

Mechanisms of larval transport: vertical distribution of bivalve larvae varies with tidal conditions

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ABSTRACT: Larval transport is a key process in the life-history and population dynamics of many marine species. It is strongly influenced by ocean currents, but the influence of behavioural traits of larvae (e.g. vertical migration) on their advective dispersal is poorly understood. In the absence of field data, predictions of population connectivity are often based on hydrodynamic models and assume that larvae behave as passive particles. Variations in the vertical distribution of early and late stage larvae of *Mytilus* spp. were investigated in a field study in the Irish Sea, collecting discrete water samples by Niskin sampler at a range of depths at different tidal states and phases at 2 sites and on 2 dates during summer 2005. Larvae were homogeneously distributed throughout the water column during flood tide, whereas larvae were more densely aggregated in middle and bottom waters during ebb tide. Highest densities were greatest near the bottom during low flow conditions. Larval size had no effect on the patterns of vertical distribution of larvae in the water column. The relative lack of larvae in the water column during ebb tides compared to flood tides could lead to significant net transport in the direction of flood tides. If this is a widespread phenomenon, models based on the assumption that larvae behave as passive particles are unlikely to predict dispersal distances correctly.

KEY WORDS: Bivalve · *Mytilus* spp. · Larval transport · Vertical distribution · Hydrodynamics · Behaviour · Modelling

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INTRODUCTION

The life-cycle of many marine invertebrates involves a pelagic larval stage which may last for days, weeks or months, and may link populations over potentially large spatial and temporal scales (Alexander & Roughgarden 1996, Cowen et al. 2000). The scale of dispersal is an important component of an organism's life-history and strongly influences population dynamics and evolution (McQuaid & Phillips 2000, Kritzer & Sale 2004). Populations can often be modelled as metapopulations (Kritzer & Sale 2004) comprising a series of distinct sub-populations maintained by dispersal among them. In this framework, migrants can effectively recolonise sites in which the species has recently become extinct

(Hanski & Gilpin 1991). Development and maintenance of such metapopulations requires larval connectivity among and potentially within sub-populations, with high larval transport likely to reduce the risk of population extinction (den Boer 1981).

Understanding how larvae are exchanged between populations is therefore vital for prediction of population dynamics in the marine environment. It is thought that larvae are able to control their dispersal to some extent by vertical migration in relation to physical or hydrographic features (e.g. stratification by abiotic and biotic factors) (Dobretsov & Miron 2001), but this process is poorly understood. In shallow coastal seas, larvae have been shown to control the direction of net travel by ascending into the water column at certain states of the

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tide (flood, ebb, high or low water) and descending to the bottom during others (Schultz et al. 2003). However, in the absence of detailed knowledge of behaviour, larvae are considered in most cases to behave as passive particles and their movements are predicted by hydrodynamic models incorporating only the duration of larval life (Roberts 1997). The passive behavioural assumption limits the effectiveness of recruitment estimations, with models often only partially predicting population distribution (Roberts 1997, Cowen et al. 2000, Leis 2002). This simplistic approach to modelling population dynamics could lead to errors in both research and management (Carr & Reed 1993). It is therefore important to characterise behavioural traits during larval development (i.e. spawning to settlement).

Behaviour during larval development (e.g. vertical migration) has seldom been investigated for marine invertebrates, especially bivalves (Manuel et al. 1996, Maximovich et al. 1996, Dobretsov & Miron 2001). Research to date suggests that the distribution of larvae is heterogenous, with early stages staying near the water surface prior to settlement followed by movement towards the bottom by late stages to facilitate settlement (Cragg 1980). Abiotic factors (e.g. temperature, tidal cycle, tidal phase, season) and biotic factors (e.g. food availability) are thought to drive vertical migration patterns (Dobretsov & Miron 2001, Burdett-Coutts & Metaxas 2004). In mesocosms, early veligers (<200 μm) of the scallop *Placopecten magellanicus* show a preference for surface layers over discontinuity layers (e.g. thermocline) (Gallager et al. 1996). However, experiments of this type may miss much of the detail controlling patterns in nature (see den Boer 1981 for review). More specifically, the influence of tidal flow on vertical distribution and behaviour has not been investigated in detail (e.g. Butman et al. 1994, Cáceres-Martinez & Figueras 1998, Dobretsov & Miron 2001, Metaxas 2001, Pernet et al. 2003), particularly in highly turbulent systems.

The Irish Sea is a well-mixed water body (Brown et al. 2003) between the east coast of Ireland and the west coast of Britain. It contains large populations of mussels *Mytilus* spp. which are a suitable model organism for field-based studies of larval vertical distribution. They spawn in late April to late May and larvae develop planktonically for about 4 wk and settle at around 220 μm . They are abundant and readily identifiable, particularly in the Irish Sea, where there are few other species of bivalves. Two species are thought to occur in the Irish Sea, *M. edulis* and *M. galloprovincialis*; however they cannot be distinguished and are thus referred to as *Mytilus* spp. herein. This paper presents the results of a study to determine whether patterns of distribution of mussel larvae in the water column vary during different conditions of tidal flow.

The study aimed to determine whether (1) larval densities in the water column vary at a range of temporal scales (month, tidal phase, tidal state), (2) vertical distribution of larvae through the water column varies with tidal phase and state, and (3) a greater proportion of late stage (>210 μm) larvae occur near the bottom than at other depths, and a greater proportion of early stage (<210 μm) larvae occur near the surface than at other depths.

MATERIALS AND METHODS

Variation in larval density and vertical distribution.

Sampling was carried out in the Blackwater region off the coast of County Wexford in the southern Irish Sea (Fig. 1) during May/June and July/August 2005. Spawning in the region typically occurs between mid-May and early-June (A. M. Knights unpubl. data). The May/June sampling was selected to coincide with high proportions of early stage larvae (<210 μm) and the July/August sampling to coincide with high proportions of near-settlement, late stage juveniles (>210 μm). Two 100 m \times 100 m sites (Site 1: 52° 19.542' N, 6° 15.538' W; Site 2: 52° 20.036' N, 6° 15.344' W) in 25 m of water within a 4 km² area were chosen, with the criteria that both sites had similar bottom topography and were composed of slightly gravely sand. Mean current speeds at the surface and at the seabed in the region vary between 1 m s⁻¹ (surface flood), 0.85 m s⁻¹ (surface ebb), 0.70 m s⁻¹ (bottom

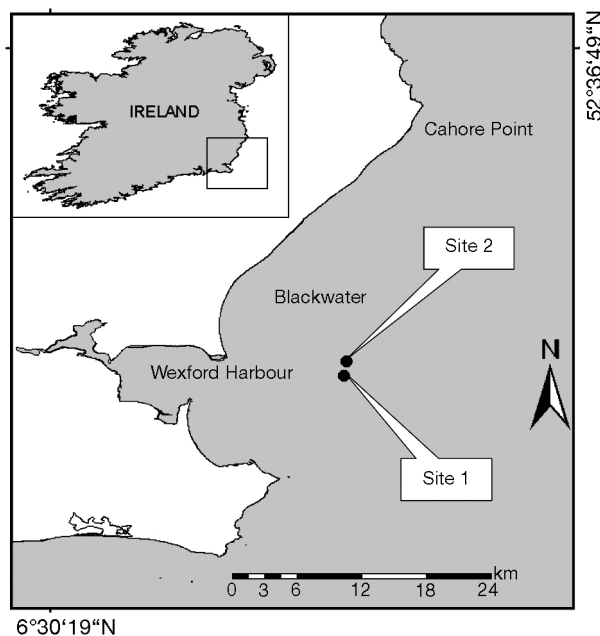


Fig. 1. Blackwater region off the coast of County Wexford in the southern Irish Sea, showing study sites

flood) and 0.6 m s^{-1} (bottom ebb) (Acoustic Current Doppler Profiler data: Aquafact International pers comm.). Average tidal range varies between +1.2 and -0.6 m during spring phases and ± 0.3 m during neap phases (Admiralty Tables 2005).

In each of the 2 periods (May/June and July/August) samples were collected at each site once during spring and once during neap tides and during the 4 tidal states of each tide: (1) flood, (2) ebb, (3) slack high water, (4) slack low water. Tidal oscillations were generated (Admiralty Tables 2005) to identify the phases and states with the most similar tidal amplitudes. The water depth was measured to the nearest 1 m using a Simrad EQ33 echo sounder, and the water column was divided into 3 equal depth zones: (1) top (0 to 8 m), (2) middle (8 to 16 m), (3) bottom (16 to 24 m). The Irish Sea is a well-mixed body of water due to strong water currents with no known hydrographic features at particular depths (Brown et al. 2003). Using a vertically mounted, messenger-operated Niskin water sampler collecting a 1 l sample, 5 replicate samples were collected from each depth zone at random intervals during the course of each tidal state (considered to be ± 1 h of maximum flood/ebb and ± 1 h high/low water). Samples were preserved in 10% industrial methylated spirit and the abundance of *Mytilus* spp. larvae was estimated using the identification keys of Loosanoff et al. (1966), Chanley & Andrews (1971), de Schweinitz & Lutz (1976) and Le Pennec (1978).

Larval densities were compared using an orthogonal 5-factor design (1: site [random], 2: time [random], 3: phase [fixed], 4: state [fixed], 5: zone [fixed]) and analysed by analysis of variance (ANOVA) following methods described in Underwood (1997). All computation was carried out using the programme 'GMAV 5' (Underwood & Chapman 1998). Cochran's *C*-test was used to test for homogeneity of variances, and in cases of significance ($p < 0.05$), data were square-root ($x + 1$) transformed. In cases where no test was possible, interactive terms that were not significant ($p > 0.250$) were eliminated as per Underwood (1997). For terms which were significant ($p < 0.05$), Student-Newman-Keuls (SNK) (Newman 1939, Keuls 1952) procedure was used to determine which means differed.

Vertical distribution of larvae of different sizes. Fifteen larvae were randomly subsampled from each set of 5 replicate samples taken from a given depth zone at a given time. Larval shell lengths were measured ($\pm 0.5 \mu\text{m}$) using an Olympus B201 microscope and Optimas Image Analysis software (Media Cybernetics). Larvae were then divided into 2 size classes: $>210 \mu\text{m}$ (late stage) and $<210 \mu\text{m}$ (early stage). This distinction is semi-arbitrary, but is based on the approximate size of a larva at metamorphosis to a pediveliger (Carriker 1961, Lutz 1985). A series of χ^2 tests

was performed (Fowler et al. 1998) to determine whether late-development larvae were disproportionately abundant nearest the seabed in the bottom depth zone than in other depth zones, and if early development larvae were disproportionately more abundant nearest the surface in the top depth zone compared to the 2 other depth zones, during each tidal flow state (flood, ebb, high and low water). Observed frequencies were compared to expected frequencies generated on the basis of random chance, with a null hypothesis that early or late stage larval were equally likely to be present within each of the 3 depth zones.

RESULTS

Mytilus spp. larvae were found during both sampling periods, but their numbers were highly variable. The maximum density of larvae in any one sample occurred during the spring tide of May/June, with 22 l^{-1} collected. Samples without larvae were also collected during all time periods, tidal phases and states, highlighting the variability in larval density within the water column.

Variation in density of larvae in relation to time (Ti) tidal phase (Ph) and tidal state (St)

Overall, there was a 50% increase in total larval density between May/June and July/August, with an increase in mean density (\pm SD) from 4 ± 3 to $6 \pm 4 \text{ l}^{-1}$ respectively. During the spring tides of both May/June and July/August, larval densities in the water column were significantly higher during flood tides than all other tidal states. Larval densities of 8 l^{-1} in May/June and 10 l^{-1} in July/August were observed during flood tides, compared to the markedly lower densities during ebb (3 and 5 l^{-1}), high (4 and 6 l^{-1}) and low tides (4 and 5 l^{-1}) (Fig. 2, Table 1, $\text{Ti} \times \text{Ph} \times \text{St}$, $p < 0.01$, SNK procedure). During the neap tides of May/June, highest densities were again observed during flood tides (7 l^{-1}) and lowest densities during ebb tides (3 l^{-1}). During slack high and low water periods of neap tides, larval densities did not differ from densities during spring tides (Fig. 2, Table 1, $\text{Ti} \times \text{Ph} \times \text{St}$, SNK procedure). During the neap tides of July/August, no differences in larval density were found between tidal states (Fig. 2, Table 1, $\text{Ti} \times \text{Ph} \times \text{St}$, SNK procedure).

Larval densities were highly variable between sites during flood tides, with greater mean densities at Site 2 ($9 \pm 4 \text{ l}^{-1}$) than at Site 1 ($5 \pm 2 \text{ l}^{-1}$) in May/June. Conversely, in July/August greater densities were found at Site 1 ($10 \pm 3 \text{ l}^{-1}$) than at Site 2 ($8 \pm 3 \text{ l}^{-1}$) (Fig. 2, Table 1, $\text{Si} \times \text{Ti} \times \text{St}$, SNK procedure, $p < 0.01$).

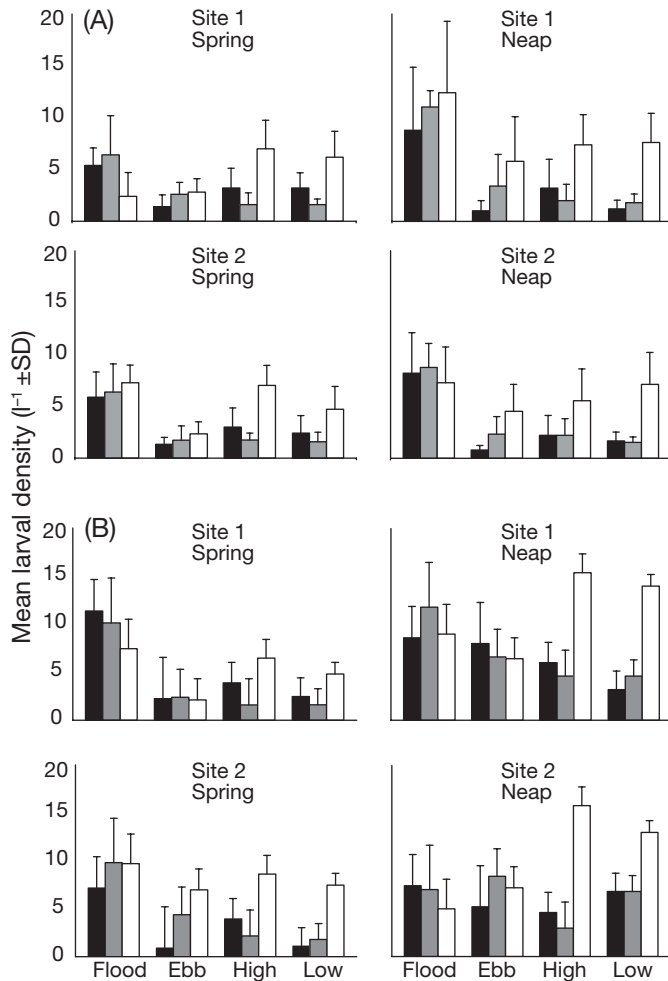


Fig. 2. *Mytilus* spp. Mean (\pm SD; $n = 5$) density of larvae in 3 depth zones: top (black), middle (grey) and bottom (white). Samples collected over 4 tidal states and during 2 tidal phases at 2 sites during (A) May/June and (B) July/August 2005

Vertical distribution of larvae in relation to tidal state

Tidal phase had no effect on the distribution of larvae in relation to depth. However, vertical distribution varied considerably with tidal state (Table 1, $St \times Zo$, $p < 0.0006$). At maximum flow rates of flood tides, larvae were distributed homogeneously throughout the water column, with densities of $9 \pm 2 \text{ l}^{-1}$ (33%) at the surface, $10 \pm 4 \text{ l}^{-1}$ (38%) in the middle depth zone and $8 \pm 2 \text{ l}^{-1}$ (29%) in the bottom zone (Fig. 2, Table 1, $St \times Zo$, SNK procedure). During ebb tides, stratification was found between depth zones, with larval densities in the bottom ($5 \pm 2 \text{ l}^{-1}$, 42%) and middle ($4 \pm 2 \text{ l}^{-1}$, 33%) depth zones significantly higher than that within the top zone ($3 \pm 1 \text{ l}^{-1}$, 25%) (Fig. 2, Table 1, $St \times Zo$, SNK procedure, $p < 0.05$).

Table 1. *Mytilus* spp. ANOVA of larval densities in relation to site, time, tidal phase, tidal state and depth zone at Blackwater, County Wexford, in 2005. $n = 5$ replicates. Data are square-root ($x + 1$) transformed; Cochran's C -test = 0.0467, not significant. Values significant at * $p < 0.05$ and ** $p < 0.01$, respectively; -: not tested

Source	df	MS	F	p
Site (Si)	1	1.40	0.81	0.533
Time (Ti)	1	22.96	13.22	0.171
Phase (Ph)	1	6.06	-	-
State (St)	3	15.57	-	-
Zone (Zo)	2	18.24	-	-
Si \times Ti	1	1.73	7.54	0.006**
Si \times Ph	1	0.80	25.63	0.124
Si \times St	3	0.40	0.15	0.924
Si \times Zo	2	2.59	36.11	0.027*
Ti \times Ph	1	13.02	415.13	0.031*
Ti \times St	3	0.31	0.11	0.946
Ti \times Zo	2	0.16	2.28	0.305
Ph \times St	3	2.25	-	-
Ph \times Zo	2	0.00	-	-
St \times Zo	6	7.04	23.54	0.001**
Si \times Ti \times Ph	1	0.03	0.14	0.712
Si \times Ti \times St	3	2.72	11.85	0.000**
Si \times Ti \times Zo	2	0.07	0.31	0.732
Si \times Ph \times St	3	0.74	8.84	0.053
Si \times Ph \times Zo	2	1.24	3.28	0.234
Si \times St \times Zo ^a	6	0.27	1.09	0.460
Ti \times Ph \times St	3	1.87	22.30	0.015*
Ti \times Ph \times Zo	2	0.23	0.62	0.619
Ti \times St \times Zo	6	0.35	1.42	0.339
Ph \times St \times Zo	6	0.29	1.03	0.484
Si \times Ti \times Ph \times St	3	0.08	0.36	0.779
Si \times Ti \times Ph \times Zo	2	0.37	1.64	0.195
Si \times Ti \times St \times Zo	6	0.25	1.09	0.369
Si \times Ph \times St \times Zo ^a	6	0.21	1.45	0.333
Ti \times Ph \times St \times Zo	6	0.28	1.99	0.211
Si \times Ti \times Ph \times St \times Zo	6	0.14	0.63	0.706
Residual	384	0.23		

^aEliminated (Underwood 1997)

During periods of minimal tidal flow, larval distribution was highly stratified, with larvae tending to aggregate nearest to the seabed in the bottom depth zone (Fig. 2). During slack high water, stratification was found between all depth zones, with $9 \pm 2 \text{ l}^{-1}$ (60%) larvae captured in the bottom depth zone, $4 \pm 2 \text{ l}^{-1}$ (27%) in the top depth zone and the remaining $2 \pm 1 \text{ l}^{-1}$ (13%) in the middle zone (Fig. 2, Table 1, $St \times Zo$, SNK procedure). During low water slack tide, the highest percentage of larvae was again found in the bottom depth zone: $8 \pm 2 \text{ l}^{-1}$ (57%) (Fig. 2, Table 1, $St \times Zo$, SNK procedure). The remaining larvae were distributed evenly between the top and middle depth zones with $3 \pm 1 \text{ l}^{-1}$ (21%) and $3 \pm 1 \text{ l}^{-1}$ (21%), respectively (Fig. 2, Table 1, and SNK procedure).

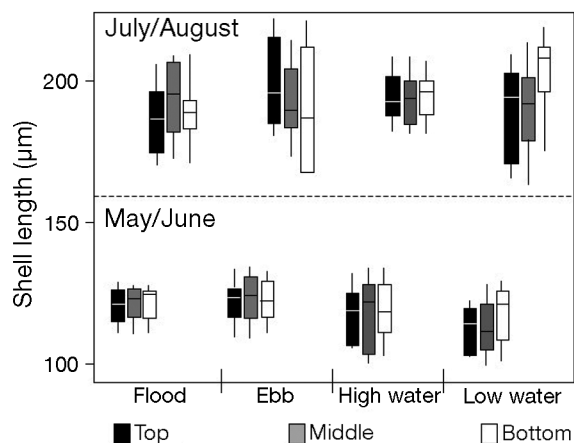


Fig. 3. *Mytilus* spp. Variation in shell length of larvae collected in May/June and July/August 2005. Larvae were randomly subsampled ($n = 15$) from a set of 5 replicate samples from each of 3 depth zones: top (0 to 8 m), middle (8 to 16 m) and bottom (16 to 24 m), over 4 tidal states: Flood, Ebb, High water and Low water. Middle lines of boxplots represent medium lengths; hinge lines (end of box) represent 25% quartiles from the median; whiskers represent 1.5 times the spread beyond the hinge

Table 2. *Mytilus* spp. Observed frequencies of early (<210 μm) and late stage (>210 μm) larvae within each depth zone during 4 tidal states, based on 15 individuals sampled from each set of 5 replicate samples per depth per tidal state

Depth zone	Tidal state			
	Flood	Ebb	High water	Low water
Early stage				
Top	29	24	30	24
Middle	27	25	30	25
Bottom	28	20	30	21
Late stage				
Top	1	6	0	6
Middle	3	5	0	5
Bottom	2	10	0	9

Vertical distribution of early and late stage veligers

The mean larval shell length (\pm SE) increased from $120 \pm 1 \mu\text{m}$ in May/June to $193 \pm 1 \mu\text{m}$ in July/August, with individuals ranging from 99 to 136 μm and from 163 to 225 μm at each time, respectively. No differences in vertical distribution in relation to depth were observed between early (<210 μm) and late (>210 μm) stage larvae (Fig. 3, Table 2). χ^2 tests of larval size frequency within each depth zone revealed that larvae of different sizes were homogeneously distributed throughout the water column. Early stage larvae were evenly distributed throughout the water column during all tidal states (Table 2), whereas late stage larvae were only homogeneously distributed during the ebb

and low water states (Fig. 3, Table 2). During flood and high water states insufficient late stage larvae were captured to enable an analysis to be performed.

DISCUSSION

Pedrotti & Fenaux (1992) described 2 modes of larval dispersal: (1) larvae may remain within a water parcel overlying the adult habitat and subjected to bottom currents, or (2) larvae may be introduced into a different water layer by current advection, and be more greatly influenced by wind-driven transport. In the present study the density of mussel larvae in the water column of the Irish Sea varied depending on tidal state. Maximum densities of larvae were captured during flood tides of both spring and neap tidal phases, whereas minimum densities were found during ebb tides. Regardless of the cause of this pattern, in the Irish Sea it would result in the net northward movement of larvae because the flood tide flows strongly northwards. These larvae would therefore be transported over greater distances in that direction (Roegner 2000, Schultz et al. 2003). The most likely explanation for the lack of larvae in our samples during ebb tides is that they were so closely associated with the seabed (samples collected in the bottom zone were at least 1 m above the seabed). This may indicate that larvae actively avoid transport during ebb tides. In contrast, the increased larval densities during flood periods may indicate an active process of resuspension to facilitate transport during flood tides. The only other possible explanations are some artifact of the sampling process that acts on ebb or flood tides but not both, or variations in actual abundance over both timescales. Neither of these is very likely. Given the limited swimming speeds of pelagic larval stages (e.g. 3 cm s^{-1} for striped bass *Morone saxatilis* [Meng 1993] and 0.25 cm s^{-1} for veligers of *Crepidula fornicata* [Hilbish et al. 1999]), Kingsford et al. (2002) argued that larvae must control their exposure to currents by partial navigation in order to control their distance and direction of dispersal. Such a mechanism may underlie the patterns documented in the present study.

The vertical distribution of planktonic larvae of *Mytilus* spp. within the Irish Sea was also highly dependent on tidal conditions, with larval abundance in different depth zones being strongly influenced by water flow characteristics. During slack water in both sampling periods, larvae were predominantly found within the bottom depth zone, with minimum numbers in the top and middle zones. It is not clear whether the aggregation of larvae within the bottom zone is an active or a passive process. It would certainly be consistent with passive sinking, although gravitational

sinking rates were not investigated. However, the stratification between the top and middle zones during slack high water, with higher densities of individuals in the top depth zone than in the middle depth zone, suggests some active buoyancy control. Active buoyancy control using mucus to control vertical position has been shown in both adult (Martel & Chia 1991) and larval (Nozais et al. 1997) stages of other organisms, although the ability of larvae to control their depth within a turbulent system is thought to be greatly limited (Roegner 2000). Larval stratification may result in either wide-scale dispersal, with larvae within the top water zone more susceptible to fast-moving surface currents capable of dispersing larvae great distances (Roegner 2000), or limited dispersal, with larvae within the bottom water zones (closer to the seabed) subjected to slower-moving bottom currents.

Aggregation of *Mytilus* spp. in the bottom zone may also increase substrate contact and facilitate settlement. If aggregation in the bottom zone is a prelude to settlement, one may expect larger larvae to be prevalent at that depth. Comparisons of larval shell lengths within each depth zone, however, indicated that larvae of different sizes were generally distributed similarly between the 3 depth zones regardless of tidal state. Earlier work on larval distribution had suggested that *Mytilus* spp. larvae exhibit 'preference' for surface waters during early veliger stages prior to descending into deeper waters close to settlement (Dobretsov & Miron 2001). Little is known about the ability of early veliger larvae to remain affixed to a substrate prior to development of the attachment apparatus. However, areas of dynamic substrate have been shown to cause involuntary resuspension in clam and cockle larvae (Bouma et al. 2001). The risk of resuspension is compounded if both high turbulence and reduced substrate contact occur simultaneously, and therefore higher densities during high flow periods are unsurprising. As a result, the dispersal of larvae, especially during flood tides is likely to occur over larger areas due to increased susceptibility to surface currents and wind-driven dispersal, with larvae behaving passively during high flow conditions.

Increased abundances in July/August correspond to the reproductive development of local and regional populations of *Mytilus* spp., with individuals typically spawning in the western Irish Sea from early May to late June (A. M. Knights unpubl. data). Shell length measurements also showed that the variation in larval size in May/June was small, as would be expected shortly after initiation of spawning. The second sampling period (July/August) occurred after all populations had completed spawning. The 'trickling' or non-synchronous spawning contributions from multiple local and regional populations (Cowen et al. 2000, Kinlan & Gaines 2003) which supply the larval pool may

account for the increased abundances from May/June to July/August. The larger variation in shell lengths during July/August would also indicate 'trickle-spawning', with variations in local population synchrony resulting in the simultaneous presence of small and large veligers within the water column. In fact, during the flood and slack high water periods few late stage larvae were captured. In slack high water periods, late stage larvae may have settled onto the seabed in an attempt to attach to a favourable substrate. During the flood tides, the lack of late stage larvae is surprising considering the increased abundances of larvae observed during this tidal state and previous suggestions of buoyancy control enabling transport during flood periods. It may be that, at this late stage, larvae are so closely associated with the bottom that they are not sampled, even when samples are collected within a few metres of the substrate (Crimaldi et al. 2002).

The influence of flow on larval settlement and motility has previously been investigated, primarily within artificial mesocosm environments using velocities up to 1 order of magnitude lower than those observed in the southern Irish Sea (Butman et al. 1994, Metaxas 2001, Pernet et al. 2003). Such work has suggested that *Mytilus* spp. larvae are unable to overcome flow rates in excess of $>40 \text{ l h}^{-1}$, with larvae acting as passive particles and displaying reduced settlement success (Pernet et al. 2003). The high tidal flow rates in the Irish Sea were associated with less stratification of larvae within the water column than in low flow tidal states. In highly turbulent systems, tidal flow rate appears to overcome any limited ability to control position within the water column. An active movement toward the surface may facilitate transport over greater spatial scales (Roegner 2000). Stratification during ebb tides of increased larval densities in the bottom depth zone and decreased larval densities in the top zone would reduce larval susceptibility to Eckman transport and limit dispersal distance, thus allowing retention within an environment (Roegner 2000, Crimaldi et al. 2002).

The present study has also shown increased densities of larvae in the water column during flood tides and reduced densities during ebb tides. Simplistic models that utilise such assumptions could over- or underestimate dispersal distances, and predictions based solely on water circulation are likely to be inaccurate (Leis 2002). Although it is not clear whether larval transfer from depth zone to depth zone is an active or passive process, the results of this study demonstrate that flow-related stratification does exist. Regardless of the mechanism, it is likely to be influential in larval transport and population dynamics. The assumption of passive larval drift (Roberts 1997) used in many fishery assessment models is therefore potentially misleading.

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LITERATURE CITED

- Admiralty Tables (2005) UK Home Office, Taunton, Somerset
- Alexander SE, Roughgarden J (1996) Larval transport and population dynamics of intertidal barnacles: a coupled benthic/oceanic model. *Ecol Monogr* 66:259–275
- Bouma H, Duiker JMC, de Vries PP, Herman PMJ, Wolff WJ (2001) Spatial pattern of early recruitment of *Malcoma balthica* (L.) and *Cerastoderma edule* (L.) in relation to sediment dynamics on a highly dynamic intertidal sand-flat. *J Sea Res* 45:79–93
- Brown J, Carrillo L, Fernand L, Horsburgh KJ, Hill AE, Young EF, Medler KJ (2003) Observations of the physical structure and seasonal jet-like circulation of the Celtic Sea and St. George's Channel of the Irish Sea. *Cont Shelf Res* 23: 533–561
- Burdett-Coutts VA, Metaxas A (2004) The effect of the quality of food patches on larval vertical distribution of the sea urchins *Lytechinus variegatus* (Lamarck) and *Strongylocentrus droebachiensis* (Mueller). *J Exp Mar Biol Ecol* 308:221–236
- Butman CA, Frechette M, Geyer WR, Starczak VR (1994) Flume experiments on food supply to the blue mussel *Mytilus edulis* L. as a function of boundary layer flow. *Limnol Oceanogr* 39:1755–1768
- Cáceres-Martínez J, Figueras A (1998) Distribution and abundance of mussel (*Mytilus galloprovincialis* Lmk.) larvae and post-larvae in the Ria de Vigo (NW Spain). *J Exp Mar Biol Ecol* 229:277–287
- Carr MH, Reed DC (1993) Conceptual issues relevant to marine harvest refuges—examples from temperate reef fishes. *Can J Fish Aquat Sci* 50:2019–2028
- Carriker MR (1961) Interrelation of functional morphology, behaviour, and autecology in early stages of the bivalve *Mercenaria mercenaria*. *J Elisha Mitchell Sci Soc* 77: 168–241
- Chanley P, Andrews JD (1971) Aids for identification of bivalve larvae of Virginia. *Malacologia* 11:45–119
- Cowen RK, Lwiza KMM, Sponaugle S, Paris CB, Olson DB (2000) Connectivity of marine populations: open or closed? *Science* 287:857–859
- Cragg SM (1980) Swimming behaviour of the larvae of *Pecten maximus* L. (Bivalvia). *J Exp Mar Biol Ecol* 93:11–45
- Crimaldi J, Thompson J, Rosman J, Lowe R, Koseff J (2002) Hydrodynamics of larval settlement: the influence of turbulent stress events at potential recruitment sites. *Limnol Oceanogr* 47:1137–1151
- den Boer PJ (1981) On the survival of populations in a heterogeneous and variable environment. *Oecologia* 50:39–53
- de Schweinitz EH, Lutz RA (1976) Larval development of the northern horse mussel *Modiolus modiolus* (L.), including a comparison with the larvae of *Mytilus edulis* L. as an aid in planktonic identification. *Biol Bull (Woods Hole)* 150: 348–360
- Dobretsov SV, Miron G (2001) Larval and post-larval vertical distribution of the mussel *Mytilus edulis* in the White Sea. *Mar Ecol Prog Ser* 218:179–187
- Fowler J, Cohen L, Jarvis P (1998) Practical statistics for field biology, 2nd edn. John Wiley & Sons, Chichester
- Gallager SM, Manuel JL, Manning DA, O'Dor RK (1996) Ontogenetic changes in the vertical distribution of giant scallop larvae, *Placopecten megellanicus*, in 9 m deep mesocosms as a function of light, food, temperature stratification. *Mar Biol* 124:679–692
- Hanski I, Gilpin M (1991) Metapopulation dynamics—brief history and conceptual domain. *Biol J Linn Soc* 42:3–16
- Hilbish TJ, Sasada K, Eyster LS, Pechenik JA (1999) Relationship between rates of swimming and growth in veliger larvae: genetic variance and covariance. *J Exp Mar Biol Ecol* 239:183–193
- Keuls M (1952) The use of studentized range in connection with an analysis of variance. *Euphytica* 1:112–122
- Kingsford MJ, Leis JM, Shanks AL, Lindeman KC, Morgan SG, Pineda J (2002) Sensory environments, larval abilities and local self-recruitment. *Bull Mar Sci (Suppl S)* 70: 309–340
- Kinlan BP, Gaines SD (2003) Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* 84:2007–2020
- Kritzer JP, Sale PF (2004) Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. *Fish Fish* 5:131–140
- Leis JM (2002) Pacific coral-reef fishes: the implications of behaviour and ecology of larvae for biodiversity and conservation, and a reassessment of the open population paradigm. *Environ Biol Fish* 65:199–208
- Le Pennec M (1978) Genèse de la coquille larvaire et postlarvaire chez divers bivalves marins. These de Doctorat d'état, Université de Bretagne Occidentale, Brest
- Loosanoff VL, Davis HC, Chanley PE (1966) Dimensions and shapes of larvae of some marine bivalve mollusks. *Malacologia* 4:351–435
- Lutz RA (1985) Identification of bivalve larvae and postlarvae: a review of recent advances. *Bull Am Malacol Union Inc (Spec edn)* 1:59–78
- Manuel JL, Gallager SM, Pearce CM, Manning DA, O'Dor RK (1996) Veligers from different populations of sea scallop *Placopecten magellanicus* have different vertical migration patterns. *Mar Ecol Prog Ser* 142:147–163
- Martel A, Chia FS (1991) Foot-raising behavior and active participation during the initial phase of post-metamorphic drifting in the gastropod *Lacuna spp.* *Mar Ecol Prog Ser* 72:247–254
- Maximovich NV, Sukhotin AA, Minichev YS (1996) Long-term dynamics of blue mussel (*Mytilus edulis* L.) culture settlements (the White Sea). *Aquaculture* 147:191–204
- McQuaid CD, Phillips TE (2000) Limited wind-driven dispersal of intertidal mussel larvae: *in situ* evidence from the plankton and the spread of the invasive species *Mytilus galloprovincialis* in South Africa. *Mar Ecol Prog Ser* 201: 211–220
- Meng L (1993) Sustainable swimming speeds of striped bass larvae. *Trans Am Fish Soc* 122:702–708
- Metaxas A (2001) Behaviour in flow: perspectives on the distribution and dispersion of meroplanktonic larvae in the water column. *Can J Fish Aquat Sci* 58:86–98
- Newman D (1939) The distribution of the range of samples from a normal population expressed in terms of an independent estimate of standard deviation. *Biometrika* 31: 20–30
- Nozais C, Duchene JC, Bhaud M (1997) Control of position in the water column by the larvae of *Poecilochaetus serpens* (Polychaeta): the importance of mucus secretion. *J Exp Mar Biol Ecol* 210:91–106

- Pedrotti ML, Fenaux L (1992) Dispersal of echinoderm larvae in a geographical area marked by upwelling (Ligurian Sea, NW Mediterranean). *Mar Ecol Prog Ser* 86:217–227
- Pernet F, Tremblay R, Bourget E (2003) Settlement success, spatial pattern and behavior of mussel larvae *Mytilus* spp. in experimental 'downwelling' systems of varying velocity and turbulence. *Mar Ecol Prog Ser* 260:125–140
- Roberts CM (1997) Connectivity and management of Caribbean coral reefs. *Science* 278:1454–1456
- Roegner GC (2000) Transport of molluscan larvae through a shallow estuary. *J Plankton Res* 22:1779–1800
- Schultz ET, Lwiza KMM, Fencil MC, Martin JM (2003) Mechanisms promoting upriver transport of larvae of two fish species in the Hudson River estuary. *Mar Ecol Prog Ser* 251:263–277
- Underwood AJ (1997) *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press, Cambridge
- Underwood AJ, Chapman MG (1998) *General model analysis of variance, 5 factor (GMAV 5)*. Institute of Marine Ecology, University of Sydney

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