

Partial migration in the northern Gulf of St. Lawrence Atlantic cod population

Arnault Le Bris^{1*}, Alain Fréchet², Peter S. Galbraith², Joseph S. Wroblewski³

¹Biology Department, Memorial University of Newfoundland, St. John's, NL, Canada

²Maurice-Lamontagne Institute, Fisheries and Oceans Canada, Mont-Joli, Qc, Canada

³Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, NL, Canada

The coexistence of resident and migratory individuals within a population is termed partial migration. Using data storage tags that record depth and temperature, we investigated the migratory behaviour of adult Atlantic cod in the northern Gulf of St. Lawrence. The geolocation problem was solved using the hidden Markov model based on daily maximum depths and bottom temperature. Reconstructed migration routes revealed undocumented partial migration in the panmictic population. Migratory individuals overwintered in relatively deep (300-500m) and warm (5°C) waters. In the spring, these migratory fish displayed extensive diel vertical movements that were interpreted as spawning behaviour. Resident individuals displayed a prolonged period of dormancy in shallow (< 50m) and near freezing (-1.5°C) coastal waters during the winter and the spring. This dormancy period was followed by foraging movements in western Newfoundland coastal waters. Limited ability of scientific survey to sample resident cod in shallow coastal waters may induce bias in the population abundance estimations.

Keywords: Partial migration, Atlantic cod, data-storage tags, northern Gulf of St. Lawrence

* Corresponding author: arnault.lebris@mun.ca ; (709) 864-2502.

Introduction

Movement is a crucial component of ecological and evolutionary responses of natural population to anthropogenic disturbances such as habitat fragmentation, climate change, intense exploitation, and species introductions (Nathan *et al.*, 2008). Movement affects trophic dynamics, communities structure, and ecosystems functioning (Schindler *et al.*, 2003; Brodersen *et al.*, 2008). Individual movement governs populations dispersal, structure, and connectivity. Movement affects our ability to assess populations status and to conserve existing biodiversity. Migration is arguably the movement type that has the most attracted the scientific curiosity. Environmental heterogeneity and stochasticity, behavioural plasticity, and trade-offs between migration and fitness-related life history traits may results in intrapopulation diversity in migration patterns (Fryxell and Sinclair, 1988; Dingle, 1996). Increasing recognition that intrapopulation diversity in migration affects populations productivity, stability, and resilience to disturbance (Hilborn *et al.*, 2003; Kerr *et al.*, 2010; Schindler *et al.*, 2010) has urged the need for understanding ultimate and proximate factors regulating intrapopulation diversity in migratory behaviours.

The coexistence of resident and migratory individuals within a population is termed partial migration. Partial migration is ubiquitous among metazoan taxa, including insects, birds, mammals, and fish (Swingland, 1983; Jonsson and Jonsson, 1993; Chapman *et al.*, 2011). Several mechanisms have been proposed to explain the maintenance of alternative migratory strategies within a population over evolutionary time. Partial migration was first thought to result from strict genetic control, with equal long-term fitness for migrants and non-migrants (Berthold, 1984; 1991). It has then been suggested, based on game theory models, that partial migration is a mixed evolutionary stable strategy (ESS, Maynard Smith and Price, 1973) arising from frequency-dependent selection (Lundberg, 1987; Kaitala *et al.*, 1993). Increasing evidences of the environmental influence on the adoption of migratory strategies, as well as lack of empirical evidence to support the mixed ESS hypothesis, has favoured the current consensus that partial migration is a conditional strategy influenced by individual characteristics such as size, sex, growth rate (Thériault and Dodson, 2003; Brodersen *et al.*, 2008; Kerr *et al.*, 2009; Chapman *et al.*, 2011).

The partial migration theory has also been used to explain intrapopulation diversity in diel vertical movements (DVM), especially departure from the classic DVM pattern of planktonic organisms. Partial diel vertical migration in the copepod *Metridia pacifica* is induced by individual variations in lipid store (Hays *et al.*, 2001). Individual size has been proposed as the conditional mechanism for partial migration in *Daphnia* population, with smaller individual not descending at dawn (Hansson and Hylander, 2009). More recently, partial diel vertical migration was documented in freshwater zooplanktivorous fish species (*Coregonus spp*) with some individuals not performing night ascend in the water column (Mehner and Kasprzak, 2011). Increasing empirical evidences suggest that the propensity for individual to perform DVM result from a conditional strategy.

Because of its commercial, historical, and cultural importance, Atlantic cod (*Gadus morhua*) is the most studied demersal fish species. Migration patterns and behaviours of Atlantic cod have long been studied, and many resident populations have been documented throughout its geographic range (see review by Robichaud and Rose, 2004). It is only recently that the paradigm of large population structure has shifted towards the reconnaissance of mechanisms promoting fine scale population structure for Atlantic cod (Green and Wroblewski, 2000; Svedäng *et al.* 2007; Hauser and Carvalho, 2008; Bradbury *et al.*, 2008). The miniaturization and increasing affordability of new tagging technologies has revolutionized the study of cod movement and has resulted in the recognition that numerous putative populations may be composed of a mixture of resident and migratory individuals (Neat *et al.*, 2006; Svedäng *et al.*, 2007). Theories offering mechanistic explanations for intrapopulation diversity in migratory behaviours have thus regained attention. Metapopulation and partial migration theories have been applied to Atlantic cod populations (Smedbol and Wroblewski, 2002; Wright *et al.*, 2006; Sherwood and Grabowski, 2010; Petitgas *et al.*, 2010).

The main objective of this research is to investigate the intrapopulation diversity in Atlantic cod migratory behaviours in the northern Gulf of St. Lawrence using data-storage tags. To test the hypothesis of partial migration in the nGSL Atlantic cod, we reconstructed cod migration routes using an hidden Markov Model based on daily maximum depth and associated temperature

recorded by the tag. A second objective is to investigate diversity in the cod vertical movements. Periodicities in depth signal were detected using Fast Fourier Transform. A complementary objective is to assess if it is feasible to geolocate demersal species tagged with data-storage tags in the Gulf of St. Lawrence.

Material and methods

Tagging procedure

In 2007, the Department of Fisheries and Oceans Canada (DFO) and the Fish Food and Allied Worker (FFAW) launched a new tagging program for Atlantic cod in the northern Gulf of St. Lawrence using data storage tags (DSTs). Cod were captured using baited handlines at multiple locations along the west coast of Newfoundland and along Quebec north shore. Tagging locations were chosen to encompass the three Northwest Atlantic Fisheries Organization (NAFO) management units in the northern Gulf of St. Lawrence (i.e. NAFO divisions 3Pn, 4R, and 4S). Cod presenting no sign of barotrauma were surgically implanted with data-storage tags inside their abdominal cavity. One traditional spaghetti tag with a unique serial number and one red tag labelled with a warning message were fixed in the dorsal musculature of cod in order to inform harvesters about the presence of the internal electronic tag. Fish were immediately released after tagging so that the overall procedure seldom took more than two minutes. Advertisement and reward campaigns (100 CADs for each DST) were launched to increase tag reporting rate. As of now, 353 adult cod (Fork Length > 40 cm) were tagged with DSTs. As the tagging program progressed, tag series LTD_1100, LAT_1400, and LAT_1500 (Lotek Wireless Inc., St. John's, Canada) were used. DSTs recorded ambient temperature ranging from -5°C to 35°C, with a minimal accuracy of 0.2°C and a minimal resolution of 0.05°C, and pressure with $\pm 1\%$ accuracy and 0.05% resolution. DSTs were programmed using the time extension recording feature in order to privilege sampling duration over frequency. As a result, sampling frequencies varied among tags from 2.5 to 60 minutes.

Oceanographic data

The Gulf of St. Lawrence is a semi-enclosed marginal sea in the northwest Atlantic. This large estuarine ecosystem has three major water influxes. Cold waters from the Labrador Shelf enter

the Gulf via the Strait of Belle Isle. Temperate Atlantic Ocean waters penetrate the Gulf through the Cabot Strait, and freshwaters arrive from the St. Lawrence river and its tributaries (Koutitonsky and Bugden, 1991). The low tidal range and the presence of a unique amphidromic point for the M2 constituent (Lu *et al.*, 2001; Saucier *et al.*, 2003) prevent the use of the tidal location method (Metcalf and Arnold, 1997; Hunter *et al.*, 2003). Instead, the geolocation method used in this study takes advantage of the Gulf complex bathymetry and pronounced temporal and spatial gradients in temperature (Figures 1 and 2).

Bottom temperature grid were obtained using all available CTD casts sampled by the DFO. Temperature profiles recorded by CTD casts were averaged into depth intervals of one meter and then interpolated onto a 2 km resolution grid using the Barnes algorithm (Galbraith, 2006). Minimum and maximum temperature measured in each of the Gulf's nine oceanographic subareas were used to bind horizontal interpolation of temperature (Galbraith *et al.*, 2011). Bottom temperature at each grid point was obtained by selecting the interpolated temperature at the depth level corresponding to a bathymetry grid obtained from the Canadian Hydrographic Service. Bottom temperature grids were obtained annually for the months of March, August, and November from 2007 to 2011. No data were available in March for water deeper than 275 m in 2007-2008 and deeper than 360 m in 2009-2010-2011 resulting in gaps in the grid. Deep water temperature is relatively constant throughout the year (Petrie *et al.*, 1996), gaps were thus filled with bottom temperature using November temperature. March bottom temperature was used for the February-May period, August bottom temperature for the June-September period, and November bottom temperature of the October-January period.

Geolocation model

A hidden Markov model was used to compute the posterior probability distribution for the daily location of tagged fish from the tagging location to the recapture location (Pedersen *et al.*, 2008; Thygessen *et al.*, 2009). As with other state-space models, hidden Markov models consist in two coupled stochastic models: the process model and the observation model (Cappé *et al.*, 2005). The process model simulates the fish movement in a two-dimensional space. The observation model refines position predicted by the movement model by comparing data recorded by the tag with data from the bathymetry and bottom temperature grid. This duality allows to address errors in both the fish movement model and the observation process. Hidden Markov models are;

therefore, well adapted to model animal telemetry data (Franke *et al.*, 2004; Patterson *et al.*, 2008).

Assuming that the movement of the fish follows a two-dimensional biased random walk, the time evolving probability density of fish location can be computed using the advection-diffusion equation (Okubo, 1980; Sibert *et al.*, 1999; Pedersen *et al.*, 2008). The advection-diffusion equation had two unknown parameters: the diffusivity D and the drift term Δ . Parameters were considered constant through time and the drift term was considered null. The advection-diffusion equation was discretised in space (*i.e.* 331x476 grid cells) and time and was solved using finite differences (Thygesen *et al.*, 2009).

Daily locations predicted by the movement model were refined using an observational likelihood. The observational likelihood consists in assigning, for each time step, a likelihood value to each grid cell based on the depth and temperature data from the grid and from the tag (Andersen *et al.*, 2007; Pedersen *et al.*, 2008). Under the assumption that cod in the Gulf of St. Lawrence visit the seafloor at least once a day (Righton and Mills, 2008), the daily maximum depth recorded by the tag was considered to correspond to the sea floor and the temperature associated with daily maximum depth was assumed to correspond to the bottom temperature. The depth contribution to the observational likelihood was computed by calculating the cumulative distribution of the Gaussian function $\phi(z; \mu_z, \sigma_z)$ over the interval $[z_1 z_2]$ where z is the daily maximum depth recorded by the tag, μ_z is the grid cell bathymetry, and σ_z is the bathymetry variance of the grid cell. The interval $[z_1 z_2]$ is defined by the tag accuracy of 1%. Similarly, the bottom temperature contribution to the observational likelihood was computed by estimating the cumulative distribution of the Gaussian function $\phi(tp; \mu_{tp}, \sigma_{tp})$ over the interval $[tp_1 tp_2]$ where tp is the daily temperature extracted from the tag, μ_{tp} is the cell bottom temperature, and σ_{tp} is the bottom temperature variance of the grid cell. The interval $[tp_1 tp_2]$ is defined by the minimal accuracy of 0.2°C of the tag temperature sensor.

Temperature and depth are assumed to be independent so that the observational likelihood value for each grid cell equals to the product of the depth and temperature contributions. When the recapture day corresponded to the last sampling day, the observational likelihood of the last day was implemented with the recapture position provided by harvesters and an uncertainty delimited by a 10 km radius circle. A 10km radius circle was considered appropriate for the recapture location uncertainty since the fishery is coastal and conducted

exclusively with fixed gears. Finally, a smoothing filter (backward swept of the estimated probability density) was used to compute the full posterior distribution conditional on all observations (Thygesen *et al.*, 2009).

Seasonal distributions

The density distribution of daily locations estimated with the geolocation model were used to infer seasonal habitats of Atlantic cod in the Northern Gulf of St. Lawrence. Daily density distribution from each individual were normalized and summed over each season. Seasonal distribution for fish exhibiting similar behaviour (migratory vs. resident) were summed and the cumulative distribution of fish location was estimated for each season, thus providing the seasonal utilization distributions (Pedersen *et al.*, 2011).

Periodicities in vertical movements

In order to detect periodicities in the vertical movement of Atlantic cod, spectral analyses using Fast Fourier Transform (FFT) were performed on depth data extracted from tags. Fourier series approximate a function with pairs of orthogonal sine and cosine terms and allow to detect hidden periodicities in a complex signal and to determine their relative importance (Chatfield, 1996). A Hanning window was used to reduce spectral leakage. Spectral analyses were performed for every month using Matlab R2012a signal processing toolbox (Mathwork, Natick, MA). Depth profiles were visually inspected to confirm results from spectral analyses.

Results

Recapture

To date, 14 of the 353 DSTs set were recovered and successfully downloaded, providing a collection of 4843 days of data. Sampling duration varied from 54 to 746 days (Table 1). Size of recaptured fish varied from 49 to 74 cm Fork Length (FL). Nine individuals were recaptured with gillnets and five with longlines. Recaptures were concentrated along the Newfoundland west and southwest coast (NAFO divisions 4R and 3Pn, Figure 1). One individual (#165) tagged in division 3Pn was recaptured in the 3Ps division suggestive of mixing (Figure 1). No fish tagged along Québec north shore (division 4S) were recaptured. Distance between tagging and

recapture locations was shorter than 20 km for eight fish, between 20 and 100 km for three fish, and greater than 100 km for three fish (Table 1).

Individual geolocation, migratory strategies, and seasonal distributions

The 14 DSTs were successfully geolocated using the hidden Markov model. Nine individuals exhibited a migratory behaviour while three individuals exhibited a resident behaviour (Table 2). Two individuals were tracked for a period too short (54 days) to infer any migratory strategy (#165 and #166, Table 2).

The nine migratory individuals displayed similar trajectories. They overwintered in the relatively deep (333 ± 109 m) and warm water ($5.32 \pm 0.5^{\circ}\text{C}$) of the Laurentian Channel (Figures 3, 4 and 5). In the spring, they migrated northward along the slopes of the Laurentian Channel, crossed the cold intermediate layer in April-May, and reached coastal shallow waters (69 ± 52 m) off western Newfoundland for the summer (Figures 3, 4 and 5). In the fall, migratory individuals started their wintering migration towards the Laurentian Channel by following the slope of the Esquiman Channel (Figures 4 and 5). Five of the nine migratory individuals were recaptured at less than 36 km from their tagging location suggestive of homing behaviour. Among this five, two individuals (#12996 and #13036) that were tracked for two years returned to the same area each summer. Estimated values for the diffusivity parameters of the advection-diffusion equation varied from 1.8 to $13.43 \text{ km}^2 \cdot \text{day}^{-1}$ (Table 2).

Three individuals displayed a resident behaviour along the west coast of Newfoundland (Figure 5). They experienced prolonged period of dormancy in shallow ($39 \pm 12\text{m}$) and near freezing ($-0.8 \pm 0.9^{\circ}\text{C}$) coastal waters during the winter and the spring (Figures 3 and 4). During the Summer and the Fall, they displayed localized movements in western Newfoundland (mean Summer depth of $62 \pm 13\text{m}$ and temperature of $4.38 \pm 2.21^{\circ}\text{C}$; mean Fall waters depth of $35 \pm 11\text{m}$ and temperature of $4.82 \pm 2.18^{\circ}\text{C}$). Resident and migratory cod thus mainly differ in their respective winter and spring habitats and share similar summer and fall feeding grounds. Estimated diffusivity values for the three individuals varied from 1 to $1.56 \text{ km}^2 \cdot \text{day}^{-1}$ (Table 2).

Two individuals (#165, #166) were tracked for only 54 days from January 8 to March 3rd 2010 thus preventing to infer any migratory strategy (Table 1). It should be noted that these two individuals overwintered in 1.3°C and 20 m deep water along the southwest coast of Newfoundland (division 3Pn) and both had a brown-red colour characteristic of inshore resident

cod (Gosse and Wroblewski, 2004). Estimated values for the diffusivity parameter were equalled to one for both individuals (Table 2).

Periodicities in vertical movements

Spectral analyses and visual inspections of depth profiles revealed three classes of periodic movements by Atlantic cod in the nGSL. Periodic movements with a frequency of two cycles per day were identified (Table 3, Figures 6a and 6b). This semi-diurnal cycle was the results of the tidal signal observed when fish are distributed on the seabed. This signal was identified during periods of residency and periods of migration (Table 3). It was expressed by resident fish during the prolonged period of inactivity during the winter and the spring, and by some migratory fish during the winter while showing limited vertically activity in the deep layer of the Laurentian Channel (Figure 3). The signal was also expressed by fish #13039 in September while migrating (Table 3).

Periodic movements of one cycle per day suggestive of diel vertical migration (DVM) were also identified. Two classes of DVM appeared: first with fish up in the water column at night DVM, and second with fish up in the water column during the daytime (Figures 6a, 6b, 6c and 6d). DVM with fish up in the water column at night were displayed by some migratory fish during the spring and by some resident fish during the summer (Table 3). Such DVM usually last several days but were not displayed by all cod. DVM could reach several hundred meters in amplitude and were characterized by clear peaks at dawn and dusk (Figure 6d). DVM with fish migrating up in the water column during the day were observed in two situations; in the spring few weeks after the previous pattern of DVM was observed, and in the fall (Table 3).

Discussion

The first objective of the study was to geolocate Atlantic cod equipped with depth and temperature data logger in the Gulf of St. Lawrence. Marine mammals and pelagic fish have previously been tracked with electronic tags in the Gulf of St. Lawrence (Jonsen *et al.*, 2005; Block *et al.*, 2009); however, this is to our knowledge the first tracking of demersal fish equipped with data logger in the Gulf of St. Lawrence. A Hidden Markov Model (HMM) (Pedersen *et al.*, 2008) was used to compute the probability density distribution of daily fish

locations. The flexibility of the HMM allowed us to adapt the observational likelihood of the state-space model in order to exploit fully bathymetry and bottom temperature gradients. The model well reconstructed migration routes for Atlantic cod in the Gulf of St. Lawrence. Bathymetry gradients induced by the presence of channels in the Gulf was the most helpful environmental feature to geolocate semi-demersal species in the Gulf. As expected, the model suffers in areas with lower depth and temperature gradients such as within the deep layers of the Laurentian Channel. This is detrimental for a very accurate identification of cod wintering grounds and it prevents from tackling issues of winter mixing with adjacent 3Ps stock. Studies on the geolocation of Atlantic cod in similar estuarine environments (*i.e.* Baltic Sea) used data loggers equipped with salinity probes (Andersen *et al.*, 2007; Neuenfeldt *et al.*, 2007). It is uncertain than salinity will help to improve geolocation accuracy on wintering grounds because of the chemical stability of the Laurentian Channel deep water masses (Petrie *et al.*, 1996).

Several additions to the geolocation model could be considered to improve its accuracy. The temporal resolution of the bottom temperature is currently limited to three months (*i.e.* March, August, and November). June bottom temperature will soon be added to the model. A second and major improvement would be the addition of a fully hidden state to estimate fish movement behaviour within the geolocation model (Patterson *et al.*, 2009; Pedersen *et al.*, 2011). This would add flexibility to the movement process and would allow for new biological inferences on habitat use. Our ongoing attempts to estimate cod migratory behaviour as a new hidden state in the Markov model have so far been unconvincing.

Reconstruction of Atlantic cod movements in the northern Gulf of St. Lawrence resulted in the identification of both migratory and resident strategies. Migratory individuals followed the typical migration pattern for Atlantic cod in the northern Gulf of St. Lawrence (nGSL) with overwintering ground located in the Laurentian Channel (3Pn area), and summer feeding grounds situated along the west coast of Newfoundland (4R area). Five out of eight migratory fish displayed a homing behaviour to their summer feeding grounds. Two of them showed remarkable homing during the two years tracked suggestive of multi-year homing to summer feeding grounds. Cod in the northern Gulf of St. Lawrence were recently documented to display homing behaviour up to three years after release (Tamdrari *et al.*, 2012) and multiyear homing to

a local spawning ground was observed in the neighbouring 3Ps cod population (Robichaud and Rose, 2001).

Three individuals displayed a previously undocumented inshore residency along the west coast of Newfoundland. Some resident individuals were tagged and recaptured at the same date and location as some migratory individuals thus stressing the need for careful interpretation of homing behaviour from traditional tagging data. Resident cod overwintered in near freezing waters. During the winter and the spring, those individuals were barely active and rested on the seabed. In order to survive in near-freezing water during the winter Atlantic cod produce antifreeze glycoproteins, which lower the plasma freezing point and protect the integrity of cell membranes at low temperatures (Goddard *et al.*, 1994). Minimizing swimming activity, as observed in this study, might be another tactic used by Atlantic cod to increase overwinter survival in cold coastal water.

None of the 68 individuals tagged along the Québec north shore in 2008 and 2009 (NAFO division 4S) were recovered. The high natural mortality observed in the population may partly explain the non-recovery of fish tagged in the 4S area (Fréchet *et al.*, 2009). Following the collapse of the stock in the mid 80's early 90's, the 4S contingent was thought to have disappeared (Swain and Castonguay, 2000; Yvelin *et al.*, 2005). Recently, ichthyoplankton surveys revealed the current presence of a spawning component in the western Gulf (Bui *et al.*, 2011), and geostatistical analysis revealed an geographic expansion of the nGSL cod population to its former area in the western Gulf (Tamdrari *et al.*, 2010). Migratory patterns and behaviours of the 4S contingent remain poorly understood. More tagging in this area, or the use of pop-up tags on large adult cod may help in understanding processes for the rebuilding of this spawning component critical to the recovery of the stock (Tamdrari *et al.*, 2010; Bui *et al.*, 2011).

Spectral and visual analyses of depth profiles recorded by DSTs revealed three periodic signals. A semi-diurnal tidal signal revealed periods of seabed association by Atlantic cod (Hobson *et al.*, 2007). Although such signal was mostly associated with winter residency, seabed association was also observed during period of migration, thus suggesting vertical activity is not necessarily correlated with horizontal activity. Similar results obtained in the North-Sea lead to the conclusion that vertical movements cannot define periods of migration or residency (Hobson *et al.*, 2009).

The second periodic signal inferred from depth profile was the occurrence of extensive diel vertical movements (DVM) with fish up in the water column at night. DVM have been long documented for Atlantic cod; however, the amplitude of the DVM observed in this study (close to 200m in some case, figure 5d) remains astonishing. Two behaviours could explained such DVM. DVM could be associated with a foraging behaviour resulting from a bottom-up continuity of DVM exhibited by planktonic organisms. The second hypothesis is that such DVM result from a spawning behaviour (Brawn, 1961; Hutchings *et al.*, 1999). Atlantic cod is thought to form spawning columns at night, which amplitude is related to the height of the water column (Rose, 1993; Fudge and Rose, 2009; Knickle and Rose, 2012). In the northern Gulf of St. Lawrence, similar DVM were identified with acoustic and bottom trawl survey during the spawning season (Ouellet *et al.*, 1997; McQuinn *et al.*, 2005). Similarities in timing and depth profiles suggest that the hypothesis of a spawning behaviour is most plausible.

The third periodic signal observed in depth profile was DVM with fish up in the water column during daytime. A speculative hypothesis behind such behaviour could be that cod are scooting for orientation clues. Ongoing work to geolocate precisely where those three periodic signals were display would help in their interpretation. Current developments in fish tagging technology offer new opportunities to identify the ecological factors that govern fishes DVM (Metcalf *et al.*, 2009; Bestley *et al.*, 2010).

Identification of resident and migratory strategies validates our original hypothesis of partial migration in the nGSL cod population and raises the question about the ecological drivers that regulate variation between individuals in their propensity to migrate? Migration occurs when moving to another habitat increases fitness despite risks of migrating. As in many other populations, migration in the nGSL cod population is thought to have evolved as a response to seasonality in environmental conditions. The Gulf of St. Lawrence represents the southernmost regular annual limit of sea ice extent in the north Atlantic (Benoît *et al.*, 2012). The timing and the extent of the wintering migration of nGSL cod is be governed by ice formation and decrease in water temperature (Fréchet 1990; Castonguay *et al.*, 1999). Inshore summer migration is governed by density dependent and independent processes including population biomass, temperature, and capelin distribution (Rose and Leggett, 1989; Tamdrari *et al.*, 2011).

Two costs for migration are the energy expenditure required to travel several hundreds of kilometres and the increased risks of predation due to higher visual exposure to predators. Benefits associated with migration are warmer wintering temperature and the presence of numerous congeners. Warmer temperature experienced in the deep layer of the Laurentian Channel facilitates the gametogenesis thus potentially benefiting migratory individuals reproduction compare to resident individuals (Kjesbu, 1994). Warmer temperature experienced during the winter also limits the energy requirement for maintenance functions and increases somatic growth (Lambert and Dutil, 1998), two other factors benefiting migratory individuals. In the spring, migratory individuals form large mono-specific spawning aggregation (Ouellet *et al.*, 1997). Spawning aggregations are thought to benefit reproduction due to higher mate availability to match individual preferences and higher fertilization success (Rowe *et al.*, 2004; Rowe *et al.*, 2007).

Using depth and temperature recorded by data-storage tags implanted in individual cod, we concluded that the partial migration theory is relevant to the dynamics of the nGSL Atlantic cod population. Indeed, the reconstruction of migration routes revealed the presence of migratory and resident behaviours in the population. Cod migratory behaviours were complex and characterized in some individuals by diel vertical movements suggestive of partial diel vertical migration. It is important to consider such contingency in current estimation of population abundance and in future spatial management plans. Several ecological trade-offs associated with migration and residency may act as ecological drivers for partial migration. The small number of cod recaptured limits population inferences and prevents a complete understanding of ultimate mechanisms that promote partial migration in the population. Understanding such mechanisms may help predict population responses to ongoing environmental changes.

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Tables and Figures

Table 1. Tagging and recapture information for 14 Atlantic cod tagged with DSTs. Asterisks indicate individuals for which the tag stopped recording before the recapture date. Distance between tagging and recapture location corresponds to the great-circle distance calculated using the haversine formula.

		Tagging				Recapture						
Fish ID	Tag Series	Date	Fork Length (cm)	Latitude (°N)	Longitude (°W)	Date	Fork Length (cm)	Latitude (°N)	Longitude (°W)	Days at liberty	Days of data	Distance (Km)
12996	LTD_1100	21/09/2007	65	49.62	-57.97	06/10/2009	71	49.65	-58.00	746	746	4
12998	LTD_1100	26/09/2007	58	49.62	-57.97	22/08/2008	63	49.61	-57.97	331	331	1
13012	LTD_1100	21/09/2007	63	49.62	-57.97	10/07/2008		51.10	-57.14	293	293	175
13036	LTD_1100	26/09/2007	49	49.62	-57.97	22/07/2009	57	49.42	-58.35	665	665	35
13039	LTD_1100	18/08/2007	60	51.43	-56.60	02/08/2008	62	51.61	-55.50	350	350	79
13363	LTD_1100	31/10/2008	55	49.62	-57.97	21/09/2009		49.69	-58.08	325	325	11
13380	LTD_1100	31/10/2008	61	49.62	-57.97	30/07/2009	65	49.50	-58.15	272	272	18
13388	LTD_1100	23/09/2008	71	49.47	-57.90	30/07/2009	73	49.52	-57.92	310	310	6
128	LAT_1400	07/11/2008	53	47.85	-59.45	26/10/2010	56	47.57	-58.73	718	718	62
423	LAT_1400	07/11/2008	72	47.85	-59.45	19/06/2009	74	49.43	-58.23	224	224	197
586	LAT_1400	31/10/2008	53	49.62	-57.97	14/10/2009		49.59	-58.00	348	348	4
165*	LAT_1500	08/01/2010	52	47.58	-58.91	17/06/2011		47.58	-55.95	525	54	120
166*	LAT_1500	08/01/2010	48	47.58	-58.91	01/08/2010	50	47.58	-58.88	205	54	2
167*	LAT_1500	01/10/2009	52	50.69	-57.43	17/08/2010	49	50.77	-57.33	320	153	10

Table 2. Geolocation statistics of the 14 Atlantic cod tagged with DSTs. M = Migratory. R = Resident. AIC = Akaike Information Criterion.

FISH ID	Track duration (day)	Diffusivity (km ² .day ⁻¹)	Stdev	AIC	Behaviour
12996	746	3.11	0.27	4475.28	M
12998	331	5.27	0.65	2154.42	M
13012	293	1.56	0.25	1903.07	R
13036	665	10.40	0.78	3150.94	M
13039	350	20	1.55	2058.17	M
13363	325	1	0	2763.47	R
13380	272	1	0.81	2171.69	R
13388	310	10	1.87	1557.40	M
128	718				M
423	224	1.80	0.20	1501.27	M
586	348	15	1.59	1489.32	M
165*	54	1	0	235.06	-
166*	54	1	0	243.89	-
167*	153	13.43	1.72	1085.08	M

Table 3. Summary of observed periodicities. DVM(1) = Diel Vertical Movements with fish up at night. DVM(2) = Diel Vertical Movements with fish up during the day. Seabed = seabed residency.

FISH ID	DVM (1)	DVM (2)	Seabed
12996	Apr	Jun	-
12998	-	-	-
13012	-	Nov	Dec-May
13036	May	Jun & Oct	Feb-Apr
13039	Apr	May	Sep
13363	Jul-Aug	-	Nov-Apr
13380	-	-	Dec-Apr
13388	Apr	-	-
128	Jul	Dec	-
423	May	-	-
586	Apr-Jun	-	-
165*	-	-	Jan-Mar
166*	-	-	Jan-Mar
167*	-	-	Jan

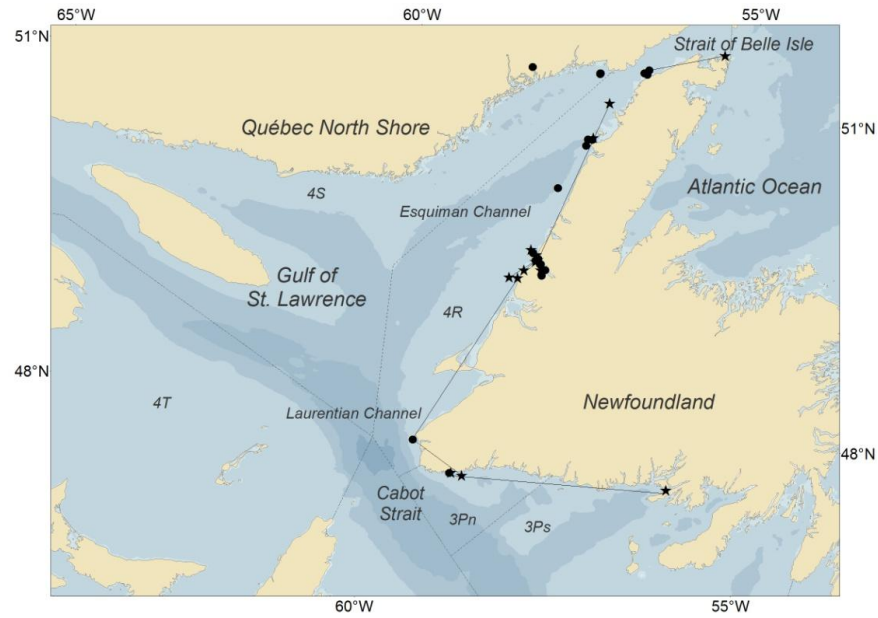


Figure 1. Map of the Gulf of St. Lawrence displaying tagging (circles) and recapture (stars) locations. The dotted lines delimit the Northwest Atlantic Fisheries Organization management units.

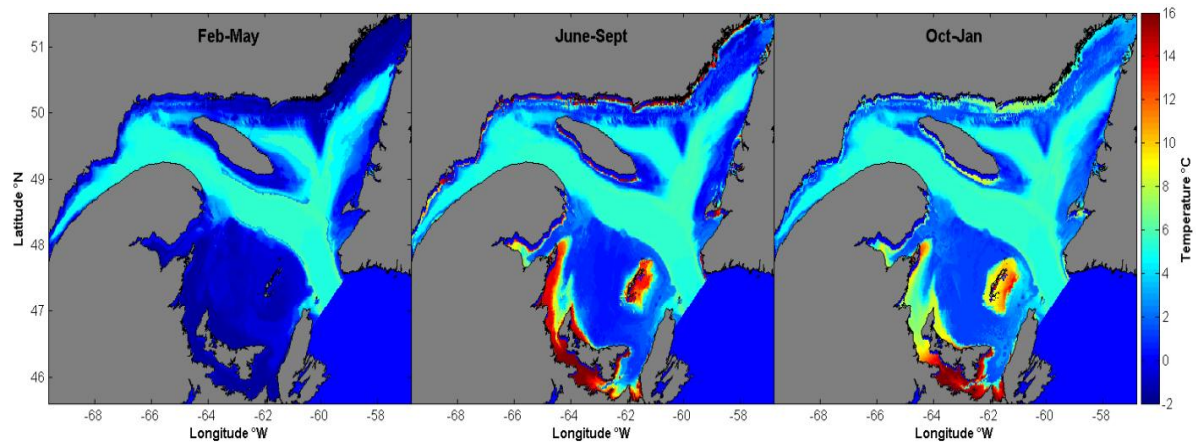


Figure 2. Bottom temperatures in the Gulf of St. Lawrence in 2011.

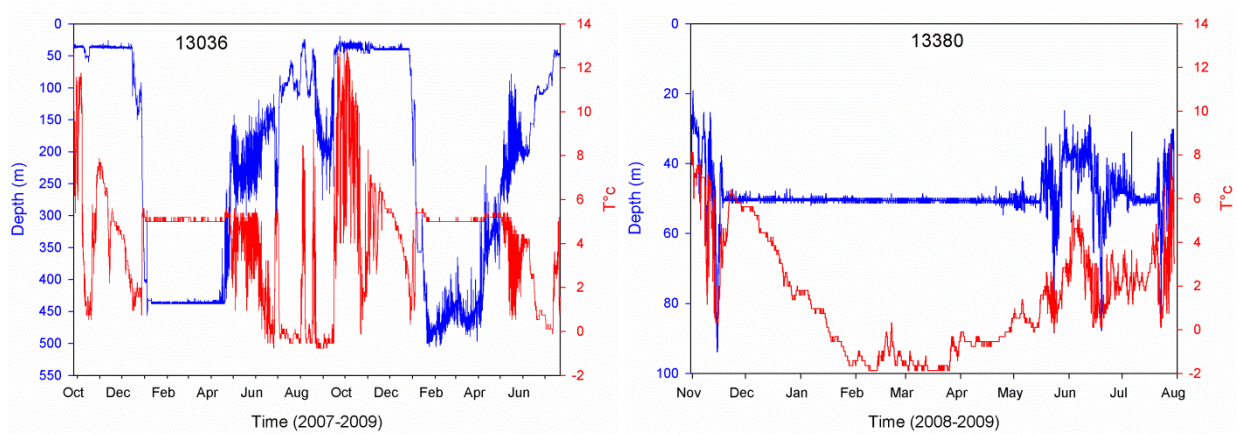


Figure 3. Depth (blue) and temperature (red) profiles of two Atlantic cod. Left: # 13036 classified as migratory. Right: # 13380 classified as resident.

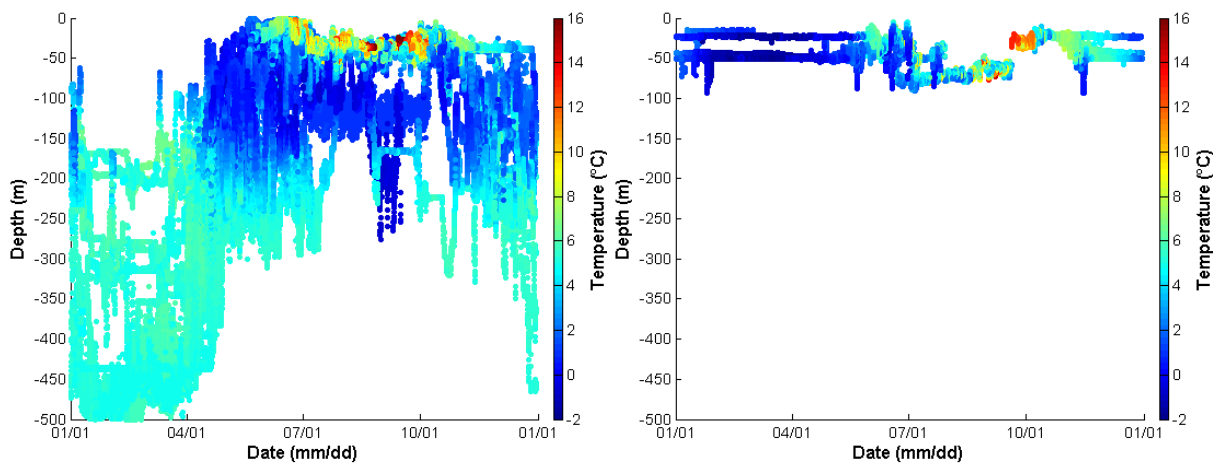


Figure 4. Depth and temperature profiles classified by behaviour. Left: migratory cod (n = 9). Right: resident cod (n = 3).

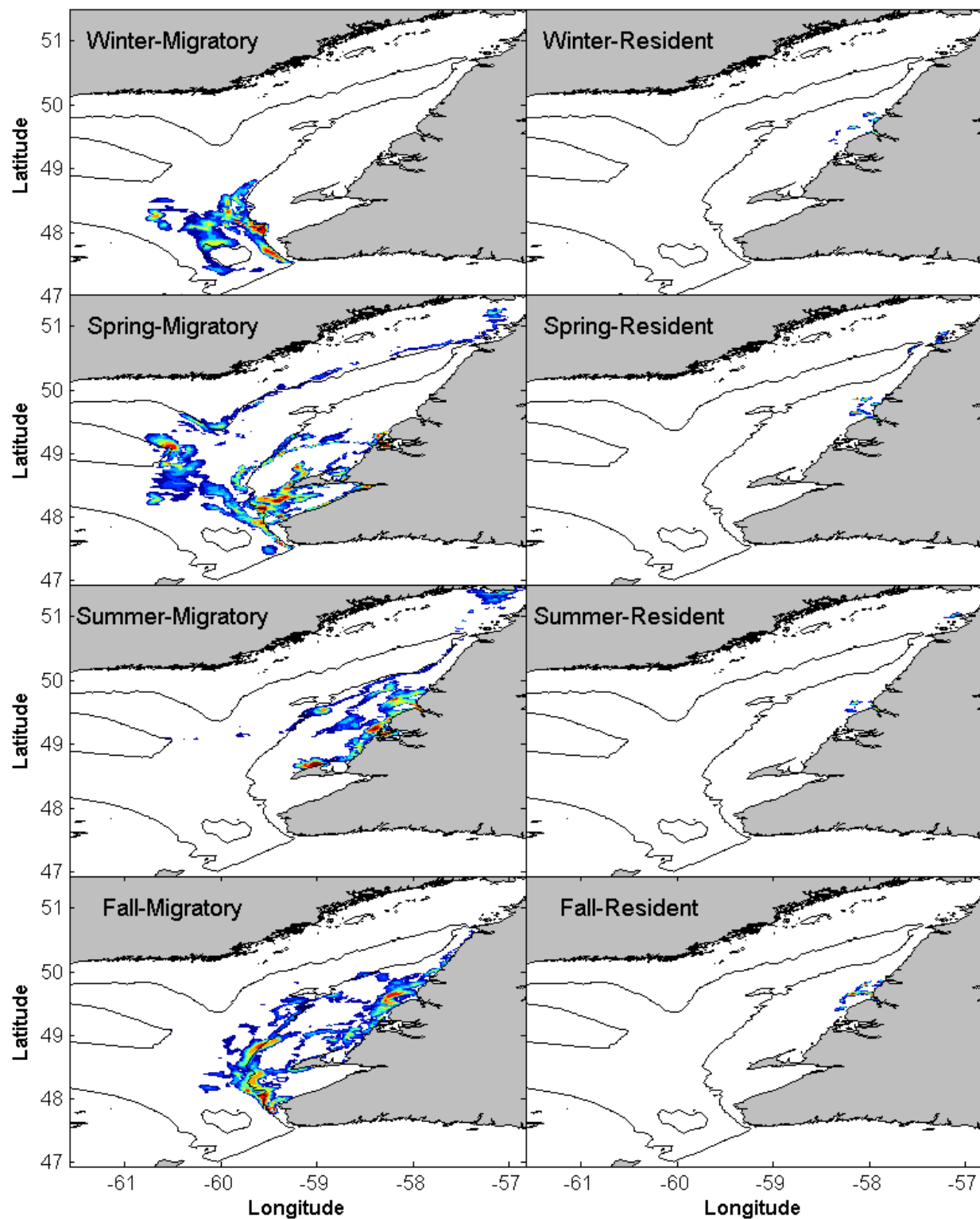


Figure 5. Seasonal utilisation distributions of northern Gulf of St. Lawrence Atlantic cod tagged with DSTs. Left: migratory cod ($n = 9$). Right: resident cod ($n = 3$).

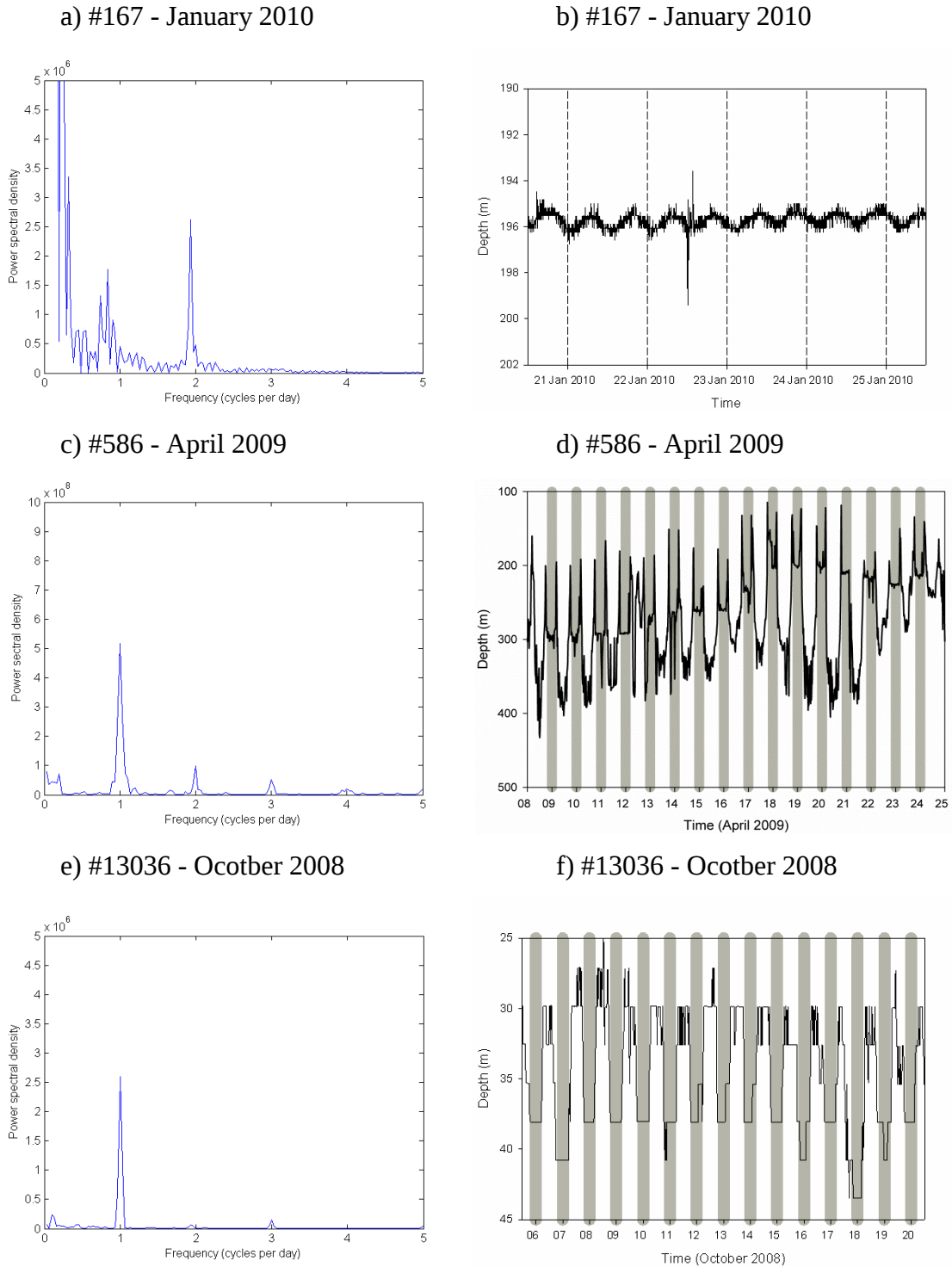


Figure 6. Examples of periodogram (left) obtained from spectral analysis with corresponding depth profile (right) for the three periodic behaviours identified. a) and b) seabed residency ; c) and d) DVM1: Diel Vertical Movements with fish up in the water column at night (grey bars) ; e) and f) DVM2: Diel Vertical Movements with fish up in the water column during daytime.