Demography of coastal Atlantic cod in relation to the establishment of a marine protected area

Jan-Harald Nordahl

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Abstract

Use a mark-recapture approach to study the demography of Atlantic cod (*Gadus morhua*) in a small (1 km^2) marine protected area (MPA) on the Norwegian Skagerrak coast. A total of 9713 Atlantic cod where tagged during 2005-2010. Inside the MPA, only hook and line fishing is allowed. Data are partly live capture-recaptures from the research fishing activity, and partly dead recoveries from commercial and recreational fishers. A high-reward system was applied to quantify the tag reporting rate from fishers. We estimated the tag reporting rate to be 72.4 % for recreational fishers and 73.8 % for commercial fishers. Based on this, our data suggests that recreational fishing has a larger impact on cod mortality than commercial fishing in this area. Adjusted for recovery rate we estimate that the recreational fishers captured 2289 of the tagged cod, corresponding to 71 % of all recoveries, while commercial fishers captured 954 fish, corresponding to 29 % of all recoveries. Capture-mark-recapture (CMR) modelling tools were used to estimate annual survival rates. Survival varied both in time and among areas. In the live-recapture model estimates apparent survival ranged between 0.3>- 0.6. The joint model the true survival range was 0.3< - 0.9. One year after protection both live-recapture model and joint model the survival estimates were higher in MPA then in the reference locality. Subjecting that the MPA might had an effect.

Contents

Introduction

Throughout the world fish stocks are threatened by overharvesting, and there is a growing concern of that fishery influence on life history evolution in target stock (e.g. (Law and Grey 1989; Law 2000; Olsen et al. 2004). For instance Beamish et al. (2006) defines that removal of large numbers of older age groups as longevity overfishing. Older age groups often have higher reproductive successes and more productivity (Beamish et al. 2006).

The Atlantic cod (*Gadus morhua*) is an important source for human food throughout of the North Atlantic Ocean (Olsen et al. 2011). Atlantic cod have the status vulnerable on IUCN Red List of Threatened Species (IUCN 2011). Current assessment of the North Sea and Skagerrak stocks indicate significant reduction in the stock size over the last decades. In the eastern part of the Skagerrak stock have suffered a near collapse (Svedäng and Bardon 2003). There is also decreasing phenotypic variability in Atlantic cod size and age in Skagerrak (Olsen et al. 2009). The coastal cod in Skagerrak is harvested by both commercial and recreational fishers (Olsen and Moland 2011). High fishing pressure may be a cause of the decrease in the Atlantic cod stock in Skagerrak, and reducing the fishing pressure is a likely way to increase the stock (Julliard et al. 2001).

One management strategy for decreasing pressure is though establishment of marine protected areas (MPAs); MPAs are increasingly being acknowledged as a tool in fisheries management and conservation. MPAs may reduce the exploitation impact from the Commercial and recreational fisheries on Atlantic cod stock and give sufficient protection for stock re-establishment and protection of older age groups. However, in temperate areas the use of MPAs are still relatively uncommon and effects on local stocks remains unclear (Blyth-Skyrme et al. 2006).

In 2006 four MPAs were established on the Norwegian Skagerrak coast. The main aim of these reserves was to study the effect of small-scale protection on the local lobster population (i.e. these are lobster reserves). In these MPAs standing gear (traps, gillnet, long line) is prohibited in order to ensure a full protection of the lobster (Dahl et al. 2009). Traditional hook and line fishing is however, not regulated.

In this thesis I have studied the effects of partial protection on the demography of the Atlantic cod by conducting standard capture-mark-recapture analysis on the cod stock. A working hypothesis was that cod survival would increase inside the lobster reserve after reserve implementation. Furthermore, I used tag returns to describe the recreational and commercial cod fishery on the coastal cod, both inside and outside a MPA before and after reserve implementation. I expected that the commercial fishery would disappear from the reserve after reserve implementation since commercial fishers will mainly use standings gear.

Materials and Methods

Study species

Atlantic cod are found throughout coastal and offshore shelf areas in the North Atlantic with its main distribution area between the Bay of Biscay in the south, Novaya Zemlya and Spitsbergen, southern Greenland and south to the eastern coast of USA. Atlantic cod may attain age of 40 years, lengths of 180 cm and a weight of more than 55 kg (Pethon 2005). Probably due to long periods of over fishing such large and old individuals are rarely encountered today (Julliard et al. 2001).

Atlantic cod age sexual maturation and growth rate vary substantially both between and within populations (Olsen et al. 2008). The offshore Atlantic cod population is known for their characterized long- distance migration linked to feeding and spawning, while coastal populations like the stock in Skagerrak tend to be spatially more confined in their distribution (Knutsen et al. 2003). The Atlantic cod is a species with highly fecund and no parental care (Kjesbu 1989, Kjesbu et al. 1998). The cod do not interbreed freely, but group in local populations which stay partly isolated from each other (Knutsen et al. 2003). In Skagerrak is a mix of several local Atlantic cod populations and genetically different sub-populations are sometimes separated by little as 30 km of coastline (Knutsen et al. 2003; Espeland et al. 2007; Jorde et al 2007). Inshore basins that are largely protected from coastal currents, combined fidelity of older fish are likely mechanisms promoting this population structure (Olsen and Moland 2011). There is evidence that the nursery areas in Skagerrak coast have some influx of juveniles from offshore spawning from the North Sea (Olsen et al. 2009). Maturtion occurs at age of 2 to 3 years at a body length of 30- 50 cm (Gjøsæter et al. 1996). Only <2 % of 1 year old Atlantic cod survive to reach 6 years or more. The average generation time is 3 years (Stenseth et al. 1999; Knutsen et al. 2003). Julliard et al. (2001) did a study in Søndeledfjorden and found that the fishery was the main mortality on fish >1 year old, but fishers mainly targeted Atlantic cod that where 3 years or older.

Study area

The ocean basin delineated by the landmasses of South-eastern Norway, Denmark, and Sweden, is called the Skagerrak Sea (Knutsen et al. 2003). Our study area is in Norwegian Skagerrak from the Lillesand area to the Risør area, which defines about 80 km of coastline (Fig. 1 right). The area contains numerous small islands, skerries and fjords along the coastline. The MPA (Fig.1 left) at Flødevigen was establish in 2006 together with 3 other areas at the coastal zone in Skagerrak sea, Risør, Bulærne and Kvernskjør, to protect the endangered European lobster (*Homarus gammarus*). All MPA are relatively small, but Flødevigen is the biggest of them with an area on 1 km^2. This area is protected under the Norwegian Saltwater Fishery law, which only allows fishing with handline inside the MPA. The protection will lasting for at least 10 year period (Dahl et al. 2009).

Before 2010, a minimal legal size of 40 cm was mandated for commercial harvest, but from 2010 this regulation also applies for recreational harvest (Olsen and Moland 2011).

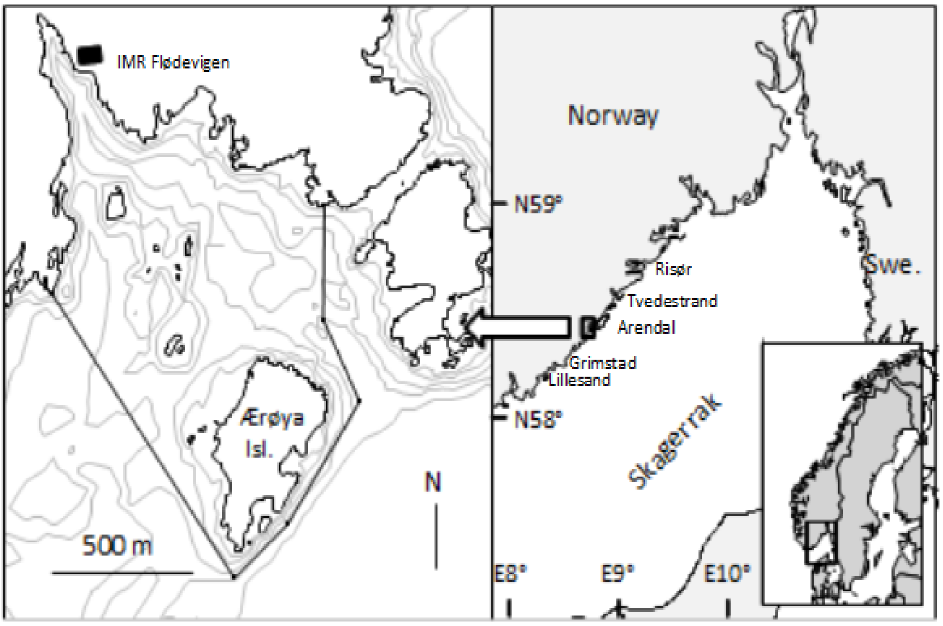

Figure 1: Map of study area. The insert at left indicates the boundaries for the marine protected area in Flødevigen

Data collection

The Atlantic cod were captured in a period between April – July, 2005-2010 (Table 1), using fyke net. The nets were usually retrieved after 1–7 days. The fishing effort varied between the years (Table 1). The traps were set at places along the coast in the three main areas, Arendal/Grimstad, Lillesand and, Risør/ Tvedestrand (Appendix Fig. 1-3).

Table 1: Tagging study period and fishing effort 2005- 2010.

Year	Period	Trap days
2005	May 14 – June 29	659
2006	April 28- July 2	1859
2007	April 25- July 1	2148
2008	April 25- July 20	1834
2009	April 1- July 20	1055
2010	April 21- June 24	883

Total length on all Atlantic cod captured where measured to the nearest 5 mm. Individuals > 250 mm were tagged in the musculature at the base of the dorsal fin with traditional T-bar tags with a printed reward of 50 NOK (yellow) or 500 NOK (red), (see also Brattey and Cadigan 2006). The purpose of this low and high-rewarding system (every 5th fish got a high reward tag) was to estimate the tag reporting rate (see below). 246 Atlantic cod < 250 mm were tagged with a small T-bar tags (0 reward). The fish with small T-bar tags were retagged reward T-bar tags when they were recaptured and had achieved length >250 mm. Some cod had lost their tag (detected as visible scar where the tag had been), and totally 78 were retagged. In 14 of the retagging cases the tag were found inside the pot. Fish that lost their tag in the pots where retagged before release. Tag cod were released immediately after tagging in the same area where they had been captured. In some cases Atlantic cod where killed (106 Atlantic cod) during tagging or taken by seabirds (26 cod).

We also recaptured a substantial number of tagged cod during our annual tagging program. These fish were measured and released alive at the point of capture. Therefore our data consist of a combination of dead recoveries from recreational and commercial fishes as well as live recaptures from our own sampling. This distinction is important when selecting the proper capture-mark-recapture modeling tool (see below). To quantified the fishing pressure from tourist we also distinguished between local fishers having a postal address within Aust-Agder county and fishers from other parts of Norway and abroad.
Upon returning tags, most fishers reported the date position of capture, what gear used and the fishers address. Along the border of the MPA it was often hard to accurately decide if a returned tag form a fish caught inside or outside the MPA based on information from the

fishers, and in all areas information on fishing gear were sometimes missing (37% from recreational fishers and 21.5 % from commercial fishers).

Data analysis

We have based our analysis on several assumptions: i) Tagged samples are representative of the coastal cod population, and that tagged fish mixed with untagged fish in the area; ii) There was no loss of tags; iii) survival rates were not significantly affected by tagging; iv) the tag recoveries were reported correctly; v) the fate of each tagged fish was independent; and vi) all tagged Atlantic cod within the cohort had the same pattern of survival rate and recovery probability (Pollock et al. 2004).

To estimate the reporting rate of the standard tag we have assumed a 100% return rate of the high-reward tags (Pollock et al. 2002). The standard tag delivery rate (λ,%) was estimated from:

$$\lambda = 100(R_S N_R)/(R_R N_S) \qquad (1).$$

Where Rs is the number of standard tag returned, N_s is the number of standard tags released, R_R is the number of high reward tags returned, and N_R is the number of high reward tag returned (Pollock et al. 2001).

A CMR model approached Lebreton et al. (1992) was used to estimate survival probabilities using the software package program MARK (v. 6.1). In capture-mark- recapture (CMR) modelling we assume that after being tagged and released the tagged individuals may be recaptured again later on different occasions (Julliard et al. 2001).

However as the CMR data we have used are based on alive recaptures and dead recovery we applied a joint alive encounter & dead recovery model (referred to as joint model). The joint model have four estimates (Fig. 2a): true survival (*S*); which is the probability that the Atlantic cod has not died, recapture probability (*p*); which is the probability for capturing a cod that is available from the study population, fidelity probability (F); which is the probability that the cod remains in the study area, recovery probability (r); which is the probability that the tagged cod individuals are harvested and return. We also chose to include a live-recapture model because it is more simple with only two estimates (Fig. 2b): apparent survival probability (*Φ*); which is the probability that the cod has not died or emigrated from the study population, and recapture probability (*p*) (Cooch & White 2011).

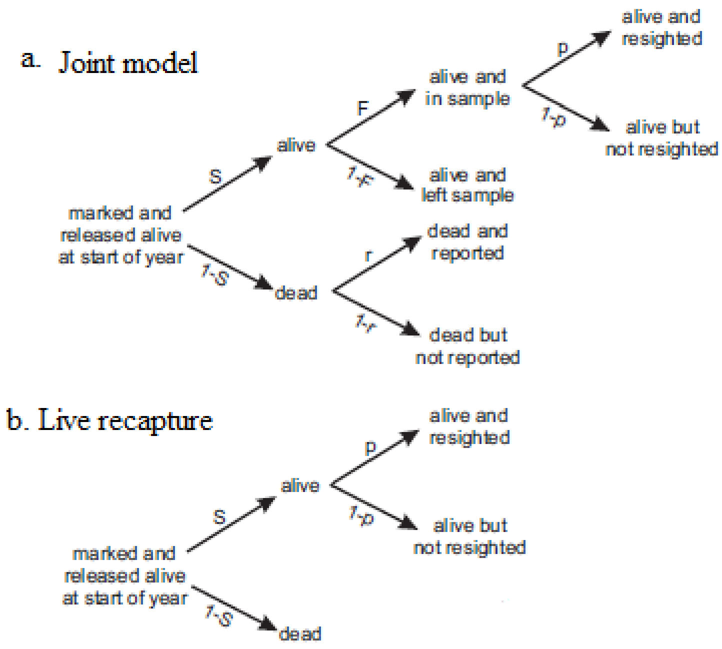

Figure 2: Simplified how the joint model and live-recapture model is estimated. Figure is from MARK book.

In the program MARK we made two datasets (Appendix table 1 and 2) for the analysis; one for the live- recaptured model and one for the joint model. The dataset were labelled with coded 1 if the cod where tagged/recaptured/ recovered or 0 for not tagged/recaptured/ recovered, one for each year in the live- recaptured model and two per year in the joint model. We modelled the data with the four study areas as separate groups in order to test if the areas have specific survival probabilities. In the cases where the cod were tagged with small tags (0 NOK reward) or it high reward tags 500 NOK (only in the joint model) or the cod died during the tagging, they were censored from the analyses. Specifically, a -1 code is used to censor the data, so the survival history after last encounter did not affect the survival estimate (Cooch & White 2011). Also, in the live recapture model, all fish reported as captured by fishers were censored after time of recovery.

Model selection

The global model in the recapture analysis revealed problems of parameter identifiability (low precision on the estimates). Preliminary analyses indicated that Arendal/ Grimstad with Lillesand had similar parameter estimates, and therefore we simplified the model by combining Arendal/ Grimstad with Lillesand to one group resulting in three groups (3g) instead of four groups. We test different models combination by changing the number of parameters in each of estimates, going left to right (see Table 3 and 4 below in the result). Number of parameters can be reduced by removing 3g, or by changing the time parameters (time dependent, constant additive effect over time or time is constant). Selection of the best model from a series of models was based on the lowest corrected Akaike Information Criterion (AICc) and likelihood corrected form of the AICc (AICc weight or normalized Akaike weights)(Burnham et al. 1995; Andersen et al. 1998). The main idea with AICc is that the more parameters included the better the fit, but the precision will decrease because you get more uncertain or variance estimates (Burnham et al. 1995, Burnham & Anderson 2002). Support is given in AICc weight which is support (scale is 0 to 1) for one given model against others model that are tested (Cooch and White 2011).

Goodness of fit

We evaluated the goodness of fit (GoF) of the full parameter global model (area and time dependent survival and recapture probabilities) from recapture analysis as recommended by Lebreton *et al*. (1992), using RELEASE GoF TEST2 and TEST 3 available in MARK . The original set were tested with RELEASE GoF TEST 2 (the catchability test) and TEST 3 (the survival test) which test that all tagged individuals have the same probability of being captured and surviving between years (White and Burnham 1999).We used RELEASE GoF TESTs on the global model live-recapture model (area * time dependent). RELEASE GoF TESTs read the censored code (-1) as normal code (1), which means the program did not stop at the last encounter, but read the entire code. This may have affected the goodness of fit test estimates, so we repeated the analysis with a reduced data set where all -1 where removed.

Results

During 2005-2010, a total of 9713 cod were tagged and released (mean size and range of sizes). A total of 1214 (12.5 % of marked cod) were seen again and re-released at least once during the research fishery. By the end of 2010 a total of 1328 (13.7%) cod were reported as harvested by recreational fishers while a total of 549 (5.7%) cod were reported harvested by commercial fishers (for details, see Table 2). Approximately a third of the marked fish were recaptured in total.

Table 2: Atlantic cod tagged in the three regions of Skagerrak during 2005-2010.

Year	Region	Tagged	Live recapture (only been recaptured)	Recoveries recreational fishermen	Recoveries commercial fishermen	Length mean (mm)	Length range (mm)
2005	Arendal/ Grimstad	500	39(18)	103	43	383,1	165-905
	MPA¤	414	79(46)	125	16	379,9	195-730
	Risør/Tvedestrand	737	150 (120)	119	22	407,8	255-930
	Lillesand	318	41(23)	56	33	422,9	250- 860
2006	Arendal/ Grimstad	625	71(55)	95	74	412,8	190-760
	MPA¤	210	51(34)	42	11	381,4	175-720
	Risør/Tvedestrand	820	179(140)	85	21	350,1	175-810
	Lillesand	422	71(36)	74	50	443,6	155-830
2007	Arendal/ Grimstad	535	78(44)	69	70	410,6	210-880
	MPA¤	309	99(72)	69	9	414,0	200-725
	Risør/Tvedestrand	871	162(137)	106	12	409,0	250-800
	Lillesand	458	86(62)	82	5	459,6	250-750
2008	Arendal/ Grimstad	297	17(14)	44	47	417,7	185-810
	MPA¤	186	38(28)	41	7	457,8	195-776
	Risør/Tvedestrand	1150	151(135)	85	10	380,6	175-700
	Lillesand	336	39(32)	42	44	452,3	160-730
2009	Arendal/ Grimstad	194	18(13)	21	12	423,4	240-720
	MPA¤	159	29(24)	13	5	449,2	230-845
	Risør/Tvedestrand	194	16(13)	15	0	451,3	295-650
	Lillesand	72	3(2)	3	4	423,4	255-790
2010	Arendal/ Grimstad	359	5(5)	11	6	334,9	290-710
	MPA¤	190	14(11)	15	0	395,5	205-870
	Risør/Tvedestrand	263	10(10)	11	0	374,6	205-735
	Lillesand	96	1(1)	8	0	363,1	165-675
Total	Arendal/ Grimstad	2510	228(149)	343 (446*)	253(343*)	397,6	175-880
	MPA¤	1468	300(215)	295(317*)	48 (71*)	406,7	165-905
	Risør/Tvedestrand	4033	447(215)	421 (566*)	65 (90*)	387,0	175-930
	Lillesand	1702	239(155)	269 (338*)	190 (190*)	440,9	165-830

¤ MPA - marine protected area.

* The total number from commercial and recreational fishers with a low/high reward model correction.

Human predation

The tag recovery rate varied among areas from 50% to almost 100% for the recreational and commercial fisheries (Fig. 3). Total recreational and commercial fishers tag recovery rate was more similar at 72.4 % and 73.8%, respectively.

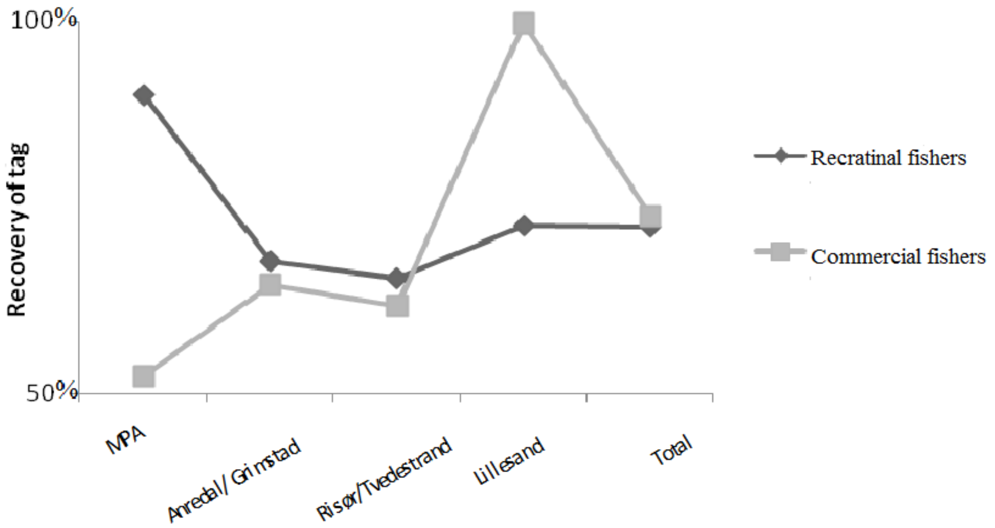

Figure 3: The tag recovery rate (%) from commercial and recreational fishers calculated using the high reward model.

Adjusted for a 72.4% and 73.8% tag recovery rate for recreational and commercial fishers, I estimate that the recreational fishers captured 2289 of the tagged cod, corresponding to 71 % of all recoveries, while commercial fishers captured 954 fish, corresponding to 29 % of all recoveries. The recreational fishers caught more cod in all areas (Fig. 4). In particular, the commercial fishers only captured a small percentage of the cod inside the protected area (Fig. 5). The same can be seen from the captured from year to year bases in the MPA. Commercial fishers captured more cod in Arendal/ Grimstad 2007 and 2008 and Lillesand 2007 and 2010. The Risør/ Tvedestrand area had totally lower capture from commercial fishers than the Arendal/ Grimstad and the Lillesand areas, but have experienced an increased activity throughout our study period.

In about 75% to about 100% of the cases cod where caught inside the study regions (Fig. 5) and only a few (0-46 cod individuals) recovered tags were recovered outside these regions. A small percent were captured in the transition area, which is cod that were tag in the MPA and 1 km from MPA border or cod that were tag within 1 km from the MPA border and then capture inside MPA.

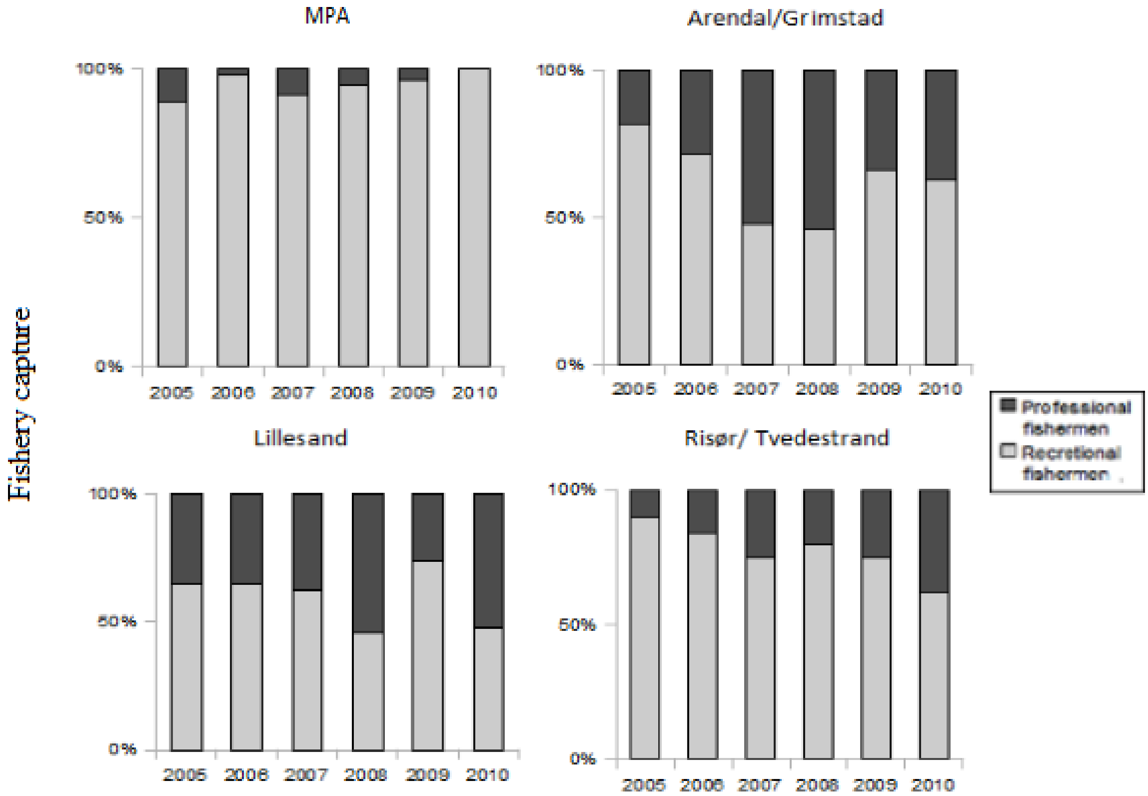

Figure 4: Cod recoveries by commercial and recreational fishers (adjusted for tag reporting rate), as percentages of total number of recoveries in four areas of the Norwegian Skagerrak coast during 2005-2010

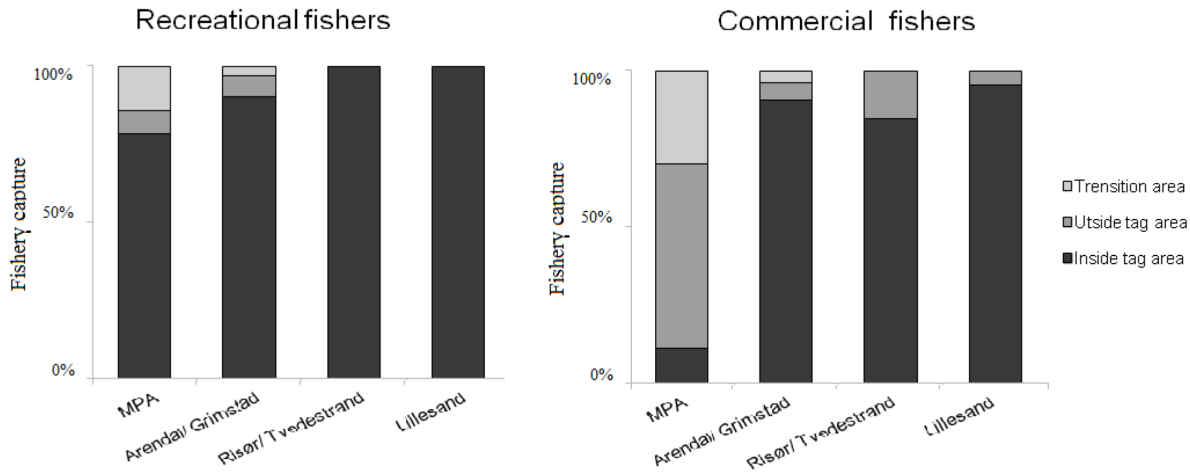

Figure 5: Percentage of Atlantic cod recaptured inside versus outside the tagging and release area. A transition zone is defined where the Atlantic cod had travelled only a short distance (about a 1 km) between areas.

Fishery and type of gear

Most of the fishing pressure is by local fishers, both recreational (49 %) and commercial (28%) (Fig. 6). Non- local fishers (Post-box outside Aust-Agder County) returned 20% of the recovered tags. Only about 2 % of the recoveries were form outside the Aust-Agder County.

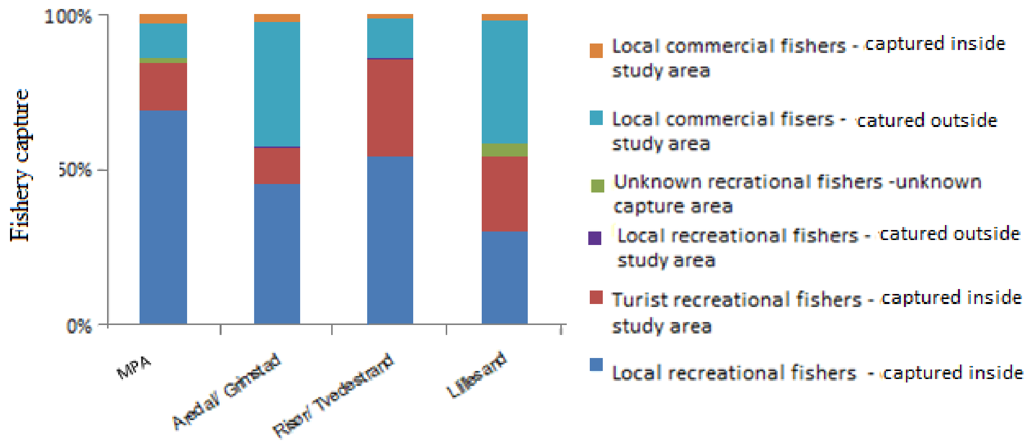

Figure 6: The percentage of captures by fisher group and region, also separating captures within the main study area (Aust-Agder County) from captures outside the main study area.

Recreational and commercial fishers reported using a variety of fishing gear (Fig. 7). Recoveries from commercial fishers were mainly by fyke nets and gillnets, while recoveries from recreational fishers were mainly by handline and gillnet (Fig. 7).

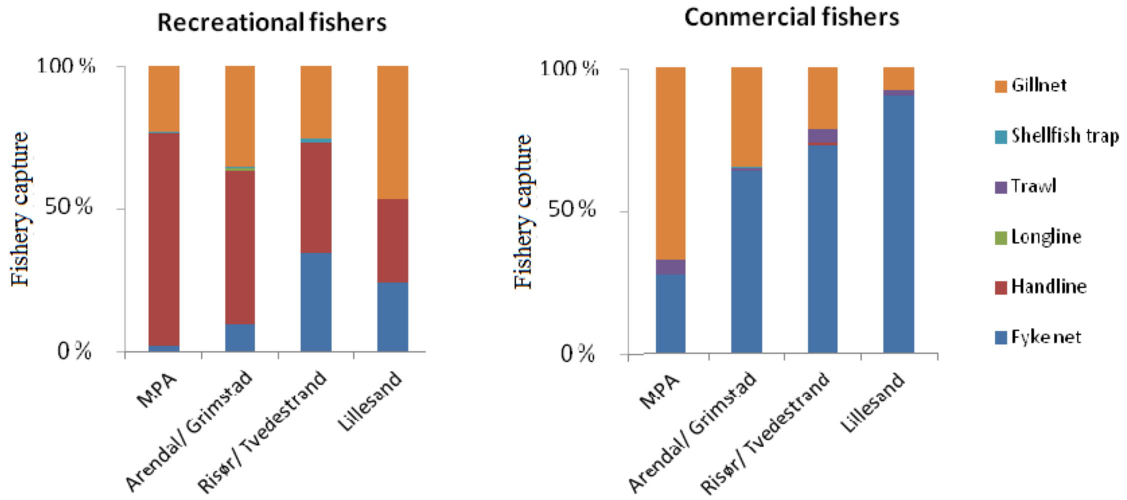

Figure 7: Type of the gear used to capture Atlantic cod in the study area by recreational and commercial fishers.

Size structure

The mean length of tagged Atlantic cod in the MPA was slightly smaller than outside the Arendal/ Grimstad region at the beginning of the study (Fig. 8), while from 2007 onwards was larger. In 2010 the mean length in the MPA was clearly higher than in the other areas.

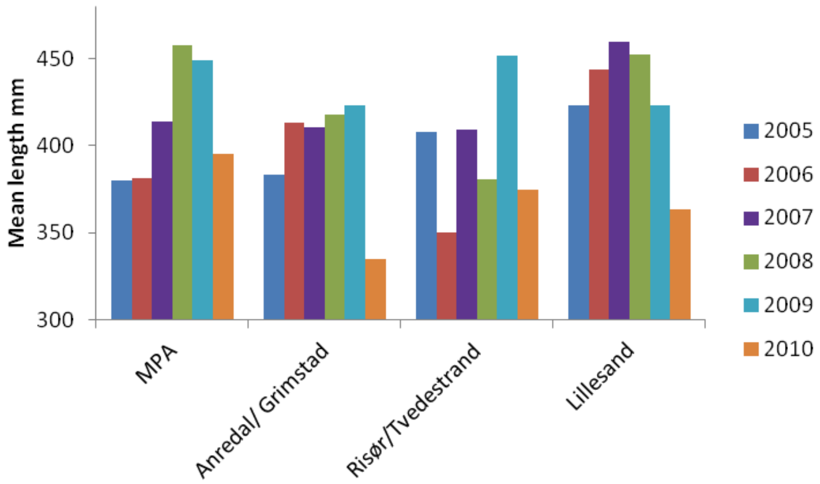

Figure 8: Mean length of the tagged Atlantic cod in the different area at different year.

Goodness of Fit

RELEASE GoF TEST 2 and TEST 3 tested for heterogeneity in catchability and survival, found the total value of both the original (p = 0.5151) and reduced data sets (p = 0.5341) varies little in the p-level (Table 3), which reveals that both the original. Both Lillesand and Risør/Tvedestrand had lower chi-square in the reduced data set than in the original. The both chi-square and degrees of freedom (dF) were higher in the original data set, while p-level was higher in the reduced data set then in the original. In both data set c-hat are <1 (Chi-square / dF), so there were no need to adjust for lack of fit.

Goodness of Fit Results (TEST 2 + TEST 3)

Data set	Area	Chi-square	dF	p-level
Original	MPA	5.9648	10	0.8182
	Arendal/ Grimstad	3.1921	10	0.9765
	Lillesand	14.5949	10	0.1475
	Risør/ Tvedestrand	16.2451	11	0.1323
	Total	39.9969	41	0.5151
Reduce	MPA	8.5966	10	0.5708
	Arendal/ Grimstad	1.9798	5	0.8519
	Lillesand	9.1491	8	0.3299
	Risør/ Tvedestrand	11.9279	10	0.2899
	Total	31.6533	33	0.5341

Model selection

The most parsimonious model live-recapture chosen based on the AICc and support (AICc weight) (Lebreton et al. 1992; Burnham & Anderson 2002), where the model that had time- and group-dependent survival- and recapture probabilities (Table 4).The most parsimonious model for the joint model was a time- and group-dependent on survival-, recapture- and recovery probabilities, and group-dependent fidelity with constant time (Table 5).

Table 4: Model selection for the Recapture model. Model parameter is survival(S) and catchability (p). Support is the AICc weights (w_i). 3g: Arendal/ Grimstad and Lillesand lumped in same group, while the MPA and Risør/ Tvedestrand was treated as separate group. Time: indicates time dependent models. The best model is in fat letters.

Model structures	AICc	No. Par	Deviance	Support
Global Model				
Φ(area*time),p(area*time)	8270.32	36	1057.53	0.1750
Φ(3g *time),p(3g* time)	**8267.92**	**28**	**1071.25**	**0.5834**
Modelling Recapture probabilities				
Φ(3g *time),p(3g+ time)	8273.06	21	1090.49	0.0762
Φ(3g *time),p(time)	8306.85	19	1128.3	0.0000
Φ(3g *time),p(3g)	8279.45	18	1102.91	0.0762
Φ(3g *time),p	8305.19	16	112.66	0.0000
Modelling Survival probabilities				
Φ(3g+ time),p(3g+ time)	8271.3	21	1088.73	0.0860
Φ(time),p(3g+ time)	8280.15	19	1101.60	0.0013
Φ(3g),p(3g+ time)	8271.74	18	1095.23	0.0860
Φ,p(3g+ time)	8281.38	16	1108.85	0.0007

Table 5: Model selection for Joint model. Model parameter is survival(S), catchability (p), recovery probability (r) and Fidelity (F). Support is the AICc Weights (w_i). 3g: Arendal/ Grimstad and Lillesand lumped in same group, while the MPA and Risør/ Tvedestrand were treated as separate group. Time: indicates time dependent models. The best model is in fat letters.

Model structures	AICc	No. Par	Deviance	Support
Global Model				
S(3g *time),p(3g* time), r(3g *time), F(3g* time)	14047.82	58	331.74	0.013
Modelling Fidelity probabilities				
S(3g *time),p(3g* time), r(3g *time), F(3g+ time)	14046.93	53	340.98	0.048
S(3g *time),p(3g* time), r(3g*time),F(time)	14046.35	51	344.46	0.101
***S*(3g *time),p(3g* time), r(3g *time),F(3g)**	**14043.1**	**50**	**343.23**	**0.514**
S(3g *time),p(3g), r(3g *time),F	14044.63	48	348.81	0.239
Modelling Recoveries probabilities				
S(3g *time),p(3g* time), r(3g +time), F(3g*time)	14050.45	43	364.74	0.013
S(3g *time),p(3g* time), r(time), F(3g* time)	14065.45	41	385.77	0.000
S(3g *time),p(3g* time), r(3g),F(3g* time)	1451.66	39	374.03	0.007
S(3g *time),p(3g* time), r, F(3g* time)	14074.35	37	400.75	0.000
Modelling Recapture probabilities				
S(3g *time),p(3g+ time), r(3g *time), F(3g)	14065.75	43	380.03	0.000
S(3g *time),p(time),r(3g *time), F(3g)	14277.28	41	395.75	0.000
S(3g *time),p(3g),r(3g *time), F(3g)	14097.28	39	419.64	0.000
S(3g *time),p, r(3g *time), F(3g)	14092.19	38	416.57	0.000
Modelling Survival probabilities				
S(3g+ time),p(3g+ time) r(3g *time), F(3g)	14072.82	43	387.11	0.000
S(time),p(3g+ time) r(3g *time), F(3g)	14086.77	41	405.1	0.000
S(3g),p(3g+ time) r(3g *time), F(3g)	14060.29	39	382.65	0.001
S,p(3g+ time) r(3g *time), F(3g)	14095.5	37	421.9	0.000

Survival estimates

A general observation of the live recapture model and the joint model was a higher estimated survival for the MPAs than in the immediate vicinity (Arendal/ Grimstad) from 2007 (Fig. 9a and 9b). The survival estimate for 2009- 2010 in both models did not converge (range of from 0 to 1), which probably is due to sparse data from that period. The recapture probability shows that higher changes for being recaptured in MPA the 3 first years (Fig. 9c), while in 2008- 2009 the recapture probability was about the same in MPA and Risør/ Tvedestrand. Both fidelity parameters on MPA and Arendal/Grimstad and Lillesand <0.50, while Risør/ Tvedestrand where a lot higher with <0.70 (Fig. 9d).

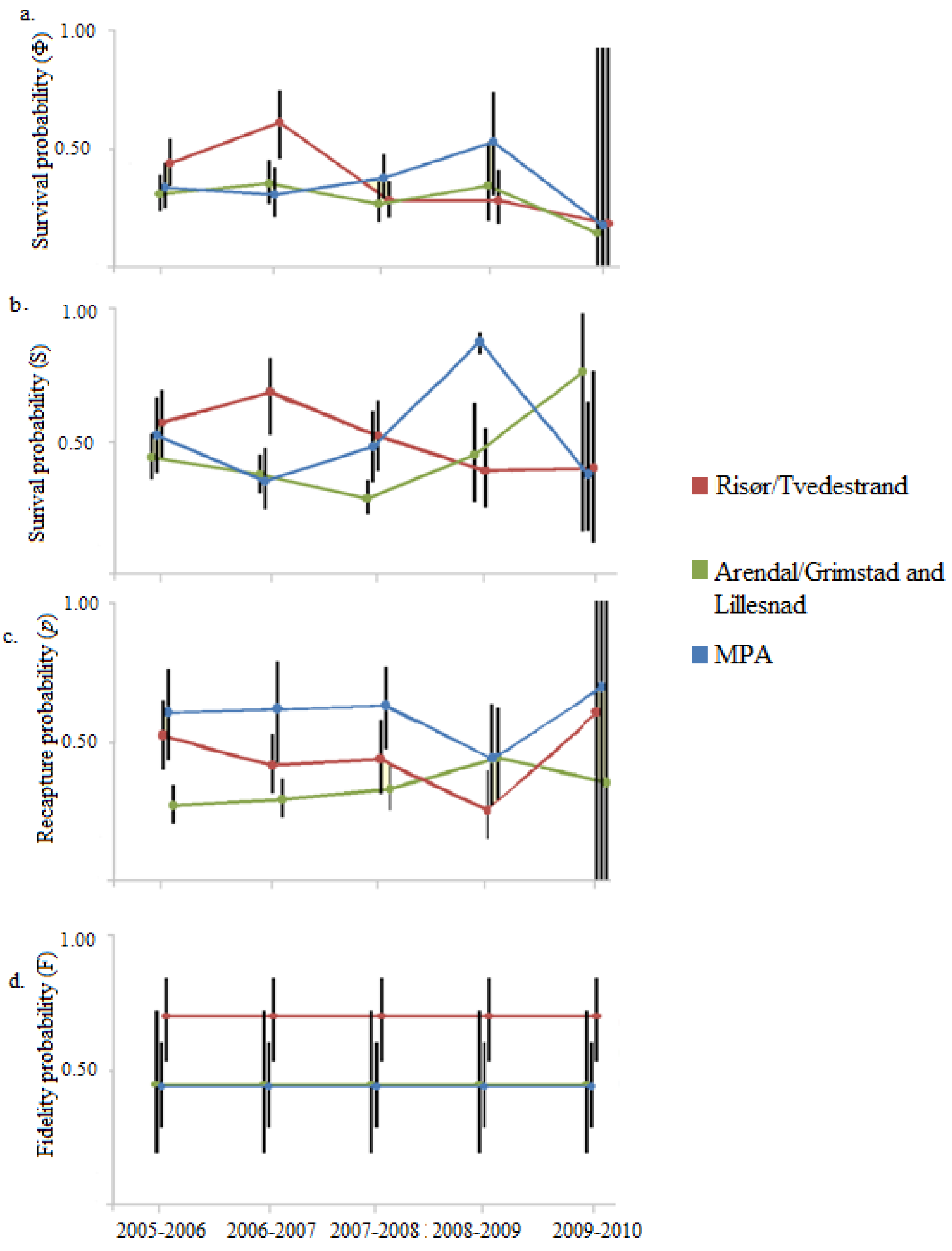

Figure 9: Survival estimates from Recapture model (apparent survival Φ), Joint model (True survival probabilities (S), Recapture probability (*p*) and fidelity (F) for Atlantic cod in the three groups with the range on each estimate.

Discussion

Differences in survival

Survival analyses revealed different trends in survival for all the study areas. In the Risør/ Tvedestrand area survival was high the first two years and then started to decrease, while in the MPA survival was low the first two years and there after started to increase. Olsen et al (2004) found that the survival probability of cod went from 0.8 to <0.3 during the stock collapse at Newfoundland. This last estimate is comparable to many of the area- and year-specific survival estimates from our live recapture model, indicating that the mortality of Skagerrak coastal cod is indeed high. The mortality at Sømskilen in Skagerrak was about the same as before the collapse in Newfoundland (Olsen and Moland 2011). Our survival estimates from the joint model (Fig. 9b) is somewhat higher, indicating that apparent survival (Fig. 9a) is an underestimate of true survival. Importantly, the emigration rate is separated from survival in the joint model (fidelity estimates), which may explain the higher survival (Bjorndal et al. 2003; Cooch & White 2011). In Søndeledfjorden at Risør the apparent survival (Φ) were 0.74-0.97 (Julliard et al. 2001), which is higher then what we got for Risør/ Tvedestrand. The bigger fjords like Søndeledfjorden might be one explanation why we had higher survival at Risør/ Tvedestrand in 2005-2007, because of better food sources or/and less predation (human or/and natural predation). However the two first survival estimates may be a part of a natural cycle that we observe. The last estimates (2009-2010) in both survival models (9a and 9b) had a high range, which does not tell anything. This can be explained by the recapture probability that year that also had high range (from 0 to 1), which suggest we had too little data that period. The higher recapture probability (Fig. 9c) in the MPA is probably because of a high effort in tagging.

Both the live recapture model and the joint model suggested that survival increased in the MPA following protection (Fig. 9a and 9b). Also, the mean length of the tagged fish was higher inside the MPA as compared to outside the MPA (Fig. 8), indicating that fish are surviving and reaching an older age (and bigger size). This suggests that MPA protect older fish from longevity overfishing.

Human predation on Skagerrak coastal cod

Recreational and commercial fishers accounted totally for 71% and 29 % of the 3243 estimated captured cod, which a counts for about 24% of the tags cod (Table 2). The most common fishing gear for recreational fishers was handline. Probably because recreational fishing is a leisure activity the main goal is not to feeding the family or making money. It is common for recreational fishers to operate from small boats. This may explain why gillnets and fyke nets are popular fishing tools. Local recreational fisher was the group that capture most of the cod at coast of Aust-Agder, but tourists also contribute significantly, accounting for a 20 % of the human predation (Fig. 6). The southern Norwegian coastline is a popular fishing area for recreational purposes in summer (Julliard et al. 2001). Our definition of local recreational fisher is that the fisher lives in Aust-Agder. We probably should have included some areas right over the border, as this did not require a long travel distances to the fishing areas studied here. This may have reduced our estimate of local fisher and increased the estimate of tourists fishers.

Commercial fishers accounted only for 29% of the captures (Table 2) which is lower than expected. During the study period the commercial fisheries had a minimal allowed size for capture cod (400mm), which may have had a negative impact on the recovery rate. Another likely reason can be that Atlantic cod is not the target species but more a by-catches for the commercial fishery in this area, which were focused on eel (*Anguilla anguilla*) and wrasses (*Labridae*). The commercial fishery after cod may have been affected negatively by the ban of eel fishery after 1 July 2009, since the eel fishery came under more strict regulations and only a few fishers obtained eel fishery license (from Institute of Marine Research in Norway) throughout 2010. The fyke net was most used fishing gear by commercial fishers, and suggested that small fishing vessels make out the main type used. Inside the MPA commercial fishers did not disappeared completely after the establishment and in 2008 and 2009 (Fig. 4) there was some fishing activity with gillnets. The fishing activity in the MPA was at the border and it may be that the position given by fishers is not accurate or that the fishing was in illegal area. However, it seems less as the fishers reported their catches.

The use of tagging

Tag loss may have affected our delivery and survival results negatively (Pollock et al. 2004). We tagged the Atlantic cod at the base of the first dorsal fin which is the place where 3.58 % of the Atlantic cod were retagged upon recaptured. We expected that a total tag loss of 3.58 % for all the tagged cod seems as a high estimate, and suggest that the fyke net make the tags fall of. In 17.9 % of the retagged cases the original tag was found inside the fyke net.

The recovery of the tags from fishers is an important source of error which we tried to correct for by applying a high reward-low reward model from Pollock et al. (2001). In that model we correct the delivery for low reward tag (50 NOK), which is more likely the true human predation in the study area. We assumed that the 500 NOK reward was high enough that it in most or all cases catches are reported, and high enough that no major errors stems from assume 100% recovery rate. We believed that this reward was not high enough that fishers “hunted” to getting high reward tags. However, if some of the high reward tags were not recovered our correction may not accurate and our resulting estimates for recovery (Fig. 3) are likely underestimated. Julliard et al. (2001) found tag delivery was 50-60% from Søndeledfjorden in the Risør area, which is similar to what we found for Risør/ Tvedestrand area (Fig. 3). Olsen & Moland (2011) conducted a study with acoustic tags in a Sømskilen (small area between Arendal and Grimstad) in Skagerrak (a area inside our study area) and found that 50 % of the tagged cod where taken by fishery within a year after tagging. Their study contained relatively few tagged cod (60 individuals) in a small area, and only covered one year. Thus it may not be directly comparable with, the present study. For instance we do not know the fish density or if fishing effort was high in Olsen & Moland (2011) study period. We find it unlikely that 50% of the cod were capture within the first year for our entire study area, but find it possible that this may apply, to parts of the area that have higher fishing pressure.

The correctness of recoveries reported is another potential source of error, and in our case the most common problem with reports of captured cod was lacking information on time, location, gear used, and where the fishers are from. In 37% and 22% of the cases information on fishing gear was lacking for recreational and professional fishermen, respectively. Thus, the present study (Fig. 7) is hampered by a potential for error regarding the use of different fishing gear.

Conclusion

Both survival analyses showed that a year after the establishment the survival of cod was higher in the MPA than outside in Arendal/ Grimstad and Lillesand. We also had a higher mean length in the MPA on year after the establishment then right outside in Arendal/ Grimstad. After establishment of the MPA human predation was 10-12% of tagged Atlantic cod, which means the human predation is lower than the natural predation (25%) observed by Olsen and Moland (2011) at Sømskilen in Skagerrak. Silvert and Moustakas (2011) found indication that several small reserves (with the same total area as a big one) had less declines in fish landings and had grater recovery speed than one large reserve. My and Silvert and Moustakas (2011) findings may encourage the management in Norway to make additional small reserves. In Norway it may be easier get support for several small reserves than a few large reserves. Large reserves will probably make more protest in the community that are affected, because they find it unfair if they loose fishing grounds. For this reason, several reserves around the country could be easier to accept.

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Appendix

Appendix table 1: Summery of the data use in Recapture model.

Observed Recaptures for Group 1: MPA

Tag year	Tagged Atlantic cod	Time period and number for recapture						Total recaptured
		Year of fist Recapture	2006	2007	2008	2009	2010	
2005	338		68	9	1	0	1	79
2006	190			35	6	0	1	42
2007	293				69	9	2	80
2008	147					48	6	54
2009	147						21	21

Observed Recaptures for Group 2: Arendal/ Grimstad

Tag year	Tagged Atlantic cod	Time period and number for recapture						Total recaptured
		Year of fist Recapture	2006	2007	2008	2009	2010	
2005	426		70	10	3	1	0	84
2006	535			69	15	4	1	89
2007	483				59	5	1	65
2008	230					25	3	28
2009	183						18	18

Observed Recaptures for Group 3: Lillesand

Tag year	Tagged Atlantic cod	Time period and number for recapture						Total recaptured
		Year of fist Recapture	2006	2007	2008	2009	2010	
2005	263		39	3	0	2	0	44
2006	339			53	4	1	0	47
2007	378				43	3	1	47
2008	273					14	10	24
2009	70						4	4

Observed Recaptures for Group 4: Risør/ Tvedestrand

Tag year	Tagged Atlantic cod	Time period and number for recapture						Total recaptured
		Year of fist Recapture	2006	2007	2008	2009	2010	
2005	662		73	34	11	5	0	123
2006	808			134	30	9	1	174
2007	893				81	19	3	103
2008	1152					131	12	143
2009	290						18	18

Appendix table 2: Summery of the data use in Joint model.

Live Encounters

Observed Recaptures for Group 1: Reserve

Tag year	Tagged Atlantic cod	Time period and number for recapture						Total recaptured
		Year of fist Recapture	2006	2007	2008	2009	2010	
2005	371		15	4	0	0	0	19
2006	190			20	2	0	0	22
2007	274				40	3	1	44
2008	191					17	2	19
2009	147						9	9

Observed Recaptures for Group 2: Arendal/ Grimstad

Tag year	Tagged Atlantic cod	Time period and number for recapture						Total recaptured
		Year of fist Recapture	2006	2007	2008	2009	2010	
2005	450		15	2	0	0	0	15
2006	535			15	1	0	0	16
2007	466				6	3	1	6
2008	241					5	10	5
2009	162						2	2

Observed Recaptures for Group 3: Lillesand

Tag year	Tagged Atlantic cod	Time period and number for recapture						Total recaptured
		Year of fist Recapture	2006	2007	2008	2009	2010	
2005	286		11	2	0	1	0	14
2006	387			21	1	0	0	21
2007	392				10	0	0	10
2008	278					4	2	6
2009	64						0	0

Observed Recaptures for Group 4: Risør/ Tvedestrand

Tag year	Tagged Atlantic cod	Time period and number for recapture						Total recaptured
		Year of fist Recapture	2006	2007	2008	2009	2010	
2005	662		29	19	4	4	0	56
2006	737			90	14	7	0	111
2007	792				31	11	2	45
2008	892					75	5	77
2009	245						9	9

Dead Encounters

Observed Recaptures for Group 1: MPA

Tag year	Tagged Atlantic cod	Time period and number for recapture							Total recaptured
		Year capture	2005	2006	2007	2008	2009	2010	
2005	352		62	45	5	1	0	1	19
2006	168			30	13	2	0	1	22
2007	230				28	16	6	0	44
2008	172					22	22	3	19
2009	138						4	6	10
2010	161							13	13

Observed Recaptures for Group 2: Arendal/ Grimstad

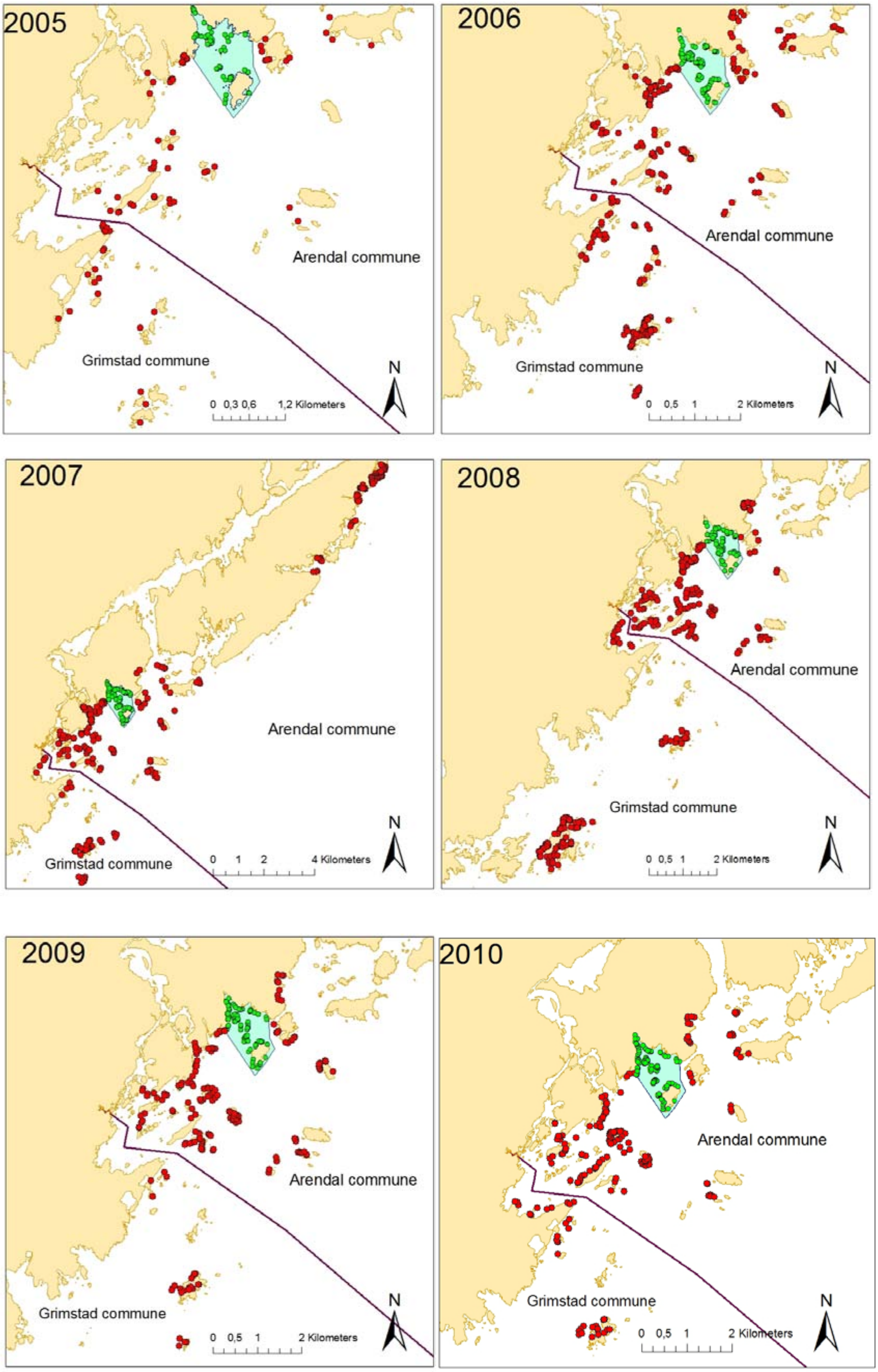
Tag year	Tagged Atlantic cod	Time period and number for recapture							Total recaptured
		Year Recapture	2005	2006	2007	2008	2009	2010	
2005	435		62	45	5	1	0	1	114
2006	519			30	13	2	0	1	46
2007	460				28	16	5	0	49
2008	236					22	22	3	47
2009	160						4	6	10
2010	284							13	13

Observed Recaptures for Group 3: Lillesand

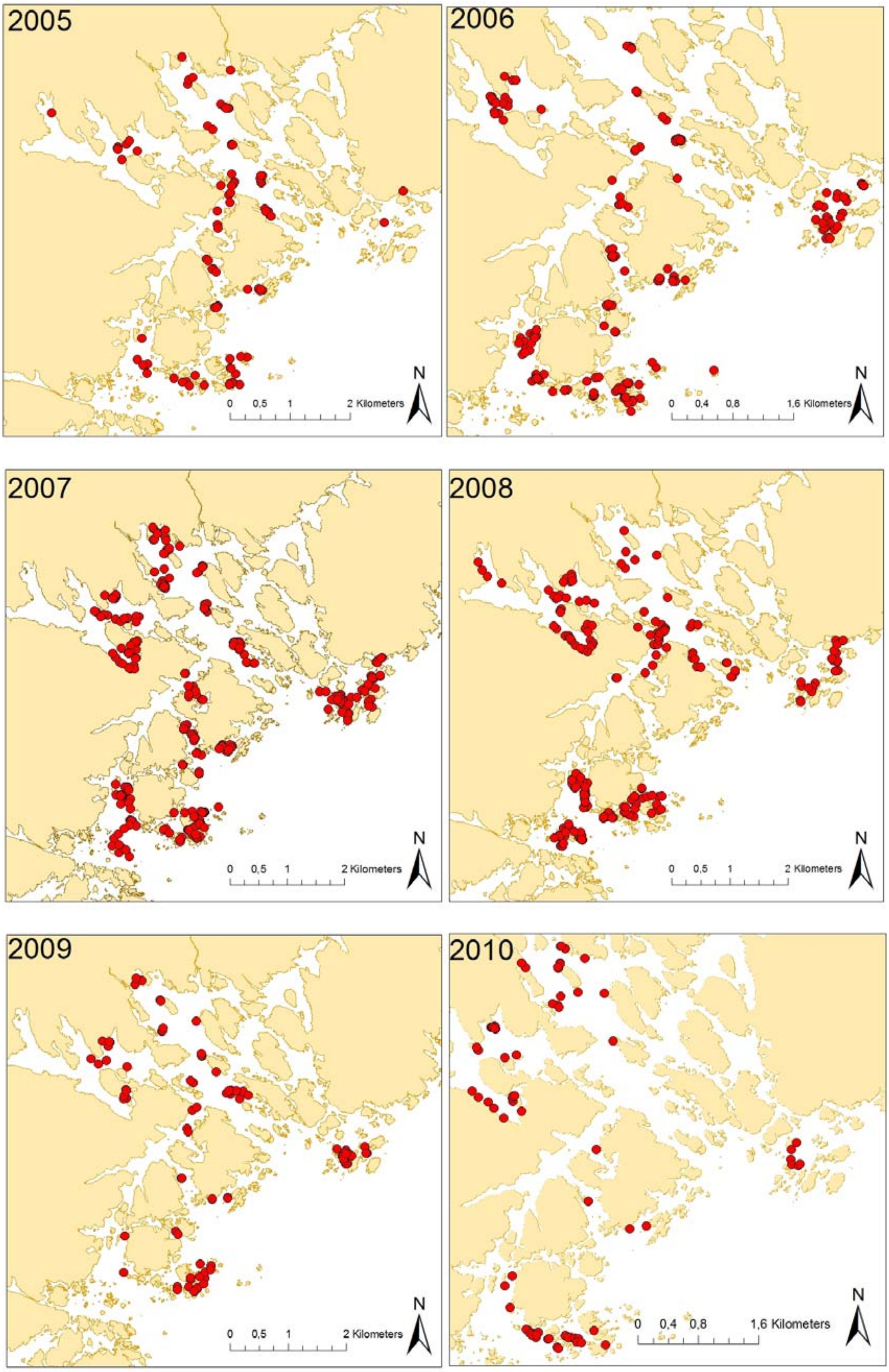
Tag year	Tagged Atlantic cod	Time period and number for recapture							Total recaptured
		Year capture	2005	2006	2007	2008	2009	2010	
2005	272		48	26	7	0	1	0	76
2006	366			85	25	4	1	0	115
2007	382				80	22	3	0	105
2008	272					55	8	4	67
2009	64						3	2	5
2010	81							7	7

Observed Recaptures for Group 4: Risør/ Tvedestrand

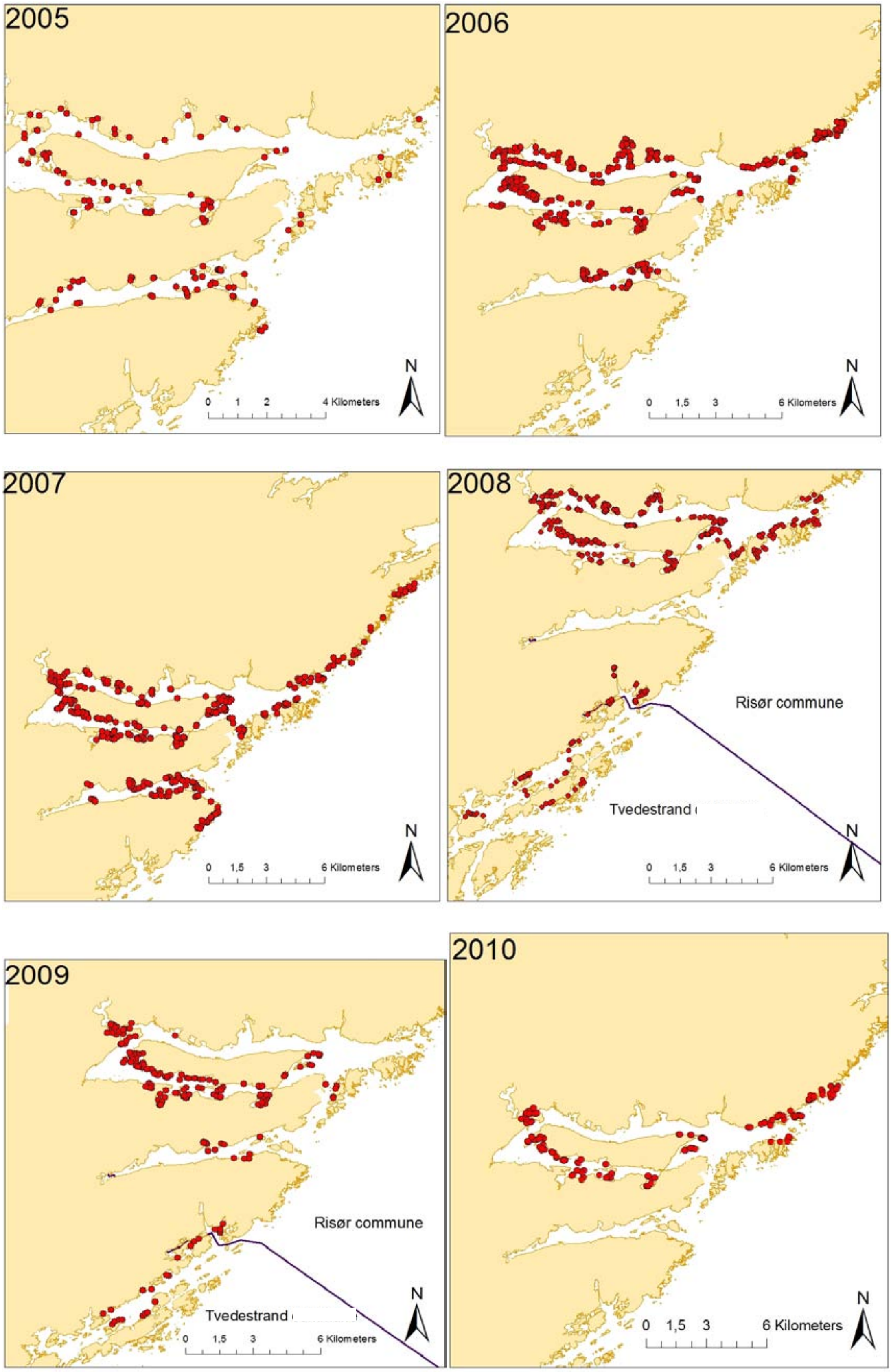
Tag year	Tagged Atlantic cod	Time period and number for recapture							Total recaptured
		Year capture	2005	2006	2007	2008	2009	2010	
2005	662		60	32	12	5	1	0	110
2006	626			37	31	12	2	0	83
2007	745				61	34	3	0	98
2008	815					37	25	3	65
2009	236						5	10	15
2010	216							7	7



Appendix figure 1**:** Trap positions in the annual (2005 – 2010) survey of Atlantic cod conducted inside the Flødevigen MPA (green) and in adjacent areas outside the MPA (red).



Appendix figure 2: Trap positions (red) in the annual (2005 – 2010) survey of Atlantic cod conducted in the Lillesand region, ≈ 30 km southwest of the Flødevigen MPA (see Fig. A1).



Appendix figure 3: Trap positions (red) in the annual (2005 – 2010) survey of Atlantic cod conducted in the Risør region, ≈ 40 km northeast of the Flødevigen MPA (see appendix figure 1).