

Wave and tide-driven flow act on multiple scales to shape the distribution of a juvenile fish (*Albula vulpes*) in shallow nearshore habitats

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Abstract

Environmental stress associated with incident flow is among the most fundamental physical factors structuring fish distributions. In shallow marine habitats, flow-related stress arises through several distinct processes, yet their combined ramifications for habitat utilization by fishes are rarely evaluated concurrently. We used hydrodynamic models to resolve spatial and temporal variability in wave- and tide-driven water velocities across the littoral zone of a subtropical island, and related these, along with other environmental predictors, to patterns in the abundance of a juvenile fish (*Albula vulpes*) as determined by 785 beach-seine samples. Exerting universally negative effects on abundance, flow-related predictors were among the most influential drivers of habitat use, particularly at landscape scales where contrasts were most apparent. Spatial gradients in the strength of wave-induced and tide-driven flow were pronounced and varied inversely across the study area, applying contradictory constraints on *A. vulpes* distributions and limiting juveniles to the small subset of habitats where near-maximal wave and tide-driven water velocities were mutually depressed over the long term. Meanwhile, within the few embayments where *A. vulpes* occurred with regularity, abundance was inversely related to short-term fluctuations in wave-driven water velocity, evidencing fine-scale movements as fish presumably sought reduced rates of flow. Juveniles were consistently absent from the remaining majority of stations regardless of temporal variability, indicating that they were unable to exploit these areas even during periods of calm. Collectively, these observations are consistent with the hypothesis that spatial and temporal variability in incident flow act simultaneously at distinct scales to structure motile fish distributions.

The physical stress imposed by the movement of water can have profound effects on organisms in aquatic environments, from freshwater streams (Statzner et al. 1988; Nikora 2010) to rocky intertidal (Denny 2006; Burrows et al. 2008) and coral reef habitats (Dollar 1982; Harborne et al. 2006). For fishes, flow-related environmental stress can impact the performance of basic ecological functions such as locomotion (Pavlov et al. 2000; Lupandin 2005) and resource acquisition (Schaefer et al. 1999; Asaeda et al. 2005) while concurrently regulating the energetic expenditures associated with these activities (Facey and Grossman 1990; Boisclair and Tang 1993; Enders et al. 2003). As such, incident flow is among the most

fundamental physical factors governing habitat utilization by fishes across a variety of freshwater (Lewis 1969; Poff and Allan 1995) and marine systems (Friedlander et al. 2003; Fulton et al. 2005).

Ambient flow is likely to have even greater ramifications for the distribution of small-bodied fishes such as juveniles, for whom habitat use is already constrained by relatively strict ecological requirements and low mobility compared to more advanced ontogenetic stages (Wilson 2008; Nash et al. 2013; Welsh et al. 2013). Small fishes achieve lower absolute swimming speeds than larger-bodied individuals, limiting the water velocities they are capable of negotiating (Brett 1965; Beamish 1978), and are subject to disturbance by a broader range of turbulence scales, increasing their susceptibility to the destabilizing effects of unsteady flows (Lupandin 2005; Webb et al. 2010). It is not surprising then that juvenile fishes exposed to elevated flow velocities exhibit comparatively large

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Additional Supporting Information may be found in the online version of this article.

reductions in prey capture success (Flore and Keckeis 1998), greater rates of flow refuging (Fulton and Bellwood 2002; Johansen et al. 2008), and can be disproportionately affected by extreme flow events (Lassig 1983; Del Signore et al. 2014). Collectively, these impacts may lead to the exclusion of smaller fishes from wave- or current-swept environments (Sagnes et al. 1997; Depczynski and Bellwood 2005; Eggertsen et al. 2016), placing major constraints on habitat utilization. While juvenile fishes should occupy relatively low-flow environments compared to adults (Blaber and Blaber 1980; Sagnes et al. 1997; Fulton and Bellwood 2002), the varying abilities of fishes to contend with moving water should nonetheless give rise to distinctive patterns of habitat use across species, (Bellwood et al. 2002; Fulton et al. 2005; Leavy and Bonner 2009), constituting a fundamental niche difference. Yet, despite the considerable attention it has received in lotic freshwater habitats, the “hydrodynamic niche” of a species is rarely included among the environmental factors used to define the essential habitat requirements of juvenile marine fishes.

Studies linking wave-driven flow to the distributions of marine organisms almost universally employ the concept of “wave exposure,” an abstraction that is seldom well defined or evaluated in a quantitative manner (Lindgarth and Gamfeldt 2005). Denny (1995) defines wave exposure as an “integrated index of the severity of the hydrodynamic environment.” Interpreted in this way, wave exposure is largely a function of coastal geomorphology, bathymetry, and prevailing climatic patterns and is thus a temporally invariant property of a point in space, giving rise to geographically varying “exposure gradients.” However, in coastal marine habitats, hydrodynamic conditions at a given location are often dynamic, dependent not only upon the relatively fixed seascape characteristics that govern wave development or dissipation but also upon temporal variability in remote and local wind forcing (Denny and Gaines 1990). While short-term fluctuations in flow-related stress may have little effect on the distributions of sessile organisms such as those found in rocky intertidal zones (Denny et al. 1985), they may nevertheless have important implications for habitat utilization by motile organisms, which can modify their position in response to changing environmental conditions (Menge and Sutherland 1987, Friedlander and Parrish 1998). Accordingly, several works examining the temporal dynamics of fish communities have linked fish abundance, diversity, and assemblage structure with changes in wave height or tidal current speed on hourly or daily scales (Lasiak 1984, Clark et al. 1996, Eggertsen et al. 2016), suggesting that fish do in fact undertake movements in response to temporally varying hydrodynamic conditions.

Although the distributions of motile organisms can be influenced by ambient flow on multiple scales (Denny et al. 2004), few studies have attempted to document directly how spatial and temporal variation in flow-related stress act

together to influence habitat utilization by marine fishes (but see Friedlander and Parrish 1998). Likewise, because of the logistical challenges involved with characterizing incident flow at ecologically-relevant scales, such works rarely quantify hydrodynamic stress in physically-meaningful terms, instead employing categorical classifications or proxies such as wind speed or wave height, which can hinder mechanistic interpretation and limit the transferability of results (Lindgarth and Gamfeldt 2005; Denny and Gaines 2007). Furthermore, most research has focused on adult fishes in topographically complex coral reef habitats, where individuals exploit fine-scale structural refugia or steep bathymetric gradients to mitigate the adversity imposed by high-flow environments (Fulton and Bellwood 2002; Johansen et al. 2008; Eggertsen et al. 2016), likely buffering the observable effects of hydrodynamic stress on distributions.

During their early ontogenetic stages, many species of tropical fish are associated with relatively unstructured shallow littoral habitats (Dahlgren and Marr 2004; Dominici-Arosemena and Wolff 2006). Littoral zone waters are hydrodynamically heterogeneous, subject to flows driven by remote swell, local wind forcing, and tidal fluctuations (Dean and Dalrymple 2004; Lowe et al. 2009), and the depth-limited shorelines that juvenile fishes often exploit as predation refugia (Paterson and Whitfield 2000) can be subject to some of the greatest wave-related stresses (Denny 2006; Webb et al. 2010). Yet, compared to coral reefs, the surf zones, tidal flats, and lagoons that make up much of tropical nearshore systems are characterized by low topographic complexity and homogeneous water depths, providing little in the way of shelter from wave- or current-induced flow. As such, hydrodynamic stress arising due to waves or tides should have substantial implications for patterns of habitat use among juvenile fishes that occupy these waters.

The present study examined the role of flow-related stress, as measured by ambient water velocity, on the distribution of juvenile *Albula vulpes*, an abundant, mobile, and ecologically important inhabitant of shallow nearshore environments. To achieve this, we employed high-resolution hydrodynamic models to estimate spatiotemporal variation in the wave-generated and tidally-driven water velocities experienced across the shallow littoral zones of a subtropical island for an extended period. We then related these factors, in conjunction with other covariates, to observed patterns in the abundance of juvenile *A. vulpes* as determined by beach-seine sampling over the course of roughly one year. Specifically, we evaluated contrasts in the relative abundance of *A. vulpes* juveniles in response to: (1) spatial gradients in long-term mean and maxima of wave-induced water velocities (akin to the traditional interpretation of “wave exposure”); (2) short-term temporal fluctuations in wave-induced water velocities, as reflected by the mean conditions in the 24 h preceding each sampling event; and (3) persistent spatial gradients in tide-induced water velocity.

Methods

Study area

Located on the eastern edge of the Bahamas archipelago, the island of Eleuthera borders the Atlantic Ocean, spanning approximately 120 km from northwest to southeast with an average width of 3 km (Fig. 1). Easterly tradewinds prevail in this region, with a greater northerly component during the dry season (November–April) and southerly component during the wet season (May–October). In the winter and early spring, approaching continental air masses can generate periods of strong westerly and northerly winds (Sealey 2006). The windward coast is characterized by a steep depth gradient and wind-fetch exceeding 6000 km, yielding a wave regime dominated by long-period oceanic swells. In contrast, the leeward coast abuts the shallow Bahamas banks and fetch is largely restricted to less than 200 km, limiting wave development to locally generated wind swell. The waters of the region are microtidal, with a mean tidal range of approximately 1 m and a maximum close to 1.2 m, leading to generally mild inshore tidal currents (Gonzalez and Eberli 1997). Differential

exposure to wind and waves coupled with markedly distinct bathymetry give rise to divergent nearshore habitats on the windward and leeward coasts. With the exception of several sheltered sounds, the windward shore comprises primarily exposed sandy beaches and semi-exposed bays, while shallow flats, mangrove creek systems, and lower energy beaches predominate to leeward.

Study species

Adult *A. vulpes* exploit a mosaic of relatively open, shallow-water habitats including reef crests, lagoons, tidal flats, and mangrove creeks, where they forage primarily on benthic invertebrates, often in large conspecific schools (Colton and Alevizon 1983; Humston et al. 2005; Murchie et al. 2013). Juveniles (< 150 mm fork length (FL)), however, are conspicuously absent from these groups, and although the habitats they occupy are not well described, evidence suggests that juveniles utilize similarly unstructured, shallow, and sparsely vegetated soft-bottom littoral zones, typically within lagoonal environments (Layman and Silliman 2002; Nero and Sealey 2006; Snodgrass et al. 2008). While *A. vulpes* adults can display a high degree of site fidelity, they are also highly mobile, commonly undertaking tide-related movements on the order of several kilometers (Humston et al. 2005; Murchie et al. 2013), and capable of traveling more than 100 km over a period of just a few days in spawning-related migrations (Haley 2009; Danylchuk et al. 2011). Given this mobility and apparent lack of structural association, and furthermore considering that the shallow littoral zones they frequent are susceptible to strong wave-driven currents, *A. vulpes* presents a fine model species for examining the effects of flow on juvenile distributions.

Fish sampling

Twenty-one sites spanning approximately 40 km along the windward and leeward coasts of Eleuthera were selected to represent a broad spectrum of littoral zone habitats characterized by diverse flow regimes. Stratified random sampling was conducted at intervals year-round, between January 2012 and April 2013, encompassing both the wet (May–October) and dry (November–April) seasons. During each sampling period, stations were visited consecutively in random order over the course of roughly 5 d. Unless precluded by logistical considerations, a minimum of three seine hauls representing a range of water depths were carried out at each station.

Sampling was conducted with a 15.2 m × 1.2 m, 3.2 mm mesh bagless beach seine. The seine was set perpendicular to shore, pulled roughly parallel to shore for 20 m, closed, and then hauled out, encompassing a total area of approximately 210 m² per sample. Over the duration of each seine haul, the composition and density of benthic vegetation (primarily *Thalassia testudinum*) was visually assessed, and at the conclusion, the proportional coverage of medium-to-dense benthic vegetation vs. unvegetated or sparsely-vegetated bottom was

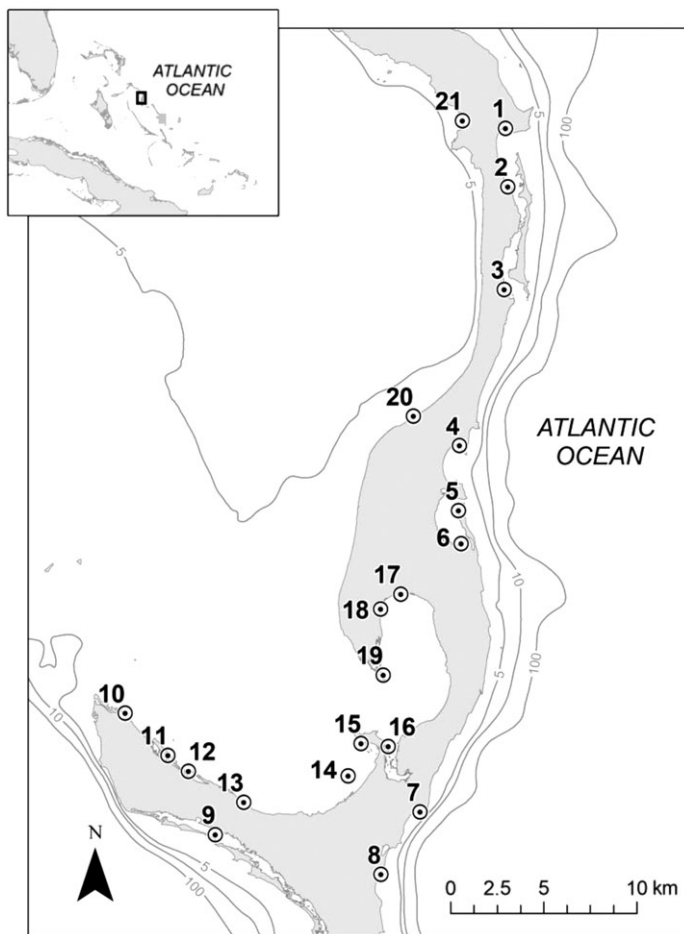


Fig. 1. Map of study area depicting the location of sampling stations. Bathymetric contours reflect water depth in meters.

estimated and recorded. Following Harborne et al. (2008), medium-to-dense vegetation was defined as seagrass standing crop densities corresponding to category 3 or greater on the visual scale described by Mumby et al. (1997). The minimum and maximum depths encountered in each haul were noted, and the approximate geographic centroid of the sampled area was recorded with a handheld global positioning system receiver. Fish specimens captured in each haul were identified to the lowest possible taxon (genus or species) and enumerated before being released. A representative subsample of individuals (up to 30 of each species) were sacrificed and retained on ice for detailed measurements and further analyses, except for large individuals (obviously exceeding 150 mm FL), which were measured on-site and released. All fish sampling for this study was approved by the University of Massachusetts Amherst Institutional Animal Care and Use Committee (protocol 2010-0005).

Hydrodynamic models

Wave- and tide-driven flow characteristics were estimated independently via discrete numerical models to manage computational demands. While this decoupling precluded the evaluation of wave–tide interactions, their omission likely had little influence on estimated hydrodynamic parameters in our study area, where small tidal ranges, mild tide-induced currents, and a generally inverse relationship between the strength of wave- and tide-driven forcing would have limited the strength of such interactions, which furthermore tend to be localized (Davis and Fox 1981). The fine-scale complexity of coastal features in the vicinity of sampling sites required that models were supplied with high-resolution bathymetric and coastline data. Accordingly, water depths in shallow near-shore regions of Eleuthera (< 6 m deep) were derived from multispectral satellite imagery (following Stumpf et al. 2003) at a horizontal resolution of 9.6 m and combined with existing lower resolution bathymetric data for deeper waters to produce a digital elevation model (DEM) of the seabed in the study area. The resulting DEM was subsequently utilized in the generation of meshes for the wave and tide model domains. Production of the bathymetric dataset is described in greater detail in Supporting Information A.

Wave model

The small water depths and incident long-period swell that typify littoral zones within the study area necessitated the consideration of shallow-water processes such as wave shoaling, refraction, and depth-limited breaking, precluding the use of less computationally demanding fetch-based models (Sundblad et al. 2014; Callaghan et al. 2015). Therefore, the properties of wave-driven flow were obtained from a simulated wave field generated with SWAN (Booij et al. 1999), a third-generation phase-averaged numerical wave model, the accuracy of which has been verified in environments characterized by similar fetches, depths, and wave climates (Lowe

et al. 2009; Mariotti and Fagherazzi 2013). To accommodate the large model domain while maintaining the fine spatial resolutions required to resolve these processes accurately, an unstructured grid was employed, ranging in resolution from 15 km at the open boundaries to less than 25 m in coastal zones. Given the large problem size, forward integration of the model over a multiyear period was not a computationally feasible alternative. Instead, a surrogate model was developed, approximating the response surface relating wind or swell forcing with hydrodynamic conditions experienced at each mesh node based on an intelligently reduced set of high-fidelity simulations (Box and Draper 1987; Queipo et al. 2005).

The range of input parameters evaluated by response surface models was determined based on frequency distributions comprising 4 years of meteorological and oceanographic observations from two nearby National Oceanic and Atmospheric Administration (NOAA) National Buoy Data Center (NBDC) stations; station SPGF1 in Grand Bahama (located approximately 300 km northwest of the study area), and Sta. 41047 (approximately 500 km east-northeast of the study area) for wind and swell data, respectively. For the wind-driven model, five wind speeds from 2.5 to 20 m s⁻¹ were evaluated for every 15° of wind angle ($n = 24$ directions), representing a total of 120 input parameter sets. In the case of remote swell, early process studies revealed that due to sheltering by adjacent islands and the northern extent of Eleuthera itself, swells originating from 180–360° and 0–30° (from south clockwise through to north-northeast) did not have a substantive impact on the study area, thus allowing the range of incoming swell directions to be truncated. Accordingly, the swell-driven model incorporated three input parameters; five swell heights (from 0.5 to 4.5 m), each with four dominant periods (from 5.5 to 14.5 s) were evaluated for every 15° of dominant swell direction between 30° and 180° inclusive ($n = 11$ directions), for a total of 220 parameter combinations. Model outputs included significant wave height, peak period, peak bottom period, bottom orbital velocity, and energy flux. Additional details on the wave model, including validation, are available in Supporting Information B.

Tide model

Tidal current velocities were estimated using the open-source software package Finite-Volume Coastal Ocean Model (Chen et al. 2006), on an unstructured mesh similar to that of the wave model but encompassing an altered spatial domain that maintained deep water where the tidal harmonics used to force the simulation were most reliable. The depth-averaged tidal model was forced at the open boundaries with sea surface elevation generated using the nine principal regional tidal harmonics (M_2 , S_2 , N_2 , K_2 , K_1 , O_1 , P_1 , Q_1 , and M_4), the amplitude and phase of which were derived from the TPX08 1/30° tidal atlas (Egbert and Erofeeva 2002). The model was forward integrated for 50 d with a time step of $\Delta t = 0.1$ s, and vertically

averaged velocity components were archived hourly for each model control volume. Flow velocity at a fixed height above the substrate was estimated by reconstructing the inertial sub-layer using the universal logarithmic profile, and the bed stress was extracted from depth-averaged simulations with hydraulic roughness set to a constant value appropriate for the prevailing substrates in the model domain. For further specifics on the production and validation of the tidal model, please see Supporting Information C.

Data analyses

Hydrodynamic predictors

Predictor variables derived from hydrodynamic models included both wave- and tide-driven water velocities, reflecting different distributional characteristics over distinct temporal scales (summarized in Table 1). Maximum bottom orbital velocity, defined as the near-bed wave-induced water velocity parallel to the seafloor in the direction of dominant flow, was selected as an appropriate metric for quantifying hydrodynamic stress associated with waves. This measure provides a widely transferable, physically interpretable representation of the wave-driven water movement experienced by bottom-associated fishes in shallow habitats and has been employed in both field and experimental studies (Fulton and Bellwood 2005; Gabel et al. 2011; Anton et al. 2014). To approximate spatial gradients in wave-related stress integrated over extended timescales (akin to the common interpretation of wave exposure), long-term mean (U_{mean}) and 99th quantile (U_{max}) bottom orbital velocity at each mesh node was estimated by interrogating the wind and swell-driven response surface models with hourly histories of forcing parameters recorded at the respective NOAA NBDC station over a 4 yr time period from 01 January 2010 to 2014, and then calculating the statistics of interest from the resulting distributions. Model outputs were then extracted at the site of each seine haul, taking the greater of wind or swell-forced velocities. Near-maximal (99th quantile) velocity was chosen over the absolute maximum to omit the most anomalous events, limiting consideration to those likely to occur on an annual basis.

To capture temporal variability in remote and local forcing, and resultant short-term fluctuations in flow-related stress, we approximated the wave-induced water velocity experienced at each seine haul location proximal to the moment of sampling. Instantaneous bottom orbital velocity ($U_{\text{inst}24}$) was estimated by interrogating the response surface models with the mean forcing parameters recorded at NBDC stations in the 24 h preceding each sampling event, using the greater of wind and swell-forced outputs. Twenty-four hours was selected as an appropriate temporal window because wave conditions do not develop nor moderate immediately in response to changing winds, but rather on the scale of several hours to days, and remote swell originating from NBDC Sta. 41047 would require many hours to reach the study area (approximately 11 h for the median wave period of 8.5 s). Moreover, we assumed that a substantial time lag is likely to be associated with the relocation of animals in response to environmental change, a conclusion supported by observations of Lasiak (1984) who found that wind speed averaged over a window of 12–48 h was a better predictor of surf-zone fish abundance than that recorded at the moment of sampling. Data exploration revealed that $U_{\text{inst}24}$ was strongly correlated with U_{mean} and U_{max} . Therefore, to preclude potential problems with multicollinearity, $U_{\text{anom}24}$ was defined as the difference between $U_{\text{inst}24}$ and U_{mean} . The resulting variable may be considered a measure of temporal wave anomaly, reflecting the departure from long-term mean conditions at a given location in the 24 h preceding a sampling event, with positive values indicating above-average water velocities.

Because most temporal variation in tide-driven flow occurs on relatively fine and predictable (semidiurnal) scales, we did not evaluate short-term fluctuations in tidal currents, but focused instead on persistent geographic gradients in the strength of tide-driven flow. Hydrodynamic stress generated by tidal exchange (U_{tide}) was quantified using the maximum current velocity associated with the M_2 (principal lunar semidiurnal) tidal component, as this reflects the typical velocities encountered on a day-to-day (6.21 h) basis at any given location (Maxwell et al. 2009). Tidal current velocities were estimated at a height of 5 cm above the substrate, to best reflect

Table 1. Hydrodynamic variable definitions.

| Hydrodynamic variables | |
|------------------------|--|
| U_{mean} | Long-term (~ 4 yr) mean wave-driven bottom orbital velocity; the greater of wind and swell. |
| U_{max} | Long-term (~ 4 yr) near-maximal (99th quantile) wave-driven bottom orbital velocity; the greater of wind and swell. |
| $U_{\text{inst}24}$ | Instantaneous wave-driven bottom orbital velocity at the time of sampling, estimated based on wind and swell conditions averaged over the 24-h period preceding a sampling event; the greater of wind and swell. |
| $U_{\text{anom}24}$ | Wave-driven bottom velocity anomaly, reflecting the instantaneous departure from long-term mean conditions (U_{mean}) at the time of sampling (i.e., $U_{\text{inst}24} - U_{\text{mean}}$) |
| U_{tide} | Maximum tidal flow velocity associated with the M_2 (principal diurnal) tidal constituent, at a height of 5 cm above the seabed, reflecting the typical maximum velocity experienced on diel timescales. |

conditions experienced by bottom-associated fishes such as *A. vulpes* (McMahon and Hartman 1989).

Biotic predictors

In addition to hydrodynamic variables, biotic habitat characteristics recorded at the time of sampling were integrated as predictors to increase model accuracy. Given the previously described benthic habitat associations of *A. vulpes* juveniles (Layman and Silliman 2002; Nero and Sealey 2006; Snodgrass et al. 2008), the proportion of sampled seabed area categorized as having medium-to-dense benthic vegetation coverage (as defined above) was incorporated as a covariate. Likewise, considering the relationship between water depth and relative predation risk in habitats akin to those studied here (Rypel et al. 2007), we included the mean water depth sampled by each seine haul (estimated by averaging the minimum and maximum depths encountered) as an explanatory variable.

Recent works have highlighted the value of taking into account biotic interactions such as competitive or facilitative relationships when modeling species distributions (Guisan and Thuiller 2005, Elith and Leathwick 2009). Using the presence or abundance of an interacting species as a predictor can improve explanatory power, (see Wisz et al. [2013] for a review), provided that its distribution is “unlinked” or independent of the focal species (Anderson 2017). Pilot sampling conducted the year prior to the present work revealed that the relatively infrequent occurrence of *A. vulpes* juveniles coincided almost exclusively with the presence of more commonly occurring mojarras (*Eucinostomus* spp.) of similar size. In remote underwater video surveys undertaken to explore this phenomenon, *A. vulpes* juveniles were observed only in the presence of and commingled within larger shoals of like-sized mojarras, among which they actively foraged. Further details on these findings are available in Supporting Information D.

The close affiliation of *A. vulpes* with eucinostomids parallels a relationship described for *Centropomus* spp., juveniles of which are thought to benefit from increased foraging efficiency and reduced predation risk as a result of associating with eucinostomid shoals (Sazima 2002). Given *A. vulpes*' rarity and nominal relative abundance among the much more numerous and widely distributed *Eucinostomus* spp., it seems likely that while eucinostomids exert a measurable effect on the distribution of *A. vulpes*, the reciprocal effect of *A. vulpes* on *Eucinostomus* spp. is comparatively negligible. Following the reasonable assumption that its relationship with *A. vulpes* was effectively unidirectional (i.e., that the distribution of *A. vulpes* did not have a meaningful influence on that of *Eucinostomus* spp.), the log-transformed abundance of *Eucinostomus* spp. in each seine haul was considered as an additional biotic predictor.

Statistical model

The observed abundance of *A. vulpes* juveniles was related to predictors using a generalized linear mixed modeling (GLMM) framework, employing a negative binomial error

distribution with the NB1 Parameterization (Cameron and Trivedi 1986) and a log link function. To manage model complexity given the relatively sparse nature of the observed abundance data, and furthermore to facilitate interpretation of results, we opted not to consider interaction terms. A random intercept was included for the factor “station” to account for the potential interdependency of observations within sampling locales arising from unmeasured environmental variation. Explanatory variables were inspected for outliers, collinearity, and variance inflation, and continuous predictors were standardized to improve model-fitting stability and interpretability of results. Covariates in the form of count data were log-transformed to reduce residual heterogeneity. The significance of fixed effects was assessed using likelihood ratio tests, and 95% confidence intervals (CI) for fixed effect coefficients were obtained via likelihood profiling. Residuals were inspected for indications of bias and heteroscedasticity and closely examined for any evidence of spatial and/or temporal autocorrelation. Model validation was carried out following methods described in Zuur et al. 2009, and posterior predictive simulations were employed to further assess model fit and to verify that distributional assumptions were met. Analyses were completed in R version 3.4.0 (R Core Team, 2017), employing the package “glmmTMB” (Brooks et al. 2017) and replicated using “glmmADMB” (Fournier et al. 2012; Skaug et al. 2016).

Results

Fish sampling

Between January 2012 and April 2013, 785 seine hauls were conducted across the 21 stations. A total of 205 juvenile *A. vulpes* (verified by genetic analyses) were collected in 57 distinct sampling events (7% of all seine hauls) and ranged from 30 to 149 mm FL with a mean length (\pm SD) of 58 ± 25 mm. When *A. vulpes* were present in seine hauls, their abundance ranged from 1 to 23 individuals, with a mean of $3.6 (\pm 3.8)$. Except for a single individual, *A. vulpes* collections were limited to just six stations (1, 2, 6, 17, 18, and 19), located entirely within three embayments (Fig. 1). Biotic habitat variables associated with each seine haul varied primarily within but also among stations (Supporting Information Table S1). *Eucinostomus* spp. were present in 482 seine hauls (61%), occurring at every station and totaling 33,147 individuals. When eucinostomids were present, there was a mean of $69 (\pm 149)$ individuals per haul, with an average length of $50 (\pm 19)$ mm FL. Eucinostomids occurred in 56 of the 57 seine hauls that contained *A. vulpes* juveniles (> 98%), accounting for 204 of the total 205 *A. vulpes* juveniles collected (> 99%). Conversely, *A. vulpes* were present in fewer than 12% of seine hauls capturing *Eucinostomus* spp. When these taxa co-occurred, *A. vulpes* typically comprised a small fraction of individuals, constituting on average less than 1% of combined total abundance.

Table 2. Minimum, maximum, and mean (± 1 SD) values of environmental predictors across the entire spatiotemporal domain of the present study. Refer to Table 1 for definitions of variables.

| | Min | Max | Mean (± 1 SD) |
|---|-------|------|--------------------|
| U_{mean} (cm s ⁻¹) | 1.1 | 42.6 | 9.5 \pm 7.9 |
| U_{max} (cm s ⁻¹) | 6.7 | 59.7 | 24.9 \pm 8.9 |
| $U_{\text{inst}24}$ (cm s ⁻¹) | 0 | 56.2 | 9.0 \pm 10.2 |
| $U_{\text{anom}24}$ (cm s ⁻¹) | -16.6 | 30.6 | -0.5 \pm 5.9 |
| U_{tide} (cm s ⁻¹) | 0.1 | 28.9 | 3.7 \pm 5 |
| Mean depth (cm) | 8 | 107 | 46 \pm 23 |
| Benthic vegetation (% cover) | 0 | 100 | 25 \pm 39 |
| <i>Eucinostomus</i> spp. (# indivs) | 0 | 1000 | 42 \pm 122 |

Hydrodynamic models

Modeled estimates of wave-induced bottom velocities and tidal current velocities (summarized in Table 2) compared closely with in situ observations recorded by others in similar habitats and water depths (Hine et al. 1981; Fulton and

Bellwood 2005; Eckman et al. 2008). Remotely generated long-period swell dominated the wave regime at windward stations, producing the maximum wave heights and bottom velocities at all but the most sheltered sites, but had little effect on leeward stations, where locally generated wind-waves predominated (Fig. 2). Estimates of long-term mean bottom orbital velocity, U_{mean} , at seine haul locations ranged from 1.1 to 42.6 cm s⁻¹ with a mean (\pm SD) of 9.4 (\pm 7.8) cm s⁻¹, and varied significantly across stations (Kruskal Wallis $\chi^2 = 637.4$, $df = 20$, $p \leq 0.0001$), with the greatest velocities occurring at windward sites exposed to remote swell (e.g., Sta. 4, 7, and 8) and the lowest occurring in tidal creeks or sounds with limited fetch (e.g., 2, 9, 11, 12, and 19) (Supporting Information Table S2). Long-term near-maximal bottom velocity, U_{max} , ranged from 6.7 to 59.8 cm s⁻¹, with a mean of 25.3 (\pm 8.9) cm s⁻¹, and also differed significantly among stations (Kruskal Wallis $\chi^2 = 656.75$, $df = 20$, $p \leq 0.0001$), again with the greatest velocities occurring at windward stations subject to remote swell (e.g., 4, 7 and 8) but also at leeward-side beaches with relatively uninterrupted westward fetch and minimal sheltering by reefs (e.g., 20 and 21) (Fig. 3). The overwhelming

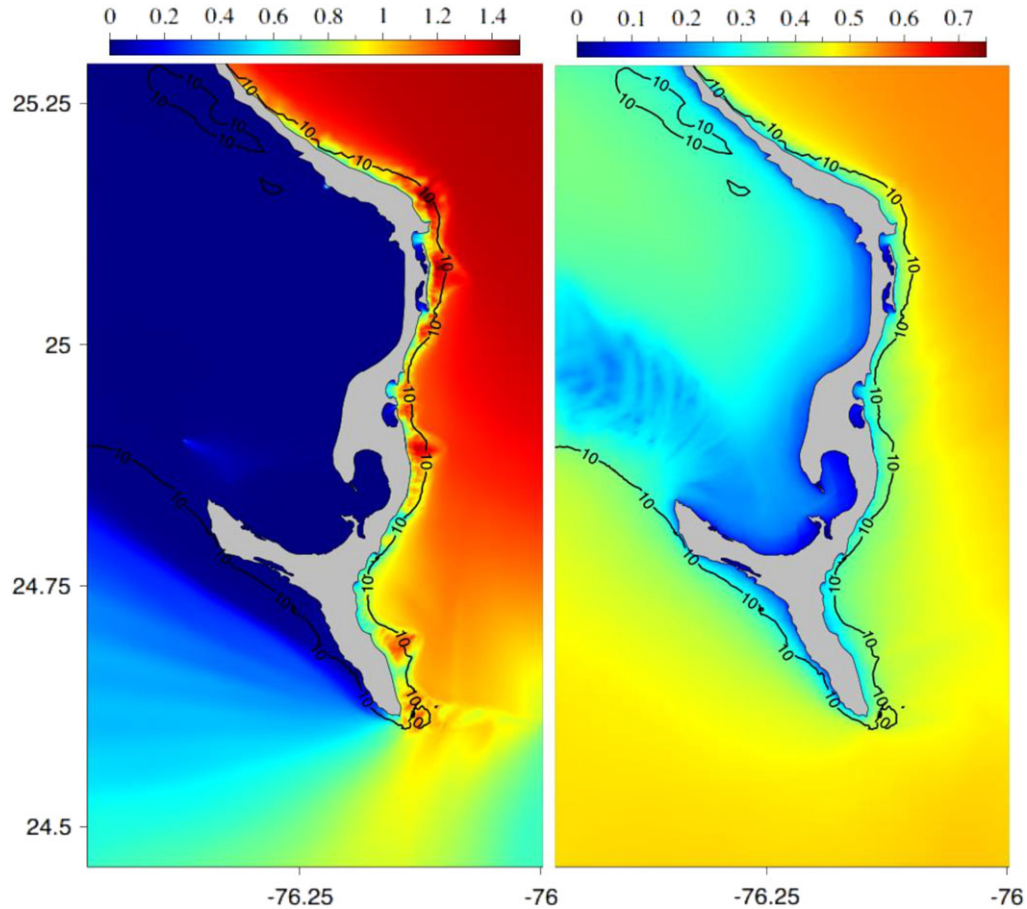


Fig. 2. Mean significant wave heights (in meters) for remote swell (left panel) and wind-driven (right panel) waves within the study area, based on simulated wave fields computed using SWAN. The 10-m isobath is shown for reference. Note the difference in the range of wave height scales depicted in the color gradient ramps.

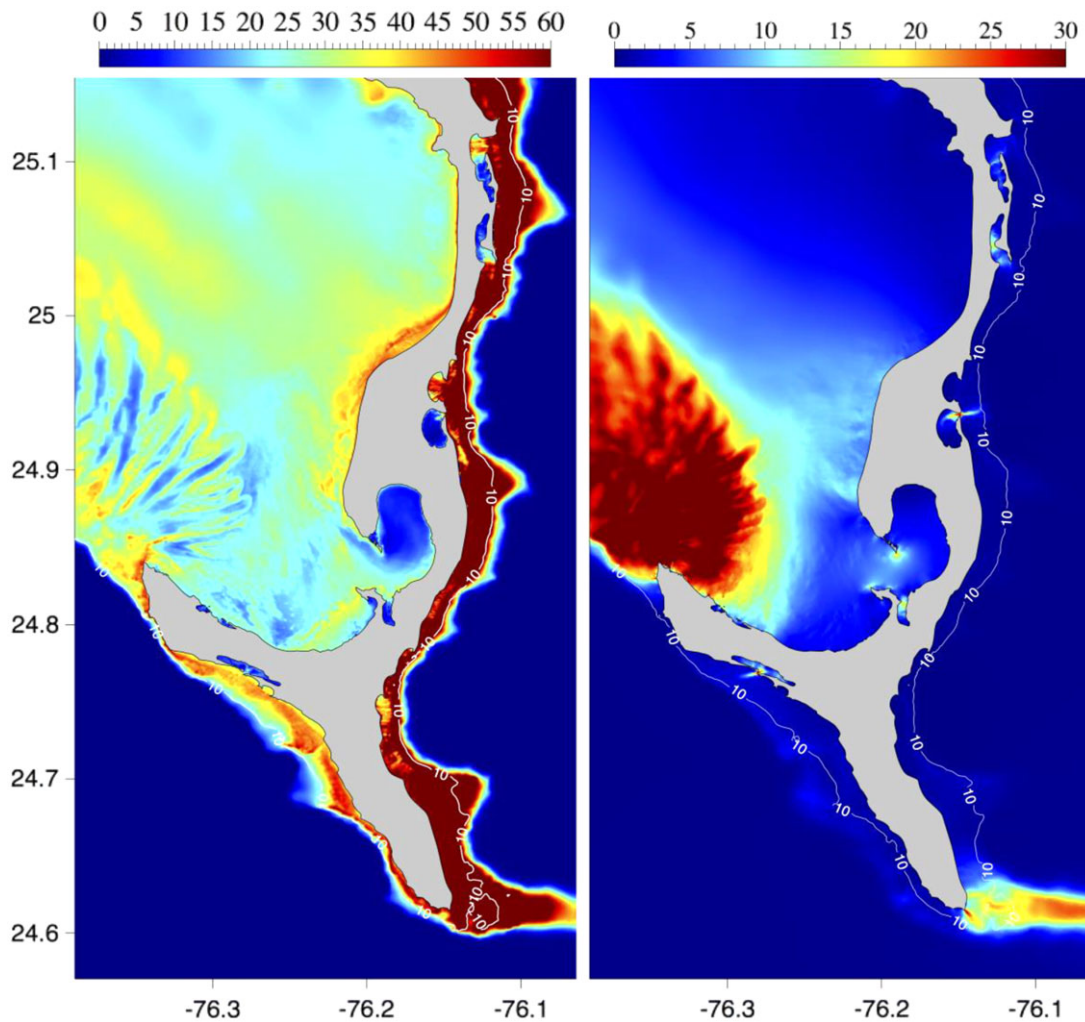


Fig. 3. Near-maximal (99th quantile) wave-induced bottom orbital velocity for wind and swell combined, termed U_{\max} (left panel), and maximum tidal current velocities associated with the M_2 (principal lunar semidiurnal) constituent at a height of 5 cm above the substrate, termed U_{tide} (right panel), as estimated by hydrodynamic models. To better depict variability within areas of interest (i.e., at sampling stations), maximum values depicted by the color gradient ramps have been truncated to 60 and 30 cm s^{-1} for U_{\max} and U_{tide} , respectively. The 10-m isobath is shown for reference.

majority of variation in both U_{mean} and U_{\max} occurred between stations, with comparatively little intra-station variance (Fig. 4). Instantaneous bottom velocity proximal to the time of sampling, $U_{\text{inst}24}$, ranged from 0 to 56.2 cm s^{-1} , with a mean of 8.9 (± 10.2) cm s^{-1} , and varied significantly between stations (Kruskal Wallis $\chi^2 = 440.75$, $\text{df} = 20$, $p \leq 0.0001$), displaying inter-station variability of similar magnitude to U_{\max} . Corresponding instantaneous departures from long-term mean bottom velocity, $U_{\text{anom}24}$, ranged from -16.7 to $+30.6$ cm s^{-1} , with a mean of 0.5 (± 5.9) cm s^{-1} . While significant differences in $U_{\text{anom}24}$ were detected among stations (Kruskal Wallis $\chi^2 = 104.69$, $\text{df} = 20$, $p \leq 0.0001$), the magnitude of these differences was small compared to that of intra-station variability (Fig. 5).

Consistent with the microtidal nature of the study area, estimated tidal currents were generally mild, with maximum

near-bed velocity, U_{tide} , averaging 3.7 (± 4.9) cm s^{-1} . Nonetheless, prominent spatial gradients existed (Fig. 3), with velocities ranging from 0.1 to 28.9 cm s^{-1} . Mean values within stations ranged from effectively zero to upward of 18 cm s^{-1} , with the fastest currents typically occurring at stations proximal to flow obstructions or constrictions such as the mouths of creeks or sounds (e.g., 9 and 10), and near-zero velocities occurring along open shorelines or beaches within protected basins or embayments. The majority of this variation occurred at broad spatial scales, leading to large and significant differences between stations (Kruskal Wallis $\chi^2 = 700$, $\text{df} = 20$, $p \leq 0.0001$) (Fig. 4). In general, persistent gradients in tidal current strength were inversely related to corresponding gradients in the intensity of wave-driven flow (Supporting Information Table S3), with the strongest negative correlation occurring between U_{tide} and U_{\max} (Spearman's rank order correlation, $\rho = -0.387$, $p \leq 0.0001$).

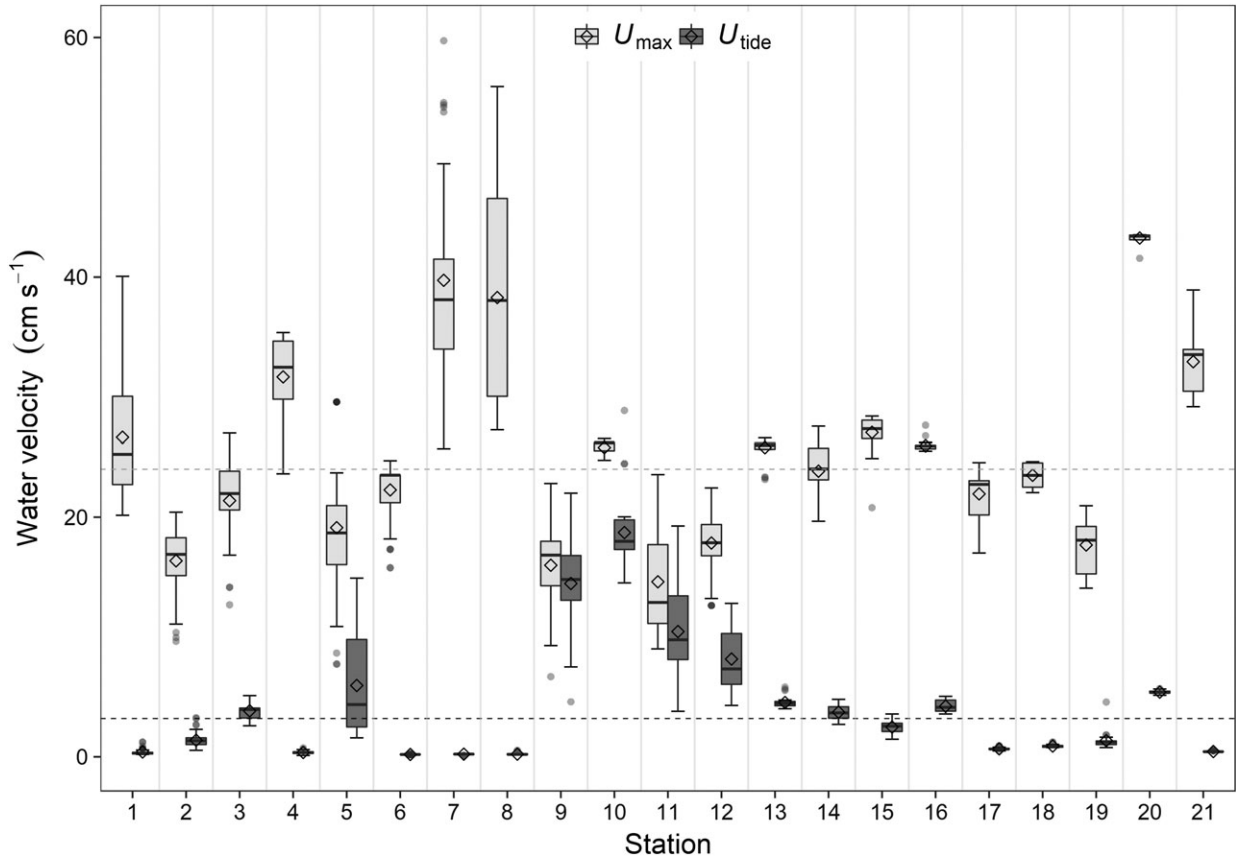


Fig. 4. Boxplots of near-maximum wave-driven (U_{\max} , with light gray fill) and tide-driven (U_{tide} , in dark gray fill) near-bed water velocities at sampling locations, grouped by station. Diamonds indicate means; dots signify outliers.

Relationships between *A. vulpes* and flow

Wave-induced 24-h mean bottom velocities ($U_{\text{inst}24}$) coinciding with *A. vulpes* collections averaged $4.4 (\pm 5.2)$ cm s^{-1} and ranged from 0 to 24.2 cm s^{-1} (Table 3); however, the vast majority (97%) of individuals were collected in samples with $U_{\text{inst}24} < 12 \text{ cm s}^{-1}$. Corresponding 24-h anomalies from long-term mean velocities ($U_{\text{anom}24}$) ranged from -7.4 to 3.3 cm s^{-1} , with a mean of $-1.8 (\pm 2.6) \text{ cm s}^{-1}$; 93% of individuals occurred when departures were no greater than 2 cm s^{-1} above the long-term average at a site. Near-maximal long-term wave-driven water velocities (U_{\max}) estimated at locations where *A. vulpes* occurred ranged from 10.4 up to 30.1 cm s^{-1} , with a mean of $20.5 (\pm 4.1) \text{ cm s}^{-1}$, and 95% of individuals occurred at sites with $U_{\max} < 24.2 \text{ cm s}^{-1}$. Tidally driven flow velocities (U_{tide}) associated with *A. vulpes* occurrences were mild and typically represented a small fraction of corresponding wave-driven velocities at a given location, averaging only $1.1 (\pm 1.3) \text{ cm s}^{-1}$. Except for a single outlying individual, *A. vulpes* juveniles were limited to locations where maximum tidal current velocity (U_{tide}) did not exceed 3.2 cm s^{-1} .

In the reduced GLMM, the abundance of *A. vulpes* juveniles was inversely correlated with both spatial and temporal variation in the strength of wave-driven flow (Table 4). Although

U_{mean} was not significantly linked, both U_{\max} and $U_{\text{anom}24}$ exerted roughly equivalent negative effects on abundance per unit (i.e., cm s^{-1}) increase in flow velocity, evidenced by their similar raw regression coefficients. However, the standardized effect of long-term near-maximal velocity (U_{\max}) on *A. vulpes* abundance was nearly twice that of 24-h departure from long-term mean velocity ($U_{\text{anom}24}$), attributable to the markedly greater variability of U_{\max} . Despite its much lower magnitudes, tidal flow velocity (U_{tide}) exerted a significant negative effect on abundance approximately four times that of an equivalent per unit increase in U_{\max} or $U_{\text{anom}24}$, with a standardized effect comparable to that of both wave-related metrics (U_{\max} and $U_{\text{anom}24}$) combined.

Spatial gradients in long-term wave-induced flow maxima (U_{\max}) were coarse grained, varying at broad scales consistent with the dominant features of coastal geomorphology, consequently driving patterns of abundance at the level of distinct embayments or water bodies (i.e., between stations or groups of adjacent stations). In contrast, as one might expect, temporal departures from long-term mean velocities ($U_{\text{anom}24}$) differed relatively little between stations but exhibited substantial variation within them, influencing abundance at finer spatial scales (i.e., within stations or clusters of stations). Notably,

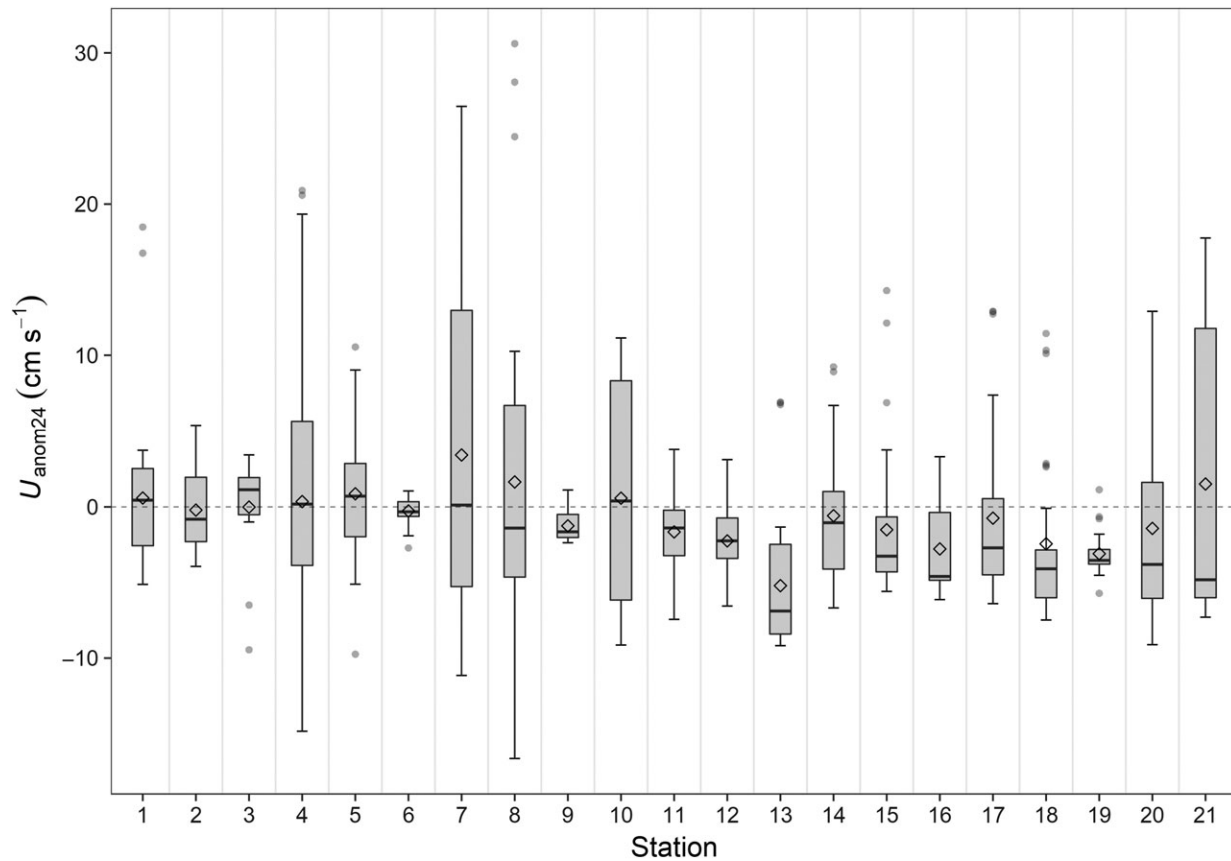


Fig. 5. Boxplot of 24-h wave-driven bottom velocity anomaly (U_{anom24}) estimated to occur at sampling locations, grouped by station. Diamonds indicate means; dots signify outliers.

only 11 stations (2, 3, 5, 6, 9, 11, 12, 14, 17, 18, and 19) were characterized by mean near-maximal wave-induced water velocities (U_{max}) equal to or less than the maximum instantaneous velocity that coincided with the occurrence of *A. vulpes* juveniles over the course of the study period ($U_{inst24} = 24.2 \text{ cm s}^{-1}$). Due to the inverse relationship between the magnitudes of U_{max} and U_{tide} , the spatial constraints placed on *A. vulpes* distributions by fixed gradients in tidal flow were largely at odds with those imposed by wave-driven flow; just 11 stations (1, 2, 4, 6, 7, 8, 15, 17, 18, 19, and 21) experienced mean peak tidal current velocities equal to or below the maximum tidal

current velocity associated with the presence of juvenile *A. vulpes* during the study ($U_{tide} = 3.2 \text{ cm s}^{-1}$, excluding the single, far-outlying individual). Accordingly, when constraints imposed by U_{max} and U_{tide} were considered concurrently just five stations representing the intersection of the two aforementioned subsets (2, 6, 17, 18, and 19) were distinguished by mean long-term hydrodynamic conditions within the above-defined limits. Altogether, these five stations produced more than 93% of *A. vulpes* juveniles collected.

Discussion

Using physical models to resolve spatial gradients and temporal fluctuations in the wave- and tide-induced water velocities likely to be experienced by fishes over broad geographic extents and a prolonged time period, we were able to elucidate, quantitatively, the impacts of distinct flow types on the observed abundance of *A. vulpes* juveniles. Hydrodynamic variables were among the most influential environmental predictors, particularly at the landscape scale (i.e., between embayments) where differences were most consistent and pronounced, exerting universally negative effects on abundance and limiting *A. vulpes* to a small subset of habitats distinguished by depressed rates of flow. The lack of similar negative

Table 3. Range and mean ($\pm 1 \text{ SD}$) of hydrodynamic variables (in cm s^{-1}) for seine haul samples with *A. vulpes* juveniles present. Refer to Table 1 for definitions of variables.

| | Min. | Max. | Mean ($\pm 1 \text{ SD}$) |
|--------------|------|------|-----------------------------|
| U_{mean} | 1.9 | 25.1 | 6.2 ± 4.5 |
| U_{max} | 10.4 | 30.1 | 20.5 ± 4.1 |
| U_{inst24} | 0.0 | 24.2 | 4.4 ± 5.2 |
| U_{anom24} | -7.4 | 3.3 | -1.8 ± 2.6 |
| U_{tide} | 0.2 | 10.3 | 1.1 ± 1.3 |

Table 4. Summary of fixed effects coefficients estimated from the reduced GLMM, relating environmental covariates to the observed abundance of *A. vulpes* juveniles. Ninety-five percent confidence intervals were obtained from likelihood profiles, and *p* values were determined via likelihood ratio tests.

| Predictor variable | Coefficient | | | χ^2 | <i>p</i> |
|--------------------------|-------------------------|-----------------------|----------------|----------|----------------|
| | Estimate (standardized) | 95% CI (standardized) | Estimate (raw) | | |
| (intercept) | -5.16 | -6.5 to -4.08 | -0.23 | — | — |
| U_{\max} | -1.45 | -2.02 to -0.9 | -16.42 | 16.54 | ≤ 0.0001 |
| $U_{\text{anom}24}$ | -0.76 | -1.21 to -0.34 | -13.02 | 13.26 | ≤ 0.001 |
| U_{tide} | -2.85 | -4.65 to -1.55 | -57.48 | 16.9 | ≤ 0.0001 |
| Vegetation cover | 0.54 | -0.97 to -0.18 | -1.37 | 9.13 | ≤ 0.01 |
| <i>Eucinostomus</i> spp. | 1.65 | 1.35 to 1.96 | 0.87 | 98.71 | ≤ 0.00001 |

relationships among juveniles of other demersal fishes collected by the same sampling efforts demonstrates that the inverse correlation between *A. vulpes* abundance and ambient water velocity was not an artifact of declining gear efficiency but rather reflected true decreases in abundance.

Spatial and temporal variation in wave-related environmental stress likely act in concert to control the distribution of many fishes, yet prior to our study these factors were rarely investigated in parallel, nor measured in a consistent and physically meaningful way. By disentangling the effects of persistent geographic gradients and short-term volatility in wave forcing, we showed that incident waves act on multiple, distinct scales to regulate habitat use by *A. vulpes* juveniles. The greater predictive power of U_{\max} as compared to U_{mean} suggests that relatively rare but extreme events may delimit the boundaries of habitats used by *A. vulpes* juveniles at broad scales (i.e., among embayments), a finding consistent with observations by others that maxima are often more relevant than means when relating organismal distributions to wave-induced stresses (Denny and Gaines 1990; Gaines and Denny 1993; Denny et al. 2009). Concurrently, within stations or embayments that were habitable from the perspective of long-term maxima (U_{\max}), the perceived abundance of *A. vulpes* declined in response to momentary increases in wave-driven water velocity, signaling that juveniles undertook fine-scale long-shore or cross-shore movements, presumably seeking reduced flow velocities (Friedlander and Parrish 1998; Layman 2000). Conversely, *A. vulpes* were consistently absent from stations subject to elevated long-term flow maxima regardless of temporal fluctuations, evidencing that fish were unable to exploit these areas even during periods of relative calm.

This multiscale relationship can be explained as a logical outcome for animals with finite mobility. For sessile, site-attached organisms, the hydrodynamic suitability of a given location is effectively static, determined by the likelihood of encountering flow-related stresses that exceed one's tolerances over extended timescales, on the order of a reproductive lifetime or more (Denny et al. 1985; Denny and Gaines 1990; Denny et al. 2004). In contrast, highly mobile organisms can

respond to adverse ambient conditions by seeking more favorable environments, in which case the habitability of a location may be dynamic, a product of flow variability on finer temporal scales (Menge and Sutherland 1987). Most demersal fishes fall somewhere between these extremes, demonstrating mobility but also bounded by varying degrees of site fidelity or home range limitation (Chapman and Kramer 2000; Fetterplace et al. 2016) that constrain the distances they may reasonably relocate in response to time-varying conditions (Friedlander and Parrish 1998). Such limitations on mobility and their consequences for habitat use should be particularly evident in the case of juveniles, whose truncated home ranges (Jones 2005; Nash et al. 2015; Welsh et al. 2013) correlate with the prolonged occupancy of nursery areas before recruitment to adult habitats (Robertson and Duke 1990; Smith and Sinerchia 2004).

Thus, for motile juvenile fishes, the hydrodynamic suitability of a habitat should be a function of both fixed spatial gradients and temporal fluctuations in flow, with the relative importance of these factors, and the respective scales at which they operate, mediated by mobility. At distances that fall within an individual's mobility constraints, habitat use is likely to be driven by short-term temporal variability in flow as fishes move dynamically to locate optimal conditions. Correspondingly, at scales exceeding the distance one can effectively relocate, habitat use should be governed by persistent geographic gradients in ambient flow intensity, as individuals occupy areas where the risk of encountering hydrodynamic extremes is minimized over their residency (i.e., the duration of the juvenile ontogenetic stage). The patterns in the distribution of *A. vulpes* elucidated here were consistent with this expectation, implying that while juveniles may have undertaken movements between stations within embayments (on the order of hundreds of meters to a few kilometers), mobility limitations likely precluded migration beyond the confines of a given embayment.

The influence of cyclical variations in tidal flow on the migratory patterns (Gibson 2003; Bretsch and Allen 2006) and fine-scale-habitat utilization (Auster 1987; Eggertsen et al. 2016) of fishes have been widely examined, but the

implications of persistent spatial gradients in the strength of tidal currents have received relatively little attention (but see Thresher 1983). While some juvenile fishes exploit the predictable oscillations in water velocity associated with tidal exchange (Weihs 1978; Gibson 2003), tidal flows can also inflict energetic costs and limit foraging opportunities, particularly for smaller fishes that do not employ refuging behavior or cannot profit from the enhanced delivery of planktonic prey in moving water (Hobson and Chess 1978; Auster 1987; Eggertsen et al. 2016). Accordingly, the chronic, diel stresses that accompany the occupation of habitats subject to strong tidal flows may lead some fish to avoid such areas altogether. The strong negative relationship we observed between maximum tide-driven water velocity (U_{tide}) and juvenile *A. vulpes* abundance implies that despite its comparatively low magnitude when juxtaposed with wave-driven flow, the costs of negotiating tidal currents may nonetheless present a significant obstacle to habitat utilization by *A. vulpes* juveniles.

Per unit increase in water velocity, spatial gradients in tidally-driven flow (U_{tide}) exerted a much greater negative influence on the abundance of *A. vulpes* than corresponding gradients in wave-driven flow (U_{max}). This apparent discrepancy may be explained by the differing frequency or regularity with which individuals should theoretically experience the conditions reflected by these metrics. In the case of U_{max} , estimated velocities represent only *potential* maxima that fishes are likely to encounter over an extended residency period, and thus there is a substantial component of chance in this metric; for a given individual, velocities approaching U_{max} may never arise, or may occur for only a brief total duration, on the order of hours to days. In contrast, for U_{tide} , this aspect of probability is absent; at any location, tidal flow velocities approaching U_{tide} will occur with certainty on a diel basis, lasting on the order of many minutes to hours at a time. Thus, considered over the entire term that an individual occupies a habitat, the aggregate cost incurred by a given increase in U_{tide} tide may far exceed that of an equivalent change in U_{max} , making locations characterized by even moderate tide-driven flow velocities less sustainable.

Due to the inherently different ways that wave- and tide-induced flows are altered by variation in coastal morphology and bathymetric topography, gradients in wave- and tide-driven water velocity were inversely related across the study area, a phenomenon that had important implications for *A. vulpes* distributions. Gradual depth-shoaling and shoreline constrictions tend to amplify tidal current velocities locally through the effects of continuity, whereas these same topographic characteristics tend to diminish the intensity of wave-driven flow through damping and sheltering (Dean and Dalrymple 2004). In contrast, steeply sloping bathymetric features such as the fringing coral reefs that parallel exposed coastlines can have the opposite effect, intensifying wave-driven forcing at the seabed via wave transformation and breaking yet contributing little to the amplification of tidal

currents. As such, while gradients in long-term wave-induced flow maxima (U_{max}) acted to restrict juveniles to sheltered, enclosed environments, corresponding gradients in tidal flow velocity (U_{tide}) had the opposite effect, limiting *A. vulpes* to more open bodies of water. Together, these contradictory controls excluded juveniles from the dominant fraction of littoral zone habitats in the study area, confining *A. vulpes* juveniles to meso-scale embayments where local geomorphological characteristics served to limit wave exposure without considerably magnifying tidal currents.

Biotic variables appear to have played a limited role in shaping *A. vulpes* distributions at broad spatial scales (i.e., between embayments) where contrasts in abundance were most evident. Both *Eucinostomus* spp. and the sparse vegetation with which *A. vulpes* was associated were common throughout the study area and varied primarily at the intrastation level, reflecting fine-scale spatial patchiness in their distributions. Even so, the strong predictive power of *Eucinostomus* spp. abundance suggests the relationship of *A. vulpes* with this taxon merits further investigation. Notably, *A. vulpes* juveniles were absent from the overwhelming majority (88%) of *Eucinostomus* spp. occurrences, consistent with the results of pilot sampling and indicating that the distribution of eucinostomids was largely independent from that of *A. vulpes*. Furthermore, when both species co-occurred, *A. vulpes* comprised a nominal proportion of total individuals, supporting the assumption that the presence of *A. vulpes* did not exert an ecologically meaningful effect on *Eucinostomus* spp. at the individual level. Collectively, these findings offer strong evidence that the inclusion of *Eucinostomus* spp. count as a covariate was appropriate.

Likely mechanisms behind observed fish-flow relationships

The inverse correlation we detected between the abundance of *A. vulpes* and ambient flow intensity is consistent with relationships documented among juveniles of other bottom-associated fishes (Maxwell et al. 2009; Trimoreau et al. 2013; Druon et al. 2015) and can be attributed to several possible mechanisms through which hydrodynamic stress acts to influence the habitat use of aquatic organisms (Hart and Finelli 1999; Denny 2006; Webb et al. 2010). Most directly, this negative relationship may reflect limitations of *A. vulpes*' swimming performance, a key determinant of the flow environments that fish are able to accommodate (Bellwood and Wainwright 2001; Fulton et al. 2001, 2005). The oscillatory nature of wave-driven flows makes them intrinsically unsteady, and this irregularity is amplified by turbulent eddies associated with wave-breaking in the shallow littoral zones where *A. vulpes* juveniles reside (Webb et al. 2010; Denny 2014). Likewise, in the near-bed depth strata occupied by *A. vulpes*, even relatively unidirectional (e.g., tidal) flows can be complex and turbulent due to benthic boundary layer effects (Hart et al. 1996; Carlson and Lauder 2011; Meyers and Belk 2014). The negotiation of such turbulent or unsteady flows is

inherently tied to maneuverability and stability (Liao 2007; Webb et al. 2010); yet, the streamlined fusiform body, fin arrangement, and dominant body-caudal-fin or subcarangiform swimming mode that characterize *A. vulpes* are traits thought to sacrifice stability and maneuverability (i.e., unsteady swimming performance) in exchange for optimized straight-line cruising efficiency (i.e., steady swimming performance) (Webb 1984; Blake 2004; Langerhans and Reznick 2010). Accordingly, the ability of *A. vulpes* juveniles to efficiently surmount high unsteady water velocities associated with waves or near-bed flows is probably limited.

Considering these limitations, *A. vulpes* juveniles may incur substantial costs when confronted with elevated unsteady flow velocities. Perhaps most acutely, strong wave-driven currents can displace juvenile fishes such as *A. vulpes* from the shallow littoral margins they exploit as predation refugia (Wolter and Arlinghaus 2003; Kucera-Hirzinger et al. 2008; Schludermann et al. 2013), disorienting individuals and placing them at heightened risk of mortality (Paterson and Whitfield 2000; Rypel et al. 2007). Likewise, chronic energetic outlays required to counter the perturbations caused by unsteady flows (Webb 2002; Enders et al. 2003; Roche et al. 2014) may reduce the metabolic resources available to *A. vulpes* for growth, likely translating to diminished survival among juveniles, for whom rapid growth is often critical (Anderson 1988; Sogard 1997). Growth and survival may also be adversely affected by reductions in foraging efficiency brought about by elevated rates of flow (Flore and Keckeis 1998; Schaefer et al. 1999; Gabel et al. 2011) and associated increases in turbidity (Ljunggren and Sandström 2007; Sweka and Hartman 2001; Johansen and Jones 2013), which can be of particular consequence for visually oriented predators like *A. vulpes* (Hannan et al. 2015; Higham et al. 2015; Taylor et al. 2015). Taken together, these immediate and longer-term fitness ramifications may make the occupancy of wave or current-swept environments untenable.

By quantifying hydrodynamic stresses in physically meaningful terms (i.e., water velocities), we were able to evaluate them within the context of animal performance (i.e., swimming speeds), permitting a degree of biomechanical inference regarding the mechanisms through which distinct flow types acted to influence habitat utilization by *A. vulpes* juveniles. Critical speed (U_{crit}) is a measure of swimming performance that reflects the ability of fishes to negotiate flow (Brett 1964; Plaut 2001) and has thus been adopted to predict the “critical” water velocities likely to displace juvenile fishes from shallow littoral zone habitats (Wolter and Arlinghaus 2003; Wolter et al. 2004; Kucera-Hirzinger et al. 2008). Among small juveniles, U_{crit} is closely related to body length and varies little across species sharing similar morphologies and swimming modes (Brett 1964; Flore and Keckeis 1998; Wolter and Arlinghaus 2003). As adults, *A. vulpes* achieve high critical speeds comparable to those of like-sized rheophilic salmonids (Nowell et al. 2015), with whom they share a similar fusiform

morphology and subcarangiform mode of propulsion. Assuming that the performance of juvenile *A. vulpes* is likewise comparable, a reasonable approximation of U_{crit} for individuals of the mean size captured here (58 mm FL) would fall in the vicinity of 40 cm s^{-1} (Brett and Glass 1973; Flore and Keckeis 1998; Wolter and Arlinghaus 2003).

Considered in the context of likely swimming performance, the mean instantaneous wave-driven water velocity associated with *A. vulpes* occurrence ($U_{inst24} = 4.4 \text{ cm s}^{-1}$) seems negligible, representing a small fraction of critical speed. However, if limitations on mobility make habitat suitability a function of hydrodynamic extremes likely to be experienced over an extended period, long-term near-maximal wave-driven velocity (U_{max}) should provide a more meaningful point of comparison. In this case, the mean and maximum U_{max} coinciding with *A. vulpes* occurrences (20.5 and 30.1 cm s^{-1} , respectively) correspond much more closely with predicted swimming performance, particularly when one considers the reduction of U_{crit} in unsteady or turbulent flows such as those associated with waves (Pavlov et al. 2000; Lupandin 2005). It is also noteworthy that the maximum U_{inst24} associated with the presence of *A. vulpes* (24.2 cm s^{-1}) correlated well with these values. Collectively, these observations appear to support the hypothesis that broad-scale distributional constraints are set largely by the probability of confronting acute hydrodynamic stresses produced by infrequent but extreme events. Conversely, declines in the abundance of *A. vulpes* in response to comparatively minor increases in U_{tide} and U_{anom24} (relative to U_{crit}) may signal that more chronic flow-related stresses, such as increased energetic costs or diminishing foraging efficiency, may be the principal drivers of observed negative relationships with these variables.

Incident flow may also have acted in more circuitous manners to regulate the distribution of *A. vulpes* via its effects on other organisms or the broader benthic environment. Spatio-temporal variability in wave-driven flow can have implications for the distribution and behavior of benthic invertebrates (Fenwick 1976; Bishop 2008; Gabel et al. 2008), potentially modulating the availability of *A. vulpes*' prey and consequently the value of distinct flow environments as foraging grounds. Less directly, ambient flow may have affected *A. vulpes* abundance through its role in defining basic characteristics of benthic habitats, such as the distribution of vegetation or sediments, which can affect utilization by fishes and invertebrates through a variety of mechanisms (Snelgrove and Butman 1994; Boström et al. 2006; Santin and Willis 2007).

Alternatively, environmental factors causally unrelated to flow, but nonetheless characteristic of high-flow habitats, may have acted to exaggerate the perceived negative relationship between hydrodynamic variables and *A. vulpes* abundance. For example, stations situated in mangrove creek systems (which consistently exhibited high tidal current velocities) were typified by expansive shallow intertidal zones that dried during

low tide, leaving only small channelized regions submersed throughout the tidal cycle. Thus, to remain in the shallow littoral margins they appeared to prefer, *A. vulpes* juveniles would be required to undertake substantial horizontal migrations, often on the order of hundreds of meters to kilometers, several times a day, constituting a considerable energetic burden which may ultimately reduce the utility of creek habitats. Moreover, the drastic reduction in wetted area during low tide would likely serve to concentrate nekton, leading to increased encounter rates with the predatory piscivores that are abundant in tidal creeks (Rypel et al. 2007; Murchie et al. 2015; Harborne et al. 2016) further inflating the costs of occupying these systems.

Conclusion

Broadly, this work demonstrates the fundamental yet often disregarded importance of ambient flow, or an individual's "hydrodynamic niche" in shaping habitat use by juvenile fish in coastal marine environments, mirroring observations in lotic freshwater habitats. The simultaneous consideration of stress associated with both wave and tide-driven water movement revealed that distinct flow types, and the divergent ways they are altered by coastal morphology, can act to magnify the restrictions placed on habitat utilization by hydrodynamic constraints. Furthermore, by evaluating gradients in flow over an extended spatiotemporal domain and at distinct scales, we were able to elucidate relationships that would not have been detectable using in situ observations acquired at the times of sampling, providing insights on the likely role of mobility in mediating the relationship between water movement and habitat use. Moreover, by defining flow-related stresses explicitly and in physically relevant terms, we were able to place them within the context of organismal performance, permitting additional inferences about the mechanisms underlying observed fish-flow relationships.

From the perspective of conservation, our findings indicate that low-flow habitats are a fundamental ecological requirement of *A. vulpes* juveniles, and may, given the apparent rarity of hydrodynamically-compatible environments within our study area, constitute a critical limiting factor for the replenishment of this economically valuable species. The seemingly low probability of long-distance (i.e., inter-embayment) migration by post-settlement juveniles, and their sporadic, isolated occurrence in higher-flow habitats suggest that observed distributions may reflect the results of differential post-settlement mortality. However, similar distributional patterns noted among settlement-stage *A. vulpes* larvae over the course of this study imply that habitat selection during settlement may also have played a role in determining distributions. The results of this research can be easily extended to predict suitable habitats for *A. vulpes* juveniles in other domains where appropriate hydrodynamic data is available.

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Conflict of Interest

None declared.

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