

# Dispersion of Eggs, Larvae and Pelagic Juveniles of White Hake (*Urophycis tenuis*) in Relation to Ocean Currents of the Grand Bank: A Modelling Approach

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## Abstract

White hake (*Urophycis tenuis*) is a temperate demersal fish species distributed in the northwest Atlantic. On the Grand Bank, it is concentrated mainly to the southwest where water temperatures are warmest. Survey data indicate that mature adult females aggregate on the southwest (SW) Grand Bank slope in spring and first-year juveniles settle on the southern, shallow Grand Bank in autumn. Dispersion patterns and survival potential of eggs, larvae and juveniles were investigated with respect to the effects of location (horizontal and vertical) and timing (monthly) of spawning under monthly-mean circulation fields,  $M_2$  tidal currents and associated turbulent mixing computed from a three-dimensional regional ocean circulation model. The results indicate that releases below the surface Ekman layer and in late spring have the highest chances for juveniles to settle in the southern Grand Bank nursery area in autumn. On an interannual scale, the strong recruitment of the 1999 year-class has been used as an example to examine the potential linkage between recruitment and the strength of the Labrador Current. A weak along-slope current and strong on-bank flow contributed to the strong recruitment of the 1999 year-class.

*Keywords:* GIS, Grand Bank, Labrador Current, larval dispersion, ocean current, recruitment, *Urophycis tenuis*, White Hake

## Introduction

The Labrador Current, carrying relatively cold water of Arctic origin, flows along the shelf edge off Atlantic Canada. It has strong seasonal and interannual variability in volume transport, which may have significant impacts on the biology and fisheries in Atlantic Canadian coastal and shelf seas (Han and Tang, 2001; Han, 2005). Here we provide an example of the manner in which the Labrador Current can affect the recruitment of white hake (*Urophycis tenuis* Mitchell 1815: Family Gadidae) on the Grand Bank.

White hake is a temperate demersal species distributed in the Northwest Atlantic from Cape Hatteras to southern Labrador, with dense concentrations occurring in the Gulf of Maine, Scotian Shelf, Gulf of St. Lawrence and on the southern Grand Bank (Musick, MS 1969, 1974; Bundy *et al.*, 2001; Hurlbut and Poirier, 2001; Kulka *et al.*, MS 2005). On the Grand Bank (Fig. 1), white hake are near the northern limit of their range, concentrating along the southwest slope of the Grand Bank, into the eastern

side of the Laurentian Channel and along the southwest coast of Newfoundland (Kulka *et al.*, MS 2005). Their distribution varies seasonally, with concentrations of juveniles extending onto the shallow (<80 m) part of the southern Grand Bank and into some coastal locations in the summer/autumn.

White hake is among the most fecund of fish with spawning characterized by egg release into the water column. The progeny are pelagic during the spring and summer, settling after they become juveniles (Kulka *et al.*, MS 2005). During this period, the pathways of eggs, larvae and young juveniles, and therefore the recruitment of settling juveniles can be significantly affected by meso-scale, seasonal and interannual circulation variability, particularly in relation to the Labrador Current.

Survey data show substantial fluctuations in the abundance of white hake on the Grand Bank (Han and Kulka, MS 2007). In particular, the recruitment of the 1999 year-class was very high. Presumably ocean current variability, in relation to the timing and location of spawn-

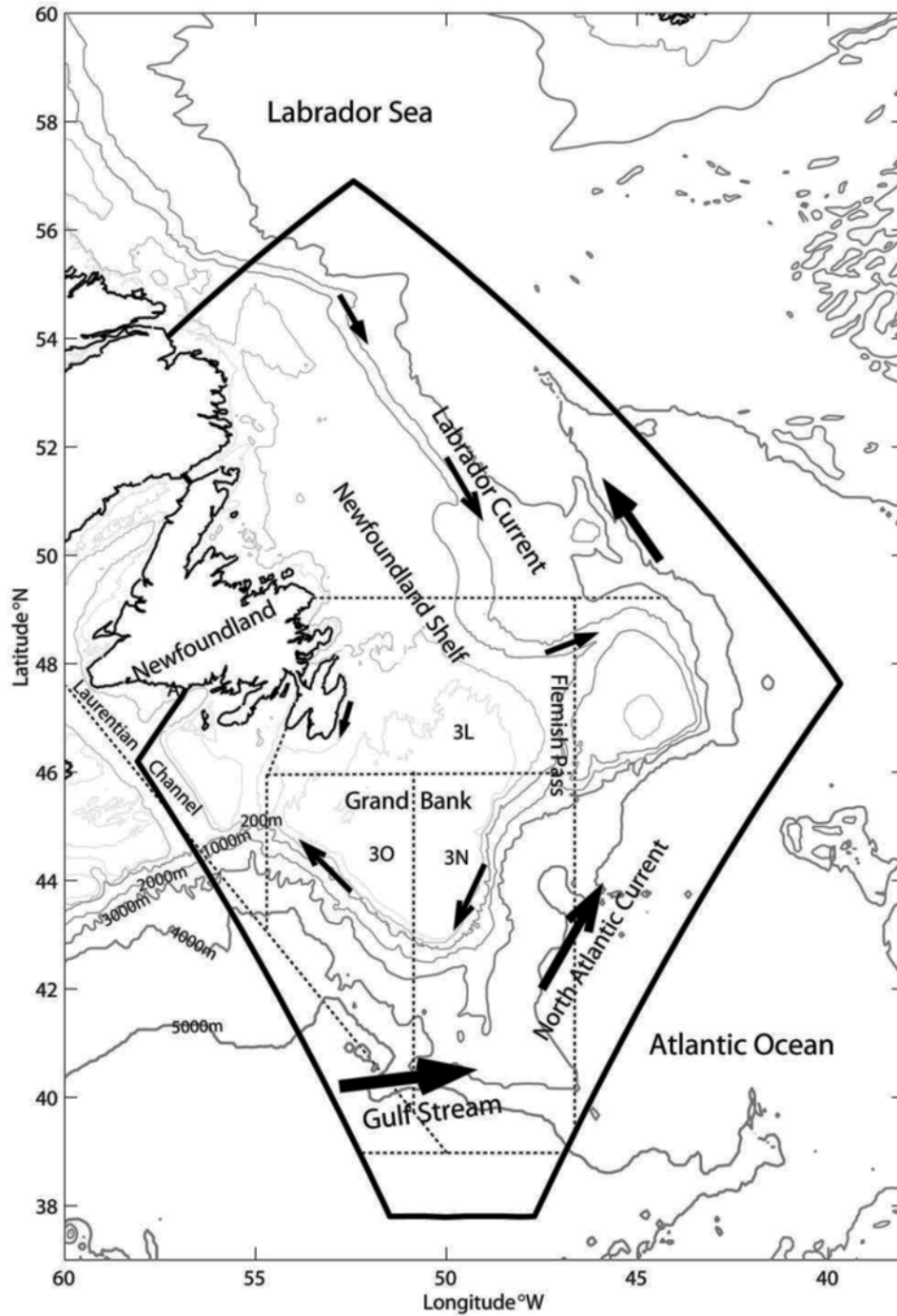


Fig. 1. Map showing the study area. Dotted lines delineate NAFO Divisions. The thick solid lines depict the open boundary locations of the ocean circulation model. Arrows identify the strength and direction of the currents.

ing may play an important or critical role in influencing white hake recruitment. The purpose of this paper is to explore how ocean currents can affect the pathways of eggs, larvae and juveniles in spring/summer and therefore juvenile recruitment in autumn of this population. Variations in the release locations and timing and their effects

on the final destination of juveniles are investigated. In addition, we discuss the role of the Labrador Current in the extremely successful 1999 year-class.

This paper is structured as follows: (i) introduction of methods for the survey and data analysis, circulation

reconstruction and dispersion model configuration, (ii) summarization of monthly mean circulation features, (iii) presentation of dispersion model results under the various circulation patterns, (iv) presentation and discussion of the dispersion patterns and recruitment of the 1999 year-class, and (v) concluding remarks.

## Material and Methods

### Survey data and analyses

Information on abundance, weight, size and maturity of white hake used in this study was collected by Newfoundland and Labrador (NL) Region, Fisheries and Oceans Canada for the purpose of estimating biomass and abundance. The data were derived from the following surveys:

1. NL demersal trawl surveys (random stratified, trawl gear, spring and autumn, post-1970 using Yankee-41.5 trawl to 1983, Engel-145 Hi-lift trawl (mesh size: 160 mm) to 1996, and Campelen-1800 shrimp trawl (mesh size: 40 mm) to date). A summary of the random stratified survey design adopted by the NL Region after 1970 can be found in Doubleday (1981).
2. Juvenile demersal surveys (Yankee-41 shrimp trawl, August-October, 1985–1994).
3. International Young Gadoids Pelagic Trawl (IYGPT) surveys (pelagic trawl at 36 m below surface, August-September, 1996-2000).

More information on these survey methods can be found in Kulka *et al.* (MS 2005).

Analysis of the distribution of different life stages of white hake integrates information on length and maturity collected for each sex. The focus of this analysis is on years when the Campelen trawl was used (1995–2004), since it captures a wider range of sizes including newly settled juveniles (recruits). Maturity data, recorded for 97% of survey sets were used to calculate maturity ogives and length at 50% maturity ( $L_{50}$  = length at which 50% of the fish were sexually mature) by sex for each Campelen survey year. Based on the analyses of sexual maturity, observations of modes in the size frequencies and preliminary information on age, white hake were assigned to three size classes corresponding to stages in the white hake life history: <25 cm - animals in their first year; 26–56 cm - juveniles older than 1 year and >57 cm - mature adults (Kulka *et al.*, MS 2005).

GIS - SPANS (Geographic Information System – Spatial Analysis System) was used to investigate the

spatial distribution of white hake with survey data. Potential mapping in SPANS (Anon, 2000) transforms points (kg per tow) to density surfaces (classified areas of similar kg per tow) by placing a circle around each point (survey set location) and averaging the values of all points that fall within the circle. The circle size selected (12 km diameter) provided complete coverage of the survey area while minimizing overlap of the circles and thus maximizing spatial resolution. The study area periphery was isolated using a ‘cookie cut’ technique (referred to as a basemap cut in SPANS). This resulted in a density surface bounded on all sides by either land or the 1000 m depth contour. The surface was stratified into 15 classes defining density of the fish, each class covering approximately the same amount of area. The method is further described in Kulka (MS 1998).

### Reconstruction of the ocean circulation

A finite-element circulation model (Han *et al.*, 2008) was used to compute ocean currents, under wind, buoyancy and tidal forcing. The model domain covers the southern Labrador Shelf, the Newfoundland Shelf and adjacent deep oceans (Fig. 1), with high resolution in shallow areas and those with steep topography. Typical node spacing is 5 km over the shelf, with a higher resolution of about 1 km for the shelf-edge Labrador Current. Initial water temperature and salinity fields are interpolated from gridded monthly mean data objectively analysed from a historical hydrographic database for the Northwest Atlantic. The wind stresses are computed from 6-hourly (once every 6 h) wind data for the period from 1990–1999 (Han, 2005). The monthly-mean wind stresses (not shown) have seasonal variations in both magnitude and direction, with the winter stress being stronger and directed more cross-shelf (offshore) than the stresses during the other seasons. The most prominent tidal constituent, the  $M_2$  tide, was also included in the model. See Han *et al.* (2008) for more details. The model reproduced 12 monthly-mean circulation fields, which were used to represent a normal year.

The finite-element model provided monthly-mean circulation climatology only. Our limited searches did not find other well validated models that sufficiently resolve the shelf-edge Labrador Current for the study region. Therefore we used satellite altimetry in conjunction with the finite-element model solution to reconstruct monthly-mean circulation fields for 1999. A long-term mean current field was calculated by averaging the 12 monthly-mean model circulation fields. The monthly near-surface circulation anomalies for April–September of 1999 were derived from weekly satellite altimetric sea surface height anomalies under the assumption of geostrophy. The satellite derived currents, with a spatial resolution of about 25 km in the study region, were linearly interpolated

onto the model grid in the horizontal. The satellite data provide near-surface geostrophic current anomalies only. To estimate subsurface current anomalies, we used two assumptions: (1) the current anomalies are depth invariant; and (2) they have a linear profile in the vertical, with the bottom current equal to zero. We also considered using the vertical structure from the climatological mean circulation and found the method is less robust presumably because the magnitude of the current anomaly is much larger than that of the mean current. Under each of the two assumptions we generated the vertical profiles of the current anomalies and added them onto the long-term model mean current field to form the total currents for April–September of 1999.

### Dispersion simulation of eggs, larvae and juveniles

The dispersion simulation considers effects of temporal variability and spatial structure of the circulation. It tracks eggs and larvae released in the monthly-mean circulation fields. The tracking method is described by Werner *et al.* (1993). In addition, estimates of the influence of unaccounted horizontal motions are obtained assuming a random walk process where additional displacements are calculated using externally specified eddy diffusivity ( $150 \text{ m}^2/\text{s}$ ) in the horizontal directions (*e.g.* Berg, 1993). Previous studies based on field experiments off the US east coast estimated the eddy mixing coefficients to be  $50\text{--}500 \text{ m}^2/\text{s}$  (Ketchum and Keen, 1955).

We chose locations for release of eggs and the area for settling of juveniles based on the observed distribution of white hake at various life stages. From examination of the gonads collected during the spring trawl survey, individuals in spawning condition were noted in April–May on the outer Grand Bank (Kulka *et al.*, MS 2005). Large, ripe and running females were reported during April and May along the southwest slope suggesting spring spawning in this location. Summer observations of maturity were not available to determine if spawning extended into that period. No mature gonads were observed in October on the Grand Bank suggesting that spawning was completed by autumn (Kulka *et al.*, MS 2005). The full extent of the spawning period on the Grand Bank is unknown since the collection of data on maturity has been restricted to April, May and October.

Based on spring survey data corresponding to the spawning time, mature females ( $>57 \text{ cm}$ ) reached their highest proportion (30–85% of the collections) along the southwest slope of the Grand Bank (mainly NAFO Div. 30) from  $51^\circ \text{ W}$  to  $56^\circ \text{ W}$  (Fig. 2). It is from these locations that it is expected that most of the white hake eggs would be released during spawning. These mature females

inhabited a wide range of depths from about 80–450 m, but were most densely concentrated between 100 and 270 m (Fig. 3). Occupancy of this depth range was consistent over time but with some interannual fluctuations.

Eggs, larvae and young juvenile white hake are pelagic. Although the distributions of eggs and larvae have not been described for the Grand Bank, the next stage in the life cycle, pelagic young of the year (YOY) were observed in August–September over most of the Grand Bank but most densely concentrated over the shallow part of the southern portion (Kulka *et al.*, MS 2005). Ninety-eight percent of observed pelagic hake were taken from an area centred at  $44^\circ 20' \text{ N}$  and  $50^\circ 50' \text{ W}$  encompassing only 4% of the Grand Bank. The timing of pelagic YOY implies that, if Grand Bank white hake have similar life history attributes to those in the Gulf of St. Lawrence, as described by Nepszy (MS 1968) and Markle *et al.* (1982), they were derived from adults which spawned in spring/summer. This implied spawning time is consistent with maturity observations from the spring Grand Bank trawl survey described above.

Newly settled juveniles were observed well offshore on the shallow part of the southern Grand Bank in the autumn at the same geographic location as the highly concentrated pelagic juveniles observed in late summer, as described above. The bottom depth at that location was 50–80 m and corresponded to the warmest location on the bank. There, the newly settled juveniles, in the range of 8–15 cm, were primarily separated from larger fish.

Hake  $<17 \text{ cm}$  (newly settled juveniles) dominated the survey catches on the shallow, southern portion of the Grand Bank in the autumn when settling of juveniles occurred (Fig. 4, coloured areas). These locations correspond closely with pelagic juveniles observed in the water column in the IGYPT surveys August–September 1994–2000 (Fig. 4, black squares). Pelagic larvae and juveniles rarely occur on the northern part of the Grand Bank, thus most settlement occurs to the south where bottom waters are warmer year round.

Spring survey data (Fig. 5) show substantial interannual fluctuations of the white hake population on the Grand Bank. The recruitment was good for the 1998–2000 year-classes, and was extremely large for the 1999 year-class. The progression of the large 1999 year-class was particularly easy to follow through time in the IGYPT and Campelen surveys. The mean date of capture of pelagic juveniles at 30 m below the surface in the IGYPT survey was 5 September. Their size ranged from 2.5–7.0 cm (mean 6.0 cm). At the same geographic location, but at 52–79 m bottom depth, newly settled juveniles

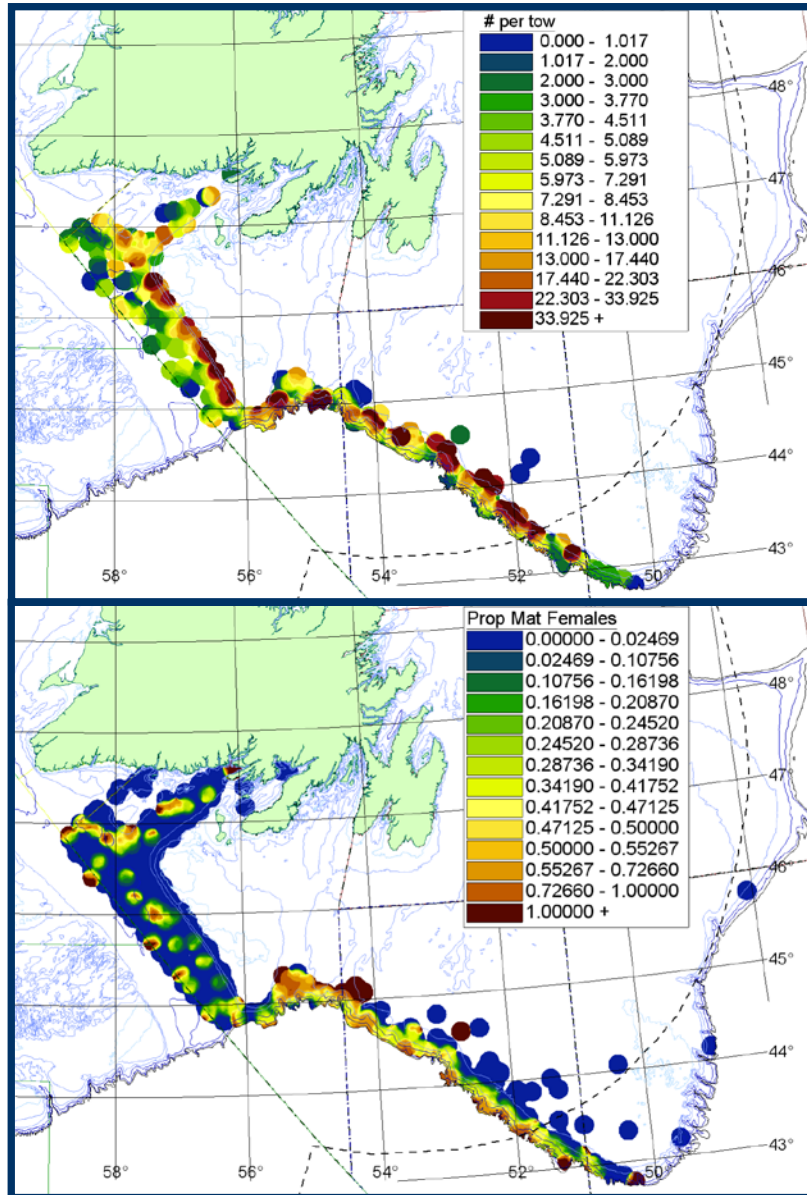


Fig. 2. Upper panel: Distribution of mature female white hake (>57 cm TL). Lower Panel: Proportion by number of mature females in the total survey catches. Data are from 1995–2004 spring trawl surveys.

were captured in the Campelen trawl in November of 1999. On 15 November 1999 (about 10 weeks after the pelagic survey), the average hake size was 13.4 cm (Fig. 6). Sets with fish of this size contained almost no larger fish indicating initial isolation from the older components. On 3 May 2000 (about 24 weeks later), large numbers of hake averaging 25.7 cm were collected (Fig. 6).

The dispersion experiments in this study treat eggs, larvae and juveniles as particles that have no vertical migration and follow the horizontal water movement under monthly mean circulation and  $M_2$  tidal currents. Three re-

lease regions are considered: (i) the SW slope region from the 100-m to 500-m isobath and from 56° W to 50° W; (ii) the SW Grand Bank region, and (iii) the Laurentian Channel region (see Fig. 7). The nursery ground is defined as the area from the 100-m isobath to 45° N and from 52° W to 50° W (Fig. 7). We have considered three positions in the vertical: (i) the 50-m depth where a high concentration of eggs is expected, (ii) the 30-m depth which is below the surface Ekman layer, and (iii) the 1-m depth which is in the Ekman layer. The release dates were 1 April, 1 May and 1 June, and the corresponding tracking times were 180, 150 and 120 d, ending on 29 September.

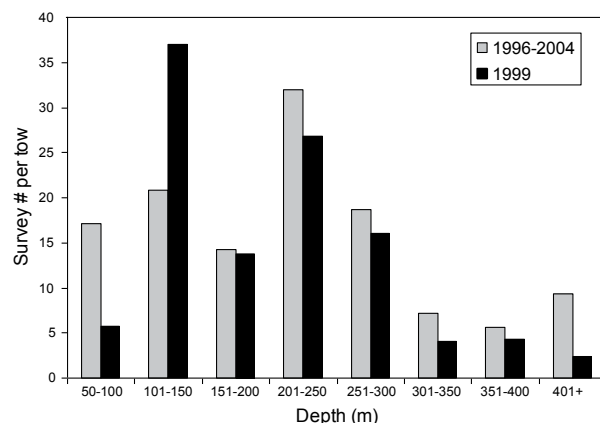


Fig. 3. Density of mature female white hake (>57 cm TL) by depth interval in the spring survey of 1999 and average over 1996–2004.

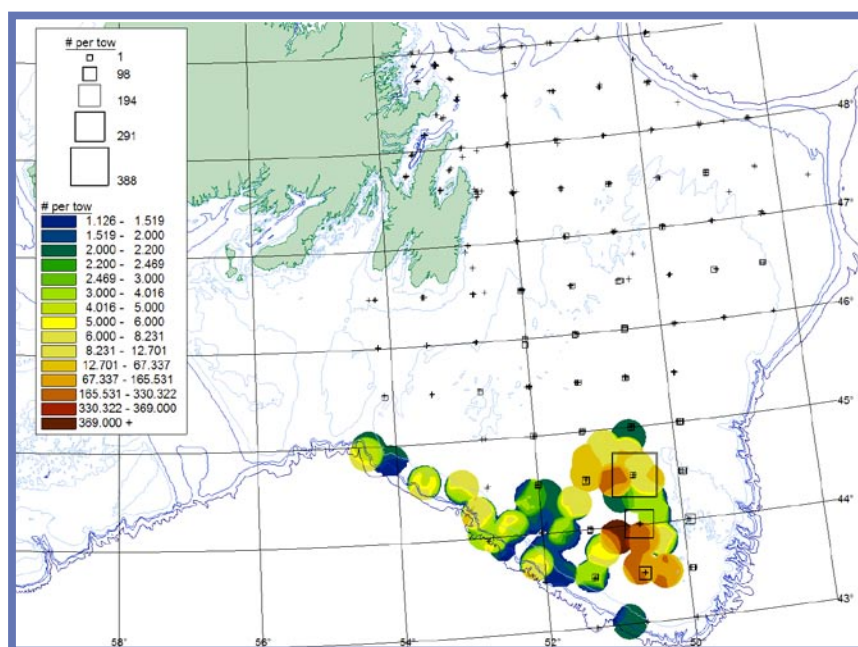


Fig. 4. Colour surface depicts the density of newly settled white hake from the Campelen autumn survey data superimposed by pelagic (~30 cm below surface) YOY from the IGYPT survey (squares). The crosses are sampled locations where no pelagic white hake were caught.

### Model circulation features

The finite-element model generated 12 monthly-mean circulation fields and the  $M_2$  tidal current field. There are strong seasonal variations in the upper-layer monthly-mean current field. For example, the Labrador Current is stronger in April than in June (Fig. 8). The spatial variability is significant, with the dominant flow along the shelf edge and to a lesser degree along the coast. Cross-shelf advective exchanges are clearly evident, for example, the offshore flow along the northern Grand

Bank edge. The cross-slope exchanges are also apparent, especially along the southeastern Grand Bank slope where the Labrador Current is entrained into the northeastward North Atlantic Current. As a result, the Labrador Current on the southwest Grand Bank slope is much weaker than on the southeast Newfoundland slope. The wind-driven Ekman flow is an important surface flow component over the Grand Bank (Fig. 9). The flow patterns between depths of 30- and 50-m indicate limited vertical shear of the horizontal current in the upper water column except within the surface Ekman layer.

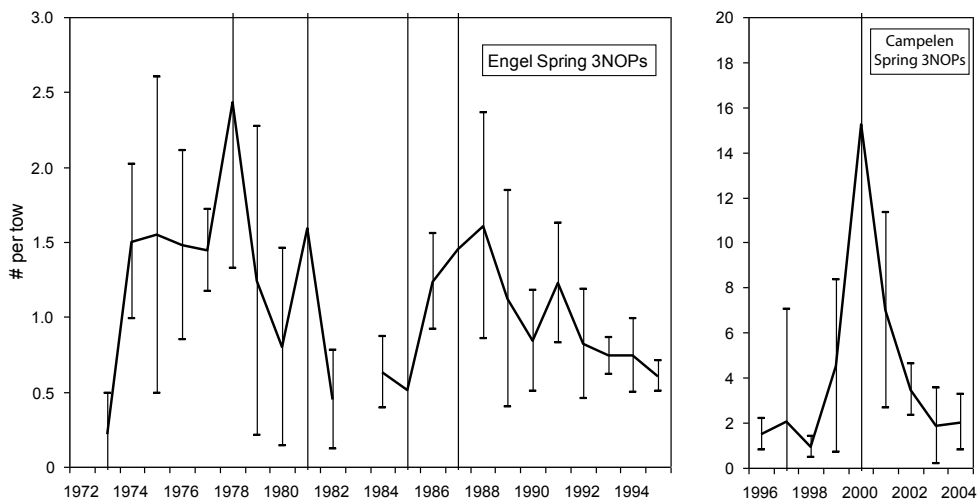


Fig. 5. Abundance of white hake in NAFO Div. 3NOPS based on spring surveys. The vertical bars show the standard deviation. Note the changes of the survey methods and scales between the two panels.

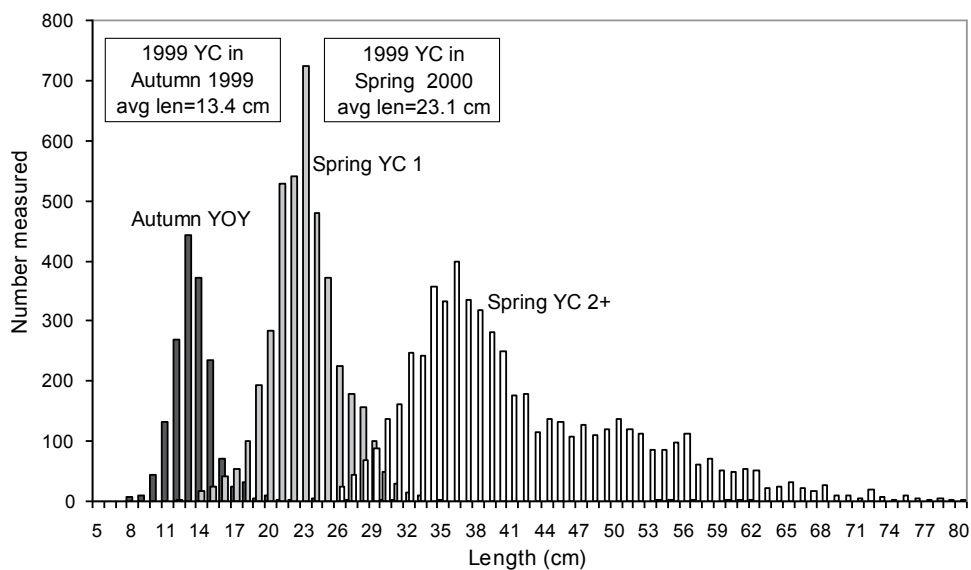


Fig. 6. Cumulative length frequencies for sets containing 1999 year-class white hake in the autumn of 1999 and spring of 2000. Individuals of other year-classes found in those sets are included (as Spring YC 2+).

There is also substantial spatial variability in tidal currents (not shown), *e.g.* with stronger currents over the shallow, southern nursery area. A detailed description of tidal currents over the Grand Bank can be found in Han (2000).

The re-constructed 1999 monthly means (Fig. 10) have weaker along-slope Labrador Current and increased on-bank flow on the SW Grand Bank edge compared with the model monthly mean currents (Fig. 8), especially with the depth-invariant assumption for the current anomalies.

These circulation differences may have important implications for the early life history of white hake.

## Dispersion Results

### Horizontal release positions

Numerical experiments were carried out for the 50-m releases from three geographical areas (Fig. 7). The distribution of particles (which represent eggs and larvae as defined in Materials and Methods) at the end of



September is shown in Fig. 11. The results indicate that a higher percentage of the particles released from the SW Bank can be available for settlement in the nursery area in early autumn compared with those released from the SW slope (Fig. 12). None were available for settlement from the Laurentian Channel release. These dispersion results are consistent with the spatial pattern of the climatological monthly-mean model circulation. Over the southern Grand Bank, the subsurface flow is relatively weak, which provides a good retention mechanism. As a result, a higher percentage of particles from the SW Bank release are available for settlement in early autumn. In contrast, the subsurface current along the shelf edge is quite strong, which carries the majority of the particles from the SW slope release downstream.

The eggs and larvae that do not enter the nursery ground are swept downstream or offshore (Fig. 11). They have little chance of becoming white hake recruits of the Grand Bank as settlement would occur off the shelf, outside of the depth range of white hake. The issue of whether they can survive somewhere else is interesting, but beyond the scope of this paper.

#### Vertical release positions

We have tracked particles released at depths of 1-m, 30-m and 50-m from the SW Bank and Slope (Fig. 12). The simulation results indicated that significantly fewer particles released at the surface (1 m) are carried to or

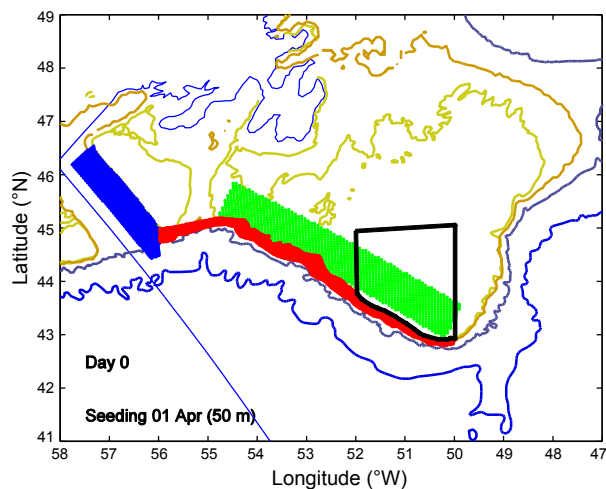


Fig. 7. Horizontal distribution of particles at the start of tracking. Green: Southwest Grand Bank (Bank); Red: Southwest Slope (Slope); Blue: Laurentian Channel. The nursery area on the south Grand Bank spans from the 100-m isobath to 45° N and from 52° W to 50° W (black polygon). The 100-, 200-, 1000-, and 3000-m isobaths are depicted.

retained inside the southern nursery area at the end of late summer compared to those released at the subsurface (30 and 50 m). Near the surface the southeastward wind-driven Ekman flow sweeps particles offshore. The reduction is more significant for the shallow bank release.

More particles from the 50-m release eventually occupy the nursery ground than from the 30-m release, and this is attributable to the vertical shear of the horizontal current. Nevertheless, the difference between the 30- and 50-m releases is less significant than between the surface and subsurface layers.

#### Release time

Analysis of survey data suggested a spring spawning season, possibly spanning several months. Here we

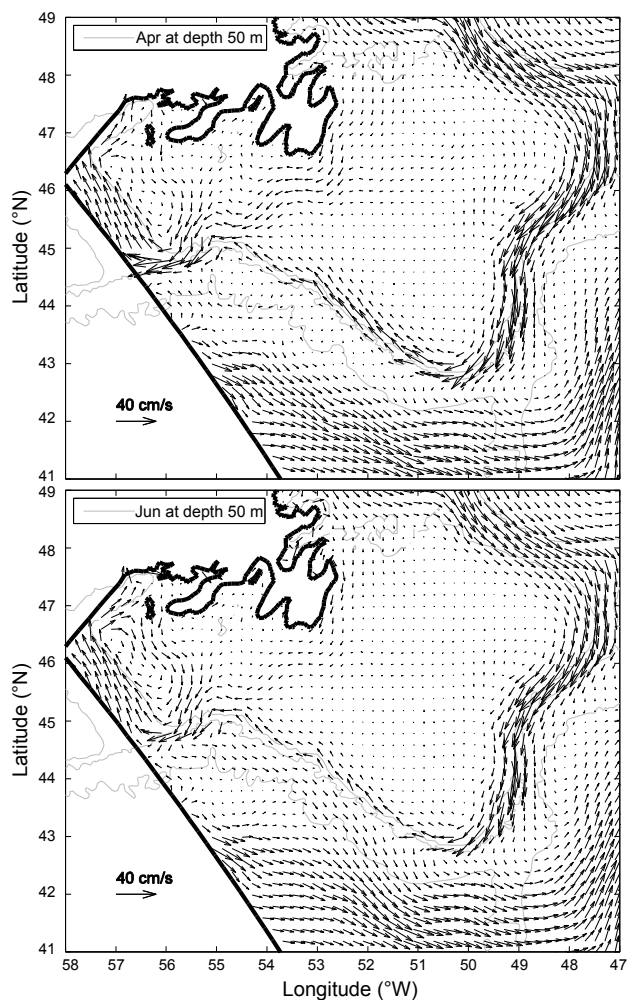


Fig. 8. Model circulation fields at 50-m in April (top) and June (bottom). The model fields have been subsampled for clarity of presentation. The 200-, 1000-, and 3000-m isobaths are depicted.



examine the impacts of spawning timing on dispersal. The results from the 50 m release on 1 April, 1 May and 1 June indicate that juveniles from late spring spawning have the highest chances to settle in the southern Grand Bank nursery ground (Fig. 12). There is a persistent westward flow along the shelf edge, with moderate seasonal variation (strong in spring and weak in summer). Under an early release, eggs and subsequently larvae and juveniles experience stronger ocean currents over a longer period prior to their settlement in the nursery area. Therefore they can be carried further downstream by advection or further offshore by entrainment.

### Dispersion and recruitment in 1999

We considered releases at 1- and 50-m from the major spawning area in the horizontal (SW Slope). There are interesting changes in the temporal patterns and autumn settlement under the 1999 circulation condition (Figs. 13 and 14), compared with those under the monthly-mean circulation. All three Slope releases show a rapid increase of particles in the nursery area nearly immediately (Fig. 14a). The result under the depth-invariant current anomaly assumption has high fluctuations and a high number of particles inside the nursery area during the first three months, whereas the result under the depth-linear assumption exhibits an initial increase followed by a relatively steady decline. The weakened Labrador Current and the increased on-bank flow in 1999 (Figs. 8 and 10) are responsible for the temporal patterns and increased nursery settlement. No matter whether the assumption is depth-invariant or depth-linear, the availability for settlement in 1999 is much higher than that for the monthly-mean case (*i.e.*, a normal year). For the 1-m release, the contrast between 1999 and a normal year is even more drastic (Fig. 14B).

### Discussion

Previous studies have suggested that the shelf-edge Labrador Current was intensified off central Labrador in 1995/1996 (Han and Tang, 2001; Hakkinen and Rhines, 2004). The Labrador Current pulse passed the southwest Newfoundland Slope in early 1997 (Han, 2006), reached the Scotian Slope (Han, 2007) and intruded onto the Scotian Shelf in late 1997 and early 1998 (Han, 2002). The flow along the southwest Newfoundland Slope remained westward but was much weaker in 1999 (Han, 2006). The Labrador Current variability is believed to be related to the dominant atmospheric variability in the North Atlantic – the North Atlantic Oscillation (Han and Tang, 2001; Hakkinen and Rhines, 2004; Han, 2007).

We have demonstrated that the shelf-edge current variability has profound impacts on the pathways and

destination of eggs, larvae, and pelagic juveniles of white hake since the major spawning area of this species is located along the shelf-edge. The reduced along-slope flow and increased on-bank flow in 1999 provided a much better upper-layer transport and retention mechanism for eggs and larvae on the southwest shelf edge to reach and remain in the shallow nursery ground, and this is an important necessary condition for successful recruitment of first year juveniles (Fig. 5).

Given the vertical shear in the horizontal current, effects of the vertical migration (passive by the vertical water current or self-propelled by new juveniles) are expected to be important for the horizontal movement of larvae and juveniles (*e.g.*, Kristiansen *et al.*, 2007; Fiksen *et al.*, 2007). Unlike Werner *et al.* (1993) the present study does not consider any vertical migratory behaviour or movement. Since the results from the 1-m

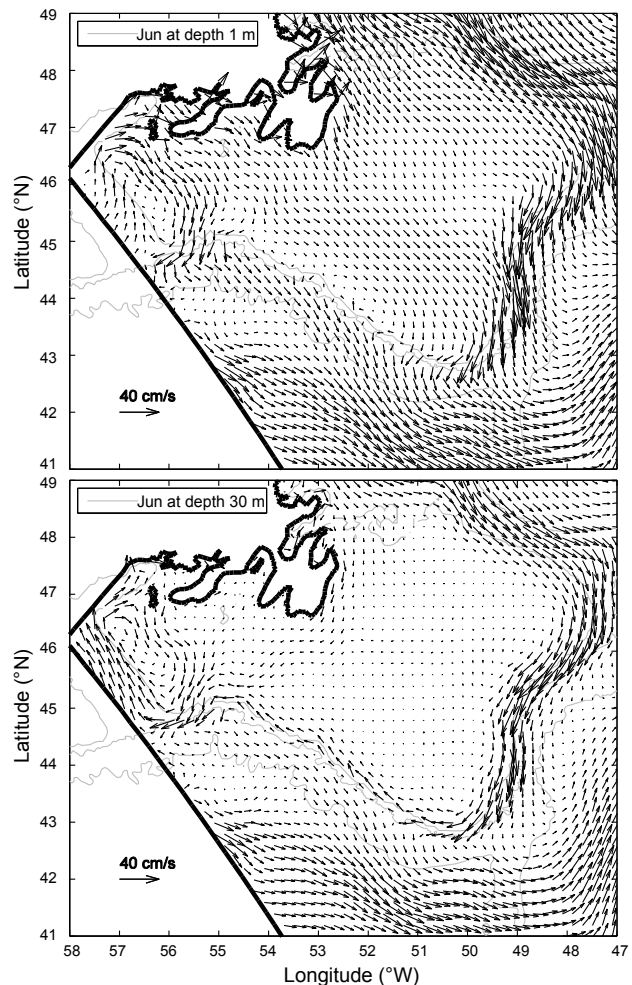


Fig. 9. Model circulation fields at the 1- and 50-m depths in June. The model fields have been subsampled for clarity of presentation. The 200-, 1000-, and 3000-m isobaths are depicted.

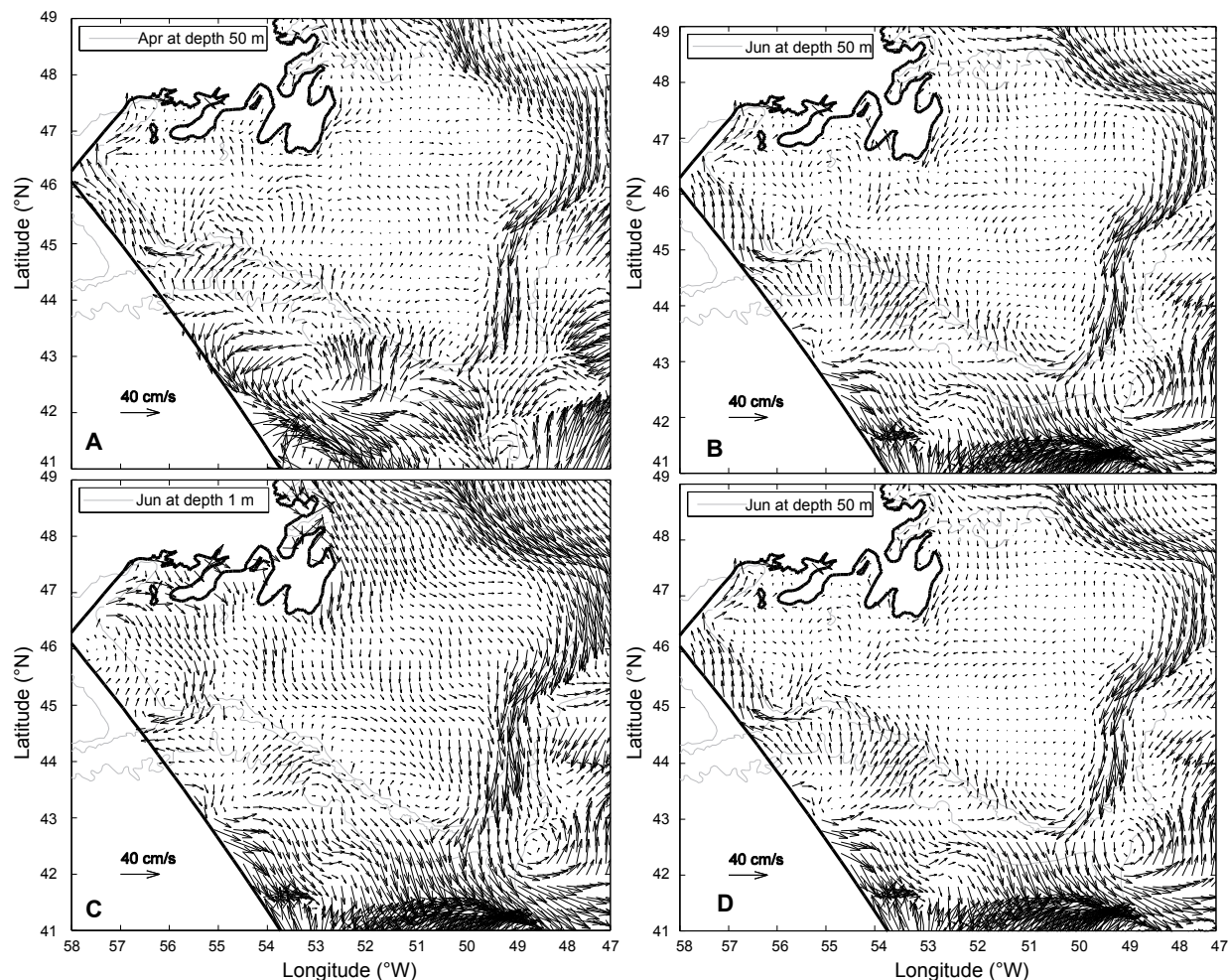


Fig. 10. The monthly circulation patterns in 1999, reconstructed from the model long-term mean circulation field and the monthly satellite-derived current anomalies. (A) 50-m in April, (B) 50-m in June, (C) 1-m in June and (D) 50-m in June. The anomaly currents are assumed to be depth-invariant in (A), (B), and (C), and to be variable linearly with depth with the bottom value of zero in (D). The 200-, 1000-, and 3000-m isobaths are also depicted.

and 50-m releases are qualitatively the same, it is unlikely that inclusion of migratory behaviour would have altered the conclusion.

Another issue is the effect of horizontal swimming capacity of larvae and pelagic juveniles from spring to August/September. Unfortunately, there is little information available on this subject. By the time they are ready to settle to the bottom in autumn, they are able to swim in a descending vertical fashion. Newly hatched larvae are capable of swimming but with a lower capacity than larger pelagic juveniles. Presumably this is a progressive capability and it is difficult to define when they become “strong” swimmers. In general, larvae/juveniles are increasingly able to move against currents as they grow but because of their small size, the magnitude of their capacity to move horizontally would not be very large at

any stage of pelagic existence. If their swimming behaviour does not change between 1999 and a normal year, it is not likely to change the recruitment difference caused by the ocean current.

The model results may also be influenced by the uncertainty associated with the assumed spawning locations in the water column. A recent study (Loher and Seitz, 2008) has shown that Pacific halibut undergo vertical migration and release eggs up in the water column. Such a migration/release pattern is thought to occur for the Atlantic cod that is more closely related to white hake (E.A. Trippel and G.A. Rose, personal communication, 2008). The egg release depth (50 m and above) assumed for white hake in our study is shallower than the depth of observed spawning aggregations (100–270 m), consistent with the pattern of Pacific halibut and Atlantic cod.

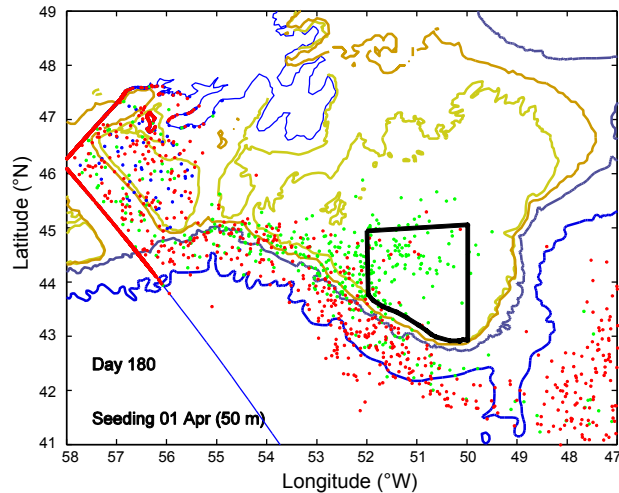


Fig. 11. Snapshot of the simulated particle distribution at the end of September. The particles were released at a depth of 50 m on 1 April. See Fig. 7 for the release locations.

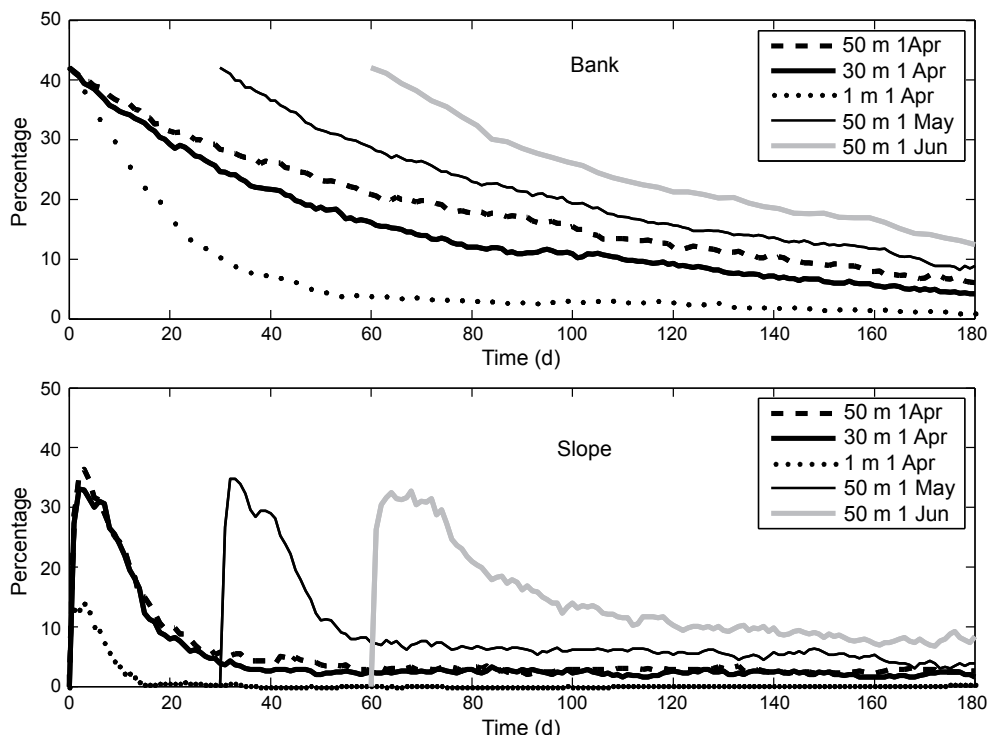


Fig. 12. The temporal evolution of the percentage of particles within the nursery area for the SW Grand Bank (top) and the SW Newfoundland Slope (bottom) releases. The particles were released at depths of 1, 30 and 50 m on 1 April, and at 50 m on 1 May and 1 June. Juveniles become demersal usually after September.

In addition to ocean currents, other factors such as spawning biomass, ocean temperature and food availability may play important roles in recruitment success. Like ocean current transport, these are all influential with respect to recruitment and presumably a favourable

combination of these factors is required for successful recruitment. Spring survey data indicated that the number of spawning females in 1999 was low and not significantly different from years when recruitment was lower than 1999 (Kulka *et al.*, MS 2005). Nevertheless,

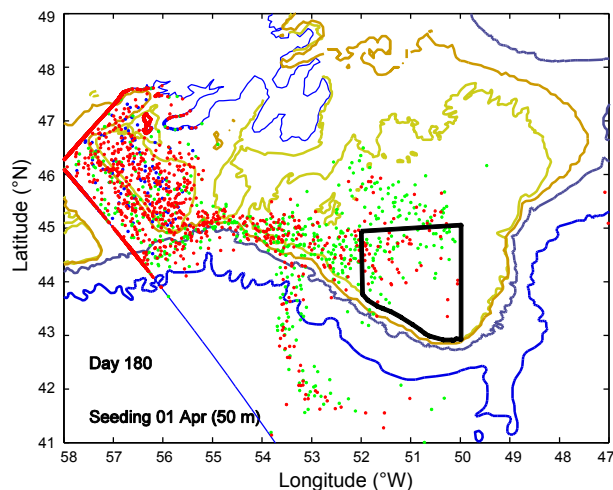


Fig. 13. Snapshot of the simulated particle distribution at the end of September for the 1999 depth-linear current anomalies case. The particles were released at a depth of 50 m on 1 April. See Fig. 7 for the release locations.

satellite ocean colour data (not shown) indicated the spring bloom in the vicinity of the nursery ground in 1999 was a few weeks earlier than normal. The early spring bloom could have significant implications for successful fish recruitment (Platt *et al.*, 2003). In addition, satellite and *in situ* data (not shown) indicated sea surface temperature was significantly warmer in 1999 than in other years and presumably more favourable for survival and growth of larvae and juveniles.

### Concluding Remarks

Field survey data indicated that the SW Grand Bank slope is a major spawning area in spring for white hake. Most of the newly settled juveniles were located in the SW Grand Bank region (the nursery area) in autumn and were separated from the population of mature white hake that are mostly on the SW Grand Bank slope. The mature spawning females are mainly located along the southwest Grand Bank edge in the depth range of 50–150 m in spring.

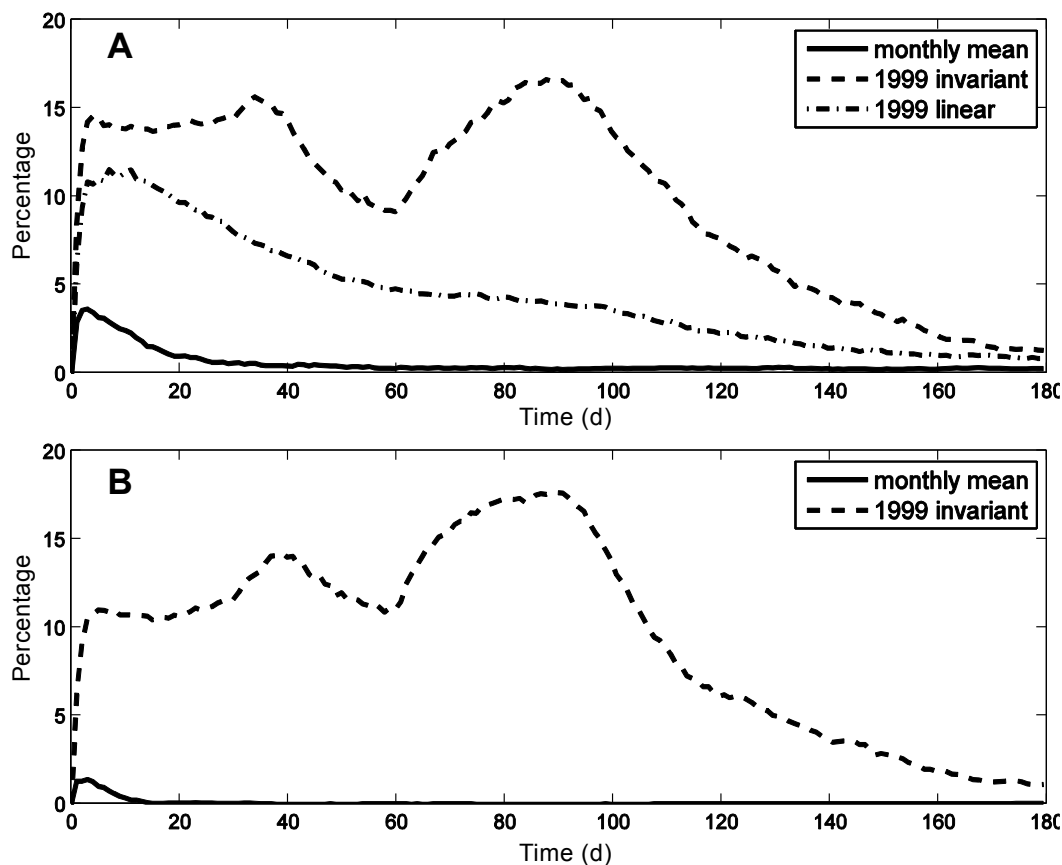


Fig. 14. The temporal evolution of the percentage of particles within the nursery area in 1999 and a normal year (under the monthly-mean circulation) for (A) the 50-m release and (B) the 1-m release. The particles were released on 1 April and tracked for six months. Juveniles become demersal usually after September.

A period of ~6 months is required for release of eggs into the water column in the spring (April and probably other months in the spring, Kulka *et al.*, MS 2005) to the time juveniles settle in shallow areas in the autumn and during this period they are subject to transport by ocean currents.

The ocean circulation in the Grand Bank region has marked spatial variability, strong along the shelf edge and upper continental slope (the shelf-edge Labrador Current) and weak over the Grand Bank. There is also significant seasonal and interannual variability in the shelf-edge Labrador Current. Along the southwest Grand Bank edge, the Labrador Current had a weaker along-slope flow and stronger on-bank component in 1999. In comparison to all years after 1995, the recruitment of the 1999 year-class was extremely good.

The dispersion model study for the major spawning area (southwest Grand Bank slope) suggests that YOY juveniles derived from late spring spawning have a higher potential to settle during autumn in the south Grand Bank nursery ground. A weaker along-slope Labrador Current and stronger on-bank flow contributed to the recruitment success in 1999. Although just one component of the ocean environmental factors in the Grand Bank ecosystem, the variability of ocean currents has important and at times critical influences on the early life stages of white hake.

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### References

- ANON. 2000. SPANS Prospector, SPANS 7.0. TYDAC Research Inc. Nepean, Ontario, Canada.
- BERG, H. C. 1993. Random Walks in Biology. Princeton University Press, 152 p.
- BUNDY, A., M. FOWLER, W. MACEACHEN, and P. FANNING. MS 2001. Assessment of the status of 4VWX/5 White Hake, 2001. *DFO Can. Sci. Advisory Res. Doc.*, 98 p.
- DOUBLEDAY, W. G. (ed.). 1981. Manual on groundfish surveys in the Northwest Atlantic. *NAFO Sci. Coun. Stud.*, 2, 7–55 p.
- FIKSEN Ø., C. JORGENSEN, T. KRISTIANSEN, F. VIKÉBO, and G. HUSE. 2007. Linking behavioural ecology and oceanography: larval behaviour determines growth, mortality and dispersal. *Mar. Ecol. Prog. Ser.*, **347**: 195–205. doi:10.3354/meps06978
- HAKKINEN, S., and P. B. RHINES. 2004. Decline of subpolar North Atlantic circulation during the 1990s. *Science*, **304**: 555–559. doi:10.1126/science.1094917
- HAN, G. 2000. Three-dimensional modeling of tidal currents and mixing quantities over the Newfoundland Shelf. *J. Geophys. Res.*, **105**: 11407–11422. doi:10.1029/2000JC900033
2002. Interannual sea level variability in the Scotia-Maine region in the 1990s. *Can. J. Remote Sens.*, **28**: 581–587.
2005. Wind-driven barotropic circulation off Newfoundland and Labrador. *Cont. Shelf Res.*, **25**: 2084–2106. doi:10.1016/j.csr.2005.04.015
2006. Low-frequency variability of sea level and currents off Newfoundland. *Adv. Space Res.*, **38**: 2141–2161. doi:10.1016/j.asr.2006.04.011
2007. Satellite observations of seasonal and interannual changes of sea level and currents over the Scotian Slope. *J. Phys. Oceanogr.*, **37**: 1051–1065. doi:10.1175/JPO3036.1
- HAN, G., and D. W. KULKA. MS 2007. Dispersion of eggs, larvae and pelagic juveniles of White Hake (*Urophycis tenuis*, Mitchell 1815) on the Grand Banks of Newfoundland in relation to subsurface currents. *NAFO SCR Doc.*, No. 21, Serial No. N5372, 27 p.
- HAN G., Z. LU, Z. WANG, J. HELBIG, N. CHEN, and B. DEYOUNG. 2008. Seasonal variability of the Labrador Current and shelf circulation off Newfoundland. *J. Geophys. Res.*, **113**: C10013. doi:10.1029/2007JC004376
- HAN G., and C. L. TANG. 2001. Interannual variation of volume transport in the western Labrador Sea based on TOPEX/Poseidon and WOCE data. *J. Phys. Oceanogr.*, **31**: 199–211. doi:10.1175/1520-0485(2001)031<0199:IVOTI>2.0.CO;2
- HURLBUT, T., and G. POIRIER. MS 2001. The status of White Hake (*Urophycis tenuis*, Mitchell) in the Southern Gulf of St. Lawrence (NAFO Division 4T) in 2000. *DFO Can. Sci. Advisory Res. Doc.*, 2001/1024, 61 p.
- KETCHUM, B. H., and D. J. KEEN. 1955. The accumulation of river water over the continental shelf between Cape Cod and Chesapeake Bay. *Deep-Sea Res.*, **3** (suppl.): 346–357.
- KRISTIANSEN, T., Ø. FIKSEN, and A. FOLKVORD. 2007. Modelling feeding, growth, and habitat selection in larval Atlantic cod (*Gadus morhua*): observations and model predictions in a macrocosm environment. *Can. J. Fish. Aquat. Sci.*, **64**: 136–151. doi:10.1139/F06-176
- KULKA, D. W. MS 1998. SPANDEX - Spans geographic information system process manual for creation of biomass indices using potential mapping. *Can. Sci. Advisory Res. Doc.*, 98/60, 28 p.
- KULKA, D. W., C. M. MIRI, and M. R. SIMPSON. MS 2005.

- Distribution and aspects of life history of white hake (*Urophycis tenuis*, Mitchill 1815) on the Grand Banks of Newfoundland. *NAFO SCR Doc.*, No. 60, Serial No. N5146, 58 p.
- LOHER, T., and A. C. SEITZ. 2008. Characterization of active spawning season and depth for eastern Pacific halibut (*Hippoglossus stenolepis*), and evidence of probable skipped spawning. *J. Northw. Atl. Fish. Sci.*, **41**: 23–36.
- MARKLE, D. F., D. A. METHVEN, and L. J. COATES-MARKLE. 1982. Aspects of spatial and temporal co-occurrence in the life history stages of the sibling hakes, *Urophycis chuss* (Walbaum 1792) and *Urophycis tenuis* (Mitchell 1815) (Pisces: Gadidae). *Can. J. Zool.*, **60**: 2057–2078. doi:10.1139/z82-265
- MUSICK, J. A. MS 1969. The comparative biology of two American Atlantic hakes, *Urophycis chuss* and *U. tenuis* (Pisces Gadidae). Ph.D. thesis, Harvard U.
1974. Seasonal distribution of sibling hakes, *Urophycis chuss* and *U. tenuis* (Pisces: Gadidae) in New England. *Fish. Bull.*, **72**: 481–495.
- NEPSZY, S. J. MS 1968. On the biology of the hake (*Urophycis tenuis* Mitchill) in the southern Gulf of St. Lawrence. MSc thesis, McGill Univ., Montreal, 69 p.
- PLATT T., C. FUENTES-YACO, and K. T. FRANK. 2003. Spring algal bloom and larval fish survival. *Nature*, **423**: 398–399. doi:10.1038/423398b
- WERNER, F. E., F. H. PAGE, D. R. LYNCH, J. W. LODER, R. G. LOUGH, R. I. PERRY, D. A. GREENBERG, and M. M. SINCLAIR. 1993. Influence of mean 3-D advection and simple behaviour on the distribution of cod and haddock early life stages on Georges Bank. *Fish. Oceanogr.*, **2**: 43–64. doi:10.1111/j.1365-2419.1993.tb00120.x
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