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Theme session Q
“Use of data storage tags”

Return migrations of Atlantic cod (*Gadus morhua* L.) to the North Sea evidenced by archival tagging of cod off the eastern Skagerrak coast

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Abstract

Here we show that cod (>40 cm) tagged off the Skagerrak coast migrated towards the North Sea, in particular, during the spawning period. Furthermore, onboard and retrospective positioning from retained archival tags by astronomical derivations of time-logged ambient light measurements depicted a migratory route to the eastern North Sea during the spawning season, and back again to the Skagerrak later in spring. The light intensity based geolocations were cross-validated with tidal location methods and experienced temperature of the tagged fish, supporting the view of a North Sea-bound migration route during the spawning period. These findings gives a strong behavioural signal with bearings on population separation and divergence in marine fish species.

Keywords: Skagerrak, North Sea, cod, light geolocation, TLM.

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Introduction

Issues on stock separation and population structure have been at the centre of fishery biology for at least a century, still without being satisfactorily resolved. Studies on marine population structures may still give rise to very contradicting interpretations, which are at least partially due to undeclared differences in perceptions and views. Differences in views on the origin of observed population structures are mostly related to the degree of connectivity between population units, the persistence of these units over time, and thereby to unequivocally diverting opinions on population structuring mechanisms in marine temperate fish species like Atlantic cod (*Gadus morhua* L.; c.f. Pawson and Jennings 1996). Conventional taggings as well as behavioural studies using archival tags have revealed structuring elements that coincide with genetically distinguished subunits, or more precisely, support population structures also elicited in genetic studies, but are also ample enough to distinguish between population units at an even finer spatial scale (e.g. Neat et al. 2005).

However, the importance of these findings cannot be assessed unless the underlying behavioural mechanisms that ultimately govern distribution, dispersal and the integrity of subunits are better understood. In other words, the true nature of the connection between putative stock units/subpopulations is the crucial point for our perception population structure and, as a consequence, of the spatial and temporal dynamics exhibited in fish stocks. These diverting perceptions are mostly founded on whether fish populations are segregated by environmental forcing (e.g. Nielsen et al. 2005) and density dependencies (e.g. Chen et al. 2005), or by a ‘learning’ process so that fish populations constitute behavioural units rather than end products of a semi-chaotic oceanic environment.

Elaborated methodologies in genetics using micro satellite DNA techniques have indicated existence of genetically divergent subpopulations in northwest Atlantic cod (Ruzzante et al. 1996, 2001), in the North Sea (Hutchingson et al. 2001), along the Skagerrak coast (Knutsen et al. 2003, 2004) as well as in other parts of the cod distribution area (e.g. Jonsdottir et al. 2001). In addition, morphometrics (e.g. otolith chemistry: Campana et al. 2000), location of spawning grounds (c.f. Brander 1994, Lawson and Rose 2000), migratory studies (Robichaud and Rose 2004) and by simple deductions from series of events in abundance of different life stages (Svedäng 2003, Cardinale and Svedäng 2004, Svedäng and Svenson 2006), have given important pieces of information on the occurrence of structuring elements in cod stocks. Considering the cod population structure in the North Sea region, comprising the eastern

English Channel, the central and northern North Sea, the Skagerrak and Kattegat, there are important pieces of population genetic information which contradict the view of one, single population unit as the simplest and least complicated theory (Hutchinson et al. 2001, Knutsen et al. 2003, 2004). However, it should be underlined that the observed level of differentiation is very small.

The very existence of sub-structuring elements indicate that cod populations are at least partially reproductively isolated. In coastal environments, resident cod populations may attain genetic differences over time. Such a population distinction is possible to incorporate into existent views on retention and dispersal of propagules in marine temperate fish species. However, in an “open” sea environment with extensive movements of water masses, dispersal of egg and larvae may well reach areas outside a population’s core distribution area. Genetic isolation can only arise in such a case if natal philopatry is considered to be a part of cod migratory behavioural repertoire, i.e. the offspring make independent decisions on return migration to the natal area. Such evidence does not, however, exist for the moment, and to investigate the possible occurrence natal philopatry, pieces of information must be gathered from various sources and methodologies and evaluated jointly.

Circumstantial evidence for natal philopatry has been shown for cod in the eastern part of the Skagerrak. An almost total eradication of locally spawning cod aggregations along the Swedish Skagerrak coast has created a rarely encountered situation; constantly low abundance of adult cod coinciding with high abundance of juvenile cod in some years (Pihl and Ulmestrand 1993, Svedäng 2003, Svedäng and Svenson 2006). Svedäng (2003) and Cardinale and Svedäng (2004) hypothesised that most juvenile cod at the eastern Skagerrak coast had been passively transported from offshore spawning areas (Munk et al. 1995, 1999), and the following [unexpected] low abundance of adult of cod was due to return migration of juvenile and/or maturing fish when they have reached a certain size or age (Pihl and Ulmestrand 1993). This theory was supported by the fact that strong year classes of juvenile cod along both the Norwegian and Swedish Skagerrak coast have been genetically assigned to eastern North Sea cod populations (Knutsen et al. 2003, 2004). In other words, the disappearance of local spawning aggregations, presumably due to over-fishing, has created unintentionally a natural set-up for analysing homing behaviour and recolonisation processes.

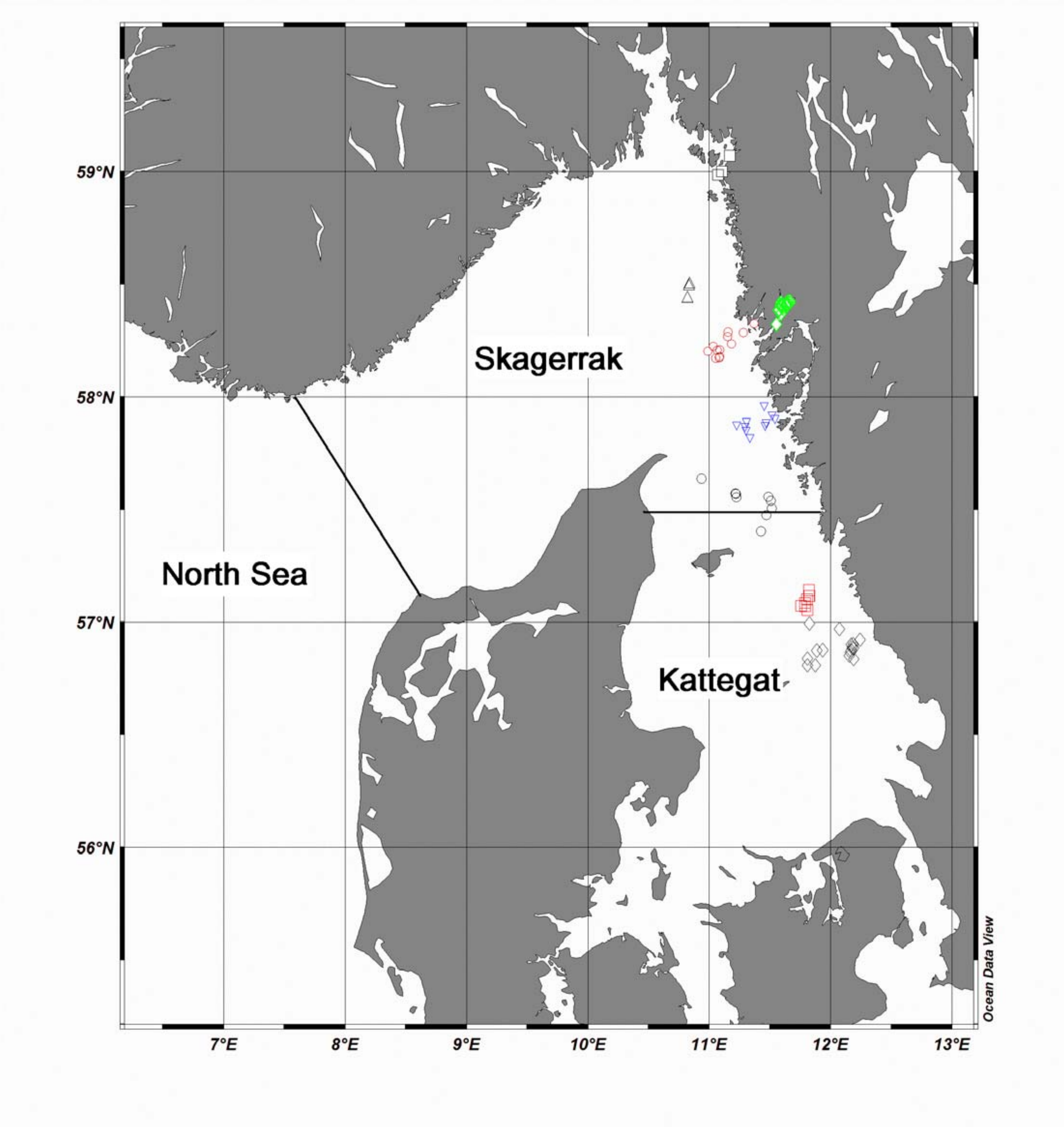


Fig. 1a. Tagging localities along the Swedish west coast 2003-2005. The Skagerrak: Kosterfjord (□); Väderöarna (Δ); off the middle eastern Skagerrak coast (○); off the southeastern Skagerrak coast (▽); southern part of the Skagerrak (○); The Skagerrak coast: the Gullmar Fjord (◊); The Kattegat: Fladen (□); middle part of the Kattegat (◊).

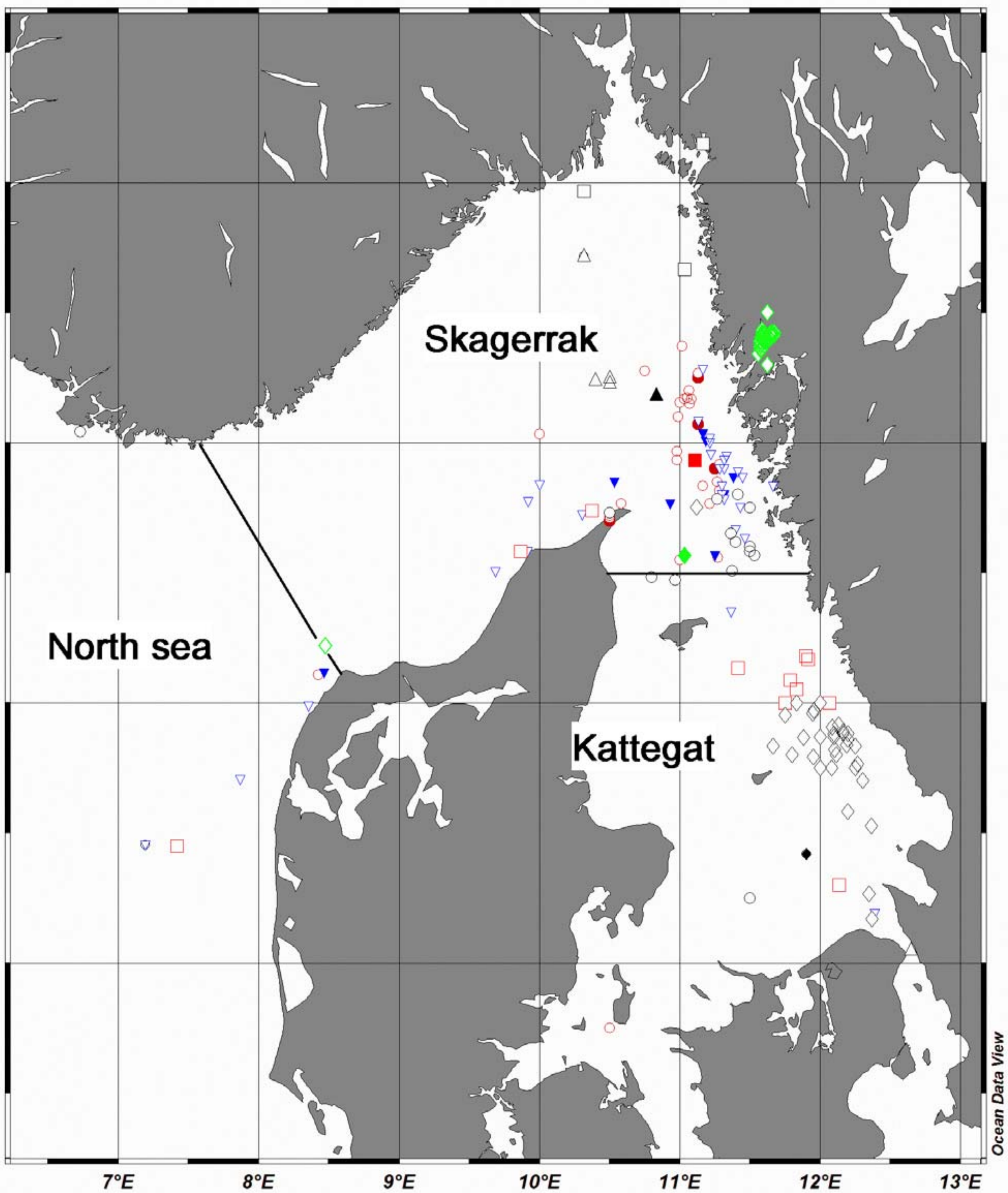


Fig. 1b. Reported positions of retained tagged cod in the Kattegat, Skagerrak and the North Sea. Filled shapes refer to fish geolocated more than 1 degree longitude west of the reported recapture position. See Fig. 1a. for further explanation of the legend.

The inclusion of archival tags as a tool into fishery biology studies represents a new opportunity to reconstruct migratory pathways of individual fish, based on stored records of various environmental signals. In contrast to most conventional tagging studies, which provide valuable however restraint information on release and recapture points, the archival tag technique has given rise to a whole battery of methods to reconstruct the location of an individual fish at sea. This virtual positioning, or geolocation, is made feasible by analysing records on various physical factors, alone or in combination, such as light (which have been used by seamen for centuries), depth (i.e. pressure) and temperature (e.g. Smith and Goodman 1986, Arnold et al. 1994, Musyl et al. 2001, Hunter et al. 2003). Records on changes in ambient light intensity level can be used for astronomical positioning with a global coverage, either by data processing onboard or by retrospective analysis on downloaded data (Musyl et al. 2001 and references therein). More detailed information on individual fish movements might give an opportunity not only to better reconstruct the dispersal of fish, but also to elucidate intrinsic migratory mechanisms.

Archival tags were deployed on cod between 2003 and 2005 along the Swedish west coast, i.e. along the Skagerrak coast, in inshore areas of the Skagerrak, in the Kattegat and the Öresund (Fig. 1a). In total, almost 800 cod have been tagged and about 40% have been reported recaptured. In this study, we have focused on tag results with relevance for elucidating the migratory behaviour of fish tagged along the Swedish Skagerrak coast with inclusion of fish from adjacent areas (i.e. northern part of the Kattegat and from the Gullmarsfjord on the Skagerrak coast) which exhibit similar migratory behavioural patterns as cod tagged in the Skagerrak. The purpose of the study was hence to investigate whether cod found along the Skagerrak coast depart from cod migratory behaviour found elsewhere along the Swedish west coast, as it can be depicted from the hypothesis that (1) they probably originate from natal spawning areas west off the Swedish Skagerrak coast, (2) they may leave their nursery areas in the eastern part of the Skagerrak for return migrations towards the North Sea (Fig. 1b).

Material and methods

Tagging procedures

Cod were tagged on several occasions in 2003-2005 at various locations along the Swedish Skagerrak coast (Table 1). In addition, fish tagged at locations in the northern part of the Kattegat and in the Gullmarsfjord on the Swedish Skagerrak coast were included into the study for comparison reasons. For all deployed fish in the study, the same tagging methodology was applied. The archival tags (Lotek model LTD 2410; www.lotek.com) were attached externally with a stainless steel wire. The wire was led through plastic sheaths incised in the back of the fish just underneath the first dorsal fin base. The fish used for tagging purposes was captured either in cages or in trawling sets of a maximum duration of 30 minutes. The caught fish were visually inspected, and only fish in good health were used in the experiments. Records on length (in cm interval), weight (in grams) and sex (if running) were taken. Release points were noted in longitude and latitude, using the vessel GPS equipment. In those cases when the fish carcass was saved at the recapture, age readings were performed on otoliths. Also, for retained fish that had not been gutted on the fishing vessels, gonadal inspection was conducted. The gonadal status was classified macroscopically according to four-stage scale. Fish in stages 1 and 2 were considered as non-maturing, whereas fish in stages 3 and 4 were considered as maturing or mature.

Table 1. The number of tagged and retained fish, the recapture rate, mean days at liberty at sea and the maximum of days at sea recorded at various localities and tagging occasions.

	Number of tagged fish	Number of retained fish	Return rate (%)	Mean days at sea	Maximum days at sea
Gullmar Fjord					
Feb-April-2004	50	17	34	126	265
May-04	53	19	36	110	362
Oct-04	18	6	33	83	196
Total number	121	42			
Skagerrak					
Nov-03	63	26	42	145	446
Mar-04	28	14	50	76	216
May-04	19	3	16	262	384
Oct-Dec-2004	75	15	20	103	236
Feb-May-2005	85	22	26	184	338
Total number	270	80			
Kattegat					
Dec-03	47	31	66	92	512
Feb-04	53	31	58	43	227
May-04	16	5	31	98	162
Total number tagged	116	67			

Archival tag characteristics and handling

The archival tag used in this study was equipped with real time clock, pressure sensor, external temperature sensor, internal temperature sensor, i.e. inside the capsulation, and a light intensity sensor (measurements band 470 nm ± 50 nm). Each tag had a data storage capacity of 83 000 datapoints. As the data can be collected at various intervals, there are several options how to optimise the use of the limited memory capacity. For example, the memory lasts for 46 days at a recording time interval of 60 s, whereas the memory lasts for 230 days at an recording time interval of 300 s. The tag can also be programmed to telescope the data, i.e. once the memory is exhausted, some data are erased in a specified manner. In this experiment, the deployed tags were programmed to store either at 60 s or 300 s intervals. The data were telescoped and retained data were saved in blocks of a minimum period of two days, and newly collected data overwrote stored data. Storing data at one minute intervals gave in most cases inevitably less days with stored data to be downloaded, but this option was nevertheless chosen for its better resolution, and therefore better opportunity to evaluate light intensity curves for geolocation purposes.

Besides the storage of time series of the four different sensors, the tag also stores day log information on parameter values during the whole deployment such as sunrise and sunset in UTC, estimated longitude and latitude (i.e. onboard processed estimates), maximum external temperature recorded during the day, maximum and minimum depths and various parameter values of SST (somewhat differing between older and newer versions of Lotek LTD 2410).

Data from retained tags were downloaded using the Tagtalk2000 version 1.1.125 software (www.lotek.com). The downloaded data was visualised with the software Viewer 2000 version 2.5.0 (www.lotek.com) . The Viewer programme gives an opportunity to export the data in xls- or csv-format.

Geolocation estimation procedures

Estimation of local noon (or local midnight) gives records on the longitude, whereas estimation of day length gives the latitude, except at times close to the equinox as the day length at these times of the year are almost equal all over the globe (Smith and Goodman 1986). Longitude is estimated by defining dusk and down at civic twilight (zenith equal to 93.44 degrees), respectively, at a particular change in light intensity, and consequently, also in time. The time angle between local noon and GMT gives thus the longitude. Although celestial methods are highly accurate in principle, the precision is impaired due to measurement errors caused, for instance, by variation cloud cover and seawater transparency, and obtained raw geolocations often deviate with hundreds of kilometres from their true positions (Welch and Eveson 1999, Musyl et al. 2001, Teo et al. 2004).

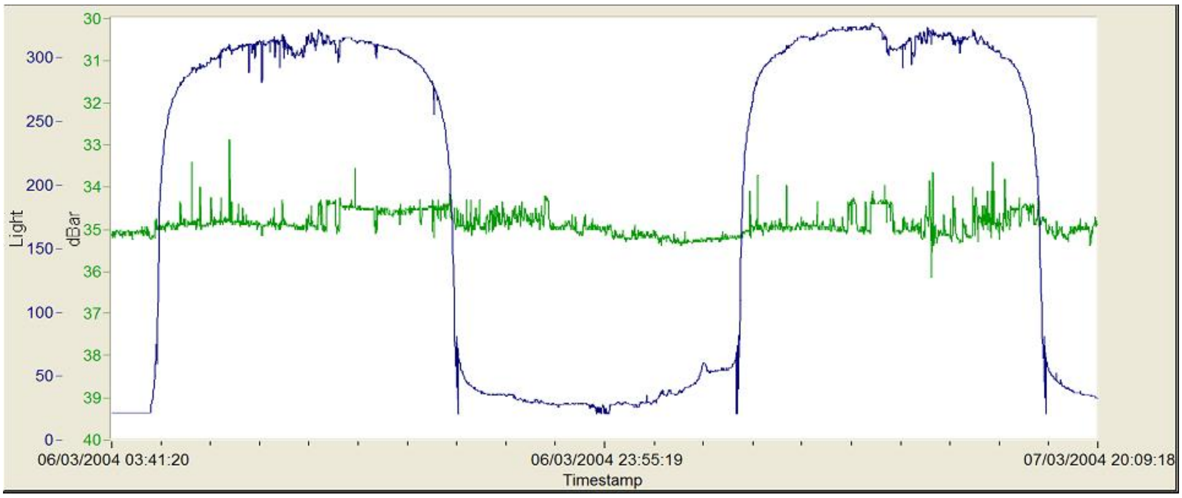


Fig. 2. Recorded relative light intensity (blue line) and pressure (dbar; green line) during two days in March in 2004, extracted from an archival tag attached to cod released in the eastern Skagerrak in November 2003.

However, it should be noticed that longitude estimation is much more precise as well as less prone to systematic deviation than latitude estimation. In case of a storing interval of 60 s, the limitations of the tag memory capacity means that light intensity recordings can be stored at a maximum of 23 two-day blocks with complete time series. These two-day blocks with recordings every minute or five minute interval may thus be retrospectively analysed for geolocation purposes. Retrospective inspection of light intensity curves (Fig. 2) gives the opportunity to judge whether obtained recordings are suitable or not for geolocation purposes. In principle, repeated longitude estimation is possible by applying several horizontal intersections of the light intensity curve, assuming the same elevation of the sun above the horizon at similar relative light intensity levels. As the archival tag stores onboard daily estimates of latitude and longitude (unless some criteria are not fulfilled and estimations of the latitude and/or the longitude are abolished), retrospective inspection gives therefore an opportunity to judge whether the automatic onboard estimates are sensible or based on distorted light records. In principle, this judgement was made by eye, considering whether the light curve was bell shaped or not.

For most retrieved tags, it was not possible to evaluate all automatic onboard geolocation estimates, due to the data storage limitations. Ideally, all onboard estimates of daily positions should be utilised, and application of Kalman filter to the analysis of tracking data was therefore considered as an objective way of sort out geographic signals from the geolocation time series, which are thus distorted to an unknown and varying extent. An extended Kalman filter tracking model has been developed for analysis of archival tagging data (Sibert et al. 2003, Nielsen 2004). In this study, we used the software package KFtrack 0.61 developed for R-statistics (www.r-project.org) for track estimation from day logged positions. However, as many onboard position estimates were calculated on distorted light data, the data sets had to be filtered in order to abolish obviously nonsensical estimates, and to let the model converge. Consequently, all estimates that departed more than ±15 degrees from the longitude 11° E, and ±20 degrees from the latitude 57° N, were excluded from the data sets. Finally, only model results on the longitude were considered as reliable and used as evidence of fish movements.

Tidal Location Model

Tidal ranges (high water to low water, or vice-versa) were extracted using a wave-fitting algorithm. Starting at each successive point in the archival tag pressure record, the algorithm searched for the best fitting sine-wave, applying a least-squares regression, using data from the following 9-h period. The period of the model waveform was constrained so that the half-tidal period could not fall below 4.5 h or exceed 7.5 h. The offset of the model was constrained so that the wave-form began with a maximum (or minimum) and continued beyond a minimum (or maximum). For each day, the best-fitting wave-form was used to calculate the times of high and low water, the tidal range, and an indication of the quality of fit (sum of squares). Estimates of time of high water and tidal range were filtered to obtain the most accurate daily estimate (based on least sum-of squares). These data were then used in the tidal location method (TLM: Hunter et al. 2003) to derive, by day, possible geographic locations where the individual may have been. During the winter and spring, when most of the North Sea is vertically mixed, daily average temperatures recorded by the archival tags were then compared to averaged sea surface temperature (SST; taken from Bundesamt für

Seeschiffahrt und Hydrographie, Hamburg), and positions at which tag temperature and SST differed by more than 1°C were excluded.

Results

Reported recapture positions

Release and recapture positions of fish tagged in the Skagerrak, the Gullmar Fjord on the Skagerrak coast, and in the northern part of the Kattegat are shown in Figure 1a,b. The number of tagged fish, return rates and mean and maximal duration at liberty at sea at various localities and tagging occasions are shown in Table 1. The distribution of reported recaptures clearly indicated a south-westerly direction of movements of the fish from tagging localities in the Skagerrak, in particular, towards the North Sea and the western part of the Skagerrak off the Danish Jutland coast. It could also be noted that some fish tagged in the Gullmar Fjord showed similar movements towards the North Sea as well as fish tagged at Fladen in the northern part of the Kattegat. Some fish tagged in the Skagerrak were also reported from the southern part of the Kattegat. A high degree of residency was, however, indicated for fish tagged in the middle of the Kattegat as well as in the Gullmar Fjord.

Geolocations of fish

Based on retrospective inspections of obtained daily light curves, day logged estimates of the longitude were evaluated. These inspections were then used for characterisation of fish horizontal movements. The tagged fish were consequently classified into the following groupings:

1. Resident in the Skagerrak.
2. Recaptured off the Danish Skagerrak coast or in the North Sea, i.e. west of longitude 10.5° E.
3. Geolocated in the western part of the Skagerrak or in the North Sea (i.e. west of longitude 10.5° E).
4. Released in the Skagerrak and recaptured in the Kattegat.
5. Released in the Kattegat and recaptured in the Skagerrak or the North Sea.
6. Released and recaptured in the Kattegat but geolocated in the Skagerrak or the North Sea.
7. Undefined movements in the deeper part of the Skagerrak (or the North Sea).

The outcome of these characterisations for fish which had been at liberty at sea for more than 30 days are shown in Table 2. For recaptured fish tagged in the Skagerrak, about 48% were either classified as resident or showing undefined movements in the deeper part of the Skagerrak, whereas 20% were recaptured in the western part of the Skagerrak or in the North Sea, and 20% were geolocated to the western part of the Skagerrak or in the North Sea. In other words, 20% of all recaptured cod tagged in the Skagerrak showed return migrations to the eastern part of the Skagerrak after visiting the North Sea or the western part of the Skagerrak. Restricting to those fish that were tagged in late autumn 2003, about 46% of all recaptured fish were either reported from the western part of the Skagerrak or the North Sea, or geolocated to these areas.

Table 2. Characterisation of fish horizontal movements based on retrospective inspections of day logged estimates of the longitude for fish more than 30 days at liberty. The following groupings were used: 1 - Resident in the Skagerrak; 2 - recaptured off the Danish Skagerrak coast or in the North Sea west of longitude 10.5° E; 3 - Geolocated in the western part of the Skagerrak (i.e. west of longitude 10.5° E) or in the North Sea; 4 -Released in the Skagerrak and recaptured in the Kattegat; 5 -Released in the Kattegat and recaptured in the Skagerrak or the North Sea; 6 - Released and recaptured in the Kattegat, but geolocated in the Skagerrak or the North Sea; 7 - Undefined movements in the deeper part of the Skagerrak (or the North Sea).

	Skagerrak				Kattegat		Skagerrak coast	
Classification of migratory behaviour	2003-2005		2003		2003-2004		2003-2005	
	Number of specimen	Proportion of classified (%)	Number of specimen	Proportion of classified (%)	Number of specimen	Proportion of classified (%)	Number of pecimen	Proportion of classified (%)
1	28	40	8	33	61	91	40	95
2	14	20	6	25			1	2.5
3	14	20	5	21			1	2.5
4	3	4	2	8				
5					3	4.5		
6					3	4.5		
7	5	7						
Unclassified	5	7	3	12				

Only two cod tagged in the Gullmar Fjord were actually reported recaptured off the coast: one was recaptured in early spring in the western part of the Skagerrak, whereas the other was reported recaptured in the south-eastern Skagerrak, but also geolocated to the North Sea during in early spring. Some of the fish tagged in the northern part of the Kattegat were either recaptured or geolocated to the Skagerrak or the North Sea.

Kalman filtering results

Stored daily estimations of the longitude and latitude gave the opportunity to conduct Kalman filtering modelling. The model converged for 15 out of 88 data sets (17%). This rather low rate of convergence is explained by the fact that for many data sets, daily position estimates were not available due to poor ambient light conditions at sea, i.e. either abolished at sea by the tag onboard modelling or discarded as representing very unrealistic estimates. However, for those cases when the Kalman filtering model produced a tracking record of the longitude, the results corresponded well with classification based singular automatic onboard estimates, retrospectively judged as reliable.

For fish recaptured in the western part of the Skagerrak or in the North Sea, the tracking results showed a general movement towards the west (Fig. 3). The results also indicated the fish to have been further to the west before being recaptured. For A11047, there was an indication that the fish might have returned to the Skagerrak in early summer 2004, and thereafter swam towards the North Sea again. The tagged fish A11130, previously designated as resident (category “1”), showed stable values of the longitude at about 11º E. Fish A11498, which had been designated as unclassified due to the lack of information on the recapture position, showed an unidirectional movement to the west.

For fish classified as moving from the eastern Skagerrak to the western part of the Skagerrak or the North Sea, and back again, the tracking results showed a general movement towards the west during early spring 2004 (Fig. 4). Notably, for fish A11525, tagged in April 2004, the tracking results indicated movements back and fro the Skagerrak during the summer and autumn 2004.

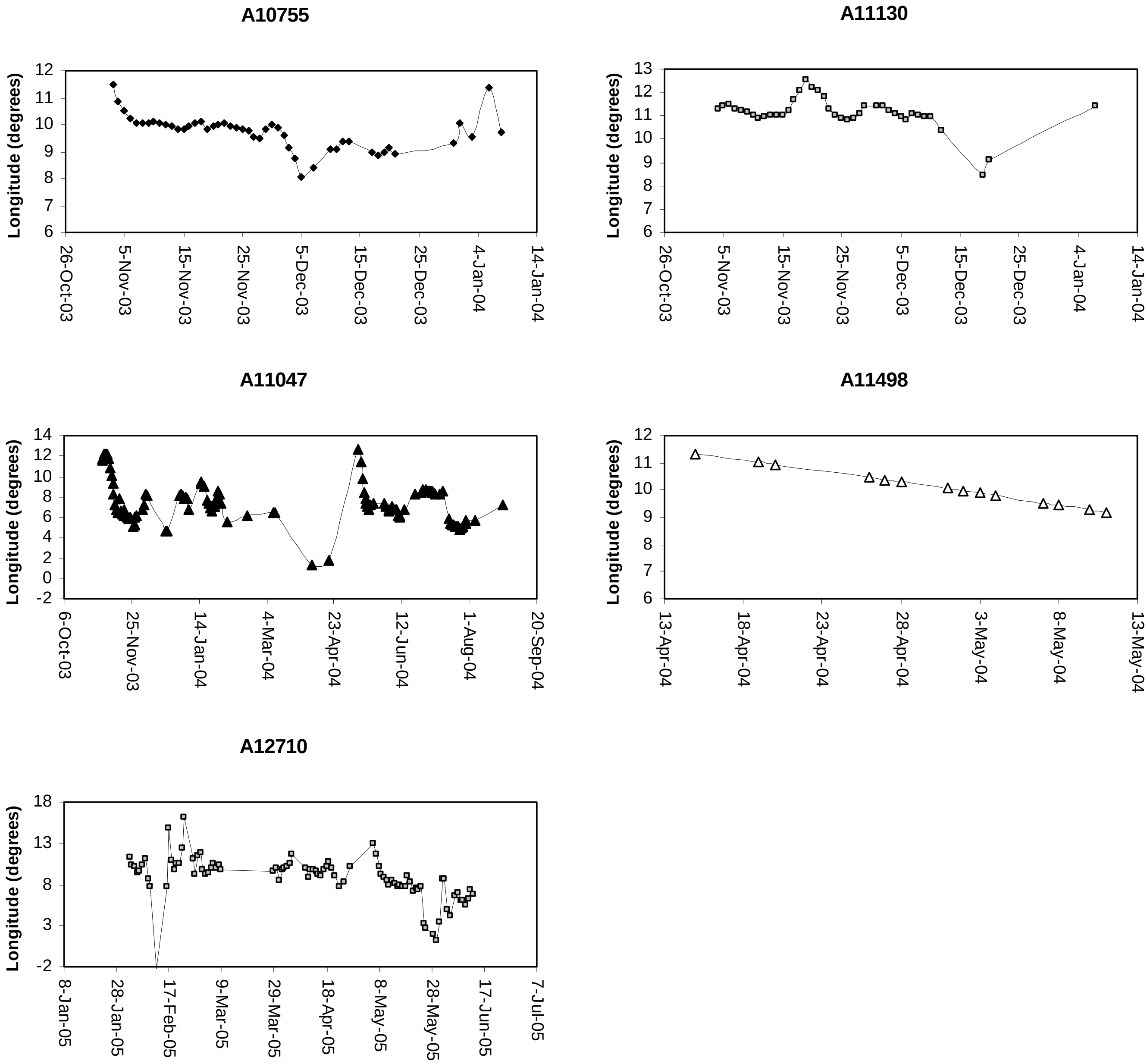


Fig. 3. Estimation by Kalman filter modelling of the longitude of archival tagged cod at liberty at sea, released in the eastern Skagerrak 2003-2005. The starting points represent research vessel GPS values, whereas the end points are the reported recapture positions. Previous, independent classification had designated the tagged cods A10755, A11047, and A12710 as fish moving from the eastern Skagerrak to the western part of the Skagerrak or the North Sea (category "2", see text for further explanation), whereas A11130 had been designated as resident (category "1"). Fish A11498 had been designated as unclassified due to the lack of information on the recapture position.

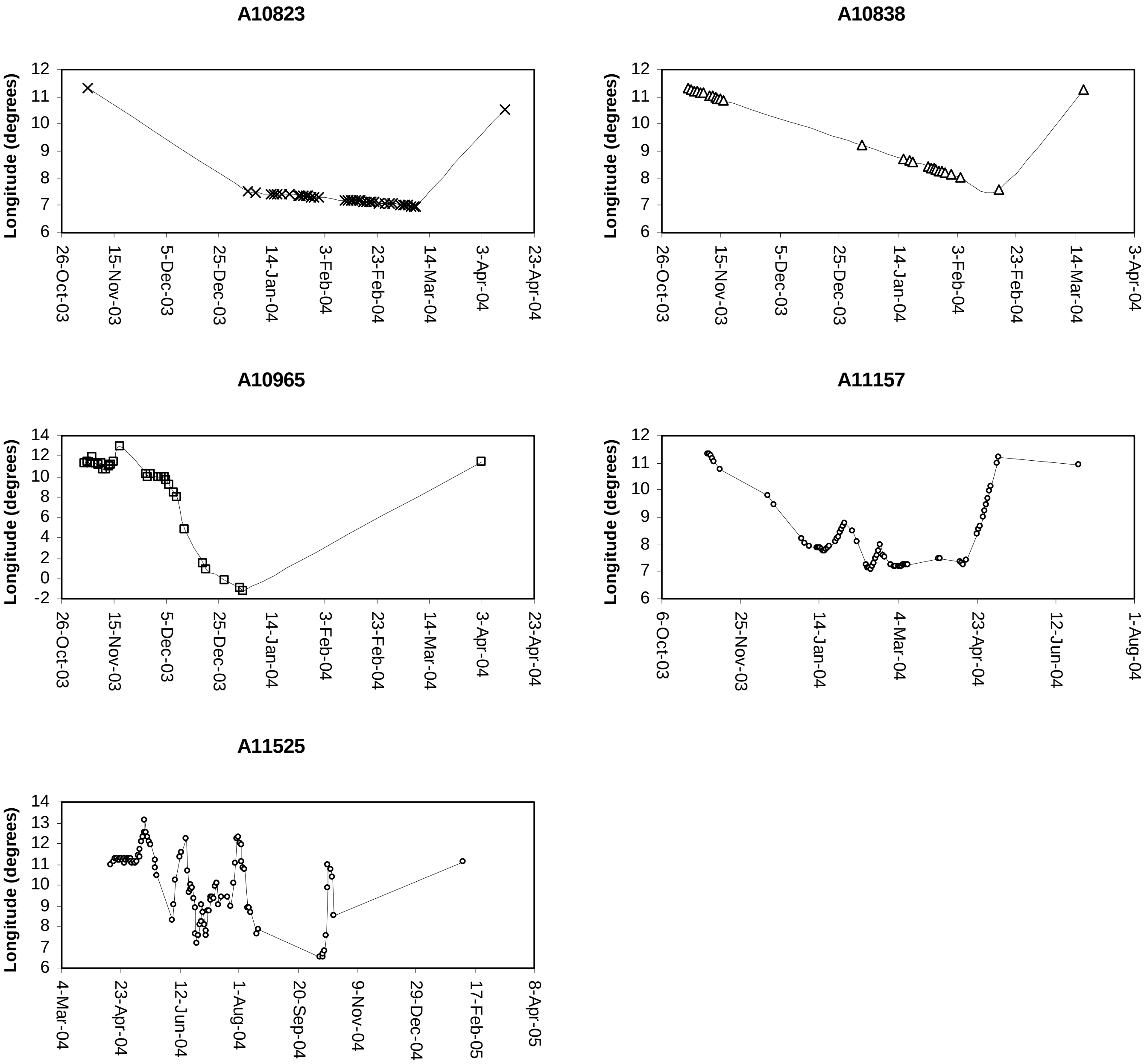
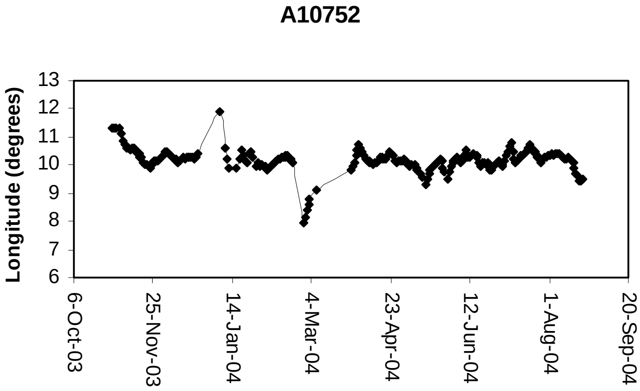
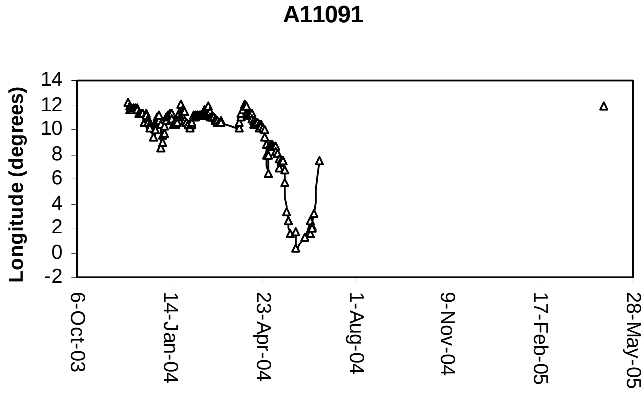


Fig. 4. Estimation by Kalman filter modelling of the longitude of archival tagged cod at liberty at sea, released and recaptured in the eastern Skagerrak 2003-2005. The starting points represent research vessel GPS values, whereas the end points are the reported recapture positions. Independent classification had designated these tagged cods as fish moving from the eastern Skagerrak to the western part of the Skagerrak or the North Sea, and back again (category “3”, see text for further explanation).





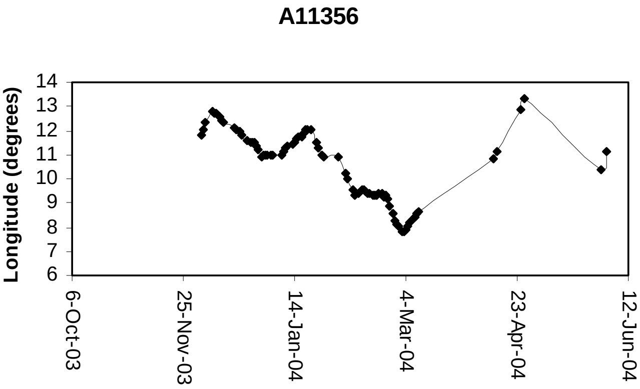


Fig. 5. Estimation by Kalman filter modelling of the longitude of archival tagged cod at liberty at sea, released in the Skagerrak and Kattegat 2003-2004. The starting points represent research vessel GPS values, whereas the end points are the reported recapture positions. Independent classification designated the tagged cod A10752 as to have moved from the Skagerrak to the Kattegat (category "4", see text for further explanation). The tagged cods A11356 and A11091 had been designated to have moved from the Kattegat to the western part of the Skagerrak or the North Sea and back again (category "6").

Independent classification designated the tagged cod A10752 as to have moved from the Skagerrak to the Kattegat (Fig. 5). The tracking results showed rather stable values of the longitude for the period at liberty. For the tagged cods A11356 and A11091, the tracking results corresponded to a movement from the Kattegat to the western part of the Skagerrak or the North Sea and back again. The fish A11091, tagged in December 2003 and recaptured in June 2005, showed an interesting indication of movements from the Kattegat towards the North Sea during summer 2004, and back again in the autumn 2004.

Tidal location modelling

For cross-checking purposes of the geolocated results, time series on experienced depths (i.e. pressure records) together with temperature data were used in tidal location modelling for a sub-set of the retained tag data (Table 3). This method gives also, advantageously, more reliable track records on the latitudes than the light geolocation method. The tracking results were in compliance with most of the light geolocation classifications, i.e. indicated a movement from the eastern Skagerrak to the North Sea or the western part of the Skagerrak. The results gave a persistent mean location signal northwest off the Danish Jutland coast for most of the fish.

Table 3. The results of tidal location modelling (average latitude and longitude), validated by comparing average temperatures recorded by the archival tags to averaged sea surface temperature for the whole period at liberty. Classification of migratory behaviour based on light geolocations are included for comparison reasons (see text for further explanations).

Classification according to light geolocations	Classification according to tidal geolocations	Tag no#	Number of validated tidal locations	Number of unique locations	Average latitude	Average longitude
2	2	A10755	105	96	55.72	6.38
3	3	A11024	89	87	56.46	4.39
2	2	A11047	51	44	56.01	6.28
3	3	A10838	29	29	55.60	5.00
2	2	A10786	135	118	56.20	5.29
3	3	A10823	88	78	56.16	6.52
3	3	A11157	114	82	56.04	5.91
6	6	A11356	480	302	54.98	5.02
7	-	A11551	0			
3	3	A11562	9	9	57.46	6.97
3	-	A11540	0			
3	3	A11554	17	17	57.64	7.20
3	3	A10957	62	39	57.63	6.68
2	2	A11045	82	67	58.06	4.78
3	3	A11655	101	83	54.65	4.26
2	2	A11630	0			
3	3	A12632	145	124	55.80	5.77
2	2	A11953	505	271	55.00	4.99
2	2	A12710	287	121	53.81	3.72
1	3	A12825	132	128	56.33	5.13
1	-	A12727	0			
1	3	A12835	184	44	55.86	6.12
1	-	A12647	0			

Biological and habitat choice differences between resident and migratory cod

Differences in biology and habitat choice was inspected for cod tagged in the Skagerrak characterised either as resident (category “1”) or migratory (categories “2” and “3”) cod, i.e. in age, size, maturity and change in mean depth during the spawning period. Significant differences in age were found between resident and migratory fish (t-test, d.f.=54, p=0.02; Table 4). No significant differences in size (length) was however found (Table 4).

Table 4. Age and length composition of retained fish originally tagged in the Skagerrak. The fish have been classified either as resident (category “1”) or migratory (category “2” or “3”). Ages are given in years and length in mm.

Migratory behaviour classification		N	Mean	Std. Deviation	Std. Error Mean
age	Resident	35	2.8571	.94380	.15953
	Migratory	21	3.4286	.74642	.16288
length	Resident	40	504.2500	100.50864	15.89181
	Migratory	30	532.3333	96.79995	17.67317

Gonadal inspection indicated that the incidence of mature or maturing was higher in migratory fish (54%) compared to resident fish (22%), although the difference was not significant on conventional p-levels (Pearson chi-square; p=0.06, Table 5).

Table 5. Classification of maturation status of retained fish originally tagged in the Skagerrak 2003-2005. The fish have been classified either as resident (category “1”) or migratory (category “2” or “3”).

Migratory behaviour classification	Maturation status		Total
	Non-maturing	Mature or maturing	
Resident	17	5	22
Migratory	6	7	13
Total	23	12	35

It was hypothesized that the migratory cod were moving into spawning areas in the eastern North Sea and therefore should have entered shallower areas, i.e. upwards in the water column during the spawning period. The lack of continuous high frequency time series on experienced depths, naturally restricts the generality of the retained time series. Instead, the daily maximum depths were used as a proxy for bottom depth, i.e. it was assumed that the fish, despite possibly exhibiting pelagic behaviour for most of the time, it at least visits the seafloor once a day.

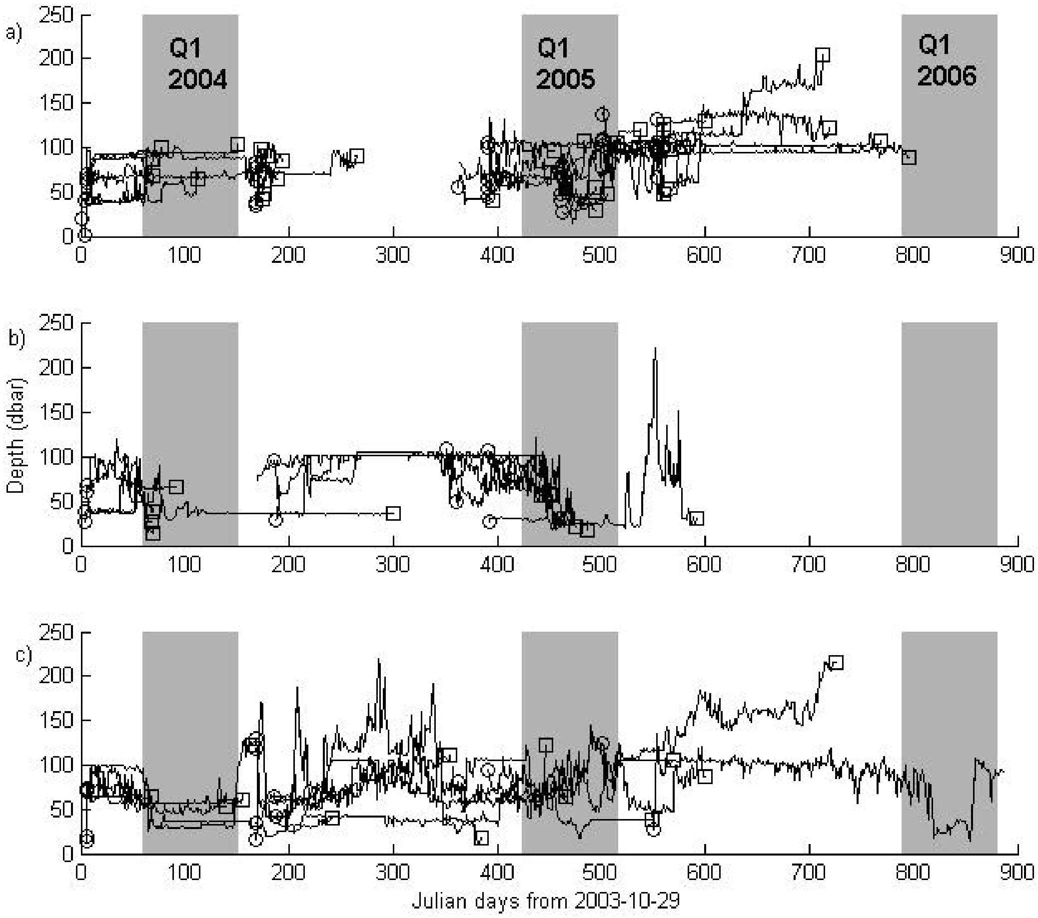


Fig. 6. Time-series of the daily maximum depths (dbar), where the first quarterof the year (Q1) is highlighted by gray shading. First day of recording is marked (○) and the last day of recording i.e. day of recapture is marked (□). The individuals are categorized as: a) category '1' resident in the Skagerrak (n=38), b) category '2' recaptured in western Skagerrak/North Sea (n=13), c) category '3' geolocated to western Skagerrak/North Sea (n=15).

Daily recorded maximum depths are plotted in Figure 6 for each of the three behavioural categories (38, 13 and 15 individuals for the categories "1","2"and "3", respectively). Recorded maximum depths varied considerably over time as well as between individuals within and between categories. It can be observed that the greatest depths were recorded during summer period, and migratory fish tended to inhabit shallower waters during the first quarter of the year.

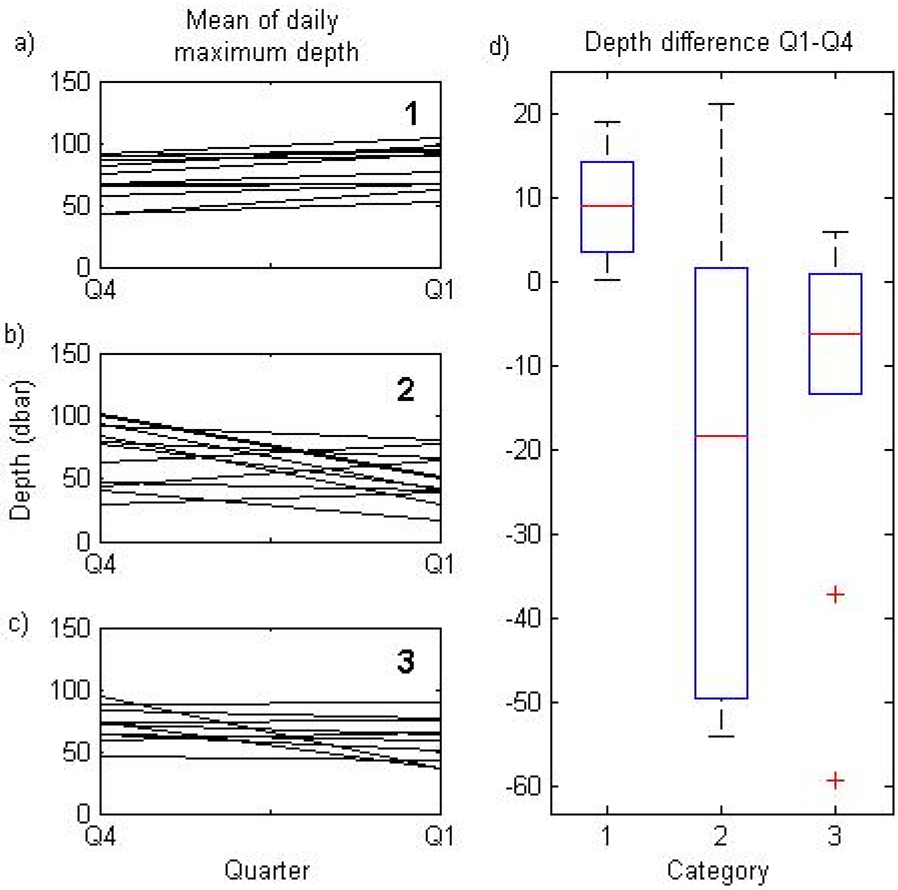


Fig 7. Left panel: Average maximum depths for the last quarter of the year (Q4) and the first quarter the subsequent year (Q4) grouped by category, where (n) is the number of individuals: a) category ‘1’ (n=12), b) category ‘2’ (n=12), c) category ‘3’ (n=10). Right panel: d) The individual differences in average maximum depth grouped by category.

To further elucidate differences in the vertical distribution behaviour the individual difference in average maximum depth has been calculated between last quarter of the year (Q4) and the first quarter in the subsequent year (Q1) (Fig. 7a-c). None of the individuals contributed with more than one difference, i.e. no fish had remained at liberty through two consecutive spawning periods.

It was found that cod categorized as resident in the Skagerrak actually tended to move into deeper waters, on average approximately 10 m deeper during the first quarter of the year (p<0.001; d.f.=11). Migratory cod, recaptured in the western part of the Skagerrak or in the North Sea, on the opposite moved upwards into about 20 m shallower waters (p=0.02, d.f.=11). The fish belonging to category '3' had a similar depth distribution in both quarters of the year (p=0.08, d.f.=9), although this group contained some of individuals with the greatest decrease in depth.

Discussion

The mark-recapture results of this study indicated pronounced differences in cod migratory behaviour between tagging locations in the Skagerrak-Kattegat area. A large proportion of the tagged cod off the Skagerrak coast moved in a westerly direction during their period at liberty. Cod tagged in the Skagerrak had in general much more extensive movements compared to fish tagged in the Kattegat. Cod tagged in the Gullmarsfjord, showed a very resident behaviour with exceptions for two cods which were recaptured in the western part of the Skagerrak, respectively in the south-eastern Skagerrak. Almost all cod in the Kattegat showed very limited movements, and the recapture positions were scattered around the releasing sites. The only fish that showed a migratory behaviour similar to the one observed in the Skagerrak were tagged in the northern part of the Kattegat, notably in the vicinity of the offshoot from the Norwegian trench, Djupa rännan. The predominance of recapture positions along the northern coast off Jutland suggests that this might be the main migratory route for cod from the eastern Skagerrak to the North Sea. One cod tagged in the south-eastern part of the Skagerrak swam across the Norwegian trench to a location close to the Norwegian coast. The depth profile (i.e. tag records on pressure) connected to this movement was not encountered in fish caught along the Danish coast, suggesting that migrations across the Norwegian trench might be of infrequent occurrence (c.f. Danielssen 1969).

The geolocation results supported the mark-recapture inference, and added complexity to the deduced migratory behaviour, changing unidirectional movements into less obvious dispersal patterns. Cod tagged off the eastern Skagerrak coast not only migrated towards the North Sea, they also showed return migrations back to the eastern Skagerrak after visiting the North Sea/western part of the Skagerrak. According to the Kalman filtering results westerly movements predominately occurred during the spawning period. Differences in age and maturity between resident and migratory cod also supports the theory of that possibly a majority of the cod in the eastern Skagerrak return to the North Sea/ western Skagerrak for spawning. Variation in depth (habitat) selection between the categories also supported this theory. Although the average of maximum depth over such along period as three months is a very crude estimate of the behaviour of an individual fish, these finding were not contradictory to the conducted migratory classifications, but supported the idea that these groupings reflect behavioural differences, besides the actual migration, most probably spawning activity.

The results in this study were also in good compliance with the outcome from earlier tagging studies in the western part of the Skagerrak (Danielssen 1969). Cod off the northern Jutland coast between longitude 9º and 10º E were tagged between 1954 and 1965. About 80% of the recaptures were made in the Skagerrak, but 14% of the tagged cod were also reported from the North Sea with a random distribution between longitude 1º and 8.5º E and between latitude 54º and 58.5º N, i.e. over the entire eastern part of the North Sea. In addition, about 5% of the tagged cod were retained from the northern part of the Kattegat (the border between Kattegat and Skagerrak here defined by a straight line from Skagen to Paternoster lighthouse). Most of the cod reported from the North Sea were caught during the first six months of the year, especially from February to April, i.e. during the most active part of spawning period for cod in the North Sea. Hence, the observations made in the 1950s and 1960s, gives strong support for conclusions made in this study of a migration route between the North Sea/western part of the Skagerrak and the eastern Skagerrak/the northern Kattegat along the northern Jutland coast.

Put together, these findings clearly suggest a strong behavioural component in the distribution pattern of cod in the eastern North Sea region, as cod tagged at different localities showed non-random, directional movements and these were in compliance with a sub-population structure already discernible from other sources of information (e.g. Munk et al. 1999, Knutsen et al. 2003, 2004, Svedäng 2003, Svedäng and Svenson 2006). In other words, even if other explanations cannot be ruled out, the studied migration of the cod tagged off the Skagerrak coast, or the cod that left the Kattegat and the Gullmarsfjord may be regarded as a part of a homing behaviour, i.e. natal philopatry, based on individual decision-making of the fish.

Robichaud and Rose (2004) stated in an extensive review of tagging studies made on cod all over its distribution area that existing data support a view on cod as species with four different modes of migratory and homing behaviour: sedentary, accurate homers, inaccurate homers and dispersers (ranging over large areas without recognisable return migrations). Genetic analysis of various cod populations have also shown that differentiation exists between relatively closely occurring subpopulations. For such differentiation to be preserved, even at low levels of genetic distances, reproductive isolation is irrefutably implied.

Nielsen et al. (2005) argued that the seemingly contradictory existence of reproductive isolation in fish populations which encounter few physical barriers, with wide distributions and dispersal of pelagic eggs and larvae, was explained by retention of juveniles to marked off watersheds. In other words, natal philopatry is not prerequisite for reproductive isolation to occur. However, genetic surveys along the Skagerrak coast have shown that the composition of young of year cod change from year to year consistently with year class strength variation in the entire Skagerrak (Knutsen et al. 2004). Thus, in years with a general low level of recruitment, juveniles were assigned to neighbouring coastal cod populations (i.e. reference material attained from adult, spawning fish), whereas in years with high levels of recruitment, the juveniles were on the contrary assigned to reference populations sampled at spawning in the western part of the Skagerrak or in the eastern North Sea. This study gives information on the mechanism why this separation between populations persist: juveniles dispersed at earlier life stages to the eastern Skagerrak leave for return migrations in a westerly direction. In addition, a previous tagging study in the 1980s along the Swedish west coast, reported a similar migratory behaviour of tagged cod juveniles (Pihl and Ulmestrand 1993). Already at this moment, most of the former coastal cod population structure was severely depleted (c.f. Svedäng 2003), and the impact on recruitment from offshore resources was obvious. At most tagging localities along the coast, the juvenile cod left their nursery areas and migrated westwards. Indications of a migration route in the opposite direction was only attained from taggings in the Gullmarsfjord. It may also be argued that juveniles coming from the North Sea to the eastern Skagerrak or to the Kattegat, do not have to make return migrations in order to find suitable spawning grounds: this energetically costly behaviour is neither consistent with the view of juvenile retention as the prime structuring mechanism.

Density-dependent effects of migration between the North Sea, Skagerrak and Kattegat have been suggested by Chen et al. (2005). Through statistical modelling of monitoring data linkages between the three watersheds were depicted, i.e. that net migrations of adult individuals take place from the North Sea to the Skagerrak and from the Kattegat to the North Sea. This study gives support for such a proposition in the sense that migrations between the areas do exist. However, the depleted states of the Kattegat cod stock (Svedäng and Bardon 2003, Cardinale and Svedäng 2004) and in the eastern Skagerrak (Svedäng 2003) are not in compliance with such a conjecture; there is no high density of cod to be found in these parts of the North Sea. More important criticism is, however, that Chen et al. in their modelling did not take the transportation of eggs and larvae into consideration, as it has been suggested to be of some importance in the modelling study by Cardinale and Svedäng (2004) and from genetic survey data (Knutsen et al. 2004). Net migration from, for instance, the Kattegat to the North Sea might well occur, but the reason for this may be related natal philopatry, following the net transportation of propagules in the opposite direction. The migrations to and fro the Skagerrak and the North Sea as revealed in this study, might also be too complicated to be properly analysed from scattered monitoring IBTS data.

Repeated homing of cod to spawning grounds have been observed in the northwest Atlantic (Green and Wroblewski 2000, Robichaud and Rose 2001). Robichaud and Rose (2002) developed some hypotheses about short-range navigation mechanisms in cod: the grunting sounds that cod make while spawning and geo-magnetism could act as potential point sources. They also speculated there was a social component to cod movements, i.e. presence of maturing conspecifics, and memory of, for instance, bathymetric structures, especially during longer distance migrations. However, this study indicated that cod tagged at various localities show multidirectional movements even in presence of resident cod as in the Kattegat or in the Gullmarsfjord. It may therefore be hypothesised that impulses to return to natal spawning grounds are imprinted at earlier life stages, as they seem to be in genera such as *Anguilla*. Analysis of otolith chemistry contents in weakfish (*Cynoscion regalis*) showed similar rates of spawning site fidelity as in birds and anadromous fishes, implying that population connectivity through larval dispersal and natal homing are the most important elements in maintenance of fish population structures (Thorrold et al. 2001).

Inference of cod population structure in West Greenland waters clearly implied natal philopatry, although irrevocable evidence seldom is provided in a singular tagging study. Besides resident inshore, fjord populations and bank populations off the Greenland Coast, return migrations of cod to Iceland, originating from episodic larval drift of Icelandic origin, is a well-studied phenomenon (e.g. Storr-Paulsen et al. 2004). In a similar manner are the Barents Sea cod (i.e. skrei) and the Norwegian coastal cod separated and able to maintain their integrity in spite of partially shared feeding grounds (Godø 1995, Nordeide 1998, Salvanes et al. 2004).

From a Bayesian point of view degrees of belief are increasing or decreasing, whereas the “hard core” of a conceptual framework is seldom open for testing (Hilborn and Mangel 1997). Regarding the Atlantic cod species complex, all inference is based on a number of assumptions and beliefs, of which only some are, at least in a singular study, open for falsification. Here we presented data on migratory behaviour that is compatible to natal homing based upon individual decision-making of the fish. Other studies on population genetics, taggings and demersal fish surveys support this kind of inference. The proximate clues for homing, if existent, are virtually unknown but are merited for further investigation.

Regarding the studied “Skagerrak population” it may be hypothesised that spawning cod in the eastern North Sea, for instance on Greater and Lesser Fisher Bank, constitute a subpopulation that utilises the strong counter-clockwise water circulation in the Skagerrak for dispersal of their propagules (c.f. Munk et al. 1995, 1999), and thereby enhance the opportunity for colonisation of large nursery areas. The return migrations to the eastern North Sea during the spawning period as well as cod roaming around in the Skagerrak for feeding during other parts of the year make perfectly sense in this regard.

References

Arnold, G.P., Greer-Walker, M., Emerson, L.S., and Holford, B.H. 1994. Movements of cod (*Gadus morhua* L) in relation to tidal streams in the southern North Sea. ICES Journal of Marine Science 51, 207–232.

Brander, K. M. 1994. The location and timing of cod spawning around the British Isles. ICES Journal of Marine Science 51, 71-89.

Campana, S.E., Chouinard, G.A., Hanson, J.M., Fréchet, A., and Brattey, J. 2000. Otolith elemental fingerprints as biological tracers of fish stocks. Fisheries Research 46, 343-357.

Cardinale, M., and Svedäng, H. 2004. Recruitment and abundance of Atlantic cod, *Gadus morhua*, in the Kattegat-Eastern Skagerrak (North Sea): evidence of severe depletion due to a prolonged period of high fishing pressure. Fisheries Research 69, 263-282

Chen, Q., Chan, K.-S., Lekve, K., Torstensen, E., Gjøsæter, J., Ottersen, G.,. and Stenseth, N. C. 2005. Population dynamics of cod *Gadus morhua* in the North Sea region: biological density-dependent and climatic density-independent effects. Marine Ecology Progress Series 302, 219-232.

Danielssen, D.S. 1969. On the migration of the cod in the Skagerrak shown by tagging experiments in the period 1954-1965. Fiskeridirektoratets Skrifter Serie Havsundersøkelser 15, 331-338.

Godø, O. R. 1995. Transplantation-tagging-experiments in preliminary studies of migration of cod off Norway. ICES Journal of Marine Science 52, 953-960.

Green, J. M., and Wroblewski, J. S. 2000. Movement patterns of Atlantic cod in Gilbert Bay, Labrador: evidence for bay residency and spawning site fidelity. Journal of the Marine Biological Association of the UK 80, 1077-1085.

Hilborn, R. and Mangel, M. 1997. The ecological detective: confronting models with data. Princeton University Press. Princeton, New Jersey. 315 p.

Hunter, E., Aldridge, J. N., Metcalfe, J. D. and Arnold, G. P. 2003. Geolocation of free-ranging fish on the European continental shelf as determined from environmental variables. Marine Biology 142, 601–609.

Hutchinson, W. F., Carvalho, G. R., and Rogers, S. I. 2001. Marked genetic structuring in localised spawning populations of cod *Gadus morhua* in the North Sea and adjoining waters, as revealed by microsatellites. Marine Ecology Progress Series, 223, 251-260.

Jonsdottir, O.D.B., Danielsdottir, A.K., and Naevdal, G. 2001. Genetic differentiation among Atlantic cod (*Gadus morhua* L.) in Icelandic waters: temporal stability ICES Journal of Marine Science 58, 114–122

Knutsen, H., Jorde, P.E., André, C., and Stenseth, Chr. 2003. Fine-scaled geographical population structure in a highly mobile marine species: the Atlantic cod. Molecular Biology 12, 385-394.

Knutsen, H. André, C. Jorde, P.E., Skogen, M.D., Thuróczy, E. and Stenseth, N.C. 2004. Transport of North Sea cod larvae into the Skagerrak coastal populations. Proceeding of the Royal Society ser B. 271, 1337-1344.

Lawson, G. L., and Rose, G. A. 2000. Small-scale spatial and temporal patterns in spawning of Atlantic cod (*Gadus morhua*) in coastal Newfoundland waters. Canadian Journal of Fisheries and Aquatic Science 57, 1011-1024.

Munk, P., Larsson, P.-O., Danielssen, D.S., and Moksness, E. 1995. Larval and small juvenile cod *Gadus morhua* concentrated in the high productive areas of a shelf break front. Marine Ecology Progress Series 125, 21-30.

Munk, P., Larsson, P.-O., Danielssen, D.S., and Moksness, E. 1999. Variability in frontal zone formation and distribution of gadoid fish larvae at the shelf break in the northeastern North Sea. Marine Ecology Progress Series 177, 221-233.

Musyl, M. K., Brill, R. W., Curran, D. S., Gunn, J. S., Hartog, J. R., Hill, R. D., Welch, D. W., Eveson, J. P., Boggs, C. H., and Brainard, R.E. 2001. Ability of archival tags to provide estimates of geographical position based on light intensity. In Electronic Tagging and Tracking in Marine Fisheries Reviews: Methods and Technologies in Fish Biology and Fisheries. J.R. Sibert & J.L. Nielsen (eds) Dordrecht: Kluwer Academic Press, pp. 343–368.

Neat, F.C., Wright, P.J., Zuur, A.F., Gibb, I.M., Gibb, F.M., Tulett, D., Righton, D.A., and Turner, R.J. 2005. Residency and depth movements of a coastal group of Atlantic cod (*Gadus morhua* L.). Marine Biology 148, 643-654.

Nielsen, A. 2004. Estimating fish movement. Ph.D. Thesis. Royal Veterinary and Agricultural University, June 2004. 119 p.

Nielsen, E.E., Grønkjær, P., Meldrup, D., and Paulsen, H. 2005. Retention of juveniles within a hybrid zone between North Sea and Baltic Sea Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Science 62, 2219–2225.

Nordeide, J. T. 1998. Coastal cod and north-east Arctic cod - Do they mingle at the spawning grounds in Lofoten? Sarsia 83, 373-379.

Pawson, M.G. and Jennings, S. 1996. A critique of methods for stock identification in marine capture fisheries. Fisheries Research 25, 203-217.

Pihl, L., and Ulmestrand, M. 1993. Migration pattern of juvenile cod (*Gadus morhua*) on the Swedish west coast. ICES Journal of Marine Science, 50, 63-70.

Robichaud, D., and Rose, G. A. 2001. Multiyear homing of Atlantic cod to a spawning ground. Canadian Journal of Fisheries and Aquatic Science 58, 2325-2329.

Robichaud, D., and Rose, G. A. 2002. The return of cod transplanted from a spawning ground in southern Newfoundland. ICES Journal of Marine Science 59, 1285-1293.

Robichaud, D., and Rose, G. A. 2004. Migratory behaviour and range in Atlantic cod: Inference from a centaury of tagging. Fish and Fisheries 5, 185-214.

Ruzzante, D. E., Taggart, C. T., Cook, D., and Goddard, S. 1996. Genetic differentiation between inshore and offshore Atlantic cod (*Gadus morhua*) off Newfoundland: Microsatellite DNA variation and antifreeze level. Canadian Journal of Fisheries and Aquatic Sciences 53, 634-645.

Ruzzante, D. E., Taggart, C. T., Doyle, R. W., and Cook, D. 2001. Stability in the historical pattern of genetic structure of Newfoundland cod (*Gadus morhua*) despite the catastrophic decline in population size from 1964 to 1994. Conservation Genetics 2, 257-269.

Salvanes, A.G.V., Skjaeraasen, J.E., and Nilsen, T. 2004. Sub-populations of coastal cod with different behaviour and life history strategies. Marine Ecology Progress Series 267, 241–251.

Sibert, J., Musyl, M. K. and Brill, R. W. 2003. Horizontal movements of bigeye tuna (*Thunnus obesus*) near Hawaii determined by Kalman filter analysis of archival tagging data. Fisheries Oceanography 12, 141–151.

Sinclair, M. 1988. Marine populations: An essay on population regulation and speciation. Washington Sea Grant Press, Seattle.

Smith, P., and Goodman, D. 1986. Determining fish movements from an “archival” tag: precision of geographical positions made from a time series of swimming temperature and depth. NOAA Technical Memorandum NMFS, NOAA-TM-NMFS-SWFC-60. Southwest Fisheries Science Center, La Jolla, CA, 92038.

Storr-Paulsen, M., Wieland, K., Hovgård, H., and Rätz, H-J. 2004. Stock structure of Atlantic cod (*Gadus morhua*) in West Greenland waters: implications of transport and migration. ICES Journal of Marine Science 61, 972-982.

Svedäng, H. 2003. The inshore demersal fish community on the Swedish Skagerrak coast: regulation by recruitment from offshore sources. ICES Journal of Marine Science 60, 23-31.

Svedäng, H. and Bardon, G. 2003. Spatial and temporal aspects of the decline in cod (*Gadus morhua* L.) abundance in the Kattegat and eastern Skagerrak. ICES Journal of Marine Science 60, 32-37.

Svedäng, H. and Svenson, A. 2006. Cod (*Gadus morhua* L.) populations as behavioural units: inference from time series on juvenile cod abundance in the Skagerrak. Symposium edition of Journal of Fish Biology (in press).

Teo, S. L. H., Boustany, A., Blackwell, S., Walli, A., Weng, K. C., and Block, B. A. 2004. Validation of geolocation estimates based on light level and sea surface temperature from electronic tags. Marine Ecology Progress Series 283, 81-98.

Thorrold, S.R., Latkoczy, C., Swart, P.K., and Jones, C.M. 2001. Natal homing in a marine fish metapopulation. Science 291, 297-299.

Welch, D.W., and Eveson, J.P. 1999. An assessment of light-based geoposition estimates from archival tags. Canadian Journal of Fisheries and Aquatic Sciences 56, 1317-1327.