hypothese dat bestandsvermeerdering een kansrijke mogelijkheid biedt werd gegeven door de resultaten van een aantal veldexperimenten die werden uitgevoerd in het kader van een ‘Stock Enhancement Program’ in het zuiden van Denemarken. De nadruk bij de experimenten lag op een vergelijking van de groei en sterfte van uitgezette vissen met die van wilde vis, en op het belang van de kenmerken van het uitzetgebied. De groei van uitgezette vis bleek gelijk, of zelfs iets hoger, dan die van de natuurlijke populatie. De sterfte was erg variabel maar verschilde niet van die van de natuurlijke populatie. Er werden geen aanwijzingen gevonden dat de wilde tarbot door uitgezette dieren werden verdrongen. De betekenis van het uitzet gebied werd onderzocht door tarbot in drie verschillende uitzetgebieden los te laten. De uitzet gebieden verschilden in de mate waarin ze aan de overheersende windrichtingen waren blootgesteld. In overeenstemming met de verwachting werd in het gebied met de hoogste blootstelling de hoogste dichtheden van de natuurlijke populatie aangetroffen. De grootste groei werd echter gemeten in een atypisch gebied met de laagste wind blootstelling.. Het effect van het uitzetgebied kon worden verklaard vanuit de verschillen in voedsel kwaliteit zoals wargenomen in de bemonsterde dieet samenstelling van wilde tarbot. Naast de keuze voor een geschikt uitzetgebied, heeft ook de lengte waarop de jonge tarbot wordt uitgezet en het conditioneren van de dieren in hun nieuwe uitzetgebied een positieve invloed op de overleving. Ten einde de sterfte van de uitgezette dieren te kunnen meten is een methode, gebaseerd op de theorie van diffusie, ontwikkeld en toegepast. Gedurende de eerste 9 dagen na het uitzetten van 7.5 cm grootte dieren was de sterfte 14% per dag. De sterfte nam af als functie van de uitzetlengte van de vis. Bij een uitzetlengte van 17cm was de sterfte verwaarloosbaar klein. Na het conditioneren van de uitgezette vis, waarbij de dieren in staat werden gesteld om te wennen aan hun nieuwe leefomgeving en ingraafgedrag te ontwikkelen, bleek de sterfte na uitzetten verwaarloosbaar klein.

Het uitzetten van kunstmatig opgekweekte jonge vis kan als een beheersinstrument worden gezien dat een aanvulling vormt voor het traditionele bestandsbeheer. Het kan worden toegepast voor soorten met een vergelijkbare levenscyclus als tarbot, waarbij de dichtheidafhankelijke processen in het vroege jeugdstadium optreedt, en waar de kosten van de productie van jonge vis opwegen tegen de opbrengstverhoging in de visserij. Als de kunstmatig gekweekte vis wordt uitgezet na afloop van de periode waarin er dichtheidafhankelijke processen optreden, kan worden verwacht dat de uitgezette dieren een bijdrage leveren aan de vermeerdering van het natuurlijke bestand. Teneinde de opbrengst van de bestandsvermeerdering te optimaliseren moet aan twee aspecten aandacht worden gegeven: 1) het selecteren van een geschikt uitzetgebied waar niet alleen de hoeveelheid voedsel maar ook de voedselkwaliteit optimale groeiconditie schept; 2) het reduceren van het verlies van vis na het uitzetten door de selectie van de optimale uitzetgrootte en door het toepassen van een periode waarin de dieren aan het uitzetgebied kunnen wennen.

Curriculum vitae:

I, Claus Reedtz Sparrevohn was born on the 28th of September 1971 in Copenhagen, Denmark. In 1990 I enrolled at the Aarhus University to study Biology, at first with the intention to specialize within physiology but later I found interest in population biology and marine ecology. In 1995 I received a Nordplus scholarship which enabled me to study one semester at the Norwegian College of Fishery Science. After Tromsø I continued to work with fishery and marine ecology and started my master thesis on growth and condition indices of Baltic cod at The Danish Institute for Fisheries Research (now known as DTU-Aqua) under the supervision of Dr. Jonna Tomkiewicz. In 2000 I was employed by Dr. Josianne Støttrup to work in the group for Marine Stock Enhancement at the DTU-Aqua’s division in Hirtshals, a group which has now become the Coastal Ecology Section. During my time in this section, I have been involved in stock enhancement of turbot, a flatfish species occurring naturally in the inner Danish waters. Focus has mainly been on three aspects of optimizing the stock enhancement of turbot; 1) to gain knowledge on which factors that defines the potential for a successful stock enhancement, 2) to minimizing the mortality of the released individuals and 3) to identify which areas that are a suitable as release habitat. Besides, I have been involved in mapping the distribution of juvenile flatfish in relation to coastal zone habitats and analyzing the interaction between fish growth, mortality, migration and habitat quality.

List of publications:

- **C.R. Sparrevohn**, J.G. Støttrup (2008). Diet, abundance and distribution as indices of turbot (Psetta maxima L.) release habitat suitability. Rev. Fish. Sci. 16: 1-10
- Carl, J.D., **Sparrevohn, C.R.**, Nicolajsen,H., Støttrup, J.G. (2008). Substrate selection by juvenile flounder Platichthys flesus L.: impact of ephemeral filamentous macroalgae. J. Fish Biol.
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