

In situ observations of Dungeness crab megalopae used to estimate transport distances by internal waves

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ABSTRACT: Larvae of many coastal organisms develop offshore and must migrate to shore to settle. Two mechanisms of migration are proposed for crustacean postlarvae: onshore swimming and transport by internal waves. In the Northeast Pacific, to swim ashore organisms must swim east. Additionally, internal wave transport distance increases when organisms swim in the direction of wave propagation. Thus, larval behavior may strongly influence onshore migration, though few studies have examined larval behavior *in situ*. Megalopae of the Dungeness crab *Metacarcinus magister* (formerly *Cancer magister*) were observed *in situ* to determine if they orient the direction of their swimming and to determine swimming speed over ground. They were not oriented to the east, rather they swam at the surface in the direction of the current at speeds of $\sim 9.8 \text{ cm s}^{-1}$ which previous work suggests should increase transport distance by internal waves. We tested the influence of these behaviors on transport by deploying a thermistor mooring for 24 d and calculating transport distances for all observed waves. We calculated transport potential for both passive particles and particles that swam with the surface current at speeds ranging from 0 to 10 cm s^{-1} . Of the 69 waves observed none would have transported passive particles, but as swimming speed of organisms increased the number of transporting waves increased dramatically. At swimming speeds of 10 cm s^{-1} , all waves would have transported larvae. Megalopae of *M. magister* do not migrate ashore by swimming east rather they swim with surface currents, which may allow them to better exploit internal waves as a transport mechanism.

KEY WORDS: Behavior · Larvae · Swimming · Internal waves · Dispersal · *Metacarcinus magister* · *Cancer magister* · Megalopae · Crab

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INTRODUCTION

Larvae of many intertidal and shallow subtidal organisms develop offshore but must migrate back to the nearshore environment to settle (Shanks 1995a). Two migration mechanisms are often proposed in the literature: swimming ashore and migration enhanced by physical oceanographic processes (Shanks 1995a). For larvae to swim ashore they must swim in the right direction and be strong swimmers. Multiple physical oceanographic processes are proposed to enhance migration such as internal waves, land/sea breezes,

shoreward propagating upwelling fronts and geostrophic flow (Shanks 1995a, Queiroga & Blanton 2004). The effectiveness of these physical mechanisms are further enhanced by organisms that swim in the right direction (whether vertically or horizontally). Thus, larval behavior may play a critical role in cross shelf dispersal (Queiroga et al. 2007). However, behaviors proposed to enhance migration are often based on findings from laboratory studies or assumptions based on larval morphology (Metaxas 2001).

Field observations of larval behavior have focused, due to their large size, on crustacean postlarvae,

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ascidian tadpoles and coral reef fish larvae (Bingham & Young 1991, Shanks 1995b). Leis & Carson-Ewart (1997) examined *in situ* swimming speeds of 54 coral reef fish larvae and found a mean swimming speed of 20.6 cm s^{-1} , a speed well above all but the fastest currents; these larvae were able to actively move through the water and, in the field, orient toward reefs. Coral reef fish larvae orient their swimming to a combination of scent, reef sounds and sun (Elliott et al. 1995, Tolimieri et al. 2000, Leis & Carson-Ewart 2003). *In situ*, decapod larvae oriented their swimming towards reef sounds and light or parallel with surface currents (Shanks 1995b, Jeffs et al. 2003, Radford et al. 2007). Off Rhode Island, American lobster larvae primarily swam northeast towards the shore (Cobb et al. 1989). *In situ* swimming speed of decapods has only been determined for late stage lobster larvae (ranging from 15 to 46 cm s^{-1} depending on species) and not for brachyuran crabs (Phillips & Olsen 1975, Cobb et al. 1989).

One physical oceanographic mechanism proposed to transport larvae is internal waves. Transport by internal waves occurs when surface current speed above the wave is greater than the wave's propagation speed (Shanks 1995b, Lamb 1997). Lamb's (1997) model states that if the surface current speed is greater than the wave phase speed, particles are transported continuously by the wave until the characteristics of the wave changes. If the surface current is slower than the wave phase speed, particles are transported a finite and short distance. The distance internal waves transport particles can be determined by (1) combining physical observations of internal waves with Lamb's (1997) model to calculate transport distance or (2) measuring transport distance *in situ* by interpolating distance from measured plankton concentration in front of and within internal waves. Studies that combine Lamb's (1997) model with physical observations report transport distances on the order of meters with rare events of 1–2 km (McManus et al. 2005, Shroyer et al. 2010). Transport distances calculated from concentrations of plankton in net tows suggest larger transport distances ranging from 3.5–23 km (A. L. Shanks unpubl. data). Thus, there is a discord between transport distances calculated from Lamb's (1997) model and *in situ* observations. From the perspective of a larva crossing the continental shelf, the differences would be significant. A possible explanation for the discord is that calculations using Lamb's (1997) model have not historically included larval behavior and previous work suggests synergistic effects of larval behavior with internal waves should greatly increase transport

distances (Shanks 1995b, Lamb 1997). Specifically if larvae are strong swimmers and swim in the direction of wave propagation, the distance they are transported by internal waves should increase dramatically (Shanks 1995b, Lamb 1997). In the field, megalopae of *Pachygrapsus crassipes* and *Lophopanopeus bellus bellus* have been observed in the surface convergence of internal waves and swimming in the direction of wave propagation, suggesting this phenomenon of increased transport distance does indeed occur (Shanks 1995b). Thus, it is likely behavior plays an important role in the transport of organisms by internal waves.

Due to their commercial importance, many studies have examined the larval dispersal and transport of the Dungeness crab (*Metacarcinus magister* Dana, 1852, formerly *Cancer magister*). Their abundance is strongly affected by recruitment processes (reviewed in Rasmuson 2013). Zoeae of *M. magister* are released in the nearshore environment during winter and are found at greater distances from shore as they develop (reviewed in Rasmuson 2013). By the time they molt into megalopae, they are far from the shore but must migrate to the nearshore environment to settle. Two laboratory studies report swimming speeds of *M. magister* megalopae ranging from 4.2 cm s^{-1} (Jacoby 1982) to 44.7 cm s^{-1} (Fernandez et al. 1994). Thus, megalopae are strong swimmers and may make the shoreward migration by swimming east; however, no studies have determined if *M. magister* megalopae orient their swimming. Conversely, correlations of daily abundance of megalopae and daily maximum tidal range suggest megalopae are transported across the continental shelf by internal waves (Johnson & Shanks 2002, Roegner et al. 2007). Thus, it is likely one of the commonly proposed migration mechanisms (swimming ashore or transport by internal waves) is the pathway by which *M. magister* return to the nearshore environment.

Therefore, due to its extensive research history and evidence that the fishery is driven by recruitment, we used *in situ* observations of *M. magister* orientation and swimming speed to test whether megalopae exhibit behaviors suggestive of cross shelf migration by swimming or transport by internal waves. We hypothesized that (1) megalopae would swim with surface currents rather than swim east. We further hypothesized that (2) the behaviors of *M. magister* megalopae would enhance transport by internal waves. We tested these hypotheses by combining our *in situ* observation data with mooring observations of internal waves to calculating potential transport distances by internal waves.

MATERIALS AND METHODS

In situ observations

Metacarcinus magister megalopae were caught in a light trap in Coos Bay, Oregon (Fig. 1; for details, see Shanks & Roegner 2007), and their swimming behavior was observed on the day of capture. Individuals were transported in a bucket of seawater equipped with an aerator to Sunset Bay, Oregon (Fig. 1), where they were released and their behavior was observed. Release sites within Sunset Bay were chosen haphazardly, and offshore distance of the releases was dictated by safety concerns. The depth of each experimental site was not determined, because observation sites were reached by kayak, and strong currents prevented depth measurements using the anchor rope.

On 15 and 22 August 2012 and 17 June 2013, using protocols similar to Shanks (1995b), megalopae were observed in order to determine if they oriented the direction of their swimming. A snorkeler observed megalopae during daylight in the upper 1 m of the water column. An individual megalopa was placed in a 225 ml jar and handed to a snorkeler. After swimming ~5 m from the kayak (alternating direction haphazardly), the snorkeler opened the jar ~1 m below the surface. Each megalopa was observed until it vanished, and its bearing was recorded. The snorkeler haphazardly oriented the location of his body relative to the sun, wave direction, surface current

and shore to minimize the effects of the snorkeler's presence. Using a compass, the snorkeler recorded the bearing of the sun and swell direction. To determine surface current direction, a 2 m weighted line with strips of plastic every 0.25 m was hung from a float at the surface of the water column. The direction of the floating strips was recorded as a bearing for the direction of the surface current. Current direction was determined in the upper 2 m of the water column since megalopae swam near the surface.

On 22 August 2012, 17 June and 30 July 2013, megalopae were released at ~1 m depth and followed to determine their horizontal swimming speeds using protocols similar to Leis & Carson-Ewart (1997). Each megalopa ($n = 10$ per date) was followed by the snorkeler for 30 s at a distance of ~1 m. Megalopae were only followed for 30 s to prevent the snorkeler from getting too far from the kayak. The snorkeler held a General Oceanics Flow Meter with a low-flow propeller (Leis & Carson-Ewart 1997). Recording time and flow meter revolutions allowed us to determine the speed of the megalopa. Surface water speeds were determined on 17 June and 30 July 2013. A plastic jar was filled with water, leaving a small air bubble, and the snorkeler followed the jar for 1 min using the same flow meter (Hamilton & Russel 1981). The jar floated with ~5 cm² of surface area exposed to the air right at the air-water interface, thus wind effects were minimal. On these dates, the speed of the water flow was subtracted from the measured swimming speed of megalopae that swam with the current and added to that of megalopae that swam against the current.

Swimming orientation data were analyzed using circular statistics (Batschelet 1981). A Rayleigh test was used to determine whether data were significantly different from random. In cases where the distributions were non-random, a V-test was used to determine if mean swimming direction was similar to the bearing of the sun, wave direction, surface current and shore. Swimming speeds were square-root transformed to ensure that the data met the assumptions of normality and homogeneity of variances. Swimming speeds from 17 June and 30 July 2013 (corrected for water speed) were compared to each other using a Student's *t*-test, while those from 22 August 2012, 17 June 2013 and 30 July 2013 (no correction for water speed was applied) were compared using ANOVA.

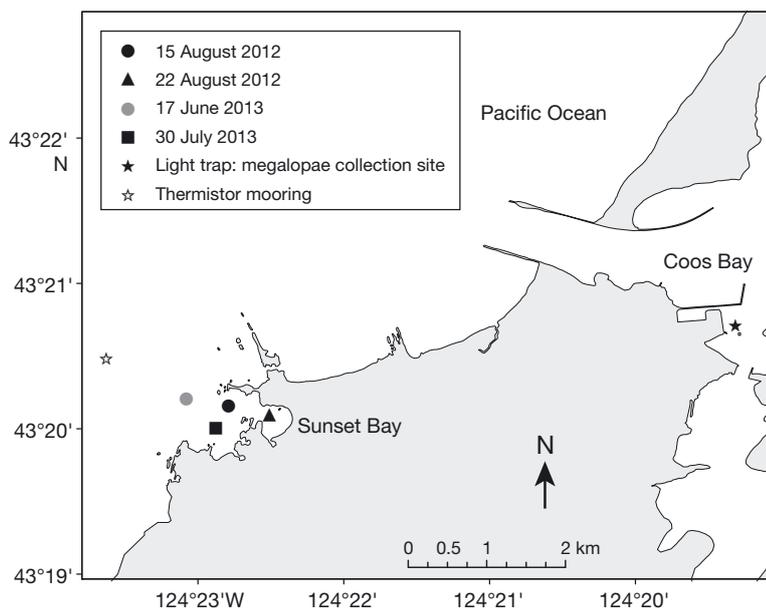


Fig. 1. Collection site for megalopae of *Metacarcinus magister* in Coos Bay, Oregon, USA, observation sites on 4 different dates in Sunset Bay, and site of thermistor mooring just outside Sunset Bay

Comparison to physical data

From 19 August to 13 September 2012, we deployed a thermistor chain in 30 m of water (Fig. 1) to observe internal waves. The thermistor chain was deployed as close to the observation locations as possible but in deep enough water to prevent loss due to boat traffic and/or wave action. Four Seabird SBE-56 thermistors were deployed at 5, 10, 15 and 19 m from the surface and recorded data every 0.5 s. Depths were chosen to provide sufficient resolution around the thermocline using the available thermistors. We used these data to describe the internal waves in the study area and calculate the probability of transport by internal waves.

McManus et al. (2005) calculated transport distance using Lamb's (1997) equation as:

$$\Delta x = 2L \left(\frac{b^2}{1-b^2} \right)^{1/2} \arctan \left[\left(\frac{b^2}{1-b^2} \right)^{1/2} \right] \quad (1)$$

where Δx is the transport distance of the particle, L is the soliton half-width, and b^2 is defined as:

$$b^2 = \frac{U_{\max}}{V - U_d} \quad (2)$$

U_{\max} is the maximum particle velocity at a specific interface, V is the linear propagation speed of the wave, and U_d is the swimming speed of the organism. However, thermistor moorings do not record current velocities, and thus McManus et al. (2005) used the following soliton solution from Holloway (1987) to convert thermistor data into velocity data:

$$\eta = \eta_0 \operatorname{sech}^2 \left(\frac{x - ct}{L} \right) \quad (3)$$

$$c = c_0 \left[1 + \frac{\eta_0}{2} \left(\frac{h_1 - h_2}{h_1 h_2} \right) \right] \quad (4)$$

$$c_0 = \left[g \frac{(\rho_2 - \rho_1)}{\rho_2} \frac{h_1 h_2}{h_1 + h_2} \right]^{1/2} \quad (5)$$

$$L^2 = \frac{4}{3} \frac{h_1^2 h_2^3}{(h_1 - h_2) \eta_0} \quad (6)$$

where η is the deviation of the thermocline from ambient, η_0 is the amplitude of the soliton, x is the horizontal position of the particle, c is nonlinear phase speed, c_0 is the linear phase speed, g is the acceleration due to gravity, and h and ρ denote the thickness and density of respective layers (h_1 and ρ_1 denote upper layers). Combining Lamb's (1997)

equation and Holloway's (1987) solution, McManus et al. (2005) proposed (assuming $U_d = 0$):

$$b^2 = \frac{U_{\max}}{c} \quad (7)$$

where U_{\max} is calculated at the surface and depth as:

$$\text{Surface } U_{\max} = c_0 \eta_0 h_1^{-1} \quad (8)$$

$$\text{Depth } U_{\max} = -c_0 \eta_0 h_2^{-1} \quad (9)$$

This allowed McManus et al. (2005) to calculate transport distance from a single thermistor chain despite not having velocity data.

An assumption of McManus et al. (2005) was that $U_d = 0$; however, the focus of our study was on the contribution of swimming speed of an organism and therefore we used

$$b^2 = \frac{U_{\max}}{c - U_d} \quad (10)$$

to calculate transport distance. We calculated U_{\max} (using Eq. 8) only for the surface of the water column, because megalopae swam at the surface in all of our observations.

Using these equations, we calculated transport probability for passive and actively swimming organisms exhibiting the behaviors we observed in *M. magister* megalopae. To find internal waves in the mooring data, data were interpolated onto a 0.2 m grid and plots of daily average temperature generated to determine the depth of the thermocline. On all days the average thermocline depth was 12 m. The temperature record from the 10 m thermistor (the thermistor closest to the thermocline) was assessed visually for the presence of internal waves of elevation and depression (Fig. 2). For each wave observed variables needed for the above equations were recorded. Transport calculations require estimates of density above and below the thermocline. Density was calculated from the 10 and 15 m thermistors using the equation of state of seawater with zero pressure and an assumed salinity of 33. Routine CTD casts conducted in this area show that salinity remains relatively constant at 33 (M. Jarvis pers. comm.).

Using the recorded data, transport distance was calculated for swimming speeds ranging from 0 to 10.0 cm s⁻¹ in 0.1 cm s⁻¹ increments. We assumed that larvae swam with the surface current, as did the *M. magister* megalopae. In the above equations in situations where $U_d = V$, the particle is transported an infinite distance by the wave until the characteristics of the wave or the organism's behavior change.

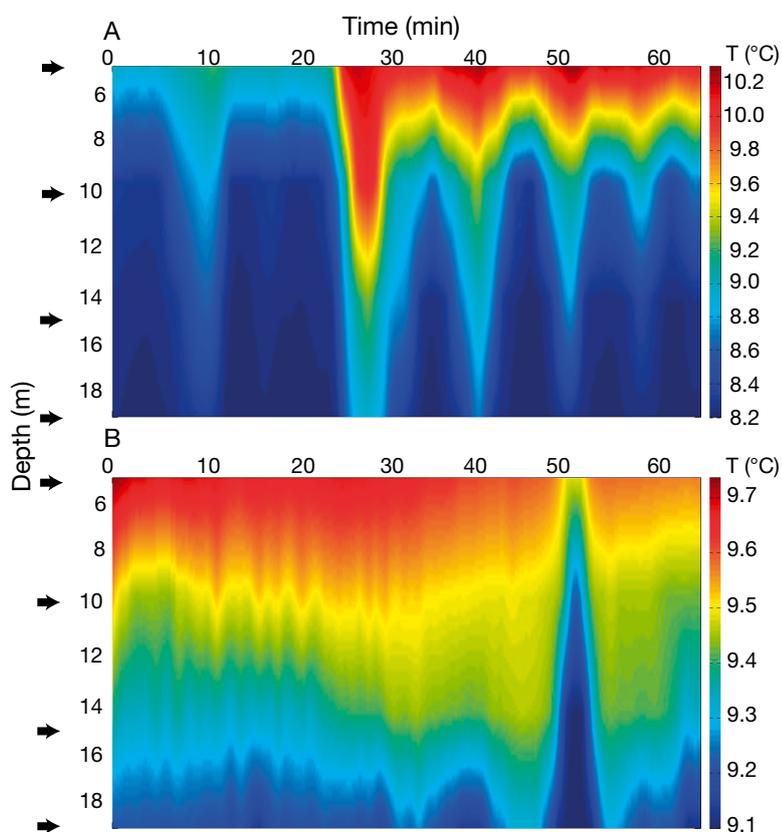


Fig. 2. (A) Internal wave of depression on 3 September 2012 and (B) internal wave of elevation on 4 September 2012 extracted from 24 d of thermistor chain data. Temperature (T) scales differ between panels. Arrows: depths of the thermistors

Our focus was to determine transport of megalopae across the continental shelf, which is ~25 km wide near our study site in Coos Bay. Since internal waves are generated at the continental shelf break by the internal tide, we considered waves to be transporting if the transport distance was ~25 km (i.e. the maximum transport distance near Coos Bay). We use the terms 'transport' and 'transporting' to denote distances <25 km and 'shelf-transport' and 'shelf-transporting' to denote distances ≥ 25 km.

We assumed that organisms were capable of reducing their swimming speed to match wave propagation speed. Based on the nature of the transport model, this means that a 'shelf-transporting' wave that occurred for larvae with swimming speeds ranging from 0 to 0.2 cm s⁻¹ was presumed to be 'shelf-transporting' for organisms with swimming speeds ranging 0 to 10.0 cm s⁻¹. Had we not made these assumptions, megalopae swimming at faster speeds would not have been transported by the waves that transported slower swimming megalopae. In marinas with turbulent eddies, *M. magister* megalopae alter

their swimming speed relative to local currents, so it is probable that megalopae do indeed reduce their speed (L. K. Rasmuson pers. obs.). The above calculations only apply to non-linear internal waves; therefore, internal bores were excluded in this analysis.

RESULTS

In situ observations

In all trials, megalopae swam up from 1 m depth to the very surface of the water, close enough to dimple the surface of the water. After release, megalopae extended their legs and spun in a circle. In most cases, megalopae did not begin swimming horizontally until their anterior end pointed in the direction of the surface current. When swimming horizontally, they tucked their legs against their carapace and swam with the surface current. In some rare instances, megalopae swam towards the observer and either clung to the observer (these individuals were excluded from analysis) or swam past the observer (included in analyses).

On all dates, the swimming direction of megalopae was significantly clustered (Fig. 3). Megalopae did not swim east or with the swell on any day (Table 1, Fig. 3). On 2 of the 3 sample days, megalopae did not swim towards the sun, while on the third day, swimming was slightly similar to the sun's bearing (Table 1, Fig. 3). Mean swimming direction on all dates was, however, statistically similar to the direction of the surface current (Table 1, Fig. 3). On one occasion, 8 megalopae were released when no surface current was detected. During this trial, megalopae appeared to swim randomly ($n = 8$, $Z = 0.90$, $p > 0.05$); however, the small sample size limits the power of the statistical test.

Mean swimming speed (prior to removal of background speed) was 11.1 cm s⁻¹ (range: 5.6–23.8 cm s⁻¹) and did not differ among sampling dates ($F_{2,27} = 0.0724$, $p > 0.05$; Table 2). Because megalopae swam with surface currents, we removed the contribution of the surface current to their swimming speed. After correcting for current speed, the average swimming speed of megalopae on 17 June and 30 July 2013 was 9.8 cm s⁻¹ (range: 5.0–23.1 cm s⁻¹) and did not differ between sampling dates ($t_9 = 0.618$, $p > 0.05$; Table 2).

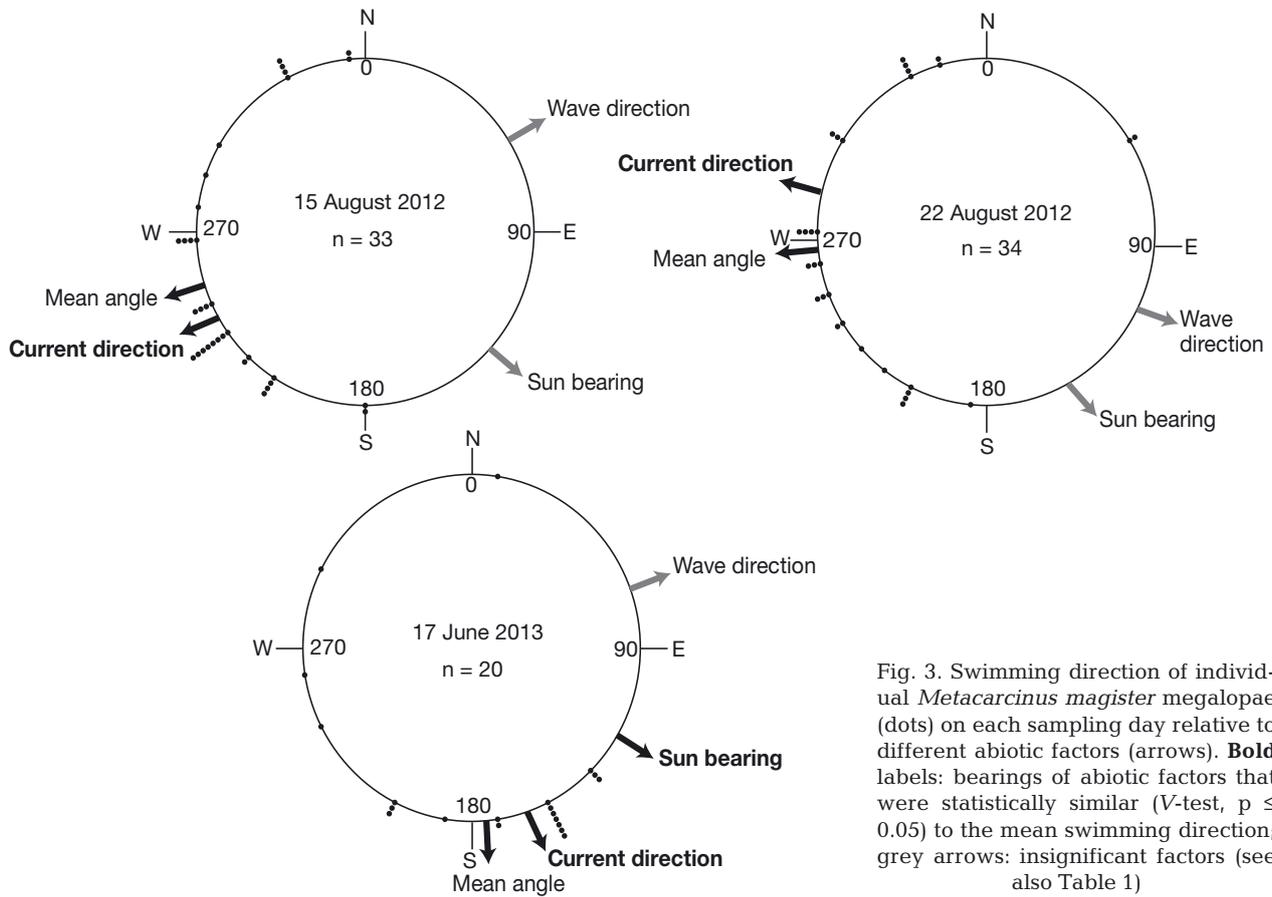


Fig. 3. Swimming direction of individual *Metacarcinus magister* megalopae (dots) on each sampling day relative to different abiotic factors (arrows). **Bold** labels: bearings of abiotic factors that were statistically similar (V-test, $p \leq 0.05$) to the mean swimming direction; grey arrows: insignificant factors (see also Table 1)

Table 1. Oriented swimming of *Metacarcinus magister* megalopae. Data were first analyzed to determine if they were significantly clustered. Mean swimming direction was compared to the bearing of abiotic factors to determine if they were statistically similar (see also Fig. 3). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Date	Rayleigh's z	Mean (\pm SE) swimming angle ($^{\circ}$)	Abiotic factor bearing	V-test u-value
15 Aug 2012	16.61***	253 \pm 43	Swell: 60 $^{\circ}$	-5.68
			Sun: 135 $^{\circ}$	-2.82
			Current direction: 240 $^{\circ}$	5.68***
22 Aug 2012	14.93***	268 \pm 47	Swell: 150 $^{\circ}$	-4.64
			Sun: 120 $^{\circ}$	-2.57
			Current direction: 280 $^{\circ}$	5.35***
17 Jun 2013	5.08***	176 \pm 63	Swell: 60 $^{\circ}$	-1.44
			Sun: 120 $^{\circ}$	1.79'
			Current direction: 160 $^{\circ}$	3.10***

Transport distances

Over 24 d, we observed 69 internal waves, 54 waves of depression and 15 waves of elevation. Waves of depression would frequently occur in rank ordered packets with the largest amplitude wave leading. Leading waves had 'idealized' soliton

shapes whereas subsequent waves in packets did not conform as well. Waves of elevation were always solitary and conformed well to the presumed shape of 'idealized' solitons. A total of 24 internal bores were observed (18 of depression and 6 of elevation), though they were not included in the analysis.

None of the waves would have been 'shelf-transporting' (distances ≥ 25 km) for non-swimming organisms (Table 3, Fig. 4). As swimming speeds of organisms increased (assuming they swam in

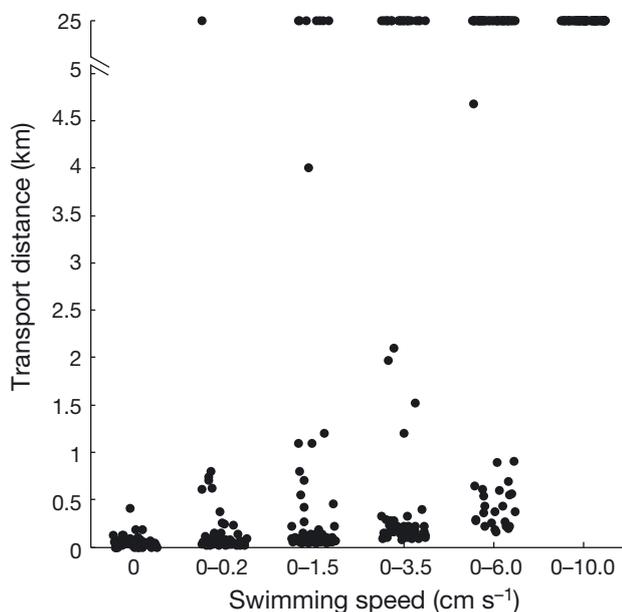
the direction of wave propagation), the number of transporting waves increased dramatically and at swimming speeds of 0–10 cm s⁻¹ all waves would have been transporting (Table 3, Fig. 4). Additionally, mean transport distance increased very slightly and maximum transport distance increased as well (Table 3, Fig. 4).

Table 2. Swimming speed (cm s^{-1} ; including and excluding water speed) of *Metacarcinus magister* megalopae. $n = 10$ on each date. NA: data not available since water speed is unknown

Sample date	Including water speed		Swimming speed only	
	Mean \pm SE	Range	Mean \pm SE	Range
22 August 2012	11.5 \pm 1.8	5.9–21.9	NA	NA
17 June 2013	11.4 \pm 2.1	7.6–13.5	9.0 \pm 0.6	6.1–12.1
30 July 2013	10.4 \pm 0.6	5.6–23.8	10.8 \pm 2.1	5.0–23.1
Mean	11.1 \pm 0.9		9.8 \pm 1.0	

Table 3. Mean and maximum transport distance for transporting internal waves (distances < 25 km) and the number of waves considered 'shelf-transporting' (distances ≥ 25 km) out of 69 observed internal waves for larvae with different swimming speeds. 'Shelf-transporting' waves were excluded from calculations of mean and maximum values for transporting waves except at swimming speeds of 0 to 10 cm s^{-1} , because at this speed all waves were 'shelf-transporting'. See 'Materials and methods: Comparison to physical data' for an explanation of why shelf transport distance is ≥ 25 km

Swimming speed (cm s^{-1})	Transport distance (km)		No. of 'shelf-transporting' waves
	Mean	Maximum	
0 (passive)	0.05	0.41	0
0–0.2	0.11	0.80	1
0–1.5	0.24	4.00	7
0–3.5	0.30	2.10	21
0–6	0.60	4.68	44
0–10	≥ 25.00	≥ 25.00	69



DISCUSSION

Our work demonstrated that the megalopae of *M. magister* actively oriented the direction of their swimming and were capable of swimming at speeds of $\sim 10 \text{ cm s}^{-1}$. Including these behaviors in calculations of potential transport distance suggests that in the presence of an internal wave, the behaviors and swimming of *M. magister* megalopae would greatly increase transport distance.

Since the megalopae used in this study had already migrated across the continental shelf to reach Coos Bay, their swimming behaviors may have been altered. However, in offshore waters, the megalopae of *Metacarcinus magister* have been observed swimming with surface currents (L. K. Rasmuson pers. obs.), suggesting that the behaviors we observed in Sunset Bay occur offshore as well. Repeating the present study in offshore waters with megalopae collected offshore would determine whether the swimming behaviors we observed here are representative of the natural migration process of *M. magister* megalopae. Larvae of some lobsters and coral reef fish are reported to swim ashore (Leis 2002, Jeffs et al. 2005). In the Northeast Pacific, organisms trying to swim ashore would need to swim approximately towards the east. Near Coos Bay, the continental shelf is ~ 25 km wide, so organisms swimming at 9.8 cm s^{-1} would require ~ 3 d to swim across the shelf. This time period is short enough relative to the megalopa stage duration that it is possible megalopae could swim ashore. However, megalopae did not swim east on any of the sample dates (Fig. 3). Thus, the swimming direction of the *M. magister* megalopae would not have resulted in their swimming ashore.

Other studies suggest that crab megalopae and coral reef fish larvae use reef sounds as a cue for navigating to settlement sites (Leis et al. 2002, Jeffs et al. 2003). *M. magister* primarily settles on soft sediments on the continental shelf (depth varies greatly) so it seems unlikely that intertidal sounds would act as a

Fig. 4. Influence of larval swimming speed, assuming the larvae swam in the direction of wave propagation, on calculated transport distance of internal waves ($n = 69$). x-axis labels denote the range of speeds in each bin, and data points are scattered in the x-direction for ease of reading. Data at $y = 25$ km represent particles that remained in the wave and were transported until the characteristics of the wave or behavior of the organism changed

navigation cue. Sounds or chemical cues generated by either conspecifics or organisms living in soft sediments could act as a cue for navigation. However, this seems unlikely since both conspecifics and organisms living in soft sediments are common across the shelf and thus would not provide a directional cue. However, since this study was conducted over soft sediment bottoms where *M. magister* settle (L. K. Rasmuson unpubl. data) and was not designed to test orientation to bottom habitat features, we could not test this hypothesis.

In a previous study in the enclosed inland waters of Puget Sound, congeneric species (*Glebocarcinus oregonensis*, formerly *C. oregonensis*; and *Metacarcinus gracilis*, formerly *C. gracilis*) swam in the direction of the sun's bearing (Shanks 1995b). *M. magister* swam in the direction of the surface current on all 3 observation days, and on 1 of these 3 days (17 June 2013), this happened to be also similar to the direction of the sun. However, even on that day, swimming direction was more similar to the direction of the surface current ($p < 0.001$) than the direction of the sun's bearing ($p < 0.05$). Studies on *M. magister* (other congeners not as well studied) have clearly demonstrated biological differences between enclosed inland and open ocean populations (reviewed in Rasmuson 2013). For example, *M. magister* larvae from Puget Sound are smaller than open ocean larvae and adults in Puget Sound more frequently utilize intertidal habitats (reviewed in Rasmuson 2013). In a different species, *Pachygrapsus crassipes*, a recent comparative study of vertical migration from enclosed estuarine and open ocean populations suggests that estuarine populations vertically migrate while oceanic populations do not (Miller & Morgan 2013). Thus, it is possible that the observed differences between congeneric species arose from biological differences between populations that inhabit enclosed inland waters and those in the open ocean. Regardless of whether the differences (sun versus surface current orientation) were due to the study being conducted in enclosed inland waters or due to species differences, megalopae of other *Cancriidae* genera did not swim towards the east and thus likely do not swim ashore.

The behavior we observed for *M. magister* was identical to that reported for *P. crassipes* and *Lophopanopeus bellus bellus* megalopae (Shanks 1995b); megalopae swam at the ocean's surface and oriented their swimming with the direction of the surface current. In the current study, megalopae did not appear to orient their swimming when no surface current was observed, suggesting that megalopae orient

their swimming direction relative to surface currents; though more data are needed.

The average *in situ* swimming speed we measured (9.8 cm s^{-1} after correction for current speed) is intermediate between previously reported swimming speeds: 4.2 (Jacoby 1982) or 8.5 cm s^{-1} (Fernandez et al. 1994) in still water and 44.7 cm s^{-1} in a flume with a strong current (Fernandez et al. 1994). The slowest current speed tested by Fernandez et al. (1994) was 14 cm s^{-1} , whereas the current speeds we observed were $\sim 1.5 \text{ cm s}^{-1}$. The results from these 2 studies suggest that the megalopae of *M. magister* alter their swimming speed and may do so relative to local current speed.

Daily abundance at the coast of *M. magister* megalopae varies with a fortnightly periodicity that is out of phase with the spring neap tidal cycle and is highly pulsed (Johnson & Shanks 2002, Roegner et al. 2007). Fortnightly periodicity in recruitment is considered indicative of cross-shelf transport by internal waves (Shanks 1986, 2006, Pineda 1991). This recruitment pattern is not considered indicative of selective tidal stream transport, because the level of recruitment would be directly proportional to the size of the tidal prism, and thus recruitment would be in phase with and proportional to the spring neap cycle (Shanks 2002). Furthermore, concentrated patches of *M. magister* megalopae have been observed in surface convergences, some of which were internal waves (Shenker 1988, L. K. Rasmuson & A. L. Shanks pers. obs.).

Transport by internal waves occurs when the speed of the surface current over the internal wave is greater than the propagation speed of the wave. Reported horizontal current velocities over internal waves are highly variable (centimeters to meters per second; Jackson 2004). An organism swimming in the direction of the surface current would increase their speed relative to the propagation speed of the wave and thus increase the possibility of being transported by a wave. Megalopae of *L. bellus bellus* were observed swimming in the convergence over an internal wave and in the direction the internal wave was propagating (Shanks 1995b). Given the behavior of *M. magister* megalopae, e.g. swimming in the direction of the surface current, it is likely that if megalopae were exposed to flow over an internal wave they would swim with the wave (Shanks 1995b).

Over 24 d, none of the observed internal waves would have caused 'shelf-transport' (distances $\geq 25 \text{ km}$) for passive particles (Fig. 4). Calculations suggest, however, that for organisms that swim in the direction of wave propagation, many of the internal

waves would cause 'shelf-transport'. At swimming speeds of 10 cm s^{-1} , all 69 waves would have been 'shelf-transporting', so that 'shelf-transport' would have occurred daily. Thus, the behaviors exhibited by *M. magister* may dramatically increase the possibility of being transported shoreward by internal waves. We did observe 24 internal bores in our temperature record, and some of these may have caused 'shelf-transport' for passive particles, but lack of suitable models prevented us from calculating transport potential (Pineda 1991, Helfrich & Pineda 2003).

Previous studies have demonstrated that only some waves transport megalopae (Shanks 1983, 1988, Shanks & Wright 1987). However, our data suggest that *M. magister* megalopae would have been transported by all of the waves we observed. This is inconsistent with work showing that recruitment of *M. magister* megalopae is pulsed (values can change by more than 3 orders of magnitude fortnightly; Shanks 2013). Our mooring was deployed where the water column depth was only 30 m. The waves we observed likely had been slowed by friction on the bottom in shallow water and thus were travelling at speeds that larvae could more easily match. Thus it is possible that the greater variability of internal wave speeds and amplitude in deeper waters would decrease the number of waves that could potentially transport megalopae significant distances. For this hypothesis to be tested, daily recruitment of megalopae should be correlated with high frequency measurements of internal waves at different sites across the continental shelf to determine the characteristics of a transporting internal wave.

Our study indicates that *M. magister* megalopae swim in the direction of a surface current and swim at speeds of $\sim 10 \text{ cm s}^{-1}$. Transport by internal waves occurs if the speed of the surface current over the wave is greater than the speed of the wave. As an increasing number of studies examine larval behavior in situ it is essential to understand how these findings influence how larvae migrate back to settle. We have demonstrated that larval behavior greatly increases transport by internal waves, and since internal tides, and thus waves, are ubiquitous around the world, future work will likely demonstrate that larvae of many species are transported by internal waves.

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LITERATURE CITED

- Batschelet E (1981) Circular statistics in biology. Academic Press, New York, NY
- Bingham BL, Young CM (1991) Larval behavior of the ascidian *Ecteinascidia turbinata* Herdman; an in situ experimental study of the effects of swimming on dispersal. *J Exp Mar Biol Ecol* 145:189–204
- Cobb JS, Wang D, Campbell DB, Rooney P (1989) Speed and direction of swimming by postlarvae of the American lobster. *Trans Am Fish Soc* 118:82–86
- Elliott JK, Elliott JM, Mariscal RN (1995) Host selection, location, and association behaviors of anemonefishes in field settlement experiments. *Mar Biol* 122:377–389
- Fernandez M, Iribarne OO, Armstrong DA (1994) Swimming behavior of Dungeness crab, *Cancer magister* Dana, megalopae in still and moving water. *Estuaries* 17:271–275
- Hamilton PV, Russel BJ (1981) Field experiments on the sense organs and directional cues involved in offshore-oriented swimming by *Aplysia brasiliana* Rang (Mollusca: Gastropoda). *J Exp Mar Biol Ecol* 56:123–143
- Helfrich K, Pineda J (2003) Accumulation of particles in propagating fronts. *Limnol Oceanogr* 48:1509–1520
- Holloway PE (1987) Internal hydraulic jumps and solitons at a shelf break region on the Australian North West Shelf. *J Geophys Res* 92:5405–5416
- Jackson CR (2004) An atlas of internal solitary-like waves and their properties, 2nd edn. Global Ocean Associates, Alexandria, VA
- Jacoby C (1982) Behavioral responses of the larvae of *Cancer magister* Dana (1852) to light, pressure and gravity. *Mar Behav Physiol* 8:267–283
- Jeffs A, Tolimieri N, Montgomery JC (2003) Crabs on cue for the coast: the use of underwater sound for orientation by pelagic crab stages. *Mar Freshw Res* 54:841–845
- Jeffs AG, Montgomery JC, Tindle CT (2005) How do spiny lobster post larvae find the coast? *N Z J Mar Freshw Res* 39:605–617
- Johnson J, Shanks AL (2002) Time series of the abundance of the post-larvae of the crabs *Cancer magister* and *Cancer* spp. on the southern Oregon coast and their cross-shelf transport. *Estuaries* 25:1138–1142
- Lamb K (1997) Particle transport by nonbreaking, solitary internal waves. *J Geophys Res* 102:18641–18660
- 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 Fishes* 65:199–208
- Leis JM, Carson-Ewart BM (1997) *In situ* swimming speeds of the late pelagic larvae of some Indo-Pacific coral-reef fishes. *Mar Ecol Prog Ser* 159:165–174
- Leis JM, Carson-Ewart BM (2003) Orientation of pelagic larvae of coral-reef fishes in the ocean. *Mar Ecol Prog Ser* 252:239–253
- Leis JM, Carson-Ewart BM, Cato DH (2002) Sound detection *in situ* by the larvae of a coral-reef damselfish (Pomacentridae). *Mar Ecol Prog Ser* 232:259–268
- McManus MA, Cheriton OM, Drake PJ, Holliday DV, Storzlazzi CD, Donaghay PL, Greenlaw CF (2005) Effects of physical processes on structure and transport of thin zooplankton layers in the coastal ocean. *Mar Ecol Prog Ser* 301:199–215
- 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

- Miller SH, Morgan SG (2013) Pheotypic plasticity in larval swimming behavior in estuarine and coastal crab populations. *J Exp Mar Biol Ecol* 449:45–50
- Phillips B, Olsen L (1975) Swimming behaviour of the puerulus larvae of the western rock lobster. *Mar Freshw Res* 26:415–417
- Pineda J (1991) Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. *Science* 253:548–549
- Queiroga H, Blanton J (2004) Interactions between behaviour and physical forcing in the control of horizontal transport of decapod crustacean larvae. *Adv Mar Biol* 47: 107–214
- Queiroga H, Cruz T, dos Santos A, Dubert J and others (2007) Oceanographic and behavioural processes affecting invertebrate larval dispersal and supply in the western Iberia upwelling ecosystem. *Prog Oceanogr* 74:174–191
- Radford CA, Jeffs AG, Montgomery JC (2007) Directional swimming behavior by five species of crab postlarvae in response to reef sound. *Bull Mar Sci* 80:369–378
- Rasmuson LK (2013) The biology, ecology and fishery of the Dungeness crab, *Cancer magister*. *Adv Mar Biol* 65: 95–148
- Roegner GC, Armstrong DA, Shanks AL (2007) Wind and tidal influences on larval crab recruitment to an Oregon estuary. *Mar Ecol Prog Ser* 351:177–188
- Shanks AL (1983) Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. *Mar Ecol Prog Ser* 13:311–315
- Shanks AL (1986) Tidal periodicity in the daily settlement of intertidal barnacle larvae and an hypothesized mechanism for the cross-shelf transport of cyprids. *Biol Bull* 170: 429–440
- Shanks AL (1988) Further support for the hypothesis that internal waves can cause shoreward transport of larval invertebrates and fish. *Fish Bull* (Seattle) 86:703–714
- Shanks AL (1995a) Mechanisms of cross-shelf dispersal of larval invertebrates and fish. In: McEdward L (ed) *Ecology of marine invertebrate larvae*. CRC Press, Boca Raton, FL, p 323–367
- Shanks AL (1995b) Orientated swimming by megalopae of several eastern North Pacific crab species and its potential role in their onshore migration. *J Exp Mar Biol Ecol* 186:1–16
- Shanks AL (2002) Internal tides and the biology of continental shelf waters. In: Castilla JC, Largies JL (eds) *The oceanography and ecology of the nearshore and bays in Chile*. Proceeding of the International Symposium on Linkages and Dynamics of Coastal System: Open Coasts and Embayments, Santiago, Chile 2000. Ediciones Universidad Católica de Chile, Santiago, p 3–27
- Shanks AL (2006) Mechanisms of cross-shelf transport of crab megalopae inferred from a time series of daily abundance. *Mar Biol* 148:1383–1398
- Shanks AL (2013) Atmospheric forcing drives recruitment variation in the Dungeness crab (*Cancer magister*), revisited. *Fish Oceanogr* 22:263–272
- Shanks AL, Roegner GC (2007) Recruitment limitation in Dungeness crab populations is driven by variation in atmospheric forcing. *Ecology* 88:1726–1737
- Shanks AL, Wright W (1987) Internal-wave-mediated shoreward transport of cyprids, megalopae, and gammarids and correlated longshore differences in the settling rate of intertidal barnacles. *J Exp Mar Biol Ecol* 114:1–13
- Shenker J (1988) Oceanographic associations of neustonic larval and juvenile fishes and Dungeness crab megalopae off Oregon. *Fish Bull* (Seattle) 86:299–317
- Shroyer EL, Moum JN, Nash JD (2010) Vertical heat flux and lateral mass transport in nonlinear internal waves. *Geophys Res Lett* 37:L08601, doi:10.1029/2010GL042715
- Tolimieri N, Jeffs A, Montgomery JC (2000) Ambient sound as a cue for navigation by the pelagic larvae of reef fishes. *Mar Ecol Prog Ser* 207:219–224

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