

REVIEWS

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Foraging behavior can influence dispersal of marine organisms

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Abstract

It has become increasingly apparent that widely varying behaviors of organisms (e.g., ontogenetic depth preference, selective tidal stream transport, position maintenance) can significantly influence dispersal and connectivity between nearby populations. However, more common day-to-day behaviors, such as foraging, are often assumed to have little effect on dispersal at larger scales (tens to thousands of kilometers). In this review, we (1) place foraging within the context of current knowledge on behaviors that influence dispersal and transport, (2) provide evidence for foraging behavior as a driving mechanism of distributions, and (3) present a meta-analysis of dispersal distances estimated for three dispersal hypotheses (passive, swimming directly against currents, and foraging behavior) from 59 studies that document oceanographic conditions and in situ organism distributions. Results of the analyses reveal that when foraging and aggregative behaviors are considered, dispersal distances for larvae and zooplankton could be hundreds of kilometers less than many current dispersal estimates. Reduced transport because of foraging implies that individual populations might be more isolated than currently accepted. These findings suggest that fine-scale organism behaviors should be considered in models aimed to improve conservation efforts.

Since humans took to the seas for food, fisherfolk have understood the importance of finding the 'honey hole' to maximize catch per unit effort (Healey et al. 1990). Observations of multiple trophic levels, from phytoplankton to whales, aggregated in or near fronts and clines (areas often termed 'honey holes') have elicited several hypotheses concerning how physical processes and behavior influence organismal distributions and dispersal in the ocean (Wolanski and Hamner 1988; *see* reviews by Metaxas 2001; Genin 2004). However, the interactive effects of increased biological activity, organism behavior, and the physical environment of fronts and clines on the transport and dispersal of marine organisms have not been fully explored.

Behaviors that allow organisms to take advantage of spatial and temporal flow reversals, which occur at relatively long time scales (~12 h or more; e.g., ontogenetic depth preference, diel migration, selective tidal stream transport), have been studied and reviewed extensively in recent years (*see* reviews by Forward and

Tankersley 2001; Sponaugle et al. 2002; Naylor 2006; Levin 2006). These reviews focus on how interactions between physical mechanisms and behavior can lead to directed horizontal transport or retention and, thus, have significant effects on horizontal advection. Behaviors of competent larvae that allow them to reach adult habitats, such as selective tidal stream transport (Forward and Tankersley 2001) or active swimming against a downwelling current yielding surface transport by internal waves or internal transport by bores (Shanks 1985; Pineda 1999), also suggest that larvae are able to remain relatively close to adult habitats (Shanks and Brink 2005). In addition to species-specific behaviors producing directed transport, many larvae show behaviors that could be specific to preferred habitats. For example, Shanks and Brink (2005) showed distinctly different distributions of four invertebrate taxa that appeared linked to habitat restrictions. These authors further speculated that many larvae have a wide variety of behavioral adaptations allowing them to remain close to shore.

Increasing attention is paid to the ability of zooplankters to influence their distributions over a wide range of spatial and temporal scales (*see* reviews by Folt and Burns 1999, Metaxas 2001, Naylor 2006). Recent reviews have focused on biological drivers (Folt and Burns 1999), selective tidal stream transport (Forward and Tankersley 2001), swimming behavior in turbulence (Metaxas 2001), vertical swimming behavior and depth preference (Sponaugle et al. 2002; Genin 2004), and circa-tidal and diel migrations (Naylor 2006). However, few, if any, studies focus on how

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foraging behaviors could indirectly influence horizontal transport at large spatial scales throughout the life cycle or pelagic larval duration.

As is well known, only a portion of the spatial variation of zooplankton can be explained by physical mechanisms alone (more recently, Wiafe and Frid 1996; reviewed by Folt and Burns 1999; McManus et al. 2005). Biological drivers have been consequently invoked to explain the remainder. Folt and Burns (1999) discussed several potential drivers of zooplankton distributions, including diel migration, predator avoidance, foraging behavior, and mate finding, with respect to observed physical mechanisms of aggregation (e.g., vertical swimming in convergent flows; Genin 2004). It is probable that all of these drivers influence distributions of zooplankton in situ to varying extents.

In this review, we focus on (1) why, because of the lack of direct associations between zooplankton and prey, foraging has not been found to explain many previous observations; (2) how foraging might parsimoniously explain a large portion of such observed distributions; and (3) how foraging can influence large-scale dispersal (10^0 to 10^3 km). For the remainder of this discussion, we explicitly define foraging as searching for prey or resources and remaining within high-resource patches, once found, through position maintenance as active responses to vertical displacements at small scales (10^{-3} – 10^{-2} ; Genin et al. 2005). Consequently, foraging behavior includes intermediate-scale (10^0 – 10^1 m) searches for prey, as well as small-scale behaviors (position maintenance) to remain within high-resource patches.

Foraging—a forgotten behavior?

In a well-mixed ocean, phytoplankton abundances would not be sufficient to maintain populations of zooplankters (Mullin and Brooks 1976). However, resources are distributed in high-density patches that can support higher trophic levels (Daro 1988). Passive accumulation in high-resource regions could take on the order of days, and once the forager is there, resources still might not be adequate for survival. Thus, strong selection should exist for zooplankters to be able to locate high-resource patches.

Grünbaum (2002) proposed a nondimensional Frost number ($Fr = c^2 T \tau / L^2$, where c is the forager speed, T is the prey patch persistence, τ is the forager turning interval, and L is the typical distance between prey patches) to estimate the availability of patchy prey to active foragers. For phytoplankton and microzooplankton, Fr is typically $\ll 1$, indicating that prey patches are not available to these organisms through foraging and that mortality and growth are likely important factors in observed distributions (Menden-Deuer and Grünbaum 2006). However, for larger zooplankton and higher trophic levels, $Fr > 1$ over realistic ranges of prey patch persistence (1 to several days) and spatial distributions (e.g., water column depths 10^2 – 10^3 m; Grünbaum 2002). These rough scaling arguments suggest that foraging is likely to be an important factor in observed distributions of mesozooplankton and higher trophic levels.

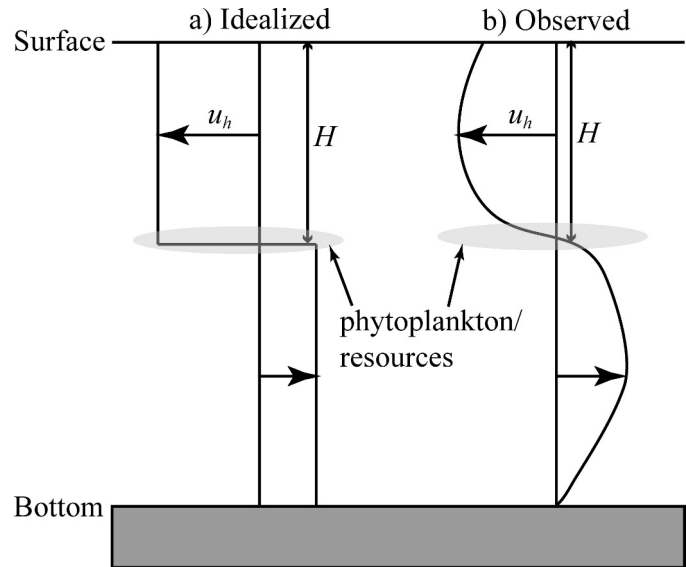


Fig. 1. (a) Idealized and (b) observed horizontal velocity profiles through water column for calculation of horizontal transport rate incorporating foraging behaviors.

Convergence and vertical shearing of the horizontal velocity field leads to phytoplankton patchiness at the scales of meters to hundreds of meters (Franks 1995; Stacey et al. 2007), although it is possible that active swimming of phytoplankton might also lead to observed aggregations and retention (e.g., Barber and Smith 1981). Consequently, the deep chlorophyll maximum is frequently located in the vicinity of flow reversals associated with fronts and clines (Fig. 1). Phytoplankton concentrations can be orders of magnitude higher in these regions (>150 mg chlorophyll a [Chl a] m^{-3}) than in surrounding waters (typically <10 mg Chl a m^{-3}) and sufficient to support consumer populations (Daro 1988; Deksheniaks et al. 2001; Cowles 2004). It has recently been suggested that organism behavioral responses to patchy environments lead to aggregations in fronts and clines, regions where flow often reverses direction, resulting in reduced horizontal transport for the individual (McManus et al. 2005; Woodson et al. 2005, 2007).

Although foraging behavior has long been considered a driver of zooplankton distributions, few observations have shown direct associations between zooplankton and prey (Folt and Burns 1999). Lack of agreement between zooplankton and prey distributions has motivated alternative hypotheses to explain these phenomena. Of them, directed swimming and position maintenance have received the most attention. Reviews by Metaxas (2001) and Genin (2004) develop conceptual models of zooplankton aggregation on the basis of turbulence intensity and vertical movement of water and zooplankters. Further, zooplankton have been directly observed to counteract vertical flow and displacement through oriented swimming behavior (Genin et al. 2005) and can consequently remain in preferred habitats (e.g., Seuront 2006). These behaviors can lead to aggregations when turbulence intensity and vertical velocities are less than the swimming speeds of the

taxa being observed. Gallagher et al. (2004) used a motility number, Mn ($Mn = U/q$, where U is the swimming speed of the taxa, and q is the root mean square [rms] turbulent velocity), as a means of quantifying the potential for zooplankton aggregation on the basis of turbulence and swimming ability. In the related field study, Mn was >1 for copepods and dinoflagellates, but not for immobile diatoms, suggesting that even very slowly swimming organisms can maintain vertical position and sustain aggregations. However, although directed responses to vertical displacements are important in defining the ability of taxa to maintain position and aggregate, these mechanisms do not necessarily explain the drivers for such behaviors.

Support for foraging as a driver of aggregation

Gallagher et al. (2004) also found that *Calanus* adults and nauplii near Georges Bank were aggregated in regions with high concentrations of the dinoflagellates *Ceratium* spp., and not in regions with high densities of diatoms. Pierson et al. (2005a,b) have shown that diatoms might not be nutritionally sufficient, and in a related study, Leising et al. (2005) showed that some copepods selectively feed on dinoflagellates. In addition, phytoplankton distributions are often segregated by taxa (e.g., Gallagher et al. 2004). Thus, bulk chlorophyll estimates might not always be appropriate measures of the influence of foraging behavior on aggregation. Fine-scale differences in zooplankton foraging behavior and prey selectivity could lead to a conclusion that foraging behavior does not explain distributions at intermediate scales (10^0 – 10^3 m). Thus, species composition of the phytoplankton must be known before foraging behavior can be excluded as a potentially important driver. The few studies that have identified phytoplankton patchiness at the species level have found strong association between zooplankton aggregations, phytoplankton distributions, and oceanographic gradients. These studies have further invoked foraging to explain the observations (Gallagher et al. 2004; Leising et al. 2005).

Vertical shearing of the water column and in situ growth have been commonly implicated in the formation of phytoplankton patchiness (Franks 1995; Gallagher et al. 2004; Stacey et al. 2007). Laboratory and modeling studies have further shown that some zooplankton tend to remain in high-resource patches once located (Tiselius 1992; Metaxas and Young 1998; Leising and Franks 2002). Intricate foraging behaviors among copepods appear inherently linked to these formation mechanisms of biological patchiness (Woodson et al. 2007). Cue hierarchies in foraging behavior encompass velocity shear, fluid density, chemical exudates, and food presence to find regions of high productivity. Such behaviors suggest that zooplankton are able to locate prey patches efficiently and could result in aggregations in these regions (Woodson et al. 2007 in press).

Zooplankton and larger organisms also might not be able to rely on passive transport to locate and exploit prey patches at temporal scales that will promote survival because of a mismatch between phytoplankton bloom

persistence (a few days to a week) and population responses of predators to increased prey (several weeks to a year or more; Mauchline 1998). Yet, organisms of multiple trophic levels are aggregated at fronts and clines. Zooplankton within high-resource patches also experience greater fitness and, unexpectedly, reduced predation in some cases (Tiselius and Jonsson 1997). Thus, one would hypothesize that zooplankton distributions follow prey distributions, and consequently larger predators aggregate in similar regions because of increased prey availability (Healey et al. 1990). Although aggregation at fronts and clines also occurs because of vertical swimming behavior in convergent flows and it is well known that some organisms in fronts and clines are not necessarily foraging (Wolanski and Hamner 1988; Genin 2004), an equally parsimonious hypothesis in many cases appears to be that organisms are following prey distributions (i.e., foraging; see Landaeta and Castro 2006).

Effect of foraging on dispersal—a meta-analysis

We searched the literature for studies that reported organism distributions and oceanographic properties. We limited our search to studies conducted after 1980 because of the availability of technology to measure in situ distributions of organisms and physical parameters. We found additional studies by searching reference lists of these studies and review articles. We then determined two criteria for inclusion of the compilation: (1) taxonomic groups of organisms are reported, and (2) concurrent physical data are reported (or data in a referenced publication are available). Fifty-nine out of 89 studies met the criteria for analysis and included species ranging from phytoplankton to whales, resulting in 99 observations of organism distributions. Out of the 59 studies that met the examination criteria (see Web Appendix 1, www.aslo.org/lo/toc/vol_52/issue_6/2701a1.pdf), 43 reported distributions of organisms associated with fronts and clines. For papers that did not report or directly measure current velocity, we reviewed cited physical oceanographic literature for the study region to determine typical currents observed (11 of out 59 studies). We grouped each observation as phytoplankton (including bacteria and microzooplankton), zooplankton (including larvae), and higher trophic levels (fishes and mammals). We then used the physical oceanographic data along with organism swimming speeds to estimate horizontal transport for organisms that (1) act as passive particles, (2) swim directly against currents, or (3) aggregate in front or cline regions as a result of foraging behaviors (i.e., can locate and remain in a preferred patch).

Fronts and clines, boundaries between disparate water bodies, are common features in the ocean, often characterized by gradients in physical properties and parameters such as density and flow velocity (Mann and Lazier 2006). In shallow coastal areas, flow often reverses direction because of fixed boundaries and the requirement of continuity. A classic example of flow reversal at a cline is the current profile in a coastal upwelling system (Fig. 1).

To calculate dispersal effects from foraging behaviors, we made five simplifying assumptions. (1) We assumed that peaks in chlorophyll (as a proxy for food in general) were associated with steep gradients in physical variables (e.g., Fig. 1). This assumption has been supported extensively in the literature (see Franks 1995; Metaxas 2001; Stacey et al. 2007). (2) We also assumed that flow in the lower layer or on the opposite side of the front was in the reverse direction, resulting in a region of near-zero velocity. On the basis of reported currents around fronts and clines, this assumption is also frequently valid. Although fronts and convergences often move horizontally as well, rates of horizontal movement are often significantly less than associated along-front currents and thus would likely have a minor effect on our order-of-magnitude dispersal estimates (Mann and Lazier 2006). (3) We assumed that current speeds were constant over the course of the calculations. As a note on this assumption, we are reporting general patterns of dispersal at large scales because of fine-scale behavior. Thus, a more realistically varying current speed will likely not have a significant effect on the general patterns of transport in this analysis but will ultimately determine dispersal for marine organisms. (4) We further assumed that organisms possess sensory and swimming capabilities to identify and remain in high-resource regions. Again, extensive reviews of fine-scale behavior of zooplankton and larvae suggest that this assumption is valid (e.g., Metaxas 2001; Folt and Burns 2004; Leis 2006). Finally, (5) we assumed that foraging behavior resulted in organisms locating and spending significant time within the region in which resources were available (e.g., Tiselius 1992; Leising and Franks 2002; Woodson et al. 2007). Field observations of organisms at fronts and clines further support this assumption (78% of all observations in this study having reported distributions associated with fronts and clines).

When the species of organism was not identified, or documented swimming speeds were not obtainable (34 out of 98 observations), we used mean values for the organism trophic class (e.g., 278 $\mu\text{m s}^{-1}$ or 1 m h^{-1} for phytoplankton, 2 mm s^{-1} for copepods and other mesozooplankton, and 2 body lengths s^{-1} for fishes and mammals; Evans and Taylor 1980; Kamykowski and McCollum 1986; Vogel 1994). Horizontal current velocities for the studies ranged between 4 and 50 cm s^{-1} , with cline depths between 3 and 400 m. Reported vertical velocities, or relative turbulent rms velocities, were on the order of 1 mm s^{-1} in all study regions, and swimming speeds varied between 200 $\mu\text{m s}^{-1}$ and 4 m s^{-1} .

We calculated a daily horizontal transport distance for each behavior (passive, Eq. 1; horizontal, Eq. 2; and foraging, Eq. 3) as

$$L_p = u_h t \quad (1)$$

$$L_h = (u_h - u_s) t \quad (2)$$

$$L_f = 2u_h [H / (u_s - v)] \quad (3)$$

where $L_{p,h,f}$ are the horizontal transport distances per day for each respective behavior, u_h is the mean horizontal

current speed (distance per day) in the upper mixed layer, u_s is the sustainable swimming speed of the organism (mean per day), v is the mean vertical current speed in the upper mixed layer or at a frontal boundary, H is the depth of the upper mixed layer, and t is time, explicitly 1 d (Fig. 1). Because fronts are often surface expressions of subsurface oceanographic gradients, we set H equal to the water depth (i.e., the cline/flow reversal region was at the surface) for observations involving surface fronts. Equations 1 and 2 are velocities multiplied by times (in the case of this analysis, 1 day = 86,400 s) yielding a distance traveled, L . In Eq. 3, the time an individual is exposed to the mean current in the upper layer is estimated as the time to swim from the cline or front to the surface and back over a 24-h period: $t = H / (u_s - v)$. For example, the time in the region of mean flow for a 10-m-deep mixed layer and a swimming speed of 2 mm s^{-1} will be 5,000 s (1.39 h). The factor of 2 in Eq. 3 was introduced to account for the upward and return movement of an organism vertically in diel migration, or it provides that an individual searches the whole water column twice each day to locate prey. However, this factor has a small influence on the observed response because of the use of a log response ratio (e.g., the factor of 2 becomes an additive factor of $\log 2 \approx 0.3$). Although it is known that many organisms do not undergo diel migration, this formulation allowed estimation of a maximum daily transport across all taxa. L_f is thus the horizontal distance an organism would be transported if it swam (or was displaced) across the entire mixed layer and back each day (perpendicular to the predominant flow direction; Fig. 1). Organisms that actively forage might not traverse this distance and could spend more time in reduced flow regions where there is increased primary production and biological activity. Hence, L_f represents a conservative estimate of restricted dispersal for these animals. $L_{h,p,f}$ thus represents the transport distance of an individual in a 24-h period under each scenario (passive, swimming against the flow, foraging). Although we did not explicitly account for turbulence in our study, we measured turbulent rms vertical velocities on the order of 1 mm s^{-1} . This potential displacement is accounted for in our use of v to correct for swimming speeds in Eq. 3.

We quantified dispersal distances with a transport distance log response ratio, LRR , defined as

$$LRR = \log(L_p / L_{h,f}) \quad (4)$$

for the active behavioral scenarios compared with the passive (control) scenario. We performed an unweighted, fixed-effects model meta-analysis, and calculated 95% confidence intervals for effect sizes by a bootstrapping technique with 9,999 recalculations for both LRR s (horizontal swimming and foraging behavior) in MATLAB (Efron and Tibshirani 1993; Hedges et al. 1999). Null hypotheses concerning behavioral influence on horizontal transport were rejected if the mean LRR and the 95% confidence intervals (calculated by a bootstrapping technique with 9,999 replications) for an organism class were >0 (e.g., $p < 0.05$; Hall 1988). LRR s and 95% confidence intervals that include zero indicate that organisms essen-

tially act as passive particles with respect to horizontal transport. *LRRs* for swimming against the flow and foraging behavior were compared with a bootstrapping hypothesis test (Efron and Tibshirani 1993). Regression revealed that other factors (current speed, thermocline depth) did not significantly contribute to the observed patterns ($R^2 < 0.015$; $p > 0.231$ in all cases; data available upon request). We repeated this analysis for each of the four zooplankton subgroups.

We then compiled data on the pelagic larval duration (PLD), size and swimming speed at release, oviparity versus viviparity, duration to hatching, and developmental rate for all invertebrate and vertebrate larvae reported from the incorporated studies (Chia et al. 1984; Strathmann 1987; Fishbase, www.fishbase.org; see Web Appendix 1). Larvae that were known not to feed during any stage of their PLD were excluded from analysis. These parameters were incorporated into transport calculations to determine maximum dispersal distances for passively and actively behaving organisms. For each day of the PLD, swimming speed was calculated on the basis of documented values for developmental rate, swimming speed at release, and swimming speed at competency because many larvae develop quickly and swimming abilities change significantly over the PLD. Transport was calculated each day (with the use of developmental data) of the PLD and summed to get a maximum total transport distance.

Out of 59 studies that met our search criteria, 78% reported organism aggregations associated with fronts, clines, or increased biological activity. Phytoplankton aggregations (12 of 14 observations) were almost always associated with steep gradients in density, temperature, and flow velocity. Zooplankton and larger organism aggregations also were commonly associated with physical oceanographic gradients and increased primary production (56 of 70 and 9 of 13 observations, respectively). Observations of multiple trophic levels aggregated at fronts and clines are common in the literature and support hypotheses that reduced horizontal transport as a result of foraging behavior could be an important factor in marine, and especially coastal, habitats. Our analyses revealed that phytoplankton and microzooplankton act as passive particles with respect to horizontal transport. These organisms cannot significantly affect horizontal transport by ocean currents under most oceanographic regimes but can influence vertical distributions (Fig. 2a; although see Barber and Smith 1981). At the other end of the size spectrum, adult fishes and mammals can adjust their horizontal transport simply by swimming directly against horizontal currents. These results are consistent with hypotheses and assumptions used in marine ecology and, specifically, in coupled models of physical circulation and larval dispersal. However, another pattern developed for the zooplankton group, wherein organisms cannot swim directly against flows, but indirectly influence horizontal transport through foraging behavior. This result contradicts hypotheses and model assumptions that lump zooplankton with phytoplankton in their ability to respond to oceanographic conditions and consequently affect horizontal transport. Our results further indicated that all

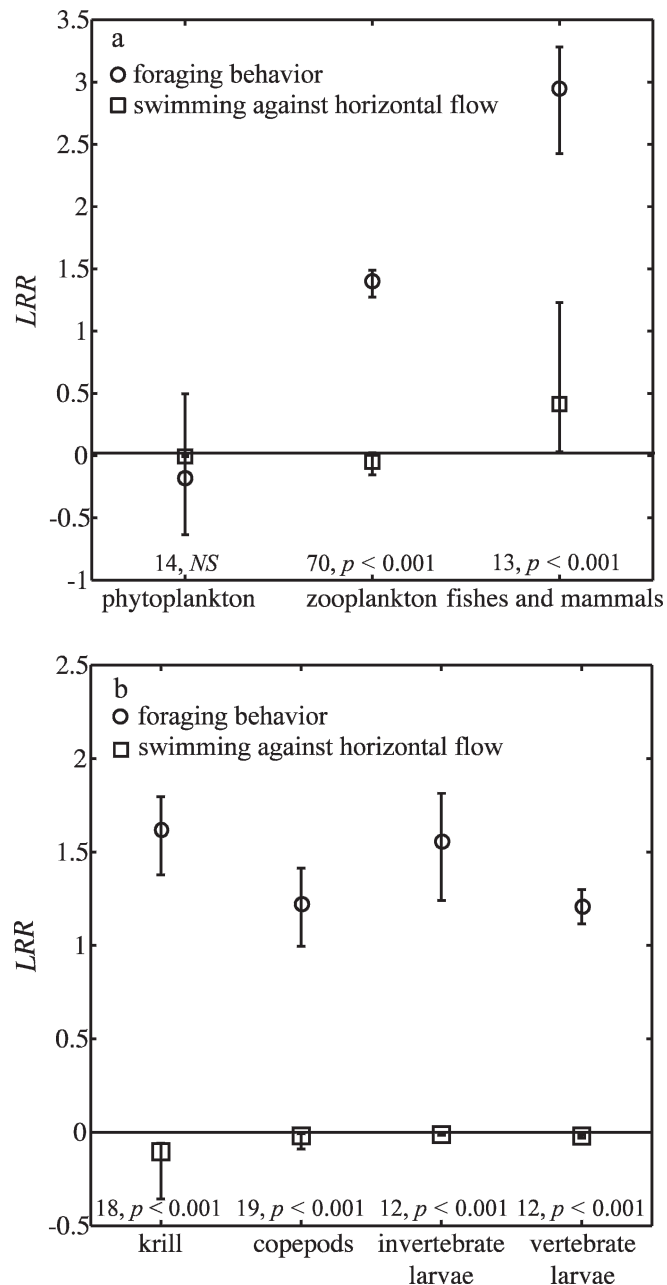


Fig. 2. *LRR* for (a) three primary organism classes and (b) four zooplankton groups to maintain horizontal position in the ocean if (1) organisms can only maintain position by swimming against a flow and (2) if organisms forage or actively aggregate in a zone of minimal flow (e.g., thermocline). The indirect influence of a modeled behavior on horizontal transport is considered significant if the mean *LRR* is above zero and the 95% confidence interval (error bars) does not cross zero. Sample sizes and *p* values are given in the figure from single-factor ANOVA comparing transport within taxonomic group. Nonsignificant *p* values are represented by *NS*. Sizes for the three organism classes are < 1 mm for phytoplankton, millimeters to centimeters for zooplankton, and centimeters to meters for larger organisms.

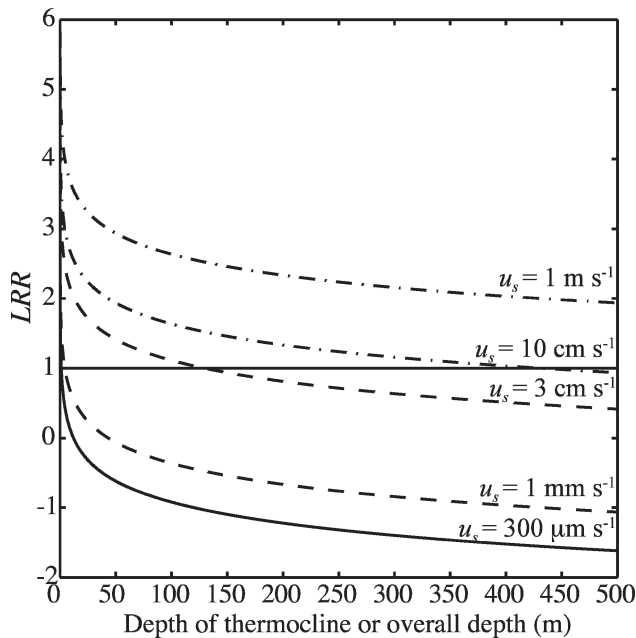


Fig. 3. LRR versus depth of thermocline or overall depth for swimming speeds of marine organisms. The point where curves intersect the solid horizontal line at $LRR > 1$ is the maximum depth at which organisms can significantly influence horizontal transport through foraging behavior.

zooplankton groups can indirectly reduce horizontal transport regardless of general size patterns across groups (Fig. 2b).

Next, we estimated the depth of a cline or the overall depth of the water column at which an organism can indirectly influence horizontal transport through foraging behaviors under our assumptions of active foraging (e.g., food is located at fronts and clines, currents are consistent and reverse direction in these regions, and organisms that actively forage will spend substantial time in these regions). For phytoplankton (and specifically motile dinoflagellates that swim at 1 m h^{-1}), this depth is approximately 1.2 m (Fig. 3). Zooplankton depths range between 4 and 130 m depending on swimming speed. For organisms that swim faster than most observed currents, LRR is almost always >1 for all cline depths, signifying an order of magnitude reduction in horizontal transport compared with passive particles.

Analysis of larval transport showed that both invertebrate and vertebrate larvae could reduce dispersal distance by an order of magnitude or more through foraging behaviors even in relatively strong flows (Fig. 3). Additionally, both groups can indirectly influence dispersal (defined as a $LRR > 1$) after only a few days in the

plankton (Table 1). Thus, foraging larvae and juveniles could indirectly reduce dispersal distances to as little as a few kilometers (Fig. 4).

Our results support hypotheses that phytoplankton and zooplankton typically are aggregated in zones of minimal flow by a combination of physical mechanisms, in situ growth, and swimming behavior (Barber and Smith 1981; Franks 1995, 2001; Stacey et al. 2007). Behavioral responses (such as foraging, feeding, and position maintenance) of zooplankton to patchy environments thus lead to aggregations in minimal flow zones where horizontal transport is significantly reduced (McManus et al. 2005; Woodson et al. 2007).

Ontogenetic depth changes and diel migration through frontal or clinal regions have been demonstrated for larvae of several invertebrate and vertebrate species (Paris and Cowen 2004). However, such behaviors might not be successful if oceanographic conditions change significantly because of large-scale events (climate change, El Niño–Southern Oscillation, Pacific Decadal Oscillation) or after long-distance dispersal to a new region (Grantham et al. 2003; Barth et al. 2007). Such behaviors are also believed to be species specific and uncommon across broad taxa. Foraging behavior, however, could also play an important role in dispersal and should be relatively consistent across many regions and taxa. Reduced horizontal transport under well-structured oceanographic regimes might explain why many species of nearshore fishes release larvae after the seasonal transition to upwelling (Love et al. 2002; Shanks and Eckert 2005). After the transition to upwelling, clines and fronts with reversals in current direction become well established as a result of density differences between cold, upwelled waters and warm surface waters (Mann and Lazier 2006). These strong gradients provide consistent oceanographic conditions under which foraging can indirectly reduce dispersal. Recent evidence showing that the larvae of fish and invertebrate species (1) prefer stratified waters (Landaeta and Castro 2006; Marta-Almeida et al. 2006), (2) follow prey distributions (Landaeta and Castro 2006), (3) are able to self-recruit (Jones et al. 1999; Swearer et al. 1999), and (4) show high genetic structuring within larval cohorts (Selkoe et al. 2006) supports our hypothesis of reduced transport via foraging behaviors. The failure of recruitment during delayed upwelling along in the California Current large marine ecosystem also suggests that development of fronts and clines in these systems is critically important to larval survival (Barth et al. 2007).

Swimming speeds that directly or indirectly affect horizontal transport are on the order of 10^0 – 10^1 mm s^{-1} , well within the capabilities of all but the youngest larvae (Table 1), further emphasizing the potential importance of local oceanographic conditions during the first few days of

Table 1. Mean and 95% confidence intervals of development age and swimming speed at which foraging behavior can reduce horizontal transport by an order of magnitude per day ($LRR > 1$) on the basis of larval capabilities and observed distributions.

Organism class	n	PLD range (days)	Age at $LRR > 1$ (days)	Swimming speed at $LRR > 1$ (mm s^{-1})
Invertebrate larvae	12	15–70	4.45 ± 0.62	2.06 ± 0.34
Vertebrate larvae	12	30–120	3.09 ± 0.51	2.59 ± 0.19

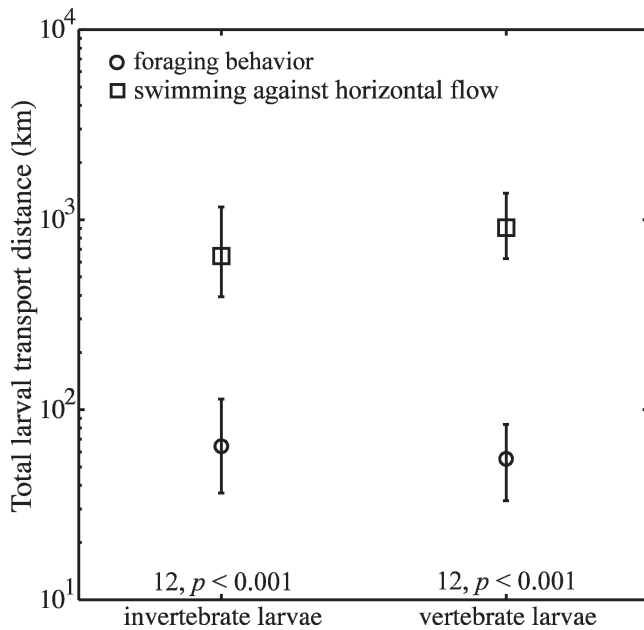


Fig. 4. Total transport distances for larvae incorporating pelagic larval duration, swimming speed at release and competency, and development rates. Distances were calculated for individual species from physical data from each study. Error bars show 95% confidence intervals. Sample size and p values given in the figure are from a single-factor ANOVA comparing transport within taxonomic group.

pelagic larval life (Sponaugle et al. 2002; Cowen et al. 2003). These swimming capabilities can effectively reduce larval transport between open-coast populations, could lead to significant retention near natal sites, and could accentuate the importance of ‘stepping stones’ in marine population connectivity where several small populations a few kilometers apart are critical (Botsford et al. 2001). Estimates of larval dispersal on the basis of our analysis also support recent suggestions that smaller, strategically distributed, marine protected areas (MPAs) should be more beneficial than a smaller number of large MPAs for many species (Cowen et al. 2006; Steneck 2006).

Flow reversals at fronts and clines are ubiquitous in coastal systems worldwide (Mann and Lazier 2006). However, larger scale physical events (mesoscale eddies, storms, relaxation from upwelling conditions, etc.) that occur at periods of roughly 15–90 d can disrupt fine-scale structure in the ocean and move organisms away from natal or preferred habitats (Sponaugle et al. 2002; Cowen et al. 2003). The ability of most larvae to influence dispersal distances from very young ages under typical oceanographic conditions, but not during rarer large-scale events, further supports hypotheses that large-scale events drive genetic connectivity and that local conditions sustain populations at ecological timescales (Narvaez et al. 2006). In this case, a network of marine protected areas would not harm genetic variation among species but in fact could promote variation across broad geographic scales, as has been recently demonstrated (Perez-Ruzafa et al. 2006).

Potential indirect effects of foraging behaviors among zooplankton on horizontal transport suggest reconsideration of many biophysical hypotheses in oceanography and marine ecology. Even though horizontal current speeds are often much greater than swimming capabilities of most zooplankton, many are able to locate and maintain position in or near high-resource patches, with the indirect consequence that horizontal transport can be significantly reduced. Importantly, this effect is potentially common in the coastal ocean on the basis of results of this global meta-analysis. Thus, foraging behavior (along with other behaviors that have been shown to influence dispersal) and fine-scale current structure cannot be overlooked, should be incorporated into coupled biophysical models, and will likely be critical for estimating transport and dispersal distances across many regions and species.

The potentially large effects of intermediate- and small-scale behaviors on dispersal and aggregation highlight the importance of three avenues of research that reach across several disciplines. First, foraging and other fine-scale behaviors need to be examined for a wider range of zooplankton and marine larvae. Second, oceanographic observations must be conducted at spatial and temporal scales relevant to the behaviors of individual organisms and must lead to the determination of species composition of distributions to elucidate appropriate driving mechanisms. Third, numerical models must capture fine-scale spatial and temporal variability of physical properties, prey patches, and behavioral responses of consumers. Each of these avenues will continue to provide critical information about how marine communities and meta-populations function and will be critical in future and continuing conservation efforts.

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