Vertical movements of Atlantic salmon post-smolts relative to measures of salinity and water temperature during the first phase of the marine migration

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Abstract

The migratory behaviour of hatchery-reared Atlantic salmon (*Salmo salar*) post-smolts during the first phase of the marine migration was examined to assess their susceptibility to salmon lice (*Lepeophtheirus salmonis*) infestations. Swimming depths of eight post-smolts relative to the measures salinity and temperature were monitored for an average of 11.4 hours following release outside the mouth of the Eio River using depth sensitive acoustic transmitters. Vertical salinity and temperature distributions were simultaneously recorded along the migratory route. Mean swimming depth was 1.7 m (individual means 0.5-2.1 m). There were no overall preferences among all the post-smolts for specific salinity concentrations. Typically post-smolts migrated the majority (68%) of their time at salinities less than 20 (brackish water), and as a result outside the reported salinity tolerances of sea lice. Furthemore, post-smolts chose the warmest water layer during their coastal migration.

Introduction

Atlantic salmon (*Salmo salar*) smolts initiate their seaward migration in spring and early summer and travel through near-coastal areas towards the open ocean to feed (Klemetsen, Amudsen, Dempson, Jonsson, Jonsson, O'Connell & Mortensen 2003). The first weeks in the marine environment are critical for their survival, being exposed to new predators, diseases and parasites (Hansen, Holm, Holst & Jacobsen 2003; Heuch, Bjørn, Finstad, Holst, Asplin & Nilsen 2005; Thorstad, Økland, Finstad, Sivertsgård, Plantalech, Bjørn & McKinley 2007). The salmon louse (*Lepeophtheirus salmonis*) is considered a serious marine parasite, and the copepod infests the migrating post-smolts and feeds on their mucus, skin and blood (Johnson & Albright 1991; Finstad, Bjørn, Grimnes & Hvidsten 2000; Heuch *et al*. 2005). A post-smolt carrying more than 11 salmon lice, or 0.75 salmon lice g^{-1} body mass, will likely not survive (Finstad *et al*. 2000; Heuch *et al*. 2005).

Typically found in coastal areas is an overlying brackish water layer from the spring freshet. Several studies have reported that salmon lice tend to avoid water with salinities less than approximately 20 (Heuch, 1995; Bricknell, Dalesman, O'Shea, Pert & Luntz 2006). As a result, brackish water layer may be viewed as an area of refuge from lice infestation for migrating Atlantic salmon post-smolts. However, studies outlining post-smolts coastal migratory behaviour, particularly in response to changes in the water temperature and salinity are severely limited. The objective of this study was to examine the migratory behaviour of post smolts along a section of the coast of Western Norway relative to changes in water temperature and salinity using acoustic telemetry.

Material and methods

The study was conducted in the Hardangerfjord system (mean depth ca. 150 meters, maximum depth 800 meters, 2.0-2.3 km wide in the study area), Western Norway. The system received a continuous freshwater input from rivers in this area, with a maximum in June and July due to snow melt and as a result, an overlying brackish water layer was present during the study period (Fig. 1).

Eight two-year-old hatchery-reared Atlantic salmon smolts from the Lærdal River were tagged with acoustic pressure (depth-sensing) transmitters (model ADT-9-short, 9x34 mm, Thelma, Norway, mass in water/air of 3.3/5.3 g). The smolts had a mean mass of 239 ± 32.0 g and a mean total length of 31.9 ± 3.4 cm (Table 1). Verification of smoltification was determined following a seawater tolerance test on 9 April. Results indicated that mean plasma chloride level of the smolts to be tagged was 146.4 mM at a temperature of 7 ºC and therefore had smoltified (Sigholt & Finstad 1990).

The smolts were tagged using the methods described in Finstad *et al*. (2005) and subsequently placed in a saltwater tank for 1-4 days to recover prior to being transported via a plastic bag to the release site outside the mouth of the Eio River (15-20 minutes transport time). Similar procedures have been used in previous studies, and smolts were observed to initiate migration shortly following release (e.g. Finstad *et al*. 2005, Thorstad, Økland, Finstad, Sivertsgård, Bjørn & McKinley 2004). Tagged smolts were released in batches with 10-15 non-tagged smolts.

Individual post-smolts were manually tracked using a boat with a VR60 receiver (VEMCO Ltd., Canada) for an average of 11.5 hours following release (Table 1). Fish position in the coastal environment was recorded every 10 minutes. Depth was continuously decoded based on the time delay between two successive acoustic pulses. On average, one depth measurement was recorded every 4 seconds. Between 6 and 19 salinity and temperature profiles were taken along the migratory route while tracking individual fish (Table 1, Fig. 2). The number of profiles was dependent on the weather conditions and fish movements. In addition, salinity and temperature measurements were also regularly taken at the actual fish swimming depth during tracking (mean 25 measurements for individual fish, Table 1). Results based on salinity and temperature profiles versus measurements taken at actual swimming depth were analysed separately, and then compared.

Descriptive statistics were based on average values for individual fish. Thus, individuals constituted the independent data points by summarising data for an individual in an average value (single summary approach, see Grafen & Hails 2002), and the basic assumption of independence in statistical analyses was not violated. Detailed results for individuals are additionally presented in table 1 and 2 and Fig. 2.

For analyses based on salinity and temperature profiles, the swimming depth was plotted over contour maps of the vertical salinity and temperature distributions using the program Minitab 14.0 (Fig. 2). Analyses were based on all depth recordings, whereas Fig. 2 is based on values averaged every 5 minutes to improve visualisation. The amount of time the post-smolts positioned themselves above (e.g. in brackish water) and below the isohaline of 20 was measured. The association between swimming depth and temperature distribution was based on the amount of time associated with any particular isotherm. The accuracy of the analyses based on isoline plots was evaluated by comparing the results with analyses of salinity and temperature measurements recorded at the actual fish swimming depth. The number of large amplitude vertical movements of each individual was also counted (defined as ≥ 1-metre movements up and down the water column in less than one minute).

The transmitters were calibrated (conditions: 25 ºC, 1000 hPa) by the manufacturer and any resulting corrections for the atmospheric pressure at the study site were applied hourly at the time when the post-smolts were followed. The transmitters' precision was ± 0.3 m. When acoustic transmitters were tracked manually, the receiver detected noise from e.g. other boats and the shoreline. Subsequently, values indicating a vertical velocity greater than 1 m s^{-1} were interpreted as acoustic noise and eliminated.

Results

The migration distance of the post-smolts from the release point at Eio River mouth to where the tracking stopped was on average 8.7 ± 3.4 km (Table 2). The post-smolts did not follow the shortest migration route; the mean distance from the release point to the outermost recording was 3.4±1.8 km, giving a mean migration efficiency of 39%. The average ground speed for individuals was 0.7 ± 0.2 bl s^{-1} (Table 2).

The mean swimming depth was 1.7 m (range of individual means: 0.5-2.1 m) (Table 1). The deepest recording for any individual was 5.6 m. The post-smolts performed an average of

2.1 (range of individual means, 0.7-3.5) large amplitude vertical movements per hour (Table 2).

The mean salinity where the post-smolts migrated was 19 (range of individual means, 18-23) and the mean temperature was 11.0 ºC (range of individual means, 9.5-12.0 ºC) (Table 1). There were differences among individuals in the salinity and temperature where they migrated (univariate ANOVA, salinity: $F = 4313.9$, $P < 0.001$, temperature: $F = 39.4$, $P < 0.001$). Based on isoline plots, the fish were swimming in brackish water (salinity < 20) on average 68% of the time (range of individual means, 25-100%) (Fig. 2, Table 2). The fish intersected the isohaline of 20 an average of 1.8 times h^{-1} (range of individual means, 0.0-8.4, Table 2). Based on the salinity recordings at the actual fish swimming depth, the post-smolts migrated in salinities < 20 on average 61% of the time (Table 1), which is similar to the results obtained based on isohalines (68%, see above). The post-smolts migrated on average 86% (range of individual means: 72-96%) of the time through the warmest water layer available in the first meters of the water column (Fig. 2, Table 2).

Discussion

The proportion of time that the post-smolts swim in brackish water (salinity < 20) versus at higher salinities may be viewed as a significant measure of the risk of infestation from sea lice for coastal migrating post-smolts. This study showed that Atlantic salmon post-smolts were swimming primarily in the top 1-3 m of the water column during the first hours after release into the fjord, where the salinity was mostly below 20. By using the low-salinity water layers, the post-smolts were likely more protected from salmon lice infestations than if they had migrated in the high salinity deep water layers.

The post-smolts did not seem to follow isohalines over longer periods, and due to variation in swimming depth during their migration, they frequently crossed isohalines. Further, the individual variation was large, and the salinity at the post-smolts' swimming depth varied significantly among individuals. Results indicated that there were no overall preferences among all the post-smolts for specific salinities.

The post-smolts migrated most of the time through the warmest water layer available. In studies of caged adult salmon, temperature preferences were observed, as salmon schooled at the maximum temperature available (e.g. Reddin, Friedland, Downton, Dempson & Mullins 2004; Oppedal, Juell & Johansson 2007). Temperature has been suggested as an important factor regulating the physiology of fishes, and distribution along a narrow temperature range may improve their metabolic processes (Oppedal *et al*. 2007). However, it is also possible that migration in the warmest water layer did not simply reflect a temperature preference, but simply a preference for migrating close to the surface for other, unknown reasons.

If there is a general tendency of post-smolts to swim in the upper 1-3 m of the water column regardless of salinity, the magnitude of freshwater input to near coastal areas may affect the salmon lice infestation risk for out-migrating post-smolts. The post-smolts will be more protected against salmon lice the further out the brackish water layer extends. This is of obvious importance for management in areas where large rivers are regulated for hydro power purposes. The water discharge, and hence the freshwater input to coastal areas, may be highly reduced during the post-smolt migration because reservoirs that have been emptied during winter are being replenished. Hence, a reduced water discharge in rivers during the post-smolt migration may increase the susceptibility of coastal migrating salmon smolts to infestation from sea lice.

The post-smolts showed a vertical migration pattern characterized by small and large (≥ 1-metre movements up and down the water column in less than one minute) amplitude vertical movements, experiencing changes in the water column salinity and temperature as they changed swimming depth. The reason for these movements is not well understood. For adult Atlantic salmon, it has been hypothesized that they perform vertical movements to search for prey, avoid predators and to recognize the way to their natal stream (Westerberg 1982; Døving, Westerberg & Johnsen 1985; Reddin *et al*. 2004).

Ground speeds recorded in this study (average: 0.7 bl s^{-1}) were slower than those recorded in another fjord system in Norway (Thorstad *et al*. 2004; Økland, Thorstad, Finstad, Sivertsgård, Plantalech, Jepsen & McKinley 2006). Differences among studies may be due to differences in current speeds, fjord characteristics, or in the fish stock origin. Slower ground speeds may have consequences for survival, as they spend longer time in fjords and coastal areas where the predation pressure may be high (e.g. Jepsen, Holte & Økland 2006), and where the vulnerability to salmon lice may be high due to extensive fish farming (e.g. Bjørn, Finstad & Kristoffersen 2001; Tully, Gargan, Poole & Whelan 1999).

Handling and tagging may influence the behaviour and swimming performance of the fish. For Atlantic salmon post-smolts, Moore, Lacroix & Sturlaugsson (2000) recommended tags to be less than 5% of fish mass to minimize effects on behaviour and survival. In the present study, this ratio (1.7-2.9%) was well below the above recommendation.

There has been a general lack of information on swimming depths of Atlantic salmon post-smolts. Unfortunately, the pressure transmitters available are too large to be implanted in wild Atlantic salmon smolts, and hatchery-reared smolts were therefore used. The possibility that wild and hatchery-reared post-smolts differ in their vertical migration behaviour cannot be completely ruled out, but these groups did not differ in other behavioural aspects during this phase of the marine migration (Økland *et al*. 2006; Thorstad *et al*. 2007).

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Table 1. Atlantic salmon post-smolts tagged with depth sensing acoustic transmitters and manually tracked outside the River Eio. Results on swimming depth, as well as salinity and temperature recorded at actual swimming depth, are also given.

Fish number	L_T (cm)	Body mass (g)	Release date (dd/ mm/yy)	Release time (hh:mm)	Hours followed	Number of salinity and temperature profiles taken during tracking	Number of salinity and temperature measurements recorded at actual fish depth (% of records at salinity < 20)	Mean swimming depth (m) (s.d., range)	Mean salinity recorded at actual swimming depth (s.d., range)	Mean temperature recorded at actual swimming depth (ºC) (s.d., range)
1	30.7	241	10/05/06	11:12	12:00	12	16 (36%)	0.5 (0.6, 0.1-1.7)	22 (6.6, 9-31)	10.0 (1.2, 7.0-14.0)
2	39.5	223	11/05/06	11:00	06:45	7	10 (90%)	1.9 (0.3, 0.4-2.6)	18 (9.2, 0-30)	9.5 (1.3, 5.5-10.5)
3	30.2	229	15/05/06	10:40	12:25	17	30 (53%)	1.7 (0.3, 0.9-2.6)	20 (5.4, 5-28)	10.5 (0.7, 7.5-12.0)
4	31.7	257	20/05/06	14:40	12:00	15	15 (33%)	0.9 (1.1, 0.0-5.6)	23 (3.1, 13-29)	12.0 (1.1, 9.0-13.0)
5	32.2	291	26/05/06	11:17	12:00	19	25 (36%)	2.1 (0.6, 0.0-3.4)	18 (6.0, 3-29)	10.0 (0.8, 10.0-11.0)
6	27.7	185	28/05/06	09:30	12:00	10	38 (100%)	1.7 (0.7, 0.1-3.4)	18 (7.4, 5-29)	10.0 (0.9, 8.0-11.0)
7	31.5	262	29/05/06	10:00	12:00	6	44 (100%)	1.7 (0.2, 0.4-2.4)	18 (4.5, 5-28)	11.5 (0.8, 8.5-12.5)
8	31.5	221	30/05/06	10:00	12:00	10	21 (38%)	2.0 (0.5, 0.4-2.2)	18 (6.7, 4-29)	11.0 (1.2, 7.5-14.0)
Mean (s.d.)	31.9 (3.4)	239 (32.0)			11:23 (1:52)	12 (4.7)	25 (61%) (11.8)	1.7 (0.8)	19 (3.0)	11.0 (1.0)

Table 2. Distance migrated, speed and vertical movements of Atlantic salmon post-smolts tracked outside the River Eio. Percentage of time the post-smolts spent in salinities < 20, percentage of time close to the highest available water temperature, and times per hour the post-smolts crossed the 20 isohaline are based on the isolines calculated from salinity and temperature profiles taken during tracking of individual fish.

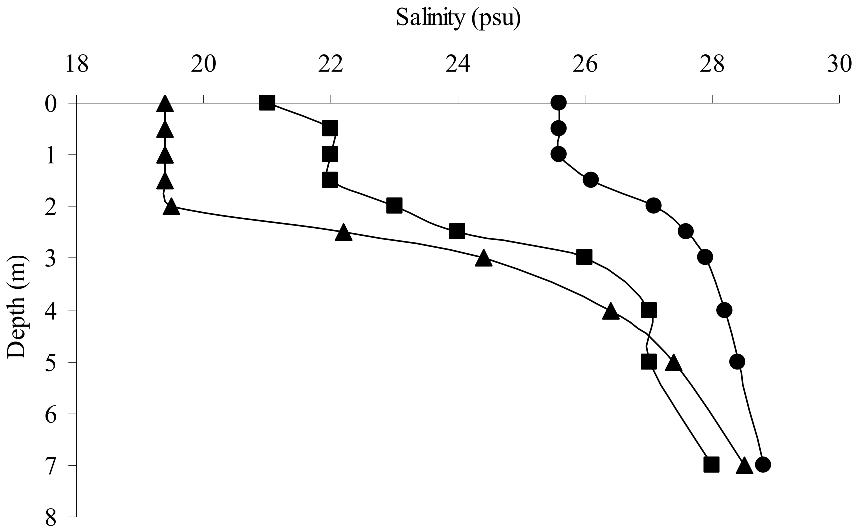
Fish number	Total distance migrated (km)	Distance from release site to outermost point in straight line (km)	Ground speed (km h^{-1})	Ground speed (bl s^{-1})	Percentage of time the post-smolts spent in salinities < 20	Percentage of time the post-smolts spent close to the highest available water temperature	Times $hour^{-1}$ the post-smolts crossed the 20 isohaline	Total number of large amplitude vertical movements	Maximum amplitude of vertical movements (m)
1	9.7	2.8	0.8	0.7	34	80	0.4	37	2.5
2	3.1	0.9	0.5	0.3	99	84	0.3	21	2
3	10.1	2.6	0.8	0.8	82	72	1.7	11	1.5
4	6.8	3.2	0.6	0.5	39	94	1.1	17	2.3
5	7.6	3.1	0.6	0.6	65	94	8.4	28	1.7
6	14.4	6.6	1.2	1.1	25	90	2.2	14	1.5
7	10.8	5.4	0.9	0.9	100	82	0.0	42	2.7
8	6.8	2.4	0.6	0.5	100	96	0.0	8	1.7
Mean	8.7	3.4	0.7	0.7	68	86	1.8	22.3	2.0
(s.d.)	(3.4)	(1.8)	(0.2)	(0.3)	(32)	(3)	(2.8)	(12.3)	(0.5)

Figure legends

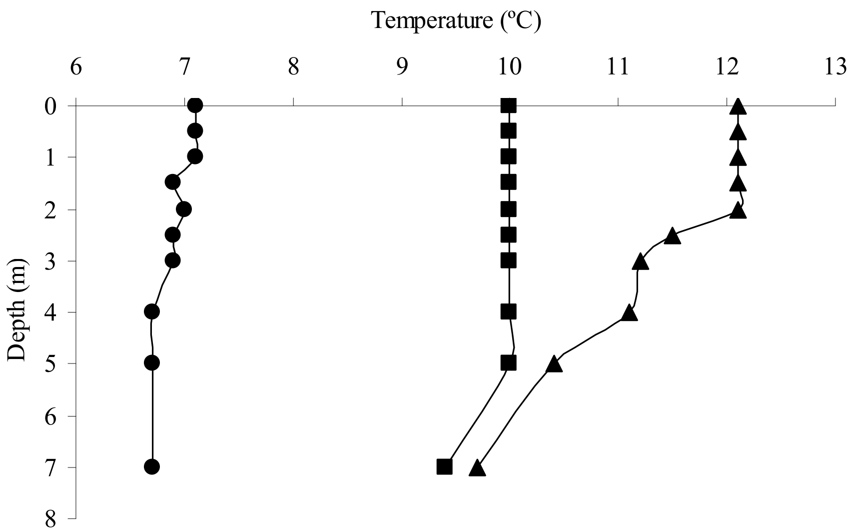
Figure 1. Salinity (a) and temperature (b) profiles in the middle of the fjord of the study area during the study period (● = 27 April, ■ = 19 May, ▲ = 31 May).

Figure 2. The post-smolts' swimming depth during tracking plotted over the contour maps of salinity (left) and temperature (right). Depth data is averaged every 5 minutes to improve visualisation. The dots indicate time and depth where salinity and temperature profiles were taken along the migratory route during tracking. The isohalines were drawn with a spacing of 2 and the isotherms with a spacing of 1 or 0.5 ºC. The thick continuous line represents the depth of the post-smolt released on the date indicated in the right corner. Time scale shows local time.

a)


Salinity (psu)
18
20
22
24
26
28
30
0
1
2
3
4
5
6
7
8
Depth (m)

b)


Temperature (ºC)
6
7
8
9
10
11
12
13
0
1
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7
8
Depth (m)

Figure 1.

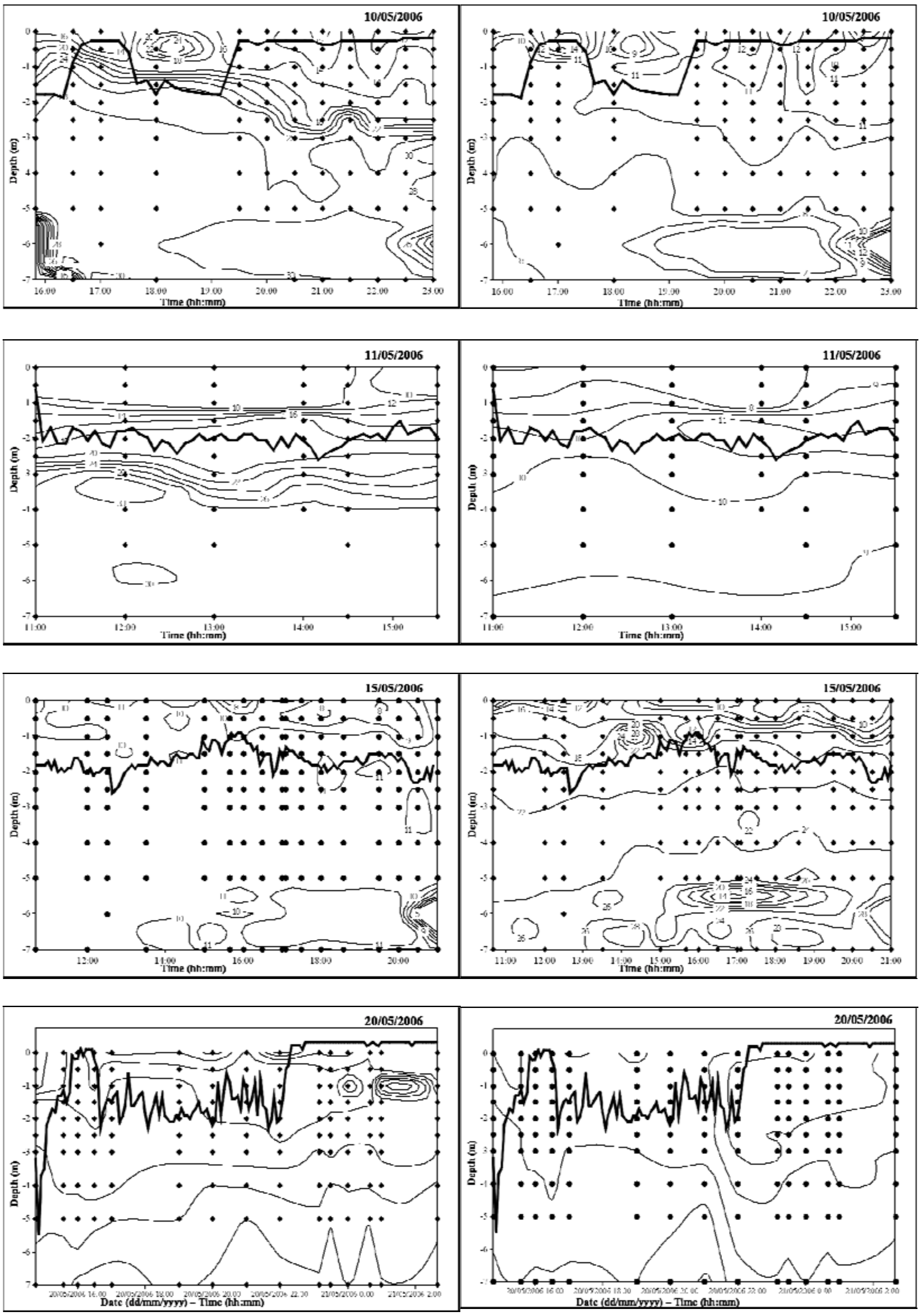
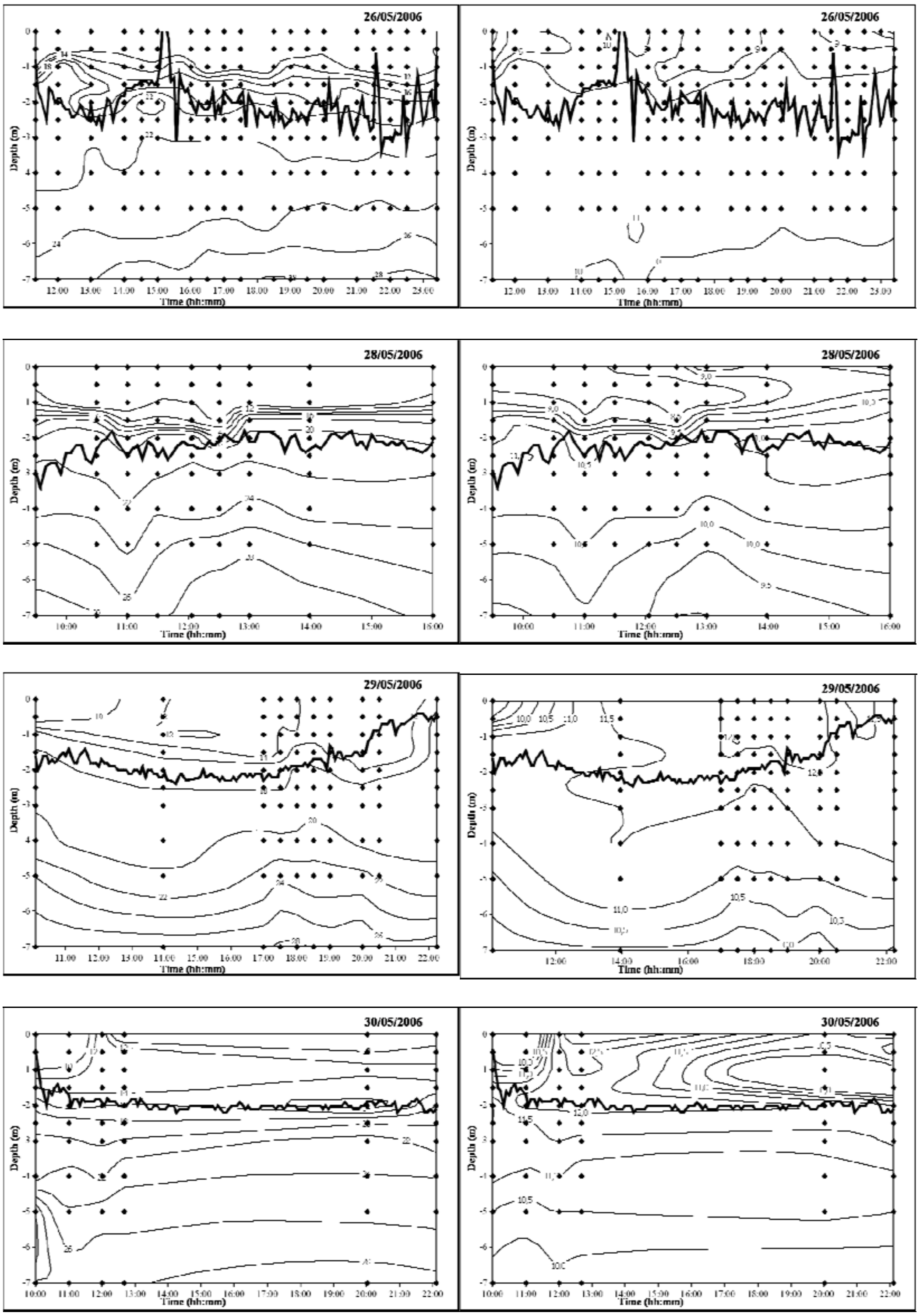


Figure 2 (continues on next page).


26/05/2006
26/05/2006
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Depth (m)
Time (hh:mm)

Figure 2.