Temperature and depth associations of porbeagle shark (*Lamna nasus*) in the northwest Atlantic

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ABSTRACT

The porbeagle (*Lamna nasus*) is a large fast-swimming pelagic shark found at high latitudes in both hemispheres. To examine the influence of temperature on porbeagle distribution, a detailed analysis of the relationship between catch rate, temperature, depth and location was carried out based on 420 temperature profiles taken during commercial fishing operations. More than half of the porbeagle were caught at temperatures of 5–10°C (at the depth of the hook); the mean temperature at gear of 7.4°C differed very little among seasons. Most of the spring fishing took place near fronts, although the affinity with fronts was not evident in the fall. Temperature at depth was a significant modifier of catch rate when included in a generalized linear model controlling for the effects of location, fishing vessel, month and year. However, sea surface temperature was a poor predictor of catch rate. The similarity between environmental and catch-weighted cumulative distribution functions confirmed suggestions that fishers sought out the most appropriate temperature range in which to set their gear. As porbeagle are among the most cold tolerant of pelagic shark species, we suggest that they have evolved to take advantage of their thermoregulating capability by allowing them to seek out and feed on abundant coldwater prey in the absence of non-thermoregulating competitors.

Key words: catch rate, cumulative distribution function, distribution, migration

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INTRODUCTION

Porbeagle sharks (*Lamna nasus*), salmon sharks (*L. ditropis*), makos (*Isurus oxyrhinchus*) and great whites (*Carcharodon carcharias*), all members of the family Lamnidae, are often found in temperate waters <22°C, which is somewhat cooler than that of many other shark species. In part, the apparent preference for cooler waters can be attributed to the presence of the retia mirabilia, a vascular heat exchange mechanism, which permits the retention of metabolically generated heat (Carey and Teal, 1969; Anderson and Goldman, 2001). However, porbeagles and their congeners are the family members found at the highest latitudes in both hemispheres, suggesting that they might be particularly cold tolerant. Common in the north Atlantic, the south Atlantic and the south Pacific, porbeagles have been caught at sea surface temperatures (SST) between 2 and 23°C, although most captures have fallen in the range of 8–20°C (Svetlov, 1978; Stevens *et al.*, 1983; Lucifora and Menni, 1998; Francis and Stevens, 2000). It is not known if the porbeagle actually inhabits such a broad temperature range, as SST may be a poor indicator of ambient temperature for this species.

It is common knowledge among fishers that oceanic fronts are the preferred catch sites for large pelagic fishes such as tunas and swordfish (Bigelow *et al.*, 1999). Anecdotal comments by porbeagle fishers suggest that the preferred areas for porbeagle fishing are also selected on the basis of proximity to fronts. Detailed monitoring of a directed fishery for porbeagle off the eastern coast of Canada has demonstrated that both catch per unit effort (CPUE) and fishing effort are highest in well-defined areas near the edge of the continental shelf (Campana *et al.*, 2002), areas where fronts are known to occur. However, the preferred fishing location moves to the north during the spring and summer of each year, suggesting that the porbeagle may be moving to maintain a preferred temperature range independent of any fronts.

Several alternative hypotheses can be invoked to explain seasonal porbeagle movements and distribution in the northwest Atlantic: (i) porbeagle restrict their distribution to the edge of the continental shelf or a particular water depth; (ii) porbeagle maintain an orientation to fronts; or (iii) porbeagle move to position themselves in a particular temperature range. A fourth hypothesis, that porbeagle move to maintain themselves within prey concentrations independent of location and temperature, is not exclusive of the above hypotheses, but can currently be examined only through inference.

As temperature profiles and accurate catch records were available for many of the porbeagle fishing sets made between 1995 and 2000, a detailed analysis of the relationship between catch rate, location, depth and temperature was possible. By making the usual assumption that porbeagle catch rate reflects local abundance, it then becomes possible to test among the various hypotheses of porbeagle distribution. The objectives of this study were to: (1) describe and test for geographic, temperature and depth effects on porbeagle catch rates; (2) test for seasonal and inter annual changes in the temperature and depth at which porbeagle are most commonly caught; (3) assess the degree of association between frontal locations and high catch rates; (4) determine if SST is an adequate descriptor of the temperature fields in which porbeagle are most commonly found. Inferences concerning the distribution and migration of porbeagle in relation to temperature and prey fields were subsequently made based on the hypothesis tests described earlier.

MATERIALS AND METHODS

Fishing location, fishing effort and catch were drawn from the logbooks of a directed longline fishery for porbeagle as part of a science industry collaborative project (Campana *et al.*, 2001). This directed fishery accounts for virtually all historical catches (Campana *et al.*, 2002). The accuracy of the logbook data is excellent for this fishery. Most of the data analysis was restricted to the offshore fleet (vessel length >33 m), as this fleet collected almost 90% of the temperature data. Water depth at each fishing location was determined retroactively based on fishing location and hydrographic charts if not indicated in fishing logs. CPUE was calculated as catch weight (kg) per hook fished. The temperature profile at the start of each fishing set was taken by fishers using expendable bathythermographs or Sealogs with a depth-sampling interval of 1–2 m. A total of 420 profiles, collected between 1994 and 2000, were used in the analysis (Table 1). Most of the profiles were collected by the offshore fleet; a total of 46 profiles, collected in 1999–2000 by scientific staff, were available for the inshore fleet (vessel length <33 m) (Table 2). Most longline sets stretched over a distance of 20–40 km, so precise allocation of the profile to each hook was not possible. However, longline sets were always set parallel to any fronts, thus the temperature variation at depth along the longline was assumed to be minimal.

Temperature at the depth of the hooks was based on the temperature profile recorded at each fishing location and the estimated mean depth of the gear. Based on temperature-depth recorders ($N = 112$) attached to gear by scientific staff, mean mid-gear depth was shallower in the fall than in the spring, but was similar across years due to the fact that the porbeagle longline gear was fished in a consistent manner by each fleet. In the spring, the fishery by the inshore fleet on the Scotian Shelf generally used 10 hooks between floats spaced at 400-m intervals, weighted at the midpoint. This produced a mean mid-gear depth of 84 m (Table 2). There was no appreciable fall fishery by the inshore fleet. The spring fishery by the offshore fleet on the Scotian Shelf, which accounted for most of the annual catch, used 32 hooks between floats spaced at 700-m intervals. Although it was not possible to attach temperature-depth recorders to the spring offshore gear, fleet captains were confident that mid-gear depth was about 100 m and that the deepest gear depth was about 160 m. The fall fishery by the offshore fleet, primarily off Newfoundland, was carried out at a mean mid-gear depth of 25–34 m, using six to seven hooks between floats spaced at 280–320-m intervals (Table 2). Accordingly, temperature at gear was estimated from each temperature profile assuming a constant gear depth of 100 m in the spring, and 34 m in the fall. Clearly, gear depth would vary with proximity to a float, making it impossible to assign an exact depth to each hook. Nevertheless, the estimate of temperature at gear was relatively insensitive (±1°C) to the exact depth of the gear in the early spring and throughout the fall, due to the depth of the gear in the near-isothermal surface waters. Larger errors, in the order of 1–3°C, might be expected in May and June if gear depth was misassigned. Surface temperature measurements were taken from the same profiles as those used to determine temperature at depth.

The influence of temperature on catch rate was evaluated by using the linear model approach of Gavaris (1980) and an enhancement of the standardized catch rate model described in Campana *et al.* (2002). As the distribution of catch rates was skewed, we used a generalized linear model with a gamma error and identity link. The use of a gamma model produces results similar to that of log-transformed catch rates, but is statistically more efficient. Subarea, fishing

Table 1. Number of temperature profiles and the mean temperature (°C) at the fishing gear associated with the catch of porbeagle in each seasonal quarter between 1994 and 2000, for the offshore fishing fleet. Profiles include those collected by fishers and scientific staff. Temperatures at mid-gear depth are based on mean depths fished in the spring (100 m on the Scotian Shelf) and fall (34 m on the Newfoundland Shelf). The associated non-fishing temperature profiles are those which were used to reconstruct the surrounding temperature field at depth, based on availability within 50 km of the fishing location in the same month and year. Yearly quarters reflect the fishing season: March–May (1), June–August (2), September–November (3) and December–February (4).

		Scotian Shelf				NF Shelf			
Year	Quarter	No. temp profiles	Mean temp at gear	Catch (mt)	Associated non-fishing profiles	No. temp profiles	Mean temp at gear	Catch (mt)	Associated non-fishing profiles
1994	1	0		0	0	0		0	0
	2	0		0	0	0		0	0
	3	4	9.3	33	154	4	6.3	13	547
	4	2	5.6	5	86	0		0	202
1995	1	25	9.4	72	654	0		0	521
	2	9	6.1	14	533	17	5.3	59	726
	3	2	9.8	5	252	3	6.0	17	600
	4	1	7.1	1	152	0		0	434
1996	1	49	9.1	67	264	0		0	537
	2	2	9.3	0	371	0		0	691
	3	0		0	206	0		0	617
	4	2	9.3	3	252	0		0	286
1997	1	19	7.5	78	443	0		0	539
	2	12	4.1	27	807	4	7.0	4	763
	3	0		0	175	0		0	741
	4	0		0	87	0		0	185
1998	1	72	7.5	178	460	1	7.0	7	453
	2	12	5.5	5	323	10	4.7	13	776
	3	0		0	229	5	8.3	17	777
	4	2	9.2	2	108	0		0	273
1999	1	50	8.2	142	393	9	9.4	25	518
	2	1	2.3	4	370	4	8.7	7	618
	3	5	9.6	3	430	37	7.3	35	630
	4	3	13.0	2	114	8	6.3	5	337
Total		272		639	6863	102		201	11771

vessel, month and year were treated as factors in the base model. As there was no reason to expect a linear relationship between temperature and catch rate, temperature was included as a factor rather than as a covariate. Therefore, temperature was binned by 2°C-intervals, and then nested within months. Both temperature at the depth of the gear and surface temperature were evaluated (in separate models).

The SST and temperature at depth data for locations surrounding fishing positions were derived from the Atlantic Fisheries Adjustment Program (AFAP) database at the Bedford Institute of Oceanography (Petrie *et al*., 1996). Temperature data were matched to the corresponding month and year of the fishing set, averaged over a 10-m interval around the mean gear depth for that area. Colour-coded maps showing temperature at depth (both from the AFAP database and the fishers' profiles) overlaid with CPUE were only examined if there were sufficient AFAP data to contour temperature at depth on all sides of the fishing location. Contours were not drawn over data gaps >20 km.

Cumulative distribution functions (CDFs) were used to compare the temperatures where porbeagle were caught compared with those areas which were fished (Perry and Smith, 1994). The unweighted CDF

Table 2. Gear depths and temperature profiles measured by scientific staff aboard large offshore and smaller inshore vessels in 1999 and 2000. SS = Scotian Shelf; NF = Newfoundland. Yearly quarters reflect the fishing season: March–May (1), June–August (2), September–November (3) and December–February (4).

		No. temp. profiles					
Year	Quarter	Offshore	Inshore	Region	Average depth (±1 SE) of gear (m)	Range of mid-gear depths (m)	Total
1999	1	0	27	SS			27
	2	0	4	SS			4
	3	37	0	NF	34 ± 1	11–69	37
		5	0	SS	27 ± 2	15–77	5
	4	8	0	NF	28 ± 4	10–52	8
2000	1	0	15	SS	84 ± 8	18–219	15
	2	0	0				0
	3	16	0	NF	25 ± 1	10–67	16
	4	0	0				0
Total		66	46				112

represents the temperatures at depth where fishing took place, while the weighted CDF indicates the temperatures associated with the same series of fishing sets, weighted by catch rate. The range of temperatures encompassed by the 10th and 90th percentiles indicates the range of temperatures where most (80%) of the fishing activity and/or catches took place. Similarities between weighted and unweighted CDFs suggest that enhanced catches are not associated with any particular range of temperatures within the range fished, while different CDFs suggest temperature associations. CDFs for the offshore fleet were first generated for each month, year and region, and then aggregated within season in the light of intermonth similarity. Statistical differences between weighted and unweighted CDFs were not tested.

RESULTS

Porbeagle distribution in relation to location and depth

Porbeagle sharks are taken almost exclusively by a Canadian directed longline fishery. This fishery focuses its effort on immature porbeagles (fork length <200 cm) on the Scotian Shelf (Shelf) in spring, and on larger, mature animals off Newfoundland and in the Gulf of St Lawrence (NF) in the fall (Fig. 1). Both inshore and offshore fleets fished the Shelf in the spring of recent years. Although the offshore fleet tended to fish near the edge of the continental shelf, the inshore fleet fished well onto the Shelf. Fishing by both fleets was minimal in the summer. In the fall, the small amount of catch taken by the inshore fleet was mainly from the Scotian Shelf, while the much larger catches by the offshore fleet were made in the Gulf of St Lawrence, off southern Newfoundland, and on the Grand Banks (NF) (Fig. 1). Since 1995, the offshore fleet has accounted for 55–70% of the annual catch (Campana *et al.*, 2001).

For the offshore fleet responsible for most of the spring catch, bottom depth varied between 35 and 3000 m, with a mean of 1165 m (SD = 876; $N = 364$) (Fig. 2). In contrast, the offshore fleet fished mainly at depths of <200 m in the fall, with a mean of 134 m (SD = 70; $N = 153$). Bottom depth was not correlated with gear depth, porbeagle catch or CPUE in the spring fishery ($P > 0.05$), although bottom depth and gear depth were positively correlated in the fall ($P < 0.05$). The fall fishery by the inshore fleet was negligible; most of its spring fishery took place on the Scotian Shelf at depths <250 m.

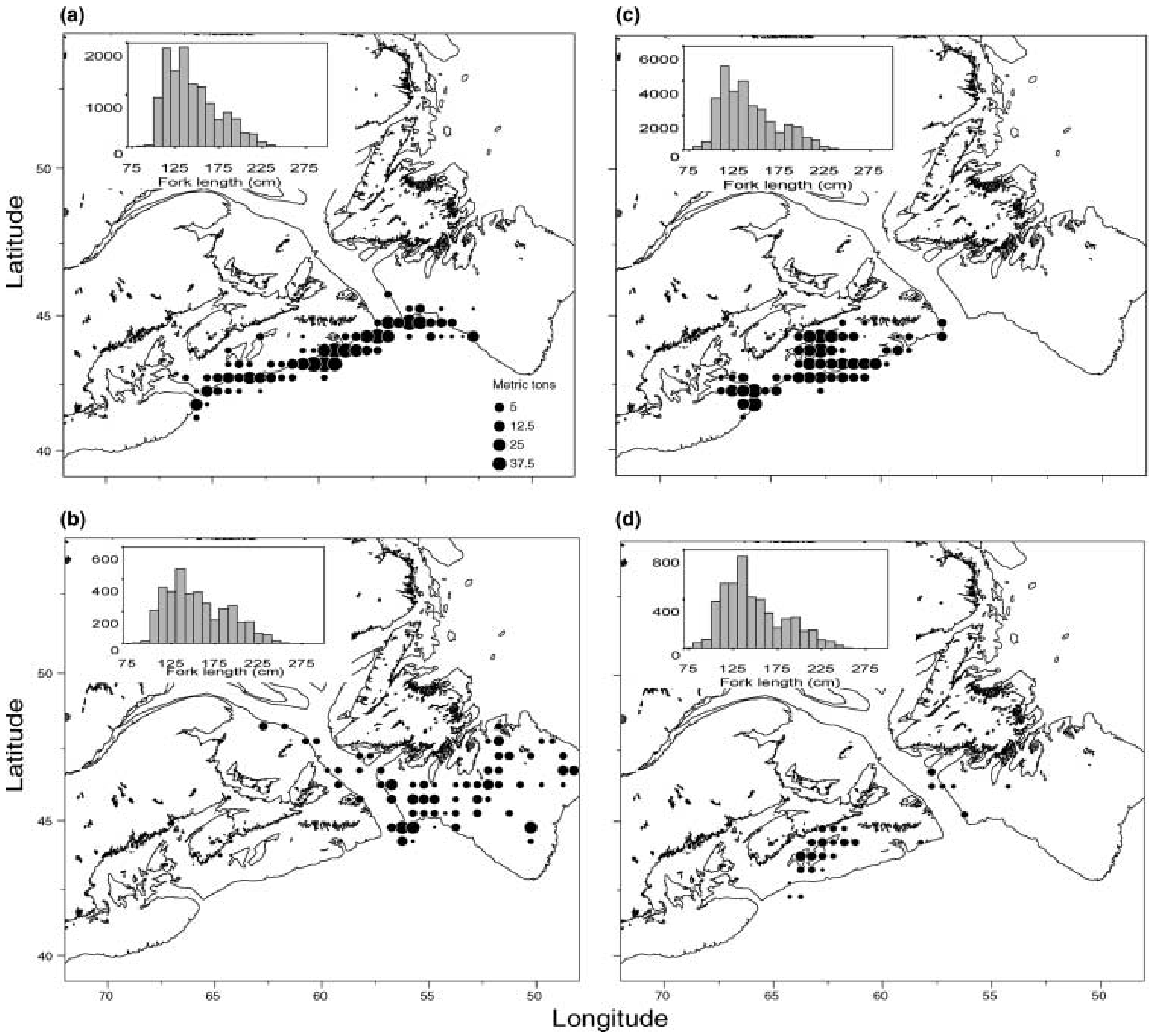
Porbeagle distribution in relation to fronts

Maps of porbeagle catch rates overlaid on the temperature field at the depth of the gear indicated that most of the spring fishing effort, particularly by the offshore fleet, was associated with frontal regions separating cool Shelf waters from warmer offshore waters (Fig. 3). The affinity with fronts was not evident in the fall fishery, despite the fact that the temperatures occupied were similar in both seasons. In general, fishing effort and higher catch rates tended to be associated with the cold-water side of the fronts.

Porbeagle distribution in relation to temperature

Examination of temperature profiles associated with porbeagle catch indicated that gear was often set above or below, but seldom within, the thermocline (Fig. 4). In most cases, the assumption of a constant gear depth for a region would not appreciably change the estimate of the temperature at the gear.

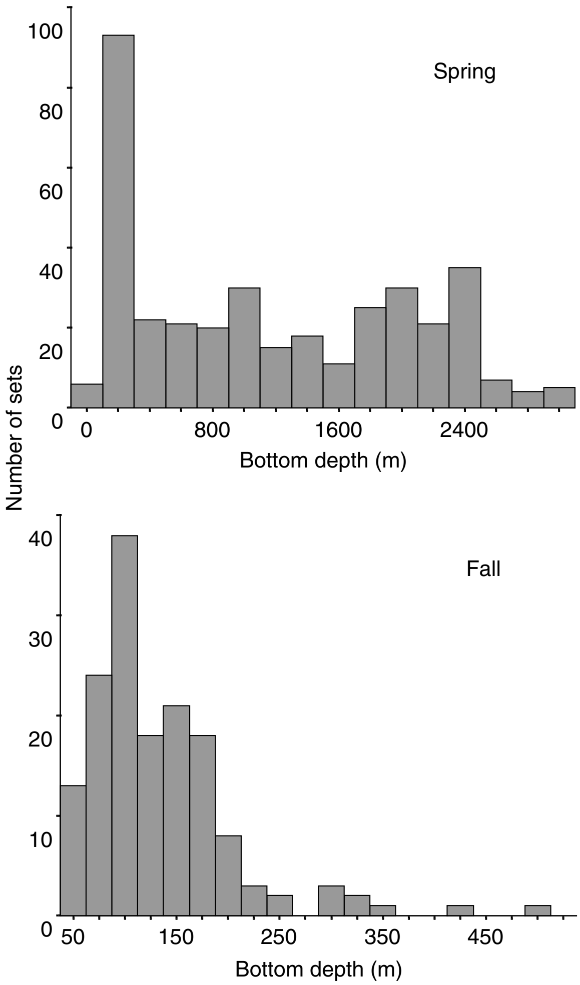
Figure 1. Catch location and associated length composition for the Canadian porbeagle fishery in spring (January–June) and fall (July–December) of 1999 and 2000. (a) Offshore vessels in spring. (b) Offshore vessels in fall. (c) Inshore vessels in spring. (d) Inshore vessels in fall. Catches have been aggregated by 10' square. Contour represents the 200-m isobath.



Porbeagle were caught at a mean gear temperature of 7.4 ± 0.3°C (mean ± 95% CI; $N = 402$), with more than 50% of the sets being made at temperatures between 5 and 10°C. The temperature at capture differed very little between seasons, with a mean temperature of 7.5 ± 0.2°C in the spring ($N = 323$) and 7.2 ± 0.3°C in the fall ($N = 79$). However, there were significant differences in the temperatures fished by the two fleets in the spring. While the offshore fleet fished at a mean temperature of 7.7 ± 0.2°C ($N = 299$) in the spring, the inshore fleet fished at 3.8 ± 0.7°C ($N = 24$). Presumably, these differences in temperature were associated with the different areas being fished (Fig. 1).

A more detailed analysis of seasonal and geographical differences in temperature at gear suggested that differences tended to be small, even when they were significant (Fig. 5). Monthly mean temperatures remained relatively constant throughout the year, varying between 5 and 10°C in virtually all months for which data were available between 1995 and 1999. A two-way ANOVA comparing monthly temperatures in the spring (March–May) offshore fishery across years found no significant differences among months ($P > 0.05$), although the year effect was significant ($P < 0.05$). A posteriori contrasts indicated that the 1995 and 1996 spring fishing seasons were carried out in waters about 2°C warmer than those fished in 1998

Figure 2. Frequency histogram of bottom depths at each of the fishing locations occupied by the Canadian offshore fleet in the spring (January–June) and fall (July–December) of 1999 and 2000.



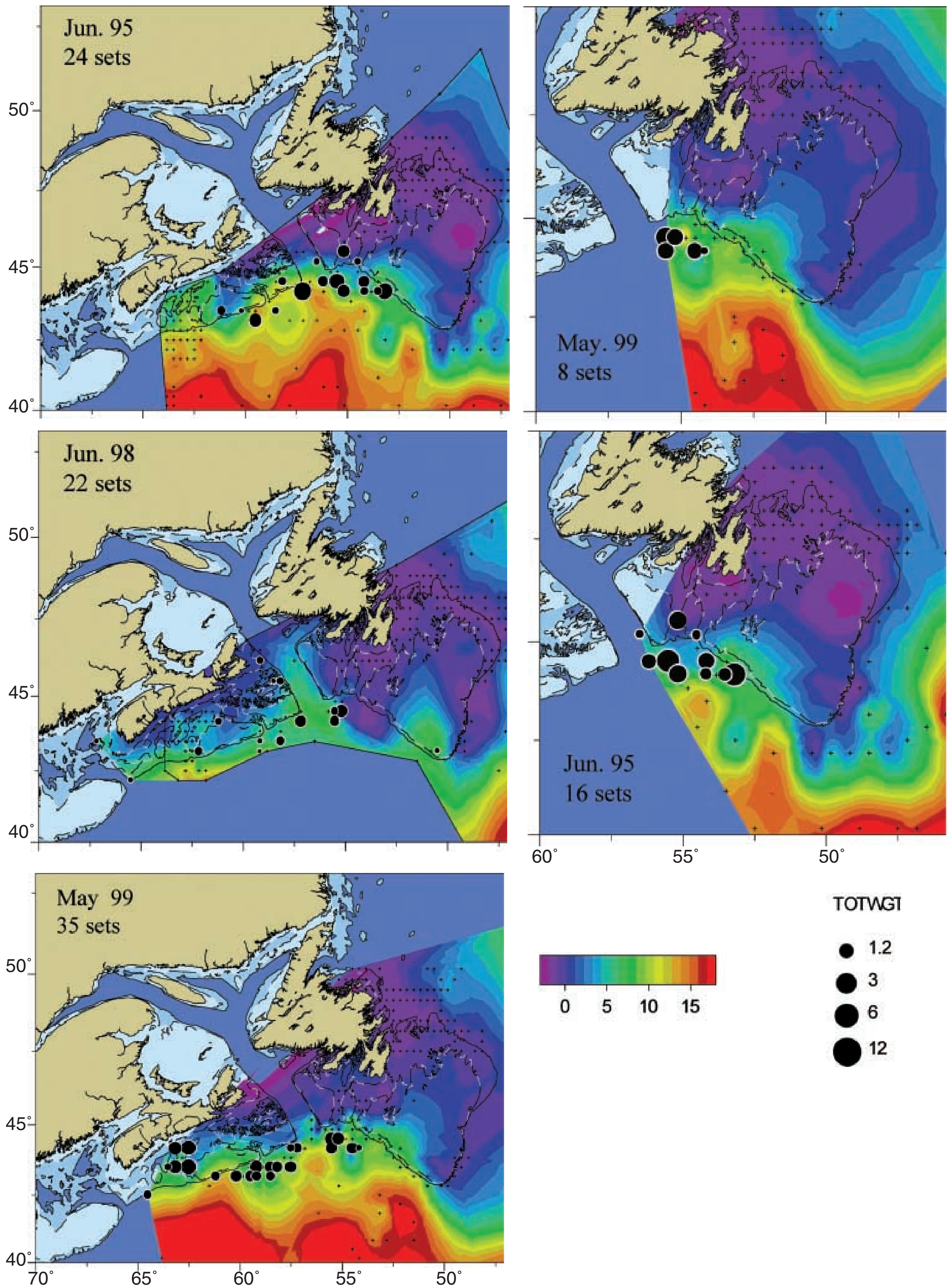
and 1999. A three-way ANOVA comparing years, months and areas was not possible, due to the presence of significant interaction terms. However, ANOVAs restricted to individual months within years indicated that there were no significant differences in temperature at gear between the Scotian Shelf and the NF region ($P > 0.05$). Nevertheless, the monthly pattern in temperatures in the NF region tended to be more variable than that on the Scotian Shelf, presumably due to the shallower depths being fished off Newfoundland.

The surface temperatures at fishing locations showed a very different pattern across months than did temperature at depth (Fig. 5). There were large month to month variations in surface temperature, increasing from about March to September in both fishing regions. Surface temperatures averaged 7.0 ± 0.2°C ($N = 313$) in the spring offshore fishery, increasing to 11.0 ± 0.5°C ($N = 35$) in the fall offshore fishery. There were no significant differences in surface temperature between regions in any given month or year ($P > 0.05$).

Figure 3. Porbeagle catch locations and catch rates (kg/hook, shown as expanding symbols scaled in size according to catch rate) in relation to the contoured ambient temperature field at the depth of the fishing gear. All catch rates exceeded zero. The temperature profiles used to generate the temperature field were available both from fishing operations (expanding symbols) and oceanographic surveys (crosses). In the spring months of most years, porbeagle fishing tended to be directed towards the cold-water side of fronts.

Weighted and unweighted CDFs were compared within fishing regions and seasons to determine if enhanced catch rates were associated with any particular range of temperatures. Seasonal CDFs indicated that fishing activity occurred most often in water temperatures of 4–12°C in the spring, and 6–10°C in the fall (Fig. 6). However, fishing temperatures varied substantially among years. For example, 70% of the fishing took place at temperatures above 8°C in the spring of 1995, while the same percentage of fishing took place at temperatures below 8°C in the spring of 1998. Despite the year to year variation in fishing temperatures, there was no clear evidence of a preferred temperature for porbeagle catches. In most years, there was little difference between the catch-weighted and unweighted CDF. Catch rates appeared slightly enhanced at temperatures between 6 and 10°C in the spring of 1999, but were slightly reduced at the same temperature range in the spring of 1997. The only year (1995) in which the catch-weighted CDF differed substantially from the unweighted CDF indicated that catch rates were highest at temperatures above 11°C, a pattern which was not evident in any other year (Fig. 6).

Temperature effects on catch rate were also analysed using a generalized linear model controlling for the effects of subarea, fishing vessel, month and year. A base model run without the inclusion of a temperature term produced results similar to those reported in Campana *et al.* (2002), wherein subarea, year, month and their interaction produced significant influences on catch rate. Temperature was not a significant factor unless nested within month, indicating that temperature influenced catch rate differently in different months (Table 3). In light of the significant year by month interaction, the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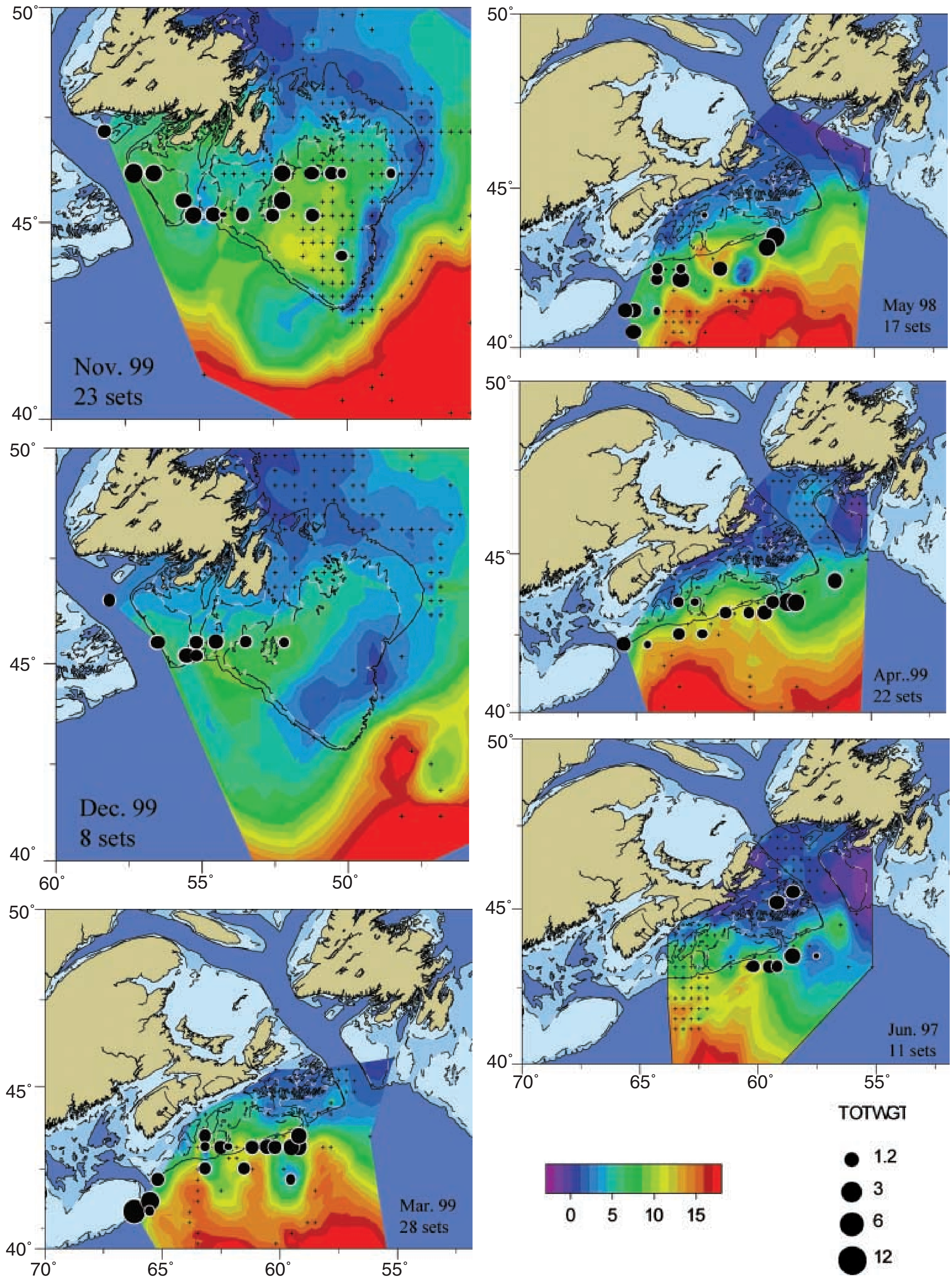
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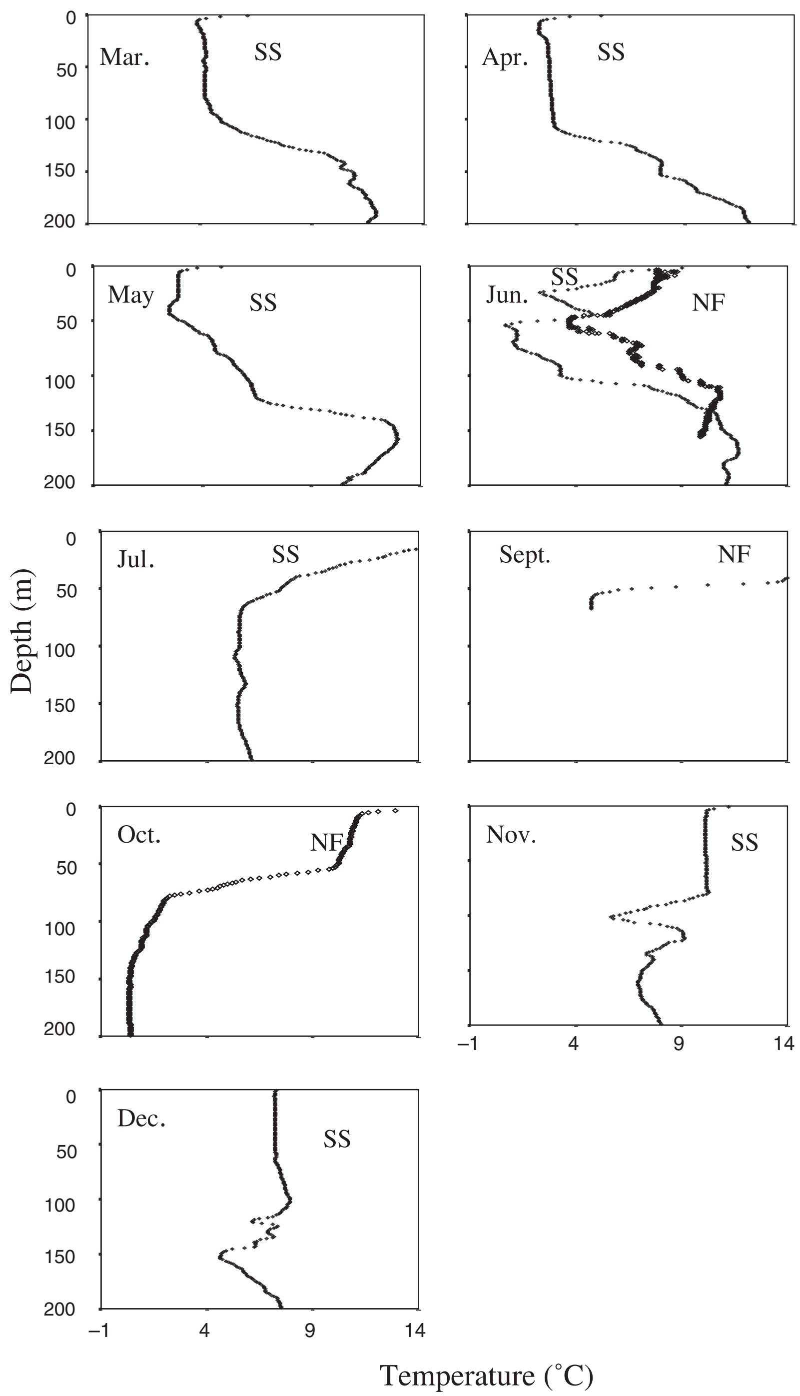


Figure 4. Representative monthly temperature profiles associated with porbeagle catch on the Scotian Shelf (SS) and off Newfoundland (NF) in 1995. The mean depth of fishing gear was 100 m on the Scotian Shelf and 34 m off Newfoundland.

analyses were then repeated year by year using only the spring Scotian Shelf data. A nested temperature effect was significant in both 1995 and 1999 ($P < 0.05$), but not in 1996–98 ($P > 0.10$). Within 1999 (the year with the most observations), standardized catch rate increased with month, but also increased with temperature within month. The pattern for 1995 was slightly different: although catch rate increased with month, it tended to decline at high temperatures within month. We interpret these results as indicating that most of the fishing effort was directed to the optimal temperature range or water mass, but that catch rates were highest at low temperatures in warm years (e.g. 1995), and at high temperatures in cool years (e.g. 1999). The magnitude of these temperature differences among years was relatively small, with marginal mean

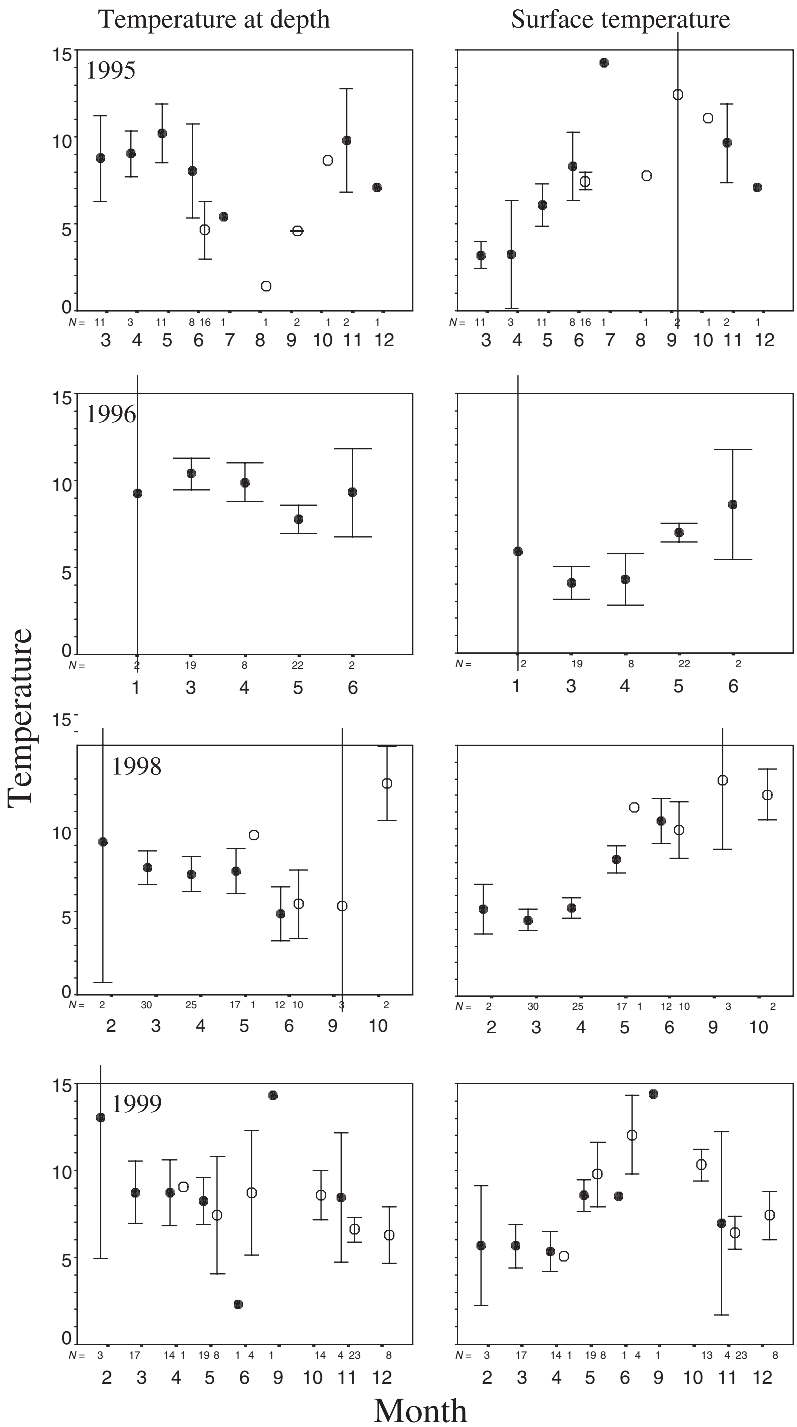


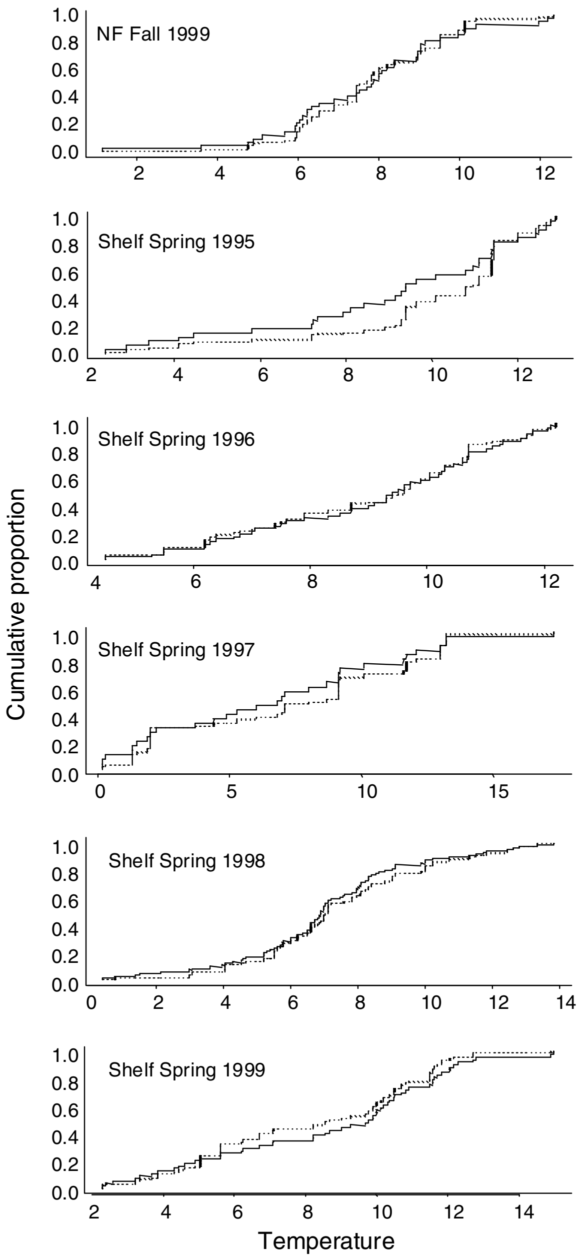
Figure 5. Mean monthly temperature at the depth of the fishing gear (left column) and at the surface (right column) for porbeagle-directed sets by the offshore fleet in which temperature profiles were collected. Shown are fishing locations on the Scotian Shelf (filled circles) and off Newfoundland (open circles). Vertical bars represent ±95% CI.

spring temperatures at the depth of the gear differing by <2°C between the warmest and coldest year on the Scotian Shelf.

Relatively few observations were available to test for a temperature effect in the fall NF fishery ($N = 63$). However, neither a nested temperature term nor month were significant in that analysis ($P > 0.10$), although year was significant ($P < 0.01$).

When surface temperature (rather than temperature at depth) was included in the catch rate model, it did not appear as a significant modifier of catch rate in any year ($P > 0.05$).

Figure 6. Cumulative distribution functions of temperature (°C) at the depth of the gear as measured on 298 fishing sets by the offshore fishing fleet. Solid lines show the distribution of temperatures of all fishing sets, while the dashed lines show the distribution of temperatures weighted by catch rate (kg/hook). Substantive deviations between the two lines indicate that porbeagle are associated with particular temperature ranges.



DISCUSSION

The porbeagle in the northwest Atlantic is a pelagic shark living and feeding at depths roughly comparable to that of the thermocline. Unlike many shark species, this shark appears to prefer cool temperate sub-surface waters. Although porbeagle were apparently tolerant of a broad range of temperatures below 13°C, the majority were caught at depths where temperatures were between 5 and 10°C. This temperature range is considerably cooler than that indicated in most of the previously published reports on porbeagle (Svetlov, 1978; Stevens *et al.*, 1983; Lucifora and Menni, 1998; Francis and Stevens, 2000). Although it is possible that porbeagle in the northwest Atlantic prefer cooler waters than those found in the southern hemisphere, it seems likely that temperature at depth is a better indicator of ambient temperature for this species than SST. This conclusion is substantiated by our analyses of distribution in relation to SST, which were more in keeping with the other published reports (all based on SST).

Tagging and distributional studies indicate that porbeagle are capable of, and actively engage in, large-scale annual migrations up and down the coast of eastern Canada between the Gulf of Maine and Newfoundland (Campana *et al.*, 1999, 2002). In principle, it should be relatively easy for the sharks to seek out preferred temperatures and water masses. The fact that much of the population maintains itself in a relatively narrow and constant temperature range throughout the year, and is consistently found in proximity to fronts in the spring, suggests that the temperature association is not coincidental. Nevertheless, the factor(s) that cue the migration and residency in such a restricted temperature range are not necessarily clear. Bottom depth appears to be unimportant. Temperature is undoubtedly a controlling factor (*sensu* Fry, 1971) through its effect on metabolic rate, which probably sets broad limits on the distributional range of porbeagle. However, this seems an unlikely explanation for such a restricted temperature range, at least by itself. Prey abundance is a more likely modifier of distribution, particularly given the observed tendency of porbeagle to be found near fronts or on productive continental shelves, where prey can be more concentrated or abundant. Indeed, Joyce *et al.* (2002) confirm that porbeagle are opportunistic piscivores, feeding primarily on midwater fishes in spring and groundfish in shallower waters in the fall. As large fast predatory fish tend to be less common in cold waters than in warm waters, there may be an evolutionary advantage for large predators that can feed in cold waters where competitors are less abundant. This advantage would be increased for thermoregulating fishes, such as porbeagle, capable of feeding and growing in colder waters than those that can be tolerated by non-thermoregulating fishes. Thus we sug-

Table 3. Fit of general linear model to porbeagle catch rate in the spring Scotian Shelf fishery. The model assumed a gamma error distribution; terms were added sequentially. The results indicate that temperature was not significant as an overall factor, but was significant when nested within month.

Term	Df	Deviance	ResidDf	ResidDev	*F* value	Pr(F)
Null			255	251.99		
Year	4	19.19	251	232.79	7.38	≪0.001
Month	5	20.24	246	212.55	6.23	≪0.001
Vessel	1	0.12	245	212.42	0.19	0.659
Temp	6	4.81	239	207.61	1.23	0.290
Temp within month	19	22.93	220	184.68	1.85	0.018
Year × month	11	26.83	209	157.84	3.75	≪0.001

gest that porbeagle have evolved to feed where prey are more abundant, selecting temperatures which are cold enough to discourage most competitors, yet remain metabolically optimal for the porbeagle.

Our results indicate that porbeagle catch rate, and by inference abundance, were highest at intermediate temperatures between 5 and 13°C, and lower at low and high temperatures. These findings are in keeping with those reported for other sharks. For instance, Bigelow *et al.* (1999) reported that the catch rate of blue sharks was greatest at temperatures of 14–18°C, and that catch rate was significantly affected by both SST and the steepness of the SST gradient at the front. Both Hazin *et al.* (1994) and Walsh and Kleiber (2001) reported that blue shark catch rate was significantly influenced by SST. In the only other published study on porbeagle, Francis and Stevens (2000) reported no change in porbeagle catch rate at temperatures (SST, not at depth) between 10 and 19°C, but reported lower catch rates at higher temperatures. Are these catch rate results compatible with the results of our CDF analyses? Despite the fact that there were differences between catch-weighted and environmental CDFs in only some years, the overall similarity suggests that fishers were accurately targeting the appropriate temperature range in which to set their fishing gear. Indeed, anecdotal comments by the fishers indicate that they used temperature measurements and the inferred proximity to frontal regions as guides for preferred fishing location. Thus we interpret these results as indicating that most of the fishing effort was directed to the optimal temperature range or water mass, a strategy commonly followed by fishers in other large pelagic fisheries (Bigelow *et al.*, 1999). Where differences existed, catch rates tended to be highest at low temperatures in warm years, and at high temperatures in cool years.

All lamnids are capable of maintaining a body temperature higher than that of the surrounding water. However, both of the *Lamna* species have the most highly developed ability to conserve metabolically generated heat (Carey and Teal, 1969; Anderson and Goldman, 2001). This heat retention capability may well explain why *Lamna* in both the Atlantic and Pacific oceans are found at higher latitudes than other species of the family. Porbeagle and salmon sharks were most often observed in temperatures of 5–10 and 8–16°C (SST), respectively (this study; Anderson and Goldman, 2001). In contrast, both whites and makos have been reported from considerably warmer waters, ranging from 15 to 22°C for both species (Carey *et al.*, 1982; Cliff *et al.*, 1989; Casey and Kohler, 1992). Thus *Lamna* appears to be the most cold-tolerant genus in the family.

In the absence of depth-stratified fishing gear, it is difficult to comment on the preferred depth range of porbeagle other than to note that they are seldom captured in the surface waters occupied by blue sharks or at depths > 200 m. As porbeagle fishing gear is usually set at night and hauled in the morning, it is entirely possible that porbeagle migrate vertically inhabiting deeper waters during the day than at night. The presence of numerous midwater fishes such as *Alepisaurus* in the stomach makes the possibility of vertical migration more likely (Joyce *et al.*, 2002). More definitive statements on depths and temperatures occupied will require archival tags capable of monitoring depth and temperature over long periods of time (Voegeli *et al.*, 2001). These studies are currently underway.

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