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Field examination of dispersion patterns of juvenile Iceland scallops (*Chlamys islandica*) in the northern Gulf of St Lawrence

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The movement of juvenile Iceland scallops, *Chlamys islandica*, was quantified in an inshore bed in the Mingan Islands, northern Gulf of St Lawrence, to examine whether the size partitioning over depth in this location, increasing scallop size with depth, results from a gradual downslope movement as scallops increase in size. Scallops of 30.0–44.9 mm and 45.0–59.9 mm in shell height were collected using SCUBA, tagged, and released in the centre of two 0.4-km^2 grids at 15 m in depth. After 7 d and 48 d, the net distance moved by the scallops from the release points did not vary between the two size groups but varied significantly between grids. The majority of scallops (70–94%) moved downslope and the mean movement vectors were not orientated in the direction of tidal currents, but rather towards increasing depth. The downslope movement of the scallops was possibly explained by more prolonged swimming bouts when scallops swam downslope. The results suggest that the spatial size partitioning of Iceland scallops at this location is caused by a gradual downslope movement as the scallops increase in size. This study provides the first experimental evidence supporting the controversial hypothesis of recruitment into adult scallop populations involving swimming of juveniles from nursery areas.

INTRODUCTION

Knowledge of processes that determine recruitment in animals is crucial to the understanding of population dynamics and for the effective management of harvested species. Scallops support important commercial fisheries in many parts of the world (Brand, 1991). Surprisingly, except for shallow-water species such as *Argopecten irradians* (Eckman, 1987; Garcìa-Esquivel & Bricelj, 1993), little is known about recruitment processes in scallops, mainly due to the difficulty of observing and sampling juveniles. Researchers from around the world have long reported a scarcity of juveniles within inshore populations of several scallop species including *Placopecten magellanicus* in North America (Baird, 1953; Kenchington et al., 1991; Giguère & Miller, 1993), *Pecten maximus* in Europe (Baird & Gibson, 1956; Mason, 1957; Thouzeau & Lehay, 1988; Minchin, 1992), *Notovola meridionalis* in Tasmania (Fairbridge, 1953) and *Chlamys islandica* in Norway and eastern Canada (Wiborg, 1963; Giguère & Miller, 1993). Some have suggested that this peculiar demographic characteristic was an artefact caused by the selectivity of the sampling methods used, generally commercial dredges (e.g. Baird & Gibson, 1956; Mason, 1957). However, use of less selective sampling methods, such as dredges lined with smaller mesh size or with narrower tooth spacing, have also been inefficient in capturing juveniles (Baird & Gibson, 1956; Mason, 1957; Giguère & Miller, 1993). These observations suggest that factors other than sampling artefacts are responsible for the widespread under representation of juveniles within inshore scallop beds.

Numerous mobile marine invertebrates show marked spatial partitioning of juvenile and adult stages (e.g. gastropods: Woodbury, 1986; asteroids: Himmelman & Dutil, 1991; urchins: Cabanac & Himmelman, 1996; crabs: Hines et al., 1987; lobsters: Wahle & Steneck, 1991) attributable to the selection of specific breeding grounds by adults, habitat selection during larval settlement or ontogenetic changes in microhabitat preferences. As with many marine invertebrates, scallops have a complex life cycle involving a planktotrophic larval stage. During their pelagic larval development, scallop larvae may drift over several kilometres owing to large-scale hydrodynamic processes (Tremblay & Sinclair, 1988). After developing in the plankton, larvae move to the bottom in search of filamentous substrata on which to settle (Larsen & Lee, 1978; Minchin, 1992; Harvey et al., 1993). Hence, both larval drift and the distribution of filamentous substrata are likely to determine the distribution of spat settlement. Consequently, the distribution of juveniles may not necessarily coincide with that of adults (Thouzeau & Lehay, 1988; Minchin, 1992; Arsenault & Himmelman, 1996a).

Scallops are renowned for their remarkable ability to swim, achieved by forcing jets of water from their mantle cavity by repeatedly opening and closing their valves (Moore & Trueman, 1971). Although swimming is generally considered to have evolved to escape predators (Yonge & Thompson, 1976), it also allows scallops to move into more favourable habitats (Baird, 1958; Winter & Hamilton, 1985; Hamilton & Koch, 1996). Swimming ability generally varies with scallop size, owing to allometric changes in body mass and shape, and often attains

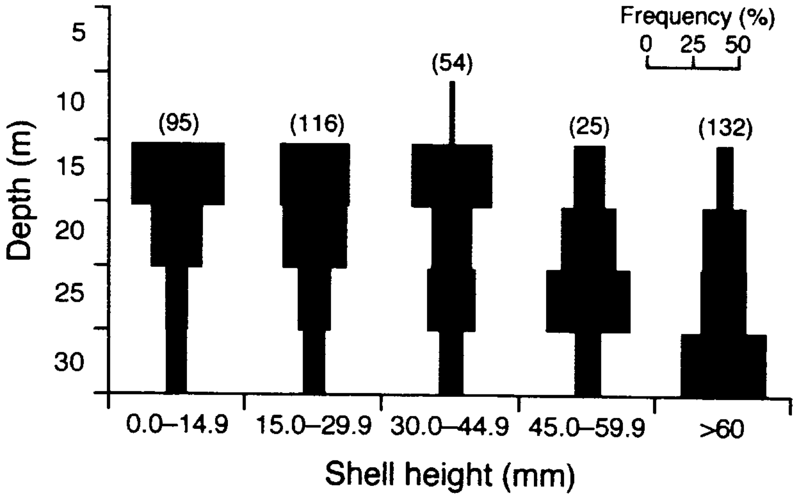

Figure 1. Depth distribution of different sized Iceland scallops, *Chlamys islandica*, as determined using SCUBA diving at Île du Fantôme in the Mingan Islands, northern Gulf of St Lawrence, eastern Canada. Numbers in parentheses correspond to the number of scallops found of each size group. Data from Arsenault & Himmelman (1996a).

a maximum in mid-sized individuals (Gould, 1971; Gruffydd, 1976; Dadswell & Weihs, 1990).

Given the complex life cycle and swimming ability of scallops, a number of researchers have hypothesized that juveniles develop in nursery areas and later recruit into adult populations using swimming (Fairbridge, 1953; Mason, 1957; Wiborg, 1963; Dadswell & Weihs, 1990; Minchin, 1992; Arsenault & Himmelman, 1996a). This would explain why so few juveniles are found within adult populations. In spite of its importance to the understanding of scallop population dynamics, this controversial hypothesis has never been examined experimentally (Fairbridge, 1953; Baird & Gibson, 1956; Mason, 1957; Posgay, 1981; Brand, 1991).

The Iceland scallop, *Chlamys islandica*, is characteristic of coastal areas of the northern North Atlantic and Arctic Oceans (Ekman, 1953) and is generally found byssally attached to coarse substrata at >30 m in depth, in areas with strong tidal currents (Wiborg, 1963; Arsenault & Himmelman, 1996a). In contrast to scallops such as *Placopecten magellanicus* and *Pecten maximus*, *C. islandica* maintains byssal attachment through the adult stage, presumably to avoid being swept away by strong currents (Vahl & Clausen, 1981). Nonetheless, *C. islandica* can readily release its byssal attachment to escape from predators or to move about the bottom (Vahl & Clausen, 1981; D.J.A., personal observation).

Chlamys islandica supports an intensive commercial fishery in the northern Gulf of St Lawrence, eastern Canada (Giguère & Miller, 1993). Stock assessment surveys in this region using commercial and small-meshed dredges at depths >30 m, have reported low numbers of juveniles (<60 mm in shell height), suggesting weak recruitment in most beds (Giguère & Miller, 1993). However, recent SCUBA observations (Arsenault & Himmelman 1996a) in an inshore Iceland scallop bed of the Mingan Islands, northern Gulf of St Lawrence, revealed a striking size partitioning over depth: the distribution of scallops gradually shifting from shallow water (15 m) to greater depths as they increase in size (Figure 1). Field experiments suggest that this size partitioning is not due to changes in size-specific mortality with depth, but rather to the greater availability of suitable substrata for larval settlement in shallow water (Arsenault & Himmelman 1996a). Further, survival of recruits in shallow water is likely to be enhanced by abundant shell litter under which juveniles hide from predators (Arsenault & Himmelman, 1996b).

These observations led Arsenault & Himmelman (1996a) to hypothesize that the size partitioning over depth results from preferential larval settlement in shallow water, followed by a gradual downslope movement as scallops increase in size. Interestingly, size partitioning is also documented in several Norwegian populations of *C. islandica*; small-sized scallops predominating near the entrance of fjords and larger individuals in the upper fjords (Wiborg, 1963; Gruffydd, 1976). Gruffydd (1976) suggests that this distribution pattern is caused by higher larval settlement at the entrance of fjords, favoured by larval drift in outflowing surface waters, followed by a gradual inward movement of scallops as they increase in size, facilitated by strong compensation currents near the bottom. The potential role of swimming in the population dynamics of *C. islandica* and other scallops has received little attention. Previous field studies of scallop swimming only consider adults (Posgay, 1981), evaluate dispersion of juveniles in aquaculture seeding operations (Parsons et al., 1992; Carsen et al., 1995; Hatcher et al., 1996) or examine size-related changes in swimming efficiency (Carsen et al., 1996). The only field study examining swimming in *C. islandica* provides an indirect estimate of daily swimming frequency in a Norwegian population, based on changes in scallop numbers in permanent quadrats (Vahl & Clausen, 1980).

The present study uses SCUBA diving to monitor the movement of tagged juvenile Iceland scallops to examine whether the size partitioning related to depth at Île du Fantôme, Mingan Islands, could result from a downslope movement as scallops increase in size.

Table 1. *Mean net distance moved (±SE), mean movement vector length (r) and vector direction (±95% confidence interval) of tagged juvenile Iceland scallops 7 and 48 d after their release on two 0.4-km^2 grids at Île du Fantôme, Mingan Islands. Rayleigh's tests were used to determine whether the mean movement vector differed from randomness. V-tests were used to examine if the direction of the mean movement vectors were significantly orientated downslope (180°) or with the direction of tidal currents (after adjusting for the axial nature of the data).*

Time (d)	Size group (mm)	Grid	Number of scallops		Distance moved (cm)	Mean movement vector		*V*-tests	
			Found	Moved		r	Direction (°M)	Downslope	Currents
7	30.044.9	West	63	53	154 ±18	0.56***	166 ±17	***	ns
		East	66	47	107 ±22	0.37**	157 ±24	***	ns
	45.059.9	West	63	48	171 ±24	0.64***	172 ±16	***	ns
		East	63	48	109 ±21	0.34**	175 ±23	***	ns
48	30.044.9	West	46	45	244 ±24	0.56***	183 ±19	***	ns
		East	45	41	109 ±22	0.44***	193 ±22	***	ns
	45.059.9	West	47	47	282 ±32	0.42***	160 ±22	***	ns
		East	56	47	130 ±16	0.38**	212 ±22	***	ns

**, $P<0.01$; ***, $P<0.001$; ns, not significant.

MATERIALS AND METHODS

The Iceland scallop bed studied was located in an east–west flowing tidal channel at the southern end of Île du Fantôme in the Mingan Islands, northern Gulf of St Lawrence (50°13′6″N 63°41′12″W; Arsenault & Himmelman, 1996a). SCUBA diving was used to monitor the movement of scallops at two sites, separated by 50 m. Transect lines were marked at 2-m intervals to make 20×20 m reference grids which subdivided each site into 100 4-m^2 areas. The centre of each grid was at about 15 m in depth. The size of the grids (each 0.4 km^2) as well as the duration of the experiment (48 d) was dictated by the logistical limitations associated with SCUBA diving, namely the limited bottom time. The experiment was performed using scallops of two size groups, 30.0–44.9 and 45.0–59.9 mm in shell height, which were collected from 15–17 m in depth. In the laboratory, a small hole was drilled in the left auricle of each scallop and a numbered tag, made of white vinyl tape (1.5×2 cm), was attached using 0.25 mm stainless steel wire (3 cm long). The mass of the tags, including the wire, was ~0.6 g. Following tagging, the scallops were maintained in the laboratory for 24 h to assess whether their condition deteriorated owing to the manipulations. On 7 July 1995, 75 scallops of each size-group were placed in a circular enclosure (40 cm in radius, 1 cm mesh) at the centre of each grid. The scallops were allowed to rehabituate to field conditions for 3 d and then, on 10 July 1995, the experiment began when the enclosures were removed. The movement of scallops was assessed by recording their position on two occasions, on 17 July 1995 and 27 August 1995, thus after 7 and 48 d, respectively. On each occasion, each grid was thoroughly searched and the position of each scallop relative to the reference transects measured using graduated T-squares. From these data, the net distance moved by each scallop from the release point (hereafter referred to as 'distance') was calculated and vector analysis used to determine the direction and length (r) of mean movement vectors (Batchelet, 1981). Only scallops which were found outside the area initially enclosed by the cages were considered to have moved and were included in the statistical analyses (the inclusion of all of the scallops in the analyses gave similar results). As a results of sampling a square grid rather than a circle, a greater distance was searched towards the corners of the grids (45°, 135°, 225° and 315°) than in any other direction. However, this is unlikely to have biased the direction of the scallop movement vectors because the size of the grids sampled was larger than the area over which the scallops dispersed. Although the initially high density of scallops at the release points (150 ind 0.5 m^2) is likely to have increased their movement rate during the first few days of the experiment, it is doubtful whether this influenced the direction of their movements. The remains of dead scallops were not collected because the latter were likely to be swept away by the strong tidal currents at the study site. Because of this, it was not possible to determine whether changes in the number of scallops between sampling dates were caused by mortality or by dispersion of scallops beyond the 0.4-km^2 sampling areas.

Current velocity and direction were recorded at 30-min intervals throughout the study using Aanderaa RCM-4S current meters which were anchored at 1 m above the bottom, at 15 m in depth, just to the east of each grid. For each grid, the mean current velocity, and the direction and velocity of the Eulerian residual current vector were calculated. The density of potential asteroid and decapod predators of scallops was estimated by sampling randomly chosen 4-m^2 quadrats in each grid (N=16 for the west grid and N=9 for the east grid). Finally, substratum characteristics were recorded in each grid by visually estimating the percentage cover of sand, gravel-rocks, algae-hydroids and shell debris in each of the 100 4-m^2 areas delineated by the reference transects.

Rayleigh's tests were used to examine if the direction of the mean movement vectors differed from randomness (Batchelet, 1981). Hotelling's T^2 parametric test was not used because the data could not be considered as originating from bivariate normal distributions. *V*-tests were used to determine whether the distributions of scallop movement directions were significantly clustered around the downslope (180°) or mean current directions (after correcting for the axial nature of the data) (Batchelet,

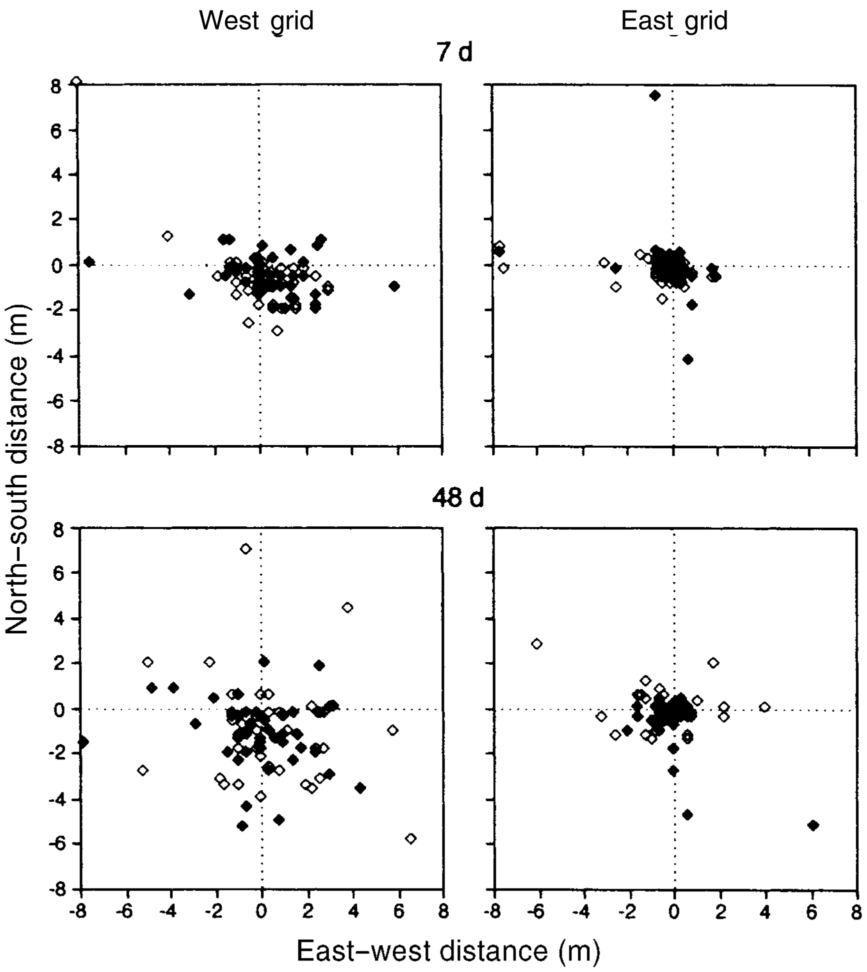

Figure 2. Position of tagged juvenile Iceland scallops (30.0–44.9 and 45.0–59.9 mm in shell height, dark and white symbols, respectively) 7 and 48 d after their release in the centre of two 20×20 m grids at Île du Fantôme, Mingan Islands. Only the centre 16×16 m area is presented, as no scallop was found beyond this area.

1981). The proportion of scallops that moved away from the release points on each grid was compared between size groups using separate χ^2-tests. Non-parametric factorial ANOVAs (Zar, 1984) were used to examine whether the distance moved by scallops from the release points after 7 d and 48 d varied between size groups and between grids. Parametric ANOVA was not used because the homoscedasticity assumption was violated and could not be corrected for by transformation of the data.

Table 2. *Summary of non-parametric ANOVAs examining the effects of scallop size (30.0–44.9 and 45.0–59.9 mm in shell height) and grid (west and east) on the net distance moved by tagged Iceland scallops from their release point after 7 and 48 d at Île du Fantôme, Mingan Islands.*

	Source of variation	df	H	P
7 d	Scallop size	1	2.37	0.124
	Grid	1	38.03	<0.001
	Scallop size×grid	1	0.03	0.874
48 d	Scallop size	1	1.82	0.178
	Grid	1	49.16	<0.001
	Scallop size×grid	1	1.30	0.254

Finally, Mann–Whitney *U*-tests were used to compare the density of each predator species in the two grids.

RESULTS

After 7 d and 48 d, the proportion of scallops that moved away from the release points did not vary between size groups in either grid ($P>0.26$ for all comparisons; Table 1). For both size groups and in each grid, the directions of the mean movement vectors were significantly different than would be expected from random movement (Table 1) and were all orientated towards the south (157–212°), which corresponded to downslope (Figure 2, Table 1). Although scallops dispersed somewhat along an east–west axis (Figure 2), their movements were not significantly orientated in the direction of tidal currents (Table 1). The mean distance moved after 7 and 48 d did not vary between the two scallop size groups but was markedly greater in the west grid than in the east grid (Tables 1 & 2). Non-significant interactions between scallop size and grid (Table 2) indicated that the differences between grids in mean distance moved were similar between scallop size groups.

Both current meters indicated that tidal currents were mainly along an east–west axis (100–280°) and thus

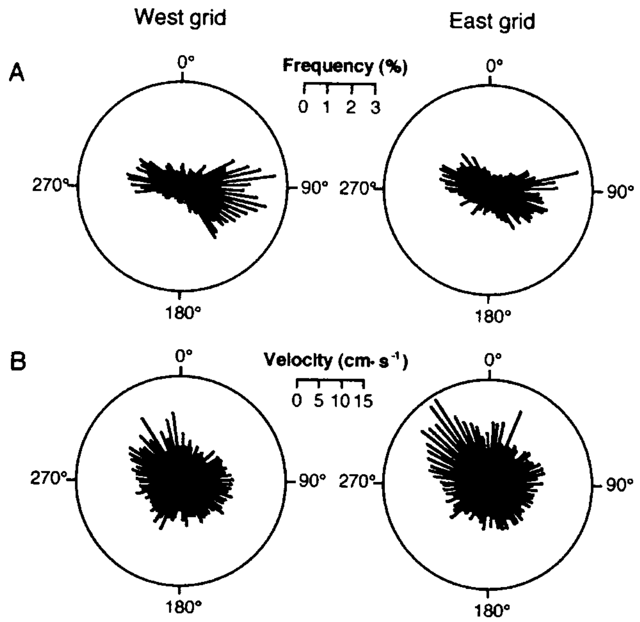

Figure 3. Frequency of tidal currents (A) and mean current velocity (B) for different orientations (5 degree-classes), as recorded by Aanderaa RCM–4S current meters anchored at 1 m above the bottom next to each of the two grids used to study the movement of juvenile Iceland scallops at Île du Fantôme, Mingan Islands.

parallel to the shoreline (Figure 3). The mean current velocity varied slightly between the west and east grids (10.2 and 11.6 cm.s^{-1}, respectively). Further, the velocity and direction of Eulerian residual current vectors varied between grids: 2.2 cm.s^{-1} at 94.4° for the west grid and 1.2 cm.s^{-1} at 16.1° for the east grid.

Densities of potential predators were similar for the two grids (Table 3). *Crossaster papposus* and *Leptasterias polaris* were the most abundant asteroids and *Hyas araneus* was the only decapod sampled. The asteroid *Asterias vulgaris* and the crab *Cancer irroratus* were not encountered in our quadrat sampling but are present in low numbers at Île du Fantôme (Arsenault & Himmelman 1996a).

The substratum on the west grid varied markedly with depth from a predominantly sandy bottom in shallow water to a mixture of sand, gravel, scattered shell debris, and rocks colonized by red algae (mostly *Ptilota serrata* and *Phyllophora truncata*) and hydroids (*Sertularia* sp.) at greater depths (Figure 4). In contrast, the substratum on the east grid was more homogeneous and consisted of a mixture of the various substrata at all depths (Figure 4).

Table 3. *Mean density (±SE) of potential predators of Iceland scallops,* Chlamys islandica*, as determined by sampling 4-m² quadrats in two 0.4-km² grids used to monitors scallop movement at Île du Fantôme. Z-values and associated probabilities (*P*) are from Mann–Whitney* U*-tests comparing the density of each predator between the two grids.*

	Mean density (ind 4 m^{-2})			
	West grid	East grid	Z	*P*
Asteroids				
Leptasterias polaris	0.56 ±0.18	0.33 ±0.17	0.69	0.49
Crossaster papposus	0.81 ±0.28	0.89 ±0.26	0.58	0.56
Decapods				
Hyas araneus	0.88 ±0.31	0.56 ±0.24	0.32	0.75

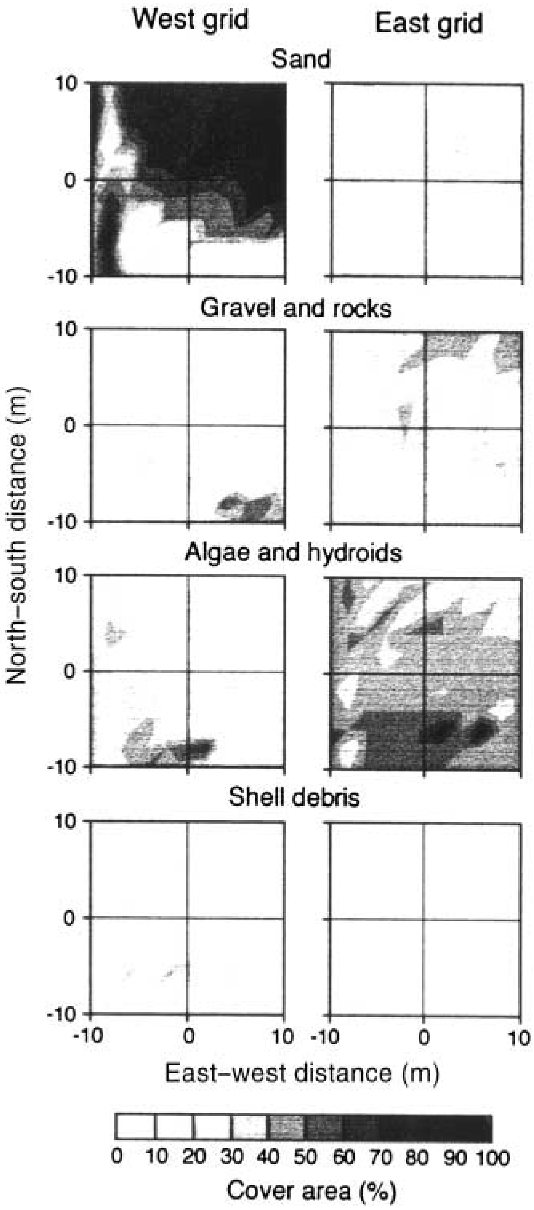

Figure 4. Contour plot showing the percentage cover of four substratum types in the two 0.4-km² grids in which the movement of tagged Iceland scallops was studied at Île du Fantôme. Substratum characteristics were determined in each of the 100 4-m² areas delimited by the reference transects.

DISCUSSION

Direction of scallop movement

Our field experiment indicated that the mean movement vectors of juvenile Iceland scallops released at Île du Fantôme were consistently orientated towards the south (157–212°), which was downslope. Whereas Posgay

(1981) suggests that scallops (*Placopecten magellanicus*) swim in random directions and that the orientation of their net movement is determined by the direction of currents, several field experiments provide contradictory evidence on the importance of currents in determining movement direction (Carson et al., 1995; Hatcher et al., 1996; Stokesbury & Himmelman, 1996). In our study, the direction of movement of Iceland scallops did not appear to be determined by the direction of tidal currents. Nevertheless, we cannot exclude the possibility that the timing of swimming bouts relative to the tidal cycle influenced the direction of movement (a downslope movement would be favoured if scallops swim more frequently when currents are orientated southward). Another possibility is that the downslope movement was due to the slope of the bottom rather than a preferential swimming direction. In a typical swimming bout, a scallop leaves the seabed at an angle of 30–50°, then the trajectory levels off so that the scallop swims horizontally, and finally, when active swimming stops, the scallop passively sinks to the seabed (Brand, 1991; D.J.A., personal observation). Given the momentum of the horizontal movement, scallops continue to move horizontally while sinking (Carsen et al., 1996; D.J.A., personal observation). Swimming bouts in the downslope direction should cover a greater distance than bouts in other directions because scallops attain a greater height above the bottom which increases the duration of passive sinking. This should result in a gradual downslope movement, even if swimming is in random directions, and downslope movement would be enhanced on steep slopes such as in our study site (15–20°). Whatever the mechanism responsible for the downslope movement, our results support the hypothesis that the size partitioning related to depth at Île du Fantôme is caused by a gradual downslope movement as scallops increase in size.

Net distance moved by scallops

As our experiment is the first field study examining the movement of individual Iceland scallops over time, it is difficult to ascertain whether the observed distances moved (1.1–2.8 m after 48 d) are characteristic of the species. Mean distances moved by Iceland scallops were much lower than those reported for other scallops. For example, Parson et al. (1992) and Hatcher et al. (1996) report mean distances moved by <25 mm tagged *Placopecten magellanicus* of 3.3 and 10 m over a similar time period (60 and 50 d, respectively). Our results are consistent with the suggestion of Vahl & Clausen (1980) that *Chlamys islandica* swims infrequently (every 31 d). Although our data indicate a higher frequency of swimming, as $>70\%$ of individuals had moved away from the release points during the first 7 d, the initial movement was possibly accentuated by the high densities at the release points. This is indicated because the increase in distance from the release points between day 7 and day 48 was less than the distance covered in the first 7 d. Given a rate of movement of 0.04 m d^{-1}, based on a mean distance of 1.93 m in 48 d for scallop sizes and grids pooled, scallops moving downslope from 15 m in depth would cover the roughly 50 m along the bottom to reach 30 m in depth in 3.4 y. Based on size–frequency distributions (Arsenault & Himmelman, 1996a) and von Bertalanffy growth curves from fisheries surveys in the Mingan Islands (Giguère et al., 1990), Iceland scallops in this region take 3–4 y to grow from 30 to 60 mm in shell height. Thus, a 30-mm scallop moving downslope at an average rate of 0.04 m d^{-1} should attain about 60 mm in shell height when it reaches 30 m in depth. Hence, the shift in the depth distribution of Iceland scallops reported by Arsenault & Himmelman (1996a) is likely to be a result of both scallop movement and growth as the scallops move downslope.

Size-related variations in distance moved and swimming frequency

In our study, we did not detect differences in the net distance moved by 30.0–44.9 mm and 45.0–59.9 mm scallops. Whereas Gruffydd (1976) reports that 30–40 mm Iceland scallops swim more frequently than either 10–20 mm or 65–75 mm individuals in a laboratory flume, the proportion of scallops which had moved away from the release points in our study did not vary between size groups. The latter observations may not be in contradiction, as in Gruffydd's study the swimming frequency of 30–40 mm scallops was only marginally greater than that of the 65–75 mm individuals (77 vs 69%). Our observations are consistent with Vahl & Clausen's (1980) report, based on repeated field observations in permanent quadrats in Norway, of a lack of size-related variations in movement frequency of 10–90 mm Iceland scallops.

Variations in scallop movement between grids

The distance moved by scallops was markedly greater in the west than in the east grid. Although Gruffydd's (1976) laboratory study indicated an increasing tendency of Iceland scallops to swim with increasing current velocity, the differences between grids in our study were not likely to be due to current velocity, as mean velocity was slightly less in the west grid where movement was markedly greater. Carsen et al. (1995) suggest that local differences in swimming frequency of juvenile *Placopecten magellanicus* may be related to differences in predator abundance, as predators often induce swimming escape responses. This also appears unlikely in our study given the similarity in predator densities in the two grids (Table 3). We suspect that the greater movement of scallops in the west grid was because of the less suitable substrata (Figure 4). Iceland scallops of the sizes used in our experiment markedly prefer coarse substrata, such as gravel and rocks (Arsenault & Himmelman, 1996a) and when found on sandy areas, as on much of the west grid, are likely to swim more often in search of sites for byssal attachment. This hypothesis is consistent with the inverse relationship between habitat suitability and the frequency of swimming reported for the scallops *Argopecten irradians* (Winter & Hamilton, 1985) and *P. magellanicus* (Stokesbury & Himmelman, 1996). Also, Hamilton & Koch (1996) demonstrated that the bay scallop *A. irradians* swam towards more suitable sea grass habitats when released on sand.

Implications and directions for future research

Our observations, in conjunction with those of Arsenault & Himmelman (1996a) in the Mingan Islands and those of Gruffydd (1976) in Norway, suggest that juvenile Iceland scallops may develop in nursery areas and later recruit into adult populations using swimming. Similar processes may be involved in the recruitment of other scallop species for which a scarcity of juveniles has been reported. To improve our understanding of population dynamics and to develop effective stock management strategies for *Chlamys islandica* and other scallops, further studies are needed: (1) to locate nursery areas associated with commercially exploited scallop beds; and (2) to evaluate the importance of swimming in recruitment processes. Given that shell litter increases survival of juvenile Iceland scallops by providing refuges against predators (Arsenault & Himmelman, 1996b), a possible management strategy would be to increase the availability of shell refuges in nursery areas to enhance juvenile survival, and ultimately recruitment into adult beds.

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