Movement and environmental preferences of Greenland sharks (*Somniosus microcephalus*) electronically tagged in the St. Lawrence Estuary, Canada

Michael J. W. Stokesbury[1,2*], Chris Harvey-Clark[1], Jeffrey Gallant[3], Barbara A. Block[2], Ransom A. Myers[1]

[1] Department of Biological Sciences, Dalhousie University, 1344 Oxford St., Halifax, Nova Scotia, Canada, B3H 4J1

[2] Tuna Research and Conservation Center, Stanford University, Hopkins Marine Station, Oceanview Boulevard, Pacific Grove, CA 93950, USA

[3] Greenland Shark and Elasmobranch Education and Research Group (GEERG) P.O. Box 483, Drummondville, Quebec, Canada, J2B 6W3

* To whom correspondence should be addressed. E-mail: mstokesb@dal.ca

Running head – Environmental preferences of the Greenland shark

Abstract

Three Greenland sharks (*Somniosus microcephalus*) were tagged with electronic tags, in Baie St. Pancrace, St. Lawrence Estuary, Quebec, Canada. One shark was tagged on 23 July 2004, with an acoustic telemetry tag. Two sharks were each tagged with a pop-up satellite archival tag (PSAT) on 27 August 2004. Two of the sharks remained in, or close to the bay, one for 47 days and the other for at least 66 days. The third shark left the bay immediately after tagging on 27 August 2004. This shark entered the main channel of the St. Lawrence Estuary, and had moved 114.9 km upstream by 1 November 2004 when the tag reported to ARGOS satellites. The tags provided a total of 179 days of data on the movement and environmental preferences of Greenland sharks in the St. Lawrence Estuary. Sharks that reported depth and ambient water temperature data from the bay showed significant diel differences in depth preferences and corresponding ambient temperatures. The sharks remained near the bottom of the water column during the day and displayed increased vertical movements at night. The shark that resided in the main channel did not show this pattern, but generally remained at deeps between 325 and 352 m. Sharks in the bay experienced water temperatures that ranged from -1.1 to 8.6 °C at depths from 0 to 67 m. In the main channel the shark experienced temperatures that ranged from 1.0 to 5.4 °C at depths from 132 to 352 m. This is the first report of numerous Greenland sharks inhabiting shallow near shore bays during summer and autumn.

Key Words – Greenland shark, depth, temperature, Vemco, tagging

Introduction

Greenland sharks (*Somniosus microcephalus*) are the only non-lamnid sharks known to live in polar waters. They can reach a total length of 7 m (Compagno 1984) and a mass of over 1000 kg (Bigelow and Schroeder 1948). Length at maturity is not known, however, adolescent sharks have been recorded as large as 311 cm total length (Beck and Mansfield 1969). They are present in the Northern hemisphere in the Atlantic Ocean, Arctic Ocean and range into southern latitudes, occupying deep waters as far south as off Georgia, United States (Herdendorf and Berra 1995).

Greenland sharks are primarily considered a benthic species, however incidental catches and sightings indicate they occupy a broad depth niche (Beck and Mansfield 1984, Herdendorf and Berra 1995). They have been taken by harpoon at the surface (Beck and Mansfield 1969), captured in the pelagic zone (Kondyurin and Myagkov 1982) and recorded by a submersible at 2,200 m (Herdendorf and Berra 1995). These sharks also display a cold thermal tolerance not evident in many sharks, as they have been tracked in ambient water temperatures below -1.5 °C (Skomal and Benz 2004).

Greenland sharks are present under land fast ice in the Canadian Arctic where they have been previously tracked using acoustic tags (Skomal and Benz 2004). In the earlier study, six sharks were tracked using tags with pressure sensors for up to 42.8 h. Although no significant depth or temperature preferences were reported, the authors did note that the sharks appeared to remain at deeper depths during the morning than in the afternoon and evening (Skomal and Benz 2004).

Studies of stomach contents (Beck and Mansfield 1969) and anthropogenic contaminants and stable isotopes (Fisk et al. 2002) of Greenland sharks, indicate that they feed on a wide variety of prey. In the Canadian Arctic, they feed upon pelagic and benthic fishes and invertebrates, and marine mammals (Beck and Mansfield 1969; Fisk et al. 2002). Fisk et al. (2002) proposed that Greenland sharks feed in the pelagic zone at the same trophic level as turbot (*Reinhardtius hippoglossoides*) and ringed seals (*Phoca hispida*), and at a higher trophic level than harp seals (*Pagophilus groenlandicus*).

Although several studies have identified their prey, the movements, environmental preferences and general life history of Greenland sharks are largely unknown. In this study we electronically tagged three Greenland sharks, using two types of electronic tagging technology. From these data, we report the movement and environmental preferences of Greenland sharks from the St. Lawrence Estuary, Canada.

Materials and methods

Greenland sharks were tagged in Baie St. Pancrace (49.288° N, 68.049° W), Province Quebec, Canada. This small bay (approximately 250 m wide and 500 m long) is located on the north shore of the St. Lawrence Estuary. It has steep walls that drop to a maximum bottom depth of 67 m. In this region the St. Lawrence Estuary is approximately 40 km wide, and has a maximum depth of approximately 350 m.

All three tags were attached to the Greenland sharks by divers using SCUBA. An acoustic telemetry tag (Vemco Ltd. V16) was applied using a sling type spear with a stainless steel barb on the end. Attached to the barb was a 10 cm long piece of stainless steel monofilament, 90.9 kg test, looped and crimped at the other end. This cable was attached to a reinforced loop of nylon connected to the transmitter. The tag transmitted pressure and depth data alternately, at 69 kHz, approximately every 30 seconds. A receiver (Vemco Ltd. VR 60) with an omni-directional hydrophone was used to initially locate the tagged shark. When the shark was located, a receiver (Vemco Ltd. VR 2) was suspended on a mooring 10 m above the bottom of the bay in which the shark was present. A minimum detection radius of 605 m was determined for the VR2 receiver. Data from the VR 2 receiver were downloaded to a laptop computer using a Vemco Ltd. VR 1 PC interface.

Pop-up satellite archival tags (PSATs) were applied using a stainless steel spear tipped with a titanium barb. A 10 cm length of 136.4 kg test monofilament, covered in shrink wrap was attached to the barb using a crimp. Attached to the monofilament was a Wildlife Computers PSAT (hardware PAT4, software 4.01e). The tags provided an end point location based on the Doppler shift of the tags' radio transmission to the Argos satellites (root mean square error of < 350 m; Taillade 1992). PSATs measured and archived, light level, ambient temperature and pressure at 60 s intervals. Also, depth and temperature data were summarized into 12 h bins prior to transmission approximating a day-night cycle. PSATs were programmed to release at 0800 Eastern Standard Time, on 1 November 2004.

Daily mean time-at-depth and time-at-temperature profiles for satellite tagged sharks were generated for each 12 h bin, by multiplying the middle value of each histogram bar by the number of observations in that bar, then dividing this value by the total number of observations included in the histogram.

Results

Three Greenland sharks were electronically tagged in the St. Lawrence Estuary. One shark was tagged with an acoustic telemetry tag and two sharks were tagged each with one PSAT. In total, the tags provided 179 days of data on Greenland shark movement and environmental preferences.

One Greenland shark was tagged with acoustic telemetry tag number 32 (Table 1) in Baie St. Pancrace, PQ, Canada, on 23 July 2004 (Fig. 1). Collection of data from this tag began on 27 July 2004 when a VR2 receiver was moored in Baie St. Pancrace. The tag reported data on ambient temperature and pressure for 47 days. Data indicate that shark 32 occupied deeper waters in the bay during the daylight hours then at night when it moved throughout the water column (Fig. 2a). This is corroborated by ambient water temperature data as the shark experienced a very narrow range of colder temperatures during the day and a more broad range of temperatures during the night (Fig. 2c). For the first 4 weeks of the track, the shark spent the majority of its time at depths below 30 m (Fig. 3a). During this time the deeper water temperatures remained consistently at or below 1 °C. However, in the fourth and fifth weeks (Fig. 3b) the shark spent more of its time in mid-water and deeper depths. By this time the upper water column had warmed and the shark was experiencing water temperatures of 2 to 3 °C in the middle of the water column (Figs. 4). The daily depth and temperature profile for this shark indicated multiple vertical movements throughout the bottom and middle portions of the water column (Fig. 5). Interestingly, the shark did not spend much time at the shallower depths, but reached a shallow point and immediately reversed and started its descent, as indicated by the sharp peaks on the depth distribution (Fig 5).

There were 176 instances (Mean = 1:21h; SD = 0.12; Max = 20:05h) when Greenland shark 32 was not recorded by a receiver for more than 30 minutes, between 28 July and 8 September 2004. These periods likely represent departures from the bay. Then the shark left the bay on 8 September 2004 at 22:38 h only to return for approximately 10 minutes on 26 September 2004. The shark was not detected from this time until removal of the receiver from Baie St. Pancrace on 1 November 2004.

Two Greenland sharks were each tagged with a PSAT, in Baie St. Pancrace, on 27 August 2004 (Table 1). Tag number 166 was attached to a female shark and tag number 581 was attached to a male shark (Table 2). The two tags each reported on the preprogrammed day, 66 days later on 1 November 2004. Tag 166 reported from Baie St. Pancrace (Fig. 1). Tag number 581 reported from 48.504° N 69.080° W, a position in the main channel of the St. Lawrence Estuary, 114.9 km to the south west (upstream) of the tagging location (Fig. 1).

Shark 166 spent the daylight hours at significantly deeper depths than the nighttime hours (paired *t*-test, $p = < 0.01$) (Fig. 6). Also, ambient temperatures experienced by the shark were significantly cooler during the day than during the night (paired *t*-test, $p = 0.04$). The shark experienced cold bottom temperatures from 27 August 2004 until 11 October 2004 when the minimum ambient water temperatures began to increase (Fig. 6).

Depth data (Fig. 7) indicate that Greenland shark 581 departed the bay on the day it was tagged. This shark exhibited no significant difference between daytime and nighttime mean depth (paired *t*-test, $p = 0.29$) or mean temperature (paired *t*-test, $p = 0.25$) (Fig. 7). The maximum depth recorded by this tag was 352 m (Table 2). The minimum depth recorded by the tag was 132 m, which occurred on two occasions, and the modal depth was 326 m. The minimum depth recorded corresponds with the coldest temperatures that the tag recorded, 1 °C. This shark spent the majority of its time at depths deeper than 250 m and at temperatures between 4 and 6 °C, with very little difference in night and day, depth distribution (Fig. 7).

Temperature and salinity profiles for the water column in the St. Lawrence Estuary taken by CTD casts between 48.580° N, 68.490° W and 48.830° N, 68.750° W on 8 June 2004 by the Department of Fisheries and Oceans, Canada, are shown in Figure 8. Corroborating the depth and temperature data from tag 581, this profile indicates that the shark resided in a highly saline deep water layer, with temperatures between 4 and 6 °C.

Discussion

This study provides 179 days of behaviour and environmental data on a sub-polar species of shark of which there is little known. While in Baie St. Pancrace, tagged Greenland sharks displayed diel depth differences. The sharks occupied mostly demersal waters during the day, and moved throughout the water column at night. Similar diel patterns were observed in a megamouth shark (*Megachasma pelagious*; Nelson et al. 1997), bigeye thresher sharks (*Alopias superciliosus*; Weng and Block 2004, Ward and Myers in Press) and school sharks (*Galeorhinus galeus*; West and Stevens 2001). Diel patterns were not found in sixgill (*Hexanchus griseus*) blue (*Prionace glauca*), crocodile (*Psuedocarcharhinus kamoharai*), oceanic whitetip (*Carcharhinus longimanus*), shortfin mako (*Isurus oxyrinchus*) and silky sharks (*Carcharhinus falciformis*) (Ward and Myers in Press) or Greenland sharks tracked under land fast ice (Skomal and Benz 2004). However, the tracks of the sharks under land fast ice were short (5-48h) and although no significant depth preferences were reported, the observed shift from deep depths in the morning to shallower depths in the afternoon and evening (Skomal and Benz 2004) are consistent with our findings. No diel depth pattern was demonstrated by the shark that moved into the main channel of the St. Lawrence Estuary. This is likely a result of the shark residing below the photic zone (depth > 300m). As Greenland sharks demonstrated diel depth differences in the shallow bay, but did not at greater depth in the main channel of the St. Lawrence Estuary, they may be demonstrating an aversion to light as has been proposed for sixgill sharks (Bigelow and Schroeder 1948; Compagno 1984).

The cold thermal tolerance displayed by the Greenland sharks in this study (< 1 °C) and under land fast ice (< -1 °C; Skomal and Benz 2004) is not a common trait in shark species, even inside of *Squalidae.* For example, other bottom dwelling squaloid sharks such as the spiny dogfish (*Squalus acanthias*; 6.62 to 9.19 °C; Shepard et al. 2002) are not known to frequent the arctic temperatures occupied by Greenland sharks. There are two other known Arctic sharks beside the Greenland shark, they are the porbeagle shark (*Lamna nasus*) and the salmon shark (*Lamna ditropis*). Both of these are endothermic laminid sharks. The porbeagle shark is generally caught at temperatures between 5 and 10 °C (Campana and Joyce 2004) and the salmon shark frequents temperatures only as low as 2 °C (Weng et al. 2003). Therefore, the cold thermal tolerance of Greenland sharks likely allows them to forage in areas where there is no competition from other shark species.

On 176 occasions between 28 July and 8 September 2004, no signals were received from Greenland shark 32 for over 30 minutes. This likely represented instances when the shark left the bay and was out of receivers range. It is possible that there are locations in the bay where a signal to the receiver might be blocked. However, it is unlikely that if a structure did exist the shark would stay under or behind it for periods of time as long as 20 hours. It is likely that in these instances, the shark left the bay, possibly to hunt. The sharks peak departure time corresponds to sunrise and just before sunset. These are times that many large pelagic predators are most active and likely hunting prey (Nakano et al. 2003). Therefore, it may be that the sharks leave the bay to feed, and therefore reside in the bay for reasons other than the abundance of prey items.

One shark left the bay on 27 August 2004 and had moved 114.9 km upstream from the tagging location, by the time the tag reported on 1 November 2004. Greenland sharks have been taken in winter in the ice fishery in the Saguenay Fjord. It is possible that the sharks present in Baie St. Pancrace are a component of this population. If so, this may have been the destination of the male shark that was moving up the St. Lawrence Estuary toward the Saguenay Fjord. More long term tagging is needed to determine the relationship of the sharks found in these two areas.

The Greenland shark that moved into the main channel of the St. Lawrence Estuary resided in the middle of the main channel, as this is the only place where the water is in excess of 300 m deep. This shark did not move through the entire water column as did the sharks that were located in the bay. The waters of the St. Lawrence Estuary east of the Saguenay Fjord are composed of three layers in summer and two in winter. In summer there is a warm surface layer, an intermediate cold layer and a deep warm layer (Lauzier and Bailey 1957). In winter there is a sub-zero mixed layer overlaying the deep warm layer (Lauzier and Bailey 1957). The deep layer retains its characteristics through the seasons (Lauzier and Trites 1958). The shark that moved into the main channel remained mostly in the deep warm (4 – 6 °C) layer. This shark made vertical migrations, however, the two shallowest depths reached were both 132m. This may indicate that a characteristic of the water structure created a barrier to the upward migration of the shark. It is unlikely that any barrier would be temperature related. In both instances that the shark moved to 132 m, the lowest temperature that it experienced was 1 °C. The sharks that resided in the bay regularly experienced temperatures < 1 °C, and Greenland sharks are known to inhabit waters with temperatures as low as -1.7 °C (Skomal and Benz 2004). The middle layer of the St. Lawrence flows downstream, as does the surface layer. However, the bottom layer flows into the St. Lawrence Estuary terminating at the Saguenay Fjord, where it is part of the production of the Gaspe Current (Lauzier and Trites 1958). Possibly the Greenland shark remained in the bottom water layer to conserve energy as it moved toward the Saguenay Fjord.

This is the first report of Greenland sharks residing in shallow near shore bays, in summer and autumn. Large numbers of sharks were observed in Baie St. Pancrace in summer 2004. For example, 11 different sharks were recorded on video on one shallow dive in low visibility. The sharks were all individually identified by different scarring patterns. No shark was recorded more than once. Therefore, the sharks in the bay appear to be seasonally plentiful (CHC unpublished data). Also, the male to female ratio of sharks identified to sex was 0.36:1 (CHC unpublished data). Therefore is the bay being used for reproduction or as a nursery? More information is needed to address these questions.

In this study, we demonstrate that when in the photic zone Greenland sharks showed diel differences in depth preferences. They occupied both very cold temperatures, and warmer temperatures than have been previously reported. Greenland sharks are seasonally plentiful in near shore shallow bays, for long periods of time. Also, the sharks in Baie St. Pancrace may be linked to the over wintering population in the Saguenay Fjord.

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Figure Legends

1. Map of the St. Lawrence River, tag release site showing Baie St. Pancrace, Quebec, where the acoustic tag data was collected, and the area in which the shark with PSAT tag 166 resided (PSAT pop off = grey triangle, offset from the bay for clarity) for the

duration of the study. Also, the pop-off position for PSAT tag 581 (grey triangle with dot) in the main channel of the St. Lawrence Estuary.

2. Record of a) depth (N = 20799) and b) ambient temperature (N = 20691) experienced by an acoustically tagged female Greenland shark while it resided in Baie St. Pancrace, Quebec, from 27 June to 9 September 2004. Data are binned hourly and standardized for sunrise at 04:59 and sunset at 20:17 these were the conditions on the first day of tracking, 28 July 2004 (circles = median, box = 1st to 3rd quartiles, whiskers = 1.5 * inter-quartile range; because of large numbers 57 outliers were removed from a., and 196 outliers were removed from b.).

3. Percentage time-at depth (bars) and water column temperature profile (line; square = mean; error bars ± one standard deviation) and for an acoustically tagged female Greenland shark while it resided in Baie St. Pancrace, Quebec, from a) 28 July to 1 September 2004 and b) 2 September to 8 September 2004.

4. Thermal profile of the water column in Baie St. Pancrace, Quebec, means calculated from temperature data measured by an acoustic tag attached to a female Greenland shark in summer 2004 for the weeks of 28 July to 3 August (grey diamond); 4 to 10 August (grey square); 11 to 17 August (grey circle); 18 to 24 August (black diamond); 25 to 31 August (black square) and 1 to 8 September (black circle).

5. Depth recorded by an acoustically tagged Greenland shark over a 24 hour period on 2 August 2004.

6. Daytime (empty symbols) and nighttime (filled symbols) depth (diamonds) and temperatures (squares) for PSAT tagged female Greenland shark 166 that resided in Baie St. Pancrace, Quebec, from 27 August to 1 November 2004 (means ± standard error).

7. Daytime (empty symbols) and nighttime (filled symbols) depth (diamonds) and temperatures (squares) for PSAT tagged male Greenland shark 581 that resided in the open channel of the St. Lawrence Estuary from 27 August to 1 November 2004 (means ± standard error).

8. Water column profile of temperature (squares; mean ± SD) and salinity (triangles; mean ± SD) from the main channel of the St. Lawrence Estuary between 48.580° N, 68.490° W and 48.830° N, 68.750° W on 8 June 2004.

Table 1. Period of deployment and data collection for electronic tags attached to Greenland sharks in Baie St. Pancrace, Quebec, in summer 2004.

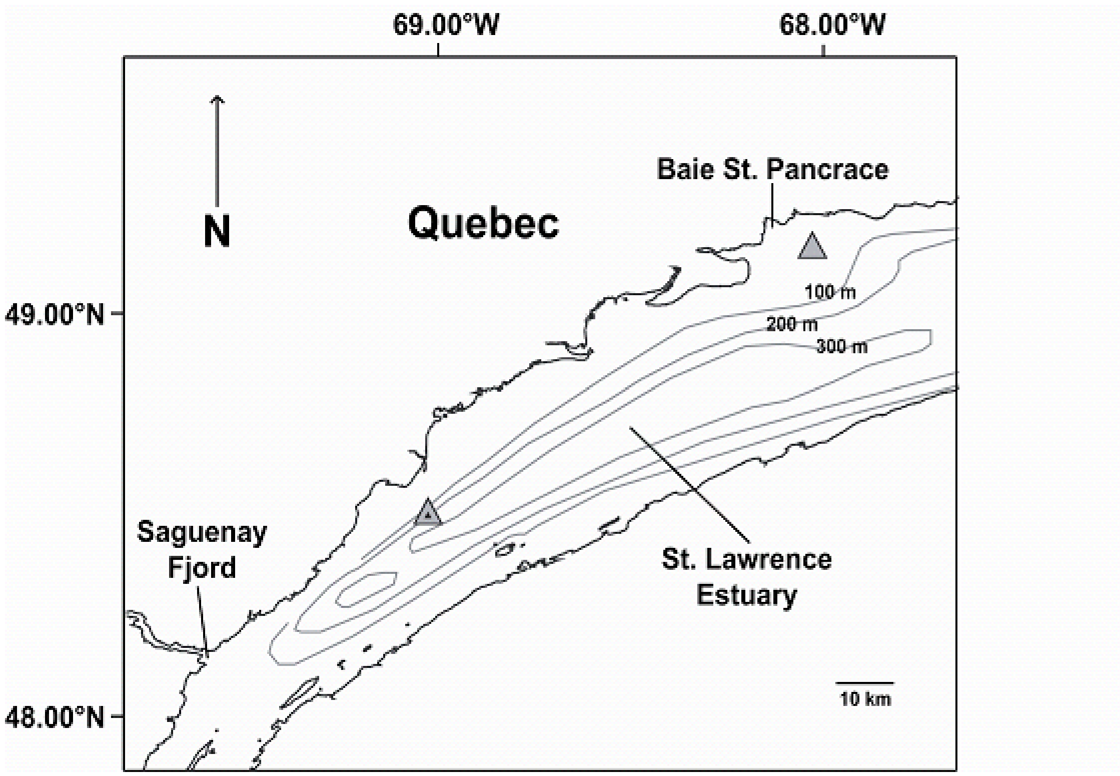
Tag #	Date of deployment	Start of data collection	End of data collection	Days of data collection
32	23/7/2004	28/7/2004	8/9/2004[a]	47
166	27/8/2004	27/8/2004	1/11/2004	66
581	27/8/2004	27/8/2004	1/11/2004	66

[a] The last date that data from tag 32 was recorded by a receiver was 26 September 2004. It is not known at what time the tag ceased to transmit.

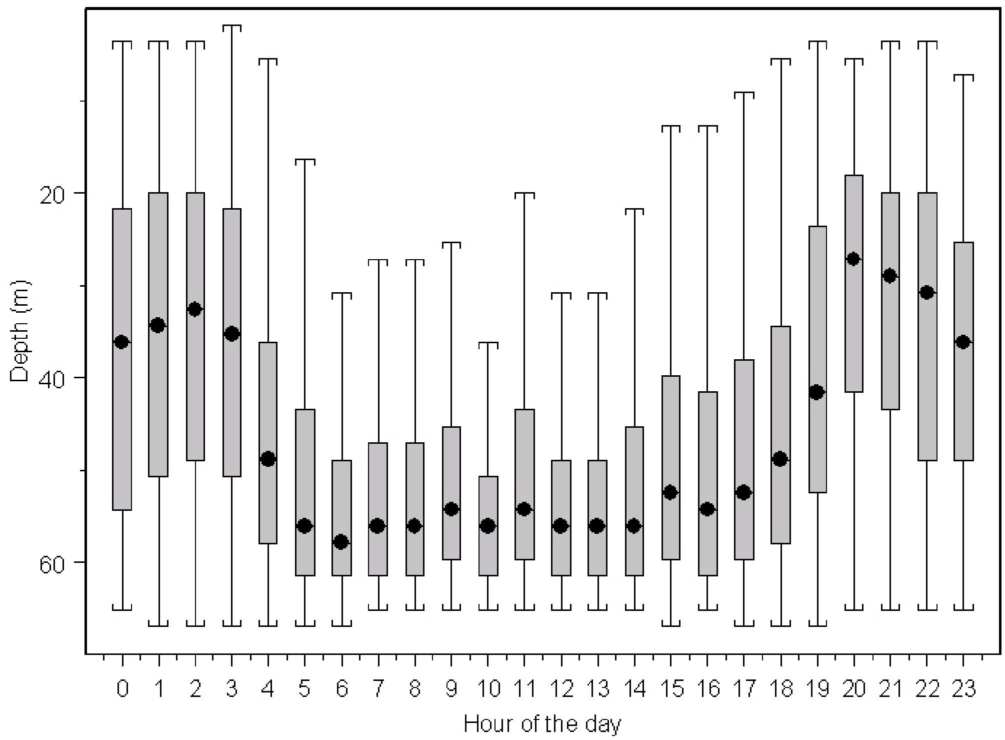
Table 2. Results of electronic tagging of three Greenland sharks in Baie St. Pancrace, Quebec, during summer 2004.

Tag #	Tag type	Estimated total length (cm)	Sex	Location of data collection	Minimum depth (m)	Maximum depth (m)	Modal depth (m)	Minimum temperature (C)	Maximum temperature (C)	Modal temperature (C)
32	V 16	235	F	Bay	1.8	67	61.5	-1.1	8.6	0.6
166	PSAT	270	F	Bay	0	72	30	0.8	7.4	3.0
581	PSAT	270	M	Channel	132	352	326	1.0	5.4	5.0

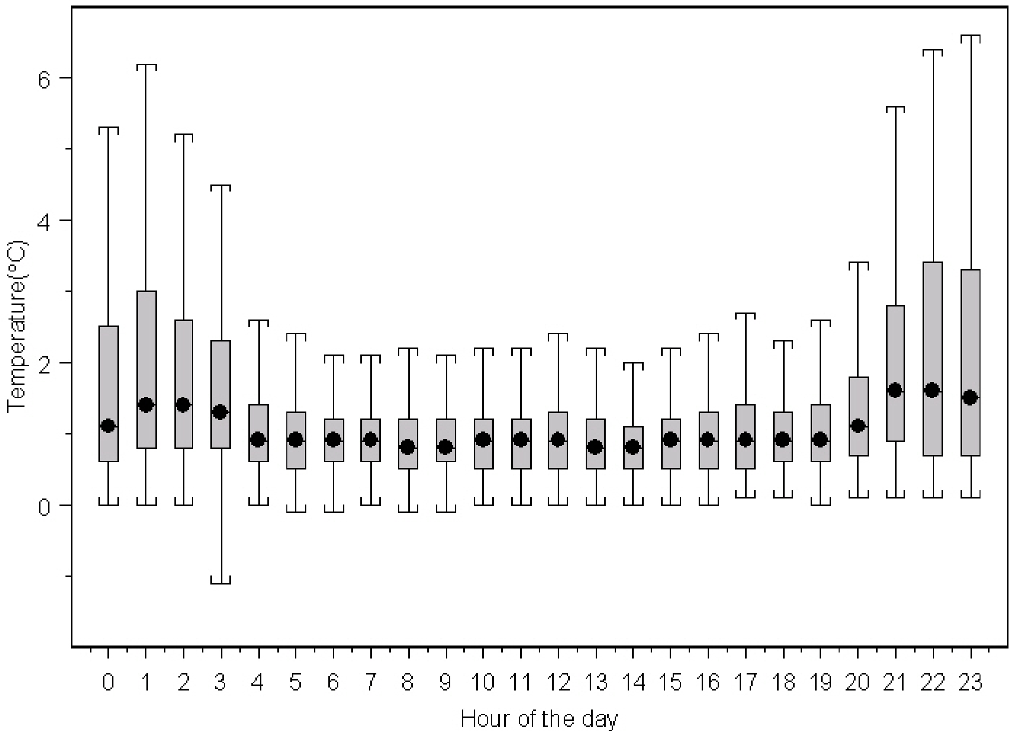
1)


69.00°W
68.00°W
N
Quebec
Baie St. Pancrace
100 m
200 m
300 m
49.00°N
48.00°N
Saguenay
Fjord
St. Lawrence
Estuary
10 km

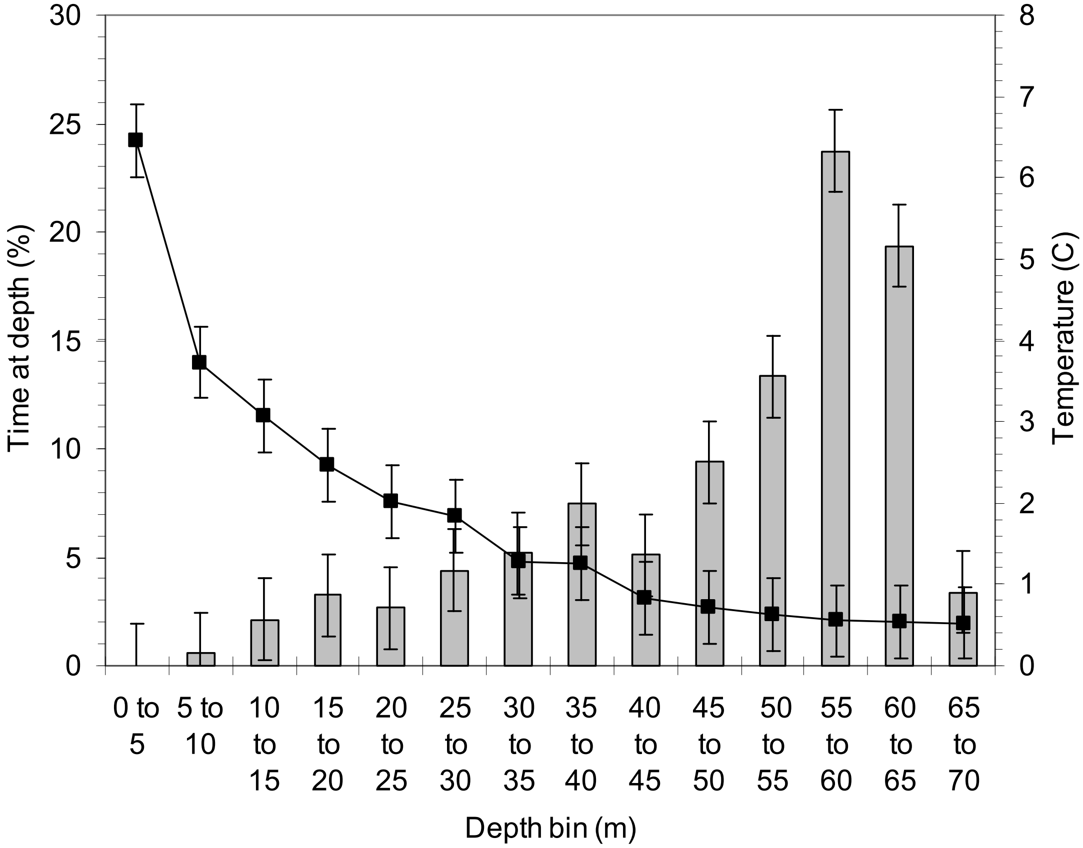
2a)


Depth (m)
20
40
60
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23
Hour of the day

b)

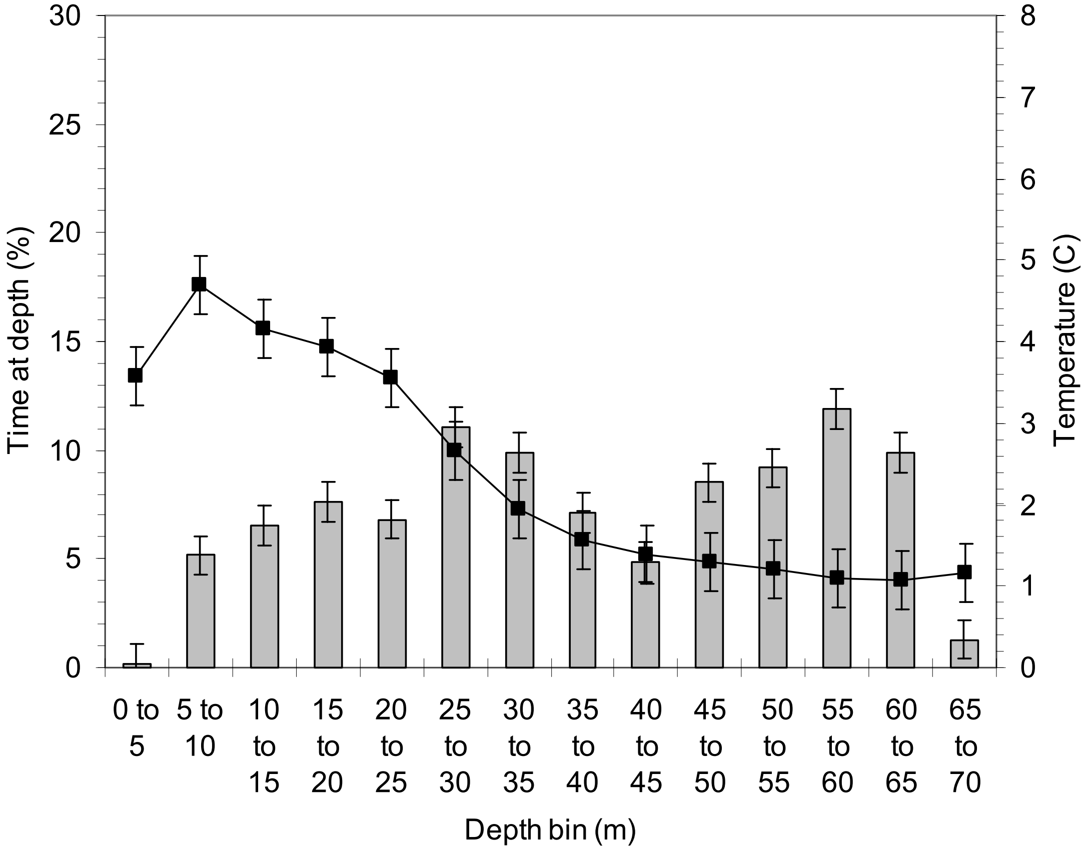

6
4
2
0
Temperature(°C)
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23
Hour of the day

3a)



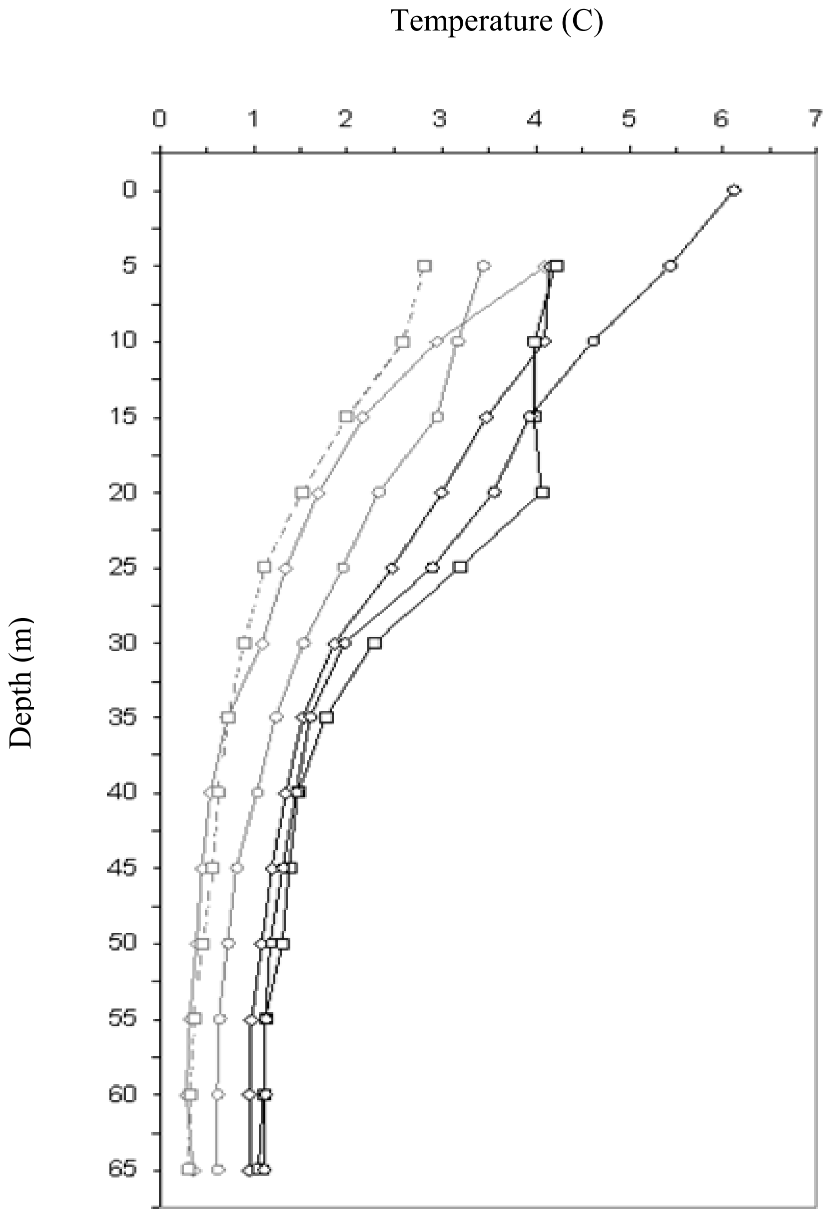
30
25
20
15
10
5
0
Time at depth (%)
8
7
6
5
4
3
2
1
0
Temperature (C)
0 to 5
5 to 10
10 to 15
15 to 20
20 to 25
25 to 30
30 to 35
35 to 40
40 to 45
45 to 50
50 to 55
55 to 60
60 to 65
65 to 70
Depth bin (m)

b)

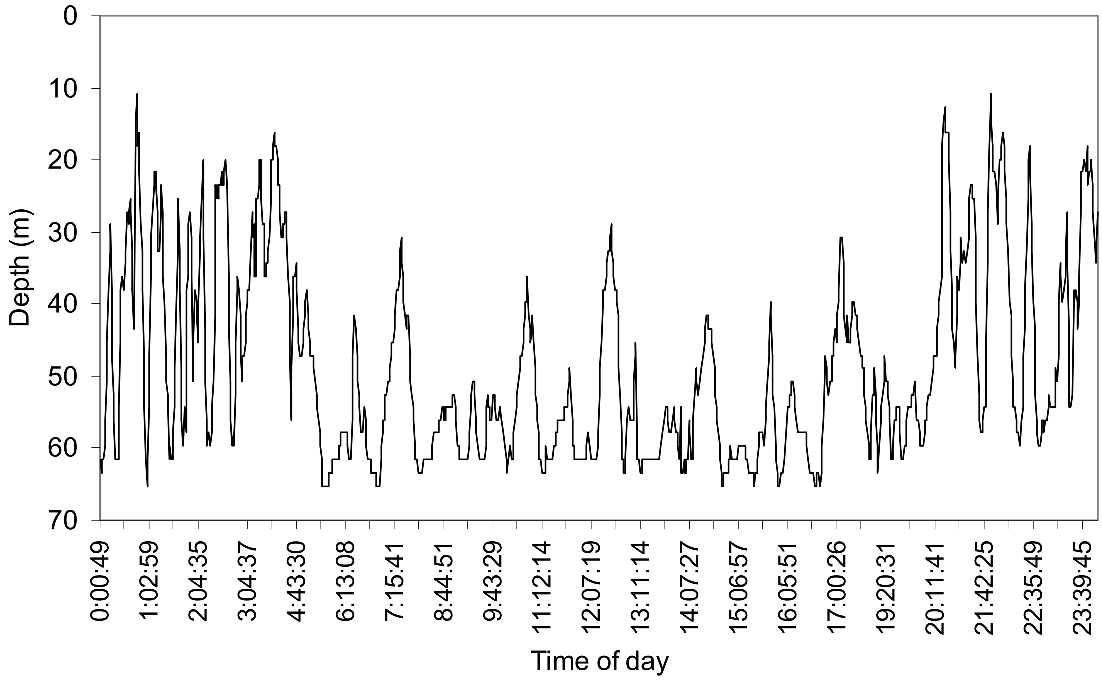


Time at depth (%)
Temperature (C)
Depth bin (m)
0
5
10
15
20
25
30
0
1
2
3
4
5
6
7
8
0 to 5
5 to 10
10 to 15
15 to 20
20 to 25
25 to 30
30 to 35
35 to 40
40 to 45
45 to 50
50 to 55
55 to 60
60 to 65
65 to 70

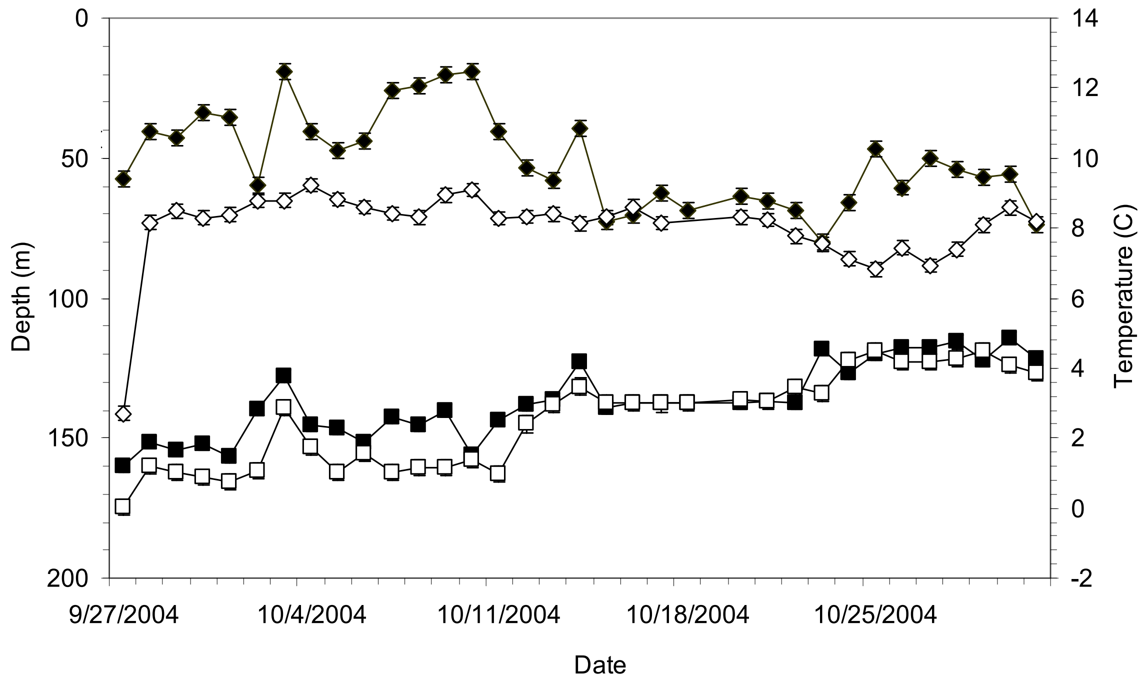
4.


Temperature (C)
0
1
2
3
4
5
6
7
Depth (m)
0
5
10
15
20
25
30
35
40
45
50
55
60
65

5.

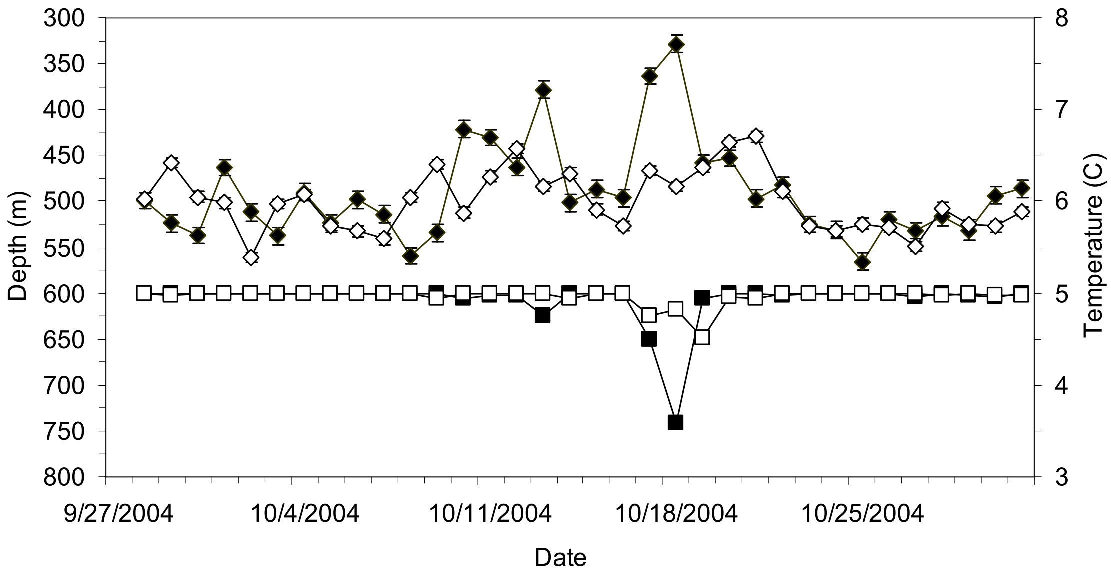

Depth (m)
0
10
20
30
40
50
60
70
Time of day
0:00:49
1:02:59
2:04:35
3:04:37
4:43:30
6:13:08
7:15:41
8:44:51
9:43:29
11:12:14
12:07:19
13:11:14
14:07:27
15:06:57
16:05:51
17:00:26
19:20:31
20:11:41
21:42:25
22:35:49
23:39:45

6.

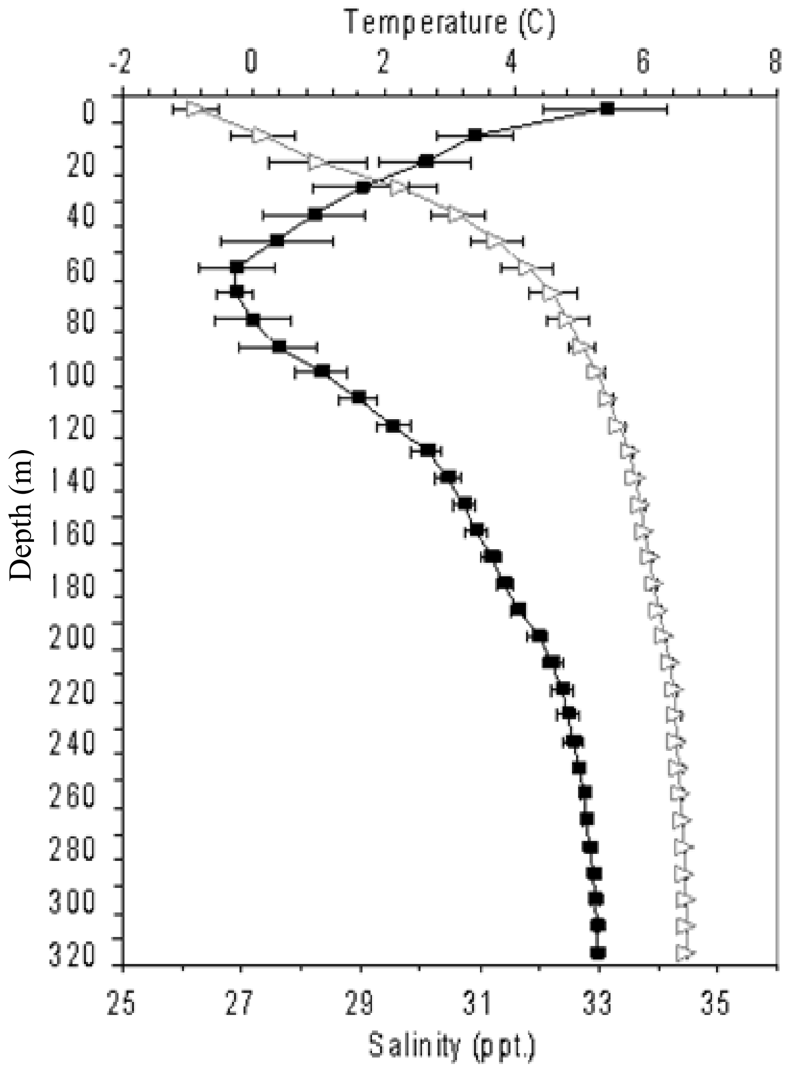


Depth (m)
Temperature (C)
Date
0
50
100
150
200
14
12
10
8
6
4
2
0
-2
9/27/2004
10/4/2004
10/11/2004
10/18/2004
10/25/2004

7.


300
350
400
450
500
550
600
650
700
750
800
Depth (m)
8
7
6
5
4
3
Temperature (C)
9/27/2004
10/4/2004
10/11/2004
10/18/2004
10/25/2004
Date

8.



Temperature (C)
-2
0
2
4
6
8
Depth (m)
0
20
40
60
80
100
120
140
160
180
200
220
240
260
280
300
320
25
27
29
31
33
35
Salinity (ppt.)