Coral Reefs (2009) 28:461–473
DOI 10.1007/s00338-009-0481-0

REPORT

# Water flow controls distribution and feeding behavior of two co-occurring coral reef fishes: I. Field measurements

**C. M. Finelli · R. D. Clarke · H. E. Robinson ·**
**E. J. Buskey**

Received: 1 August 2008 / Accepted: 7 February 2009 / Published online: 3 March 2009

**Abstract** The interaction of flowing water with reef topography creates a continuum of flow microhabitats that can alter species distributions directly via transport of organisms or propagules, or indirectly by modulating the availability of critical resources. To examine how water flow affects the distribution and feeding performance of two species of planktivorous tube blennies (Chaenopsidae), flow speed and turbulence were measured within the feeding areas of *Acanthemblemaria spinosa* and *A. aspera* at three sites within Glover's Reef, Belize. Although co-occurring, *A. spinosa* occupies topographically high locations (e.g., upright coral skeletons) while *A. aspera* occupies topographically low shelters in the coral pavement. Boundary layer theory predicts that *A. spinosa* should experience higher flow (and a higher flux of planktonic food) relative to *A. aspera*; however, complex topography and oscillatory flow require that this prediction is tested directly in the field. Within each site, the flow experienced by *A. spinosa* was, indeed, faster and more turbulent than that experienced by *A. aspera* at site-specific intermediate wave heights. When waves were small, gentle velocity gradients produced similar flows for the two species. When waves were high, flow was uniformly fast through the water column due to thinning of the benthic boundary layer. Plankton availability was similar for the species, with the exception of a greater abundance of harpacticoid copepods at the shelters of *A. aspera*. Quantitative behavioral observations suggest that the foraging strategies employed by the two fishes exploit the prevailing hydrodynamic conditions. For example, *A. spinosa*, the stronger swimmer of the two, attacks nearly 100% of the time in the water column where it can exploit the higher flux of plankton associated with faster flows, while *A. aspera* attacks primarily toward the reef surface where currents are likely to be slower and it can exploit more abundant benthic prey.

**Keywords** Chaenopsidae · Hydrodynamics · Coral reef · Feeding · Zooplankton · Planktivory

## Introduction

Planktivory and other forms of suspension feeding on coral reefs may represent an important subsidy of carbon in oligotrophic waters (Glynn 1973; Yahel et al. 1998, 2005; Genin et al. 2002; Heidelberg et al. 2004). While a majority of planktivorous fishes forage above the ocean floor where plankton is often concentrated (Hamner et al. 1988; Hobson 1991; Clarke 1992; Yahel et al. 2005), many reef suspension feeders, including various cnidarians, echinoderms, and fishes, are benthic and sessile (or nearly so) and

---

Communicated by Biology Editor Dr. Mark McCormick

C. M. Finelli (✉)
Department of Biology and Marine Biology, University of North Carolina Wilmington (UNCW), 601 S. College Rd., UNCW, Wilmington, NC 28403, USA
e-mail: finellic@uncw.edu

R. D. Clarke
Department of Biology, Sarah Lawrence College, Bronxville, NY, USA

H. E. Robinson · E. J. Buskey
University of Texas Marine Science Institute, Port Aransas, TX, USA

*Present Address:*
H. E. Robinson
Department of Integrative Biology, University of California, Berkeley, Berkeley, CA 94720-3140, USA

are subject to complex boundary layer flows (e.g., Shashar et al. 1996; Sebens et al. 1998; Madin et al. 2006). The importance of such benthic suspension feeders in controlling both phytoplankton and zooplankton biomass over the reef has recently been highlighted in several field studies (Yahel et al. 1998, 2005; Genin et al. 2002; Heidelberg et al. 2004; Motro et al. 2005).

Tube blennies of the family Chaenopsidae are abundant, if inconspicuous, planktivores inhabiting live coral and coral rubble in the eastern Pacific and Western Atlantic. Two Caribbean species, the spinyhead blenny (*Acanthemblemaria spinosa*) and the roughhead blenny (*A. aspera*), co-occur on shallow forereefs with an abundance of erect corals (especially *Acropora palmata*), where they occupy cavities in the skeletons of dead and living colonies (Smith-Vaniz and Palacio 1974; Clarke 1989, 1994). Spinyheads occur at higher locations in the corals and roughheads occur at lower locations near the substrate (Clarke 1989, 1994, 1996). Manipulative experiments suggest that the higher positions are preferred. For example, when placed in single-species groups in artificial substrates, both species distribute themselves with greatest density in the highest locations. In two-species groups, however, the spinyheads occupy the highest locations and the roughheads occupy the lowest, the same pattern as in nature (Clarke 1989). Moreover, removal experiments show that spinyhead shelters are reoccupied at higher rates (Clarke 1989).

The spatial distribution of these two species may influence their diet, feeding activity, and life histories. For example, spinyheads have a diet consisting primarily of planktonic copepods, while roughheads have a mixed diet of planktonic and benthic copepods (Clarke 1999). Moreover, when placed on artificial habitats, both species make more frequent feeding darts, have higher growth rates, and have higher fecundities at 1 m above the reef surface as compared with 0.15 m (Clarke 1992). This difference could be the result of small-scale variation in plankton density between high and low shelters (Hamner and Carleton 1979; Forrester 1991; Clarke 1999). Clarke (1999) found that during the day (i.e., when blennies feed) planktonic calanoid copepods were more abundant 1–1.5 m above the reef surface than 0–0.5 m above the reef surface, presumably increasing feeding opportunities for fishes occupying higher locations. Thus, vertical gradients in the availability of planktonic prey correspond with the observed diet for these species; primarily planktonic for *Acanthemblemaria spinosa* and mixed planktonic and epibenthic forms for *A. aspera* (Clarke 1999).

In conjunction with differential prey availability, the patterns of growth and fecundity noted for *A. aspera* and *A. spinosa* may also result from hydrodynamic conditions at higher locations that result in a greater flux of planktonic food or that enhance the ability of the fishes to capture prey. For example, Clarke et al. (2005) showed that, in the laboratory, turbulence enhances the feeding success of both *A. aspera* and *A. spinosa* over still water when feeding on evasive prey (i.e., calanoid copepods). In contrast, turbulence decreased feeding success when the prey was non-evasive (e.g., brine shrimp nauplii). Moreover, *A. aspera* modulated its attack depending on flow conditions, whereas *A. spinosa* did not. More recent flume studies have also demonstrated that increasing mean flow or turbulence increased the vulnerability of planktonic prey to predation (Robinson et al. 2007). These results suggest that feeding success may be determined through an interaction between shelter location, flow, feeding strategies, and prey escape responses.

The complex patterns of water flow over the reef have been considered an important factor in the distribution of a variety of mobile reef fishes (Bellwood and Wainwright 2001; Depczynski and Bellwood 2005). While such studies implicate the importance of swimming ability (e.g., Fulton et al. 2005), swimming mode (e.g., Fulton and Bellwood 2005), and use of refugia (e.g., Johansen et al. 2008) relative to water flow in determining habitat use, water flow may also structure fish communities via effects on feeding performance of planktivores. For example, boundary layer theory suggests that water flow (mean and turbulence) should be greater for *A. spinosa* than for *A. aspera* due to their relative position within the benthic boundary layer (BBL; Vogel 1994; Shashar et al. 1996). These conditions should favor topographically high locations inhabited by *A. spinosa* due to higher flux of prey and increased feeding performance (e.g., Clarke 1999, Clarke et al. 2005, Robinson et al. 2007). However, complex reef topography and oscillatory flow on the reef require that measurements are made directly at the location of planktivore feeding to determine the role of water flow in structuring these communities. The present study examines the prediction that *A. spinosa* experiences higher water flow than *A. aspera* and investigates the hypothesis that the distribution and feeding behavior of these species are associated with prevailing hydrodynamic conditions.

## Methods

### Field site

Studies were conducted at Glover's Reef, a 260-km$^2$ atoll 30 km east of the Mesoamerican Barrier Reef in Belize. The east side of the atoll is fully exposed to the open Caribbean Sea and is subject to the maximum wave force in the region (Gischler and Hudson 1998), while the remainder of the reef is generally less energetic. Three field sites were used and chosen due to the presence of both focal species in high abundance (Fig. 1). The SE site (Fig. 1) was situated in the spur and groove zone of the forereef near the southeastern corner of the atoll (16°45.697′ N, 87°45.821′ W). This site was exposed to the full force of ocean waves and was characterized by sand channels that were 9–12.5 m deep with spurs rising to 6–7 m deep. The NW site (Fig. 1) was a spur and groove reef at the northwest corner of the atoll (16°55.513′ N, 87°47.325′ W). This site was similar in topography to the SE site except that it was sheltered with respect to the strongest wave conditions (Fig. 1). The distance of the NW site from the research station on Middle Caye limited its usefulness. Therefore, this site was used when rough conditions precluded working at the SE site and it was not used for video observations or plankton sampling. The Patch Reef site (Fig. 1) was a small reef in the channel separating Long Caye from Northeast Caye (16°45.590′ N, 87°46.520′ W). This site was generally less energetic than either of the other sites, although it was exposed to waves entering through the channel.

## Point measurements of flow at the blenny shelter

To test the hypothesis that flow within the feeding zones of the two fish species differed, currents were measured using a Sontek acoustic Doppler velocimeter (ADV; Sontek/YSI, 16 MHz MicroADV). Individual fish were identified on the reef and the location of the shelter (bottom depth and height above the bottom) was measured. Because these fishes are so closely tied to their shelters, the shelter location is identical to the location of the fish.

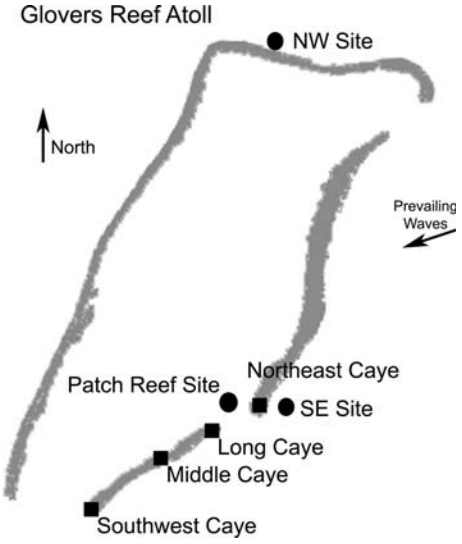

**Fig. 1** Map of Glovers Reef Atoll (Belize, Central America) showing the locations of the reef crest (*gray-shaded area*), islands (■), and the three research sites (●). Direction of prevailing winds as described in Gischler and Hudson (1998)

The ADV probe was positioned over the fish such that the sample volume was centered ~3.8 cm directly above the blenny shelter. Once the probe was in-place, blennies did not exit their shelters, thereby minimizing any contamination of the velocity record. For each measurement, the ADV probe was rigidly attached to a frame composed of 6 mm diameter stainless steel rods that was held in place on the coral using elastic shock cord. Care was taken so that no frame member was directly upstream or downstream from the sample volume. Each measurement lasted 120 s during which data were collected at 10 Hz.

Data were post-processed to ensure proper orientation of the probe relative to mainstream flow. First, the coordinate frame was rotated both horizontally and vertically to align flow measurements with prevailing flow conditions (Roy et al. 1996). Flow speed was estimated as $\sqrt{u^2 + v^2 + w^2}$, where $u$, $v$, and $w$ are, respectively, the downstream, cross-stream, and vertical components of velocity. Flow speed accounts for both the oscillatory nature of flow on the reef and for energy that is in both horizontal and vertical planes. For comparison to flume studies that used $U_{\mathrm{rms}}$ (the root mean square of downstream velocity) to describe oscillatory flow (Clarke et al. 2009), mean flow speeds measured in the field were within 6% of $U_{\mathrm{rms}}$ measured for the same time series. To derive turbulence statistics, each time series was subjected to a zero-phase displacement moving average (Matlab Filtfilt function) to estimate the mean component of the flow. The instantaneous values were then subtracted from the mean to estimate the deviations in all three dimensions. Turbulence was then approximated as the turbulent kinetic energy (TKE) according to the relation $\mathrm{TKE} = 0.5(\overline{u'u'} + \overline{v'v'} + \overline{w'w'})$, where $u'$, $v'$, and $w'$ are the instantaneous deviations from the mean of the three velocity components, and the overbar indicates temporal averaging. Significant wave height ($H_s$) was estimated from the time series of pressure measurements made simultaneously with velocity using the ADV. $H_s$ was corrected for depth attenuation using linear wave theory (Denny 1988).

Habitat characteristics (bottom depth, $H_s$, and shelter height above the bottom) were compared between the two species and three sites using a two-way analysis of variance. This test indicated significant differences between species and sites, which were then probed further with separate one-way analyses of variance with either species or site as the class variable. Because it was expected that *A. spinosa* would experience faster, more turbulent flow than *A. aspera* and it was hypothesized that these differences would vary non-linearly with wave height, the data were divided into wave height bins of 0.2 m and a one-way ANOVA was performed to test for differences in flow speed and TKE between species (one-tailed hypothesis). All data were tested for normality and homogeneity of variance; only TKE estimates showed significant departure from normality and were, therefore, log-transformed before analysis (Zar 1984).

### Reef-scale measurements of water flow

The point measurements described above were made with fine spatial ($<1$ cm$^3$) and fast temporal (10 Hz) resolution at multiple blenny shelters. To provide an estimate of flow conditions over broader temporal and spatial scales, ambient currents were measured using a small acoustic Doppler profiler (ADP, Nortek 2 MHz Aquadopp) placed on the seafloor adjacent to the sampling sites. At the SE and NW sites, the profiler was located in a sand channel adjacent to the spurs on which the ADV measurements were made; while at the Patch Reef site, the profiler was located on the sandy seafloor approximately 15 m from the reef. The choice of profiler locations was made to avoid interference from upstream or downstream obstructions or from divers working in the area. Estimates of currents at 0.2 m intervals from 0.4 to 4 m above the bottom were made at 1 Hz during each dive.

Profiler data was post-processed by parsing the raw data into 1,024 sample (17.07 min) segments. For each segment, a mean flow speed (see above) was calculated at 0.4, 1.0, 2.0, 3.0, and 4.0 m above the seafloor. In addition, significant wave height ($H_s$) was estimated and corrected for depth attenuation according to linear wave theory (Denny 1988). Because the relative magnitude of flow at various positions in the water column was of interest, each mean flow speed was normalized at 1.0, 2.0, 3.0, and 4.0 m by flow speed at 0.4 m, thus producing a ratio describing the relative changes in speed regardless of the absolute values. For consistency with point measurements of flow in tube blenny feeding volumes, the data were subdivided into wave height bins of 0.2 m and mean ratios calculated for each bin. The frequency distribution of wave heights was calculated for each site from these records.

### Field video observations

To test the association between feeding behavior and water flow, video observations of blennies were conducted at the SE and Patch Reef sites. Hydrodynamic conditions at these two sites bracketed the full range experienced by these species on Glovers Reef. The distance of the NW site from the research station on Middle Caye prevented video observations from being conducted there. Individual blennies were videotaped in situ using one of two video camcorders (Sony DCR-TRV520 or Sony CCD-TR3300) in underwater housings. The cameras were held on tripods and were left unattended to record for 12–70 min. In all cases, the placement of the camera resulted in a lateral (sagittal) view of the fish so that attacks by fish on plankton were clearly seen as rapid extensions out of the shelter. After filming in the field, videotapes were screened to determine the attack rate (number per min) and the direction of attack (toward the water column or toward the reef surface). Every attack was then digitized (Director's Cut, Miglia Technology), and the maximum distance from the shelter opening traveled by the fish was measured using video analysis software (Tracker v1.3, Open Source Physics). Thus, for each observed fish, three data points were collected: the rate of attack, percentage of attacks toward the water column or reef surface, and the maximum extended distance. These data were analyzed using two-way analysis of variance with species and site as class variables. Ambient currents were monitored during video observations using the bottom-mounted Nortek Aquadopp current profiler as described above; however, no point measurements of velocity were made at the shelters during taping, because placing the ADV probe over the shelter would result in abnormal behavior of the fish.

### Plankton sampling

To determine if food availability differed for the two species, a submersible plankton pump was used to sample plankton at blenny shelters within the SE and Patch Reef sites. The distance of the NW site from the research station on Middle Caye prevented these experiments from being conducted there. The pump design was based on the one used by Sebens and colleagues (Sebens et al. 1992; Heidelberg et al. 2004) and consisted of a 0.1-m diameter × 0.8-m long conical plankton net with 105-μm mesh suspended within a 10.2-cm diameter clear acrylic pipe. Water was drawn through the net by a battery powered bilge pump (Rule 1500 GPH) mounted downstream of the net such that plankton were caught in the net prior to reaching the pump impeller. To collect plankton from blenny shelters, a 2.5-cm internal diameter vinyl hose was fixed to the entry of the net chamber; the free end of this tube was rigidly attached to the coral head so that the tube opening was normal to the coral surface and sampled from the coral surface to 2.5 cm above the surface. The pump was calibrated immediately before and after each deployment by measuring the amount of time needed to pump a known volume of water. Live samples were fixed in formalin for several days, then rinsed with freshwater, and transferred to Lugols iodine solution prior to transport to the University of Texas Marine Science Institute where plankton were counted and identified to lowest possible taxa.

## Results

### Distribution of fishes

Flow was measured within the feeding volumes of 163 individual fishes. Roughly equal numbers of each species were sampled at the three sites, although approximately one-third fewer total fish were sampled at the Patch Reef site than at either of the forereef sites (Table 1). The distribution of fishes was markedly different within and between sites. Two-way analysis of variance revealed significant effects of both species and site (but not their interaction) on shelter heights above the bottom (overall ANOVA: $F_{5,157} = 18.26$, $P < 0.001$; species effect $F_{1,157} = 75.36$, $P < 0.001$; site effect $F_{2,157} = 5.25$, $P = 0.006$; interaction $F_{2,157} = 0.05$, $P = 0.95$). Separate one-way analyses of variance were conducted to further probe these differences. At each site, shelters inhabited by *A. spinosa* were two to four times higher than those inhabited by *A. aspera* (Table 1; ANOVA: $P < 0.001$ for each site). Shelter heights for *A. spinosa* were equal ($\sim$1 m) at all three sites (Table 1; ANOVA: $F_{2,82} = 1.64$, $P = 0.20$). In contrast, *A. aspera* at the Patch Reef site occupied shelters that were significantly higher (0.5 vs. 0.25 m) than those at either the NW or SE sites (Table 1; ANOVA with Tukey's pairwise comparisons: $F_{2,75} = 7.14$, $P = 0.002$). Finally, the hypothesis that fish were evenly distributed with regard to depth was tested. Two-way analysis of variance showed significant differences in bottom depth among both species and sites (overall ANOVA: $F_{5,157} = 155.59$, $P < 0.001$; species effect $F_{1,157} = 60.09$, $P < 0.001$; site effect $F_{2,157} = 353.55$, $P = 0.006$; interaction $F_{2,157} = 0.46$, $P = 0.63$). Tukey's pairwise comparisons showed the bottom depths at the Patch Reef site were shallower than at either the NW or SE sites, which did not differ (Table 1). Within each site, *A. aspera* occupied shelters where the bottom was about 1 m deeper than where *A. spinosa* resided (Table 1). This result was confirmed for all three sites using separate one-way ANOVAs for each site (Patch Reef $F_{1,36} = 21.14$, $P < 0.001$; NW $F_{1,60} = 32.23$, $P < 0.001$; SE $F_{1,61} = 17.52$, $P < 0.001$). The combination of height above the bed and bottom depth resulted in a pattern of fish shelter depths shown in Table 1.

### Significant wave height ($H_s$)

Significant wave heights ($H_s$) during point measurement of flow within tube blenny feeding volumes varied predictably with site. Two-way analysis of variance testing differences in $H_s$ among sites and species showed a significant site effect, but no significant species effect or interaction (overall ANOVA: $F_{5,157} = 20.11$, $P < 0.001$; species effect $F_{1,157} = 0.11$, $P = 0.074$; site effect $F_{2,157} = 49.34$, $P < 0.001$; interaction $F_{2,157} = 0.43$, $P = 0.65$). Tukey's pairwise comparisons showed that $H_s$ was lowest at the Patch Reef site, intermediate at the NW site, and highest at the SE site (Table 1).

### Point measurements of flow at the blenny shelter

The general trend at each site was for *A. spinosa* to experience faster (Fig. 2) and more turbulent (Fig. 3) flow over a wide range of wave conditions; however, statistically significant differences in mean flow speed and TKE were detected at site-specific intermediate wave heights. At the Patch Reef site where $H_s$ did not exceed 0.6 m, there was a significant difference ($F_{1,12} = 3.76$, $P < 0.05$) in mean flow speed when $H_s$ was between 0.2 and 0.4 m but not when $H_s$ was >0.4 (Fig. 2). There were no significant differences in TKE at any wave heights for the Patch Reef site (Fig. 3). At the NW site, *A. spinosa* experienced higher mean flow speed than *A. aspera* when $H_s$ was between 0.8 and 1.0 m (Fig. 2; $F_{1,18} = 12.02$, $P < 0.05$). For wave heights centered at 0.7 and 1.1 m, significant differences

**Table 1** Location and wave conditions at each field site for the two focal species (mean ± SD)

| Site | Species | *N* | Fish height above bottom (m) | Bottom depth (m) | Fish depth (m) | Significant wave height (m) |
|---|---|---|---|---|---|---|
| Patch Reef | *A. aspera* | 18 | $0.51 \pm 0.31^{a,A}$ | $4.95 \pm 0.64^{a,A}$ | $4.44 \pm 0.83^{a,A}$ | $0.46 \pm 0.15^{a,A}$ |
| | *A. spinosa* | 20 | $1.14 \pm 0.64^{b,A}$ | $3.96 \pm 0.67^{b,A}$ | $2.83 \pm 1.07^{b,A}$ | $0.45 \pm 0.12^{a,A}$ |
| NW | *A. aspera* | 31 | $0.19 \pm 0.19^{a,B}$ | $9.56 \pm 1.01^{a,B}$ | $9.37 \pm 0.99^{a,B}$ | $0.79 \pm 0.23^{b,B}$ |
| | *A. spinosa* | 31 | $0.85 \pm 0.54^{b,A}$ | $8.27 \pm 0.76^{b,B}$ | $7.42 \pm 0.86^{b,B}$ | $0.73 \pm 0.17^{b,B}$ |
| SE | *A. aspera* | 29 | $0.31 \pm 0.34^{a,B}$ | $9.20 \pm 1.07^{a,B}$ | $8.90 \pm 1.11^{a,B}$ | $0.98 \pm 0.36^{c,C}$ |
| | *A. spinosa* | 34 | $0.91 \pm 0.54^{b,A}$ | $8.16 \pm 0.90^{b,B}$ | $7.25 \pm 1.17^{b,B}$ | $1.01 \pm 0.36^{c,C}$ |

*N* is the number of measurements (=number of individual fish shelters at each site); bottom depth is the location of the seafloor directly beneath the blenny shelter; fish height is the location of the blenny shelter relative to the seafloor; fish depth is the location of the blenny shelter relative to the sea surface (bottom depth–fish height); and significant wave height is the wave conditions at the time of each measurement. Lowercase superscript letters indicate significant differences (one-way ANOVA: $P < 0.05$) between species within a site. Uppercase superscript letters indicate significant differences (one-way ANOVA: $P < 0.05$) between sites within each species

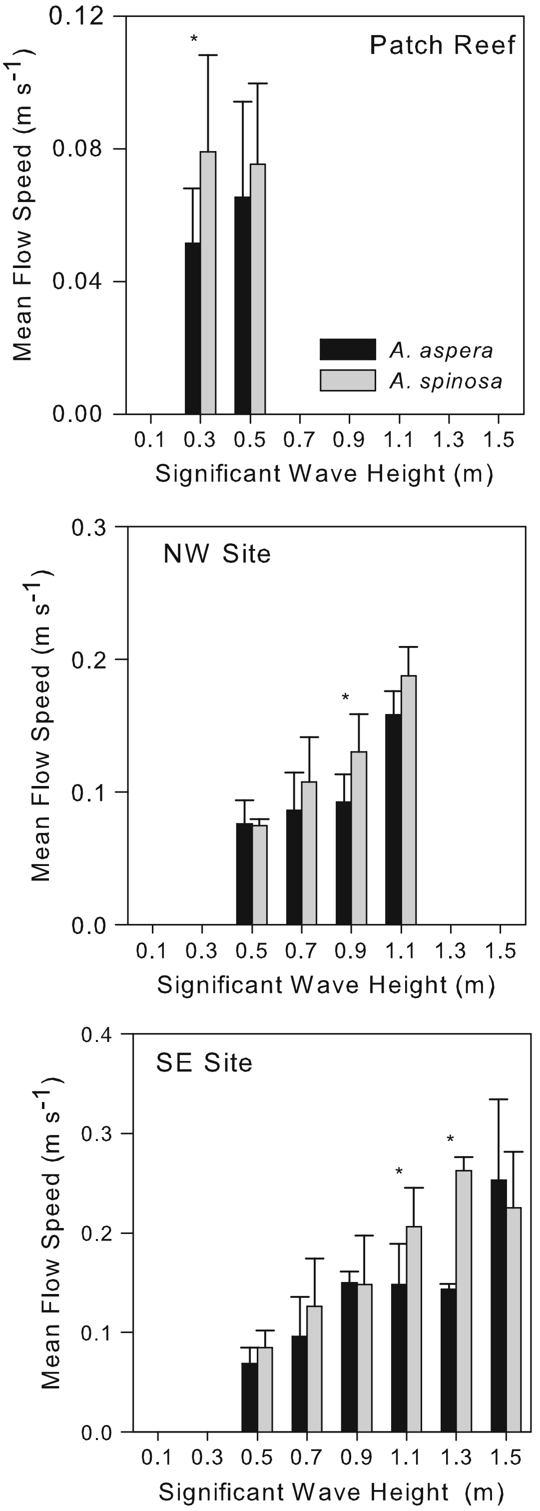

**Fig. 2** Results of flow speed measurements within the feeding volumes of two species of hemi-sessile tube blennies at three field sites. Results were compiled according to significant wave height ($H_s$) measured simultaneously with flow speed. *Error bars* indicate 1 SD. *Indicates significant difference between species at the $\alpha = 0.05$ level

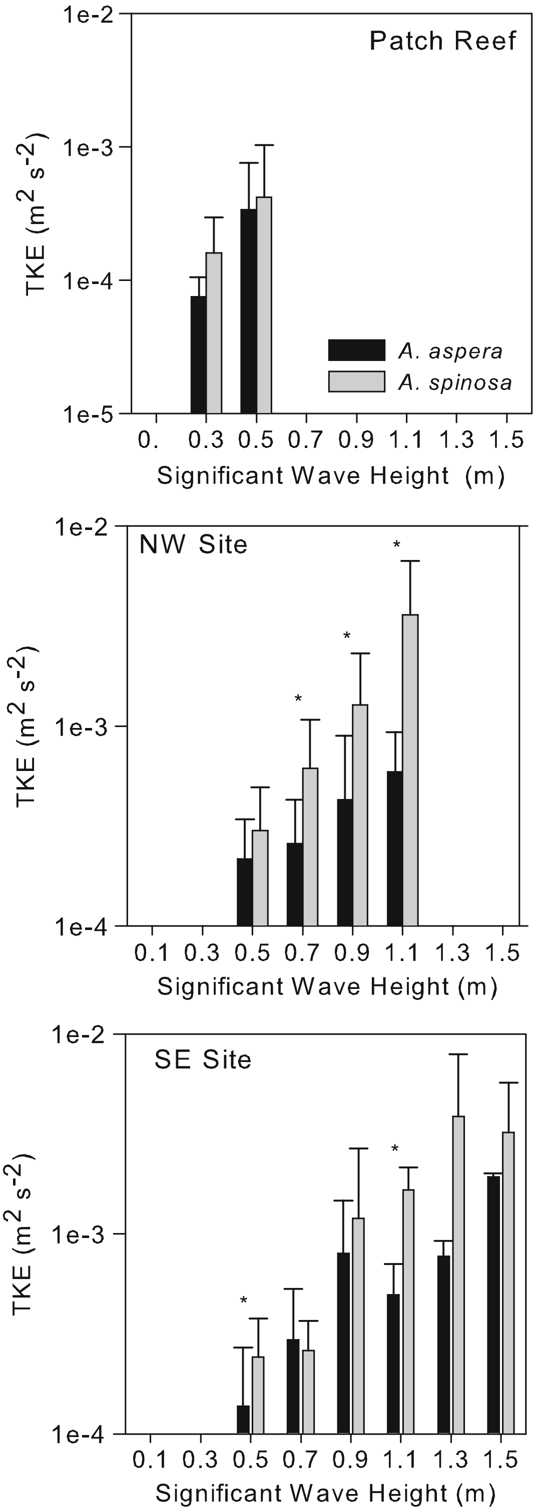

**Fig. 3** Results of measurements of turbulent kinetic energy (TKE) within the feeding volumes of two species of hemi-sessile tube blennies at three field sites. Results were compiled according to significant wave height ($H_s$) measured simultaneously with turbulence characteristics. *Error bars* indicate 1 SD. *Indicates significant difference between species at the $\alpha = 0.05$ level

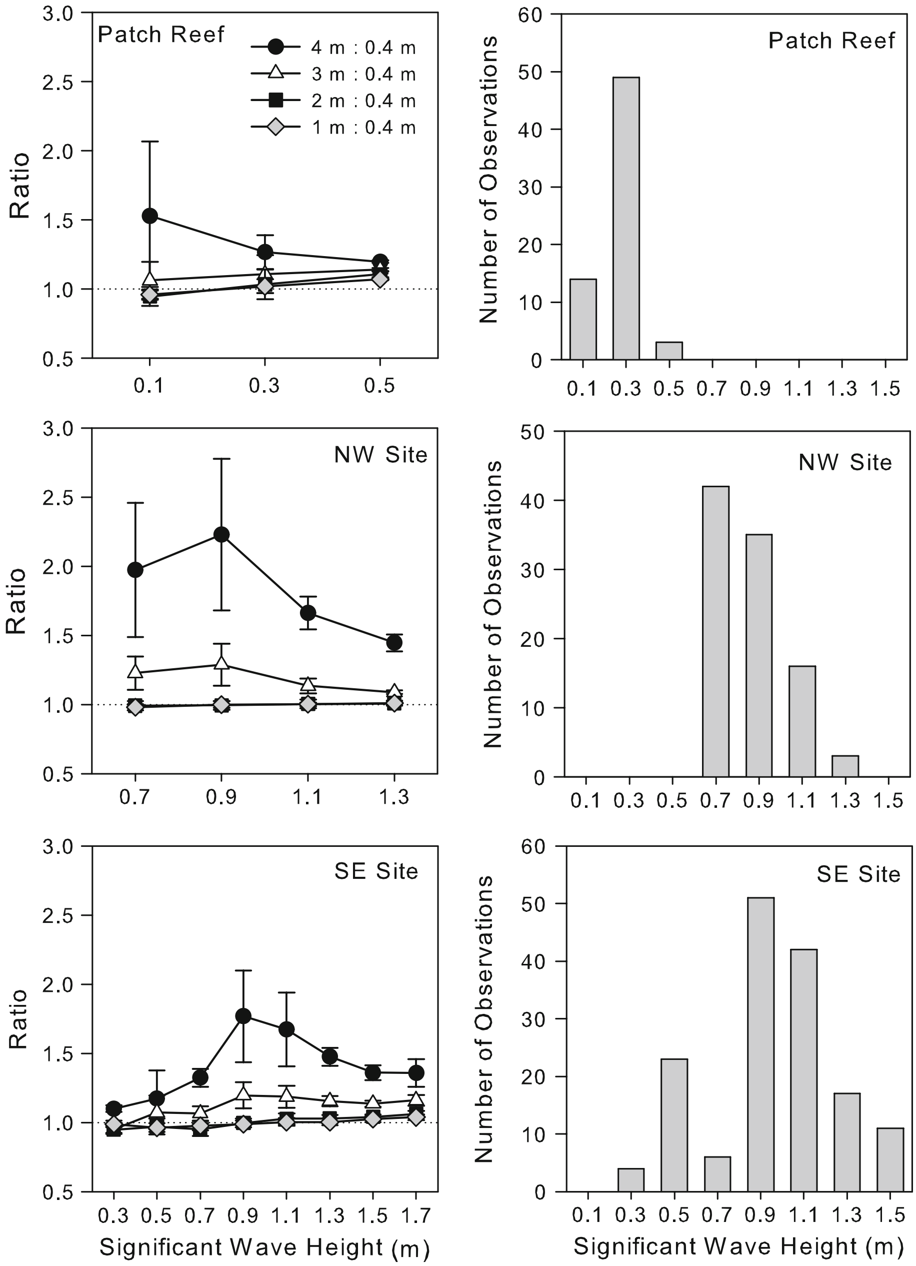

**Fig. 4** Summary of velocity profile measurements made with a bottom-mounted acoustic Doppler profiler at the three field sites. *Left-hand graphs* indicate the ratio of flow speed at various heights relative to flow speed at 0.4 m (the lowest point measured with our profiler) compiled according to significant wave height ($H_s$) at the time of measurement. Ratios > 1 indicate faster flow higher in the water column. *Right-hand graphs* indicate frequency of observing a specified significant wave height ($H_s$). *Error bars* indicate 1 SD

were not detected ($0.05 < P < 0.1$); however, the trend of higher flow for *A. spinosa* was apparent (Fig. 2). Estimates of TKE within the feeding volumes of *A. spinosa* were significantly greater than those for *A. aspera* when $H_s$ was greater than 0.6 m (Fig. 3; ANOVA: $P < 0.05$ in all cases). At the SE site, *A. spinosa* experienced significantly higher mean flow speed than *A. aspera* when $H_s$ was between 1.0 and 1.4 m (Fig. 2; $P < 0.05$ in both cases). TKE was significantly higher for *A. spinosa* at wave heights between 0.4–0.6 and 1.0–1.2 m ($P < 0.05$ in both cases). TKE experienced by the two species converged again when $H_s > 1.2$ m.

## Reef-scale measurements of water flow

Mean flow speeds within the BBL generally increased with height above the bottom and with increasing wave height ($H_s$). Within each site, mean flow speeds measured at heights of 0.4, 1.0, and 2.0 m above the bottom were roughly similar, as indicated by flow speed ratios near unity (Fig. 4). Flow speeds from 3.0 and 4.0 m above the seafloor tended to be faster relative to flow speeds at 0.4 m (Fig. 4). Site-specific patterns in flow speed ratios were also detected. At the Patch Reef site, the largest relative difference in flow speed between those measured at 4.0 m and those measured at 0.4 m occurred when $H_s < 0.2$ m (bin centered at 0.1 m, Fig. 4). In contrast, flow speeds measured at these two heights converged (i.e., ratios approached 1) as $H_s$ increased. The NW site showed a similar convergence of flow speeds measured at both 3.0 and 4.0 m with those measured at 0.4 m for $H_s > 0.8$ m. There was a slight increase in the ratio of flow speeds at 4.0 m to those at 0.4 m as $H_s$ increased from 0.6 to 1.0 m. At the SE site, maximum relative differences in flow occurred at intermediate values of $H_s$. Flow speeds measured at all heights were similar (ratios near 1) at $H_s < 0.6$ and $H_s > 1.4$ m. At $H_s$ between these values, flow speeds were divergent with the highest relative difference between flow at 0.4 and 4.0 m at an $H_s$ of 0.9 m.

The frequency distribution of $H_s$ showed that waves at each site were most commonly measured in the $H_s$ range for which there was the greatest relative difference in flow speed measured at 0.4 and 4.0 m. At the Patch Reef site, $H_s$ estimates fell within three size classes centered at 0.1, 0.3, and 0.5 m with 74% (49 of 66) of $H_s$ estimates between 0.2 and 0.4 m (Fig. 4). At the NW site, the frequency of occurrence of waves declined steadily from $H_s = 0.6$ to 1.4 m (Fig. 4). There were no estimates of $H_s < 0.6$ m from these relatively long records, although such waves were measured on shorter time scales using the Sontek ADV (e.g., Fig. 2). The SE site showed the widest variation in wave conditions, with $H_s$ estimates from 0.2 to 1.6 m. The greatest number of observations (51 of 164) fell in the bin centered at 0.9 m (range 0.8–1.0 m; Fig. 4).

## Field video observations

Fish of both species attacked prey located in the water column and on the hard surfaces adjacent to their shelters. When attacking prey in the water column, fish moved quickly with a very rapid forward thrust from their shelters. In contrast, attacks on prey at the reef surface were usually more methodical, with the fish generally approaching for a closer look and striking more slowly while curving the body to come down on the prey from above (normal to the surface).

On average, blennies of both species made feeding motions about once every 2–4 min (Fig. 5; top). A two-factor analysis of variance comparing attack rates between species and sites showed a significant site × species interaction (ANOVA: $F_{1,32} = 4.68$, $P = 0.04$) that was driven by the decline in attack rates for *A. spinosa* at the SE site relative to the Patch Reef while the attack rate of *A. aspera* remained stable (Fig. 5; top). A non-significant trend (ANOVA: $F_{1,32} = 3.64$, $P = 0.07$) toward lower attack rates at the SE site was also found, which combined with the significant interaction prompted separate analyses to be conducted for species effects at each site. At the Patch Reef, there was no difference in attack rate between the two species (ANOVA: $F_{1,15} = 1.54$, $P = 0.23$). In contrast, at the SE site *A. aspera* attacked more frequently than *A. spinosa* (ANOVA: $F_{1,17} = 5.25$, $P = 0.04$).

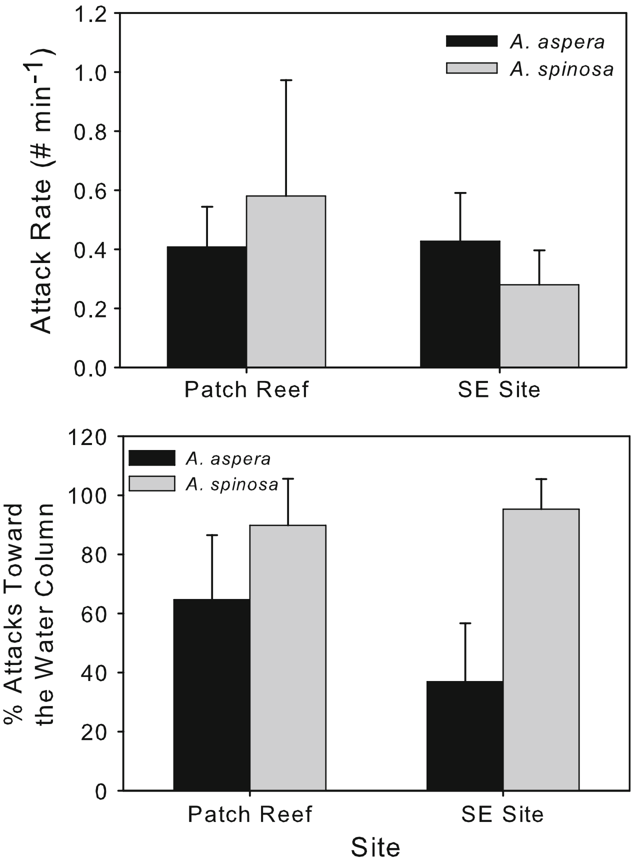

**Fig. 5** Results of quantitative video observations of tube blennies at two field sites exhibiting low wave conditions (Patch Reef) and high wave conditions (SE site). *Error bars* indicate 1 SD. *Top*: attack rate. *Bottom*: percentage of attacks directed into the water column rather than toward the reef surface

*A. spinosa* fed almost exclusively in the water column (93% of attacks at both sites) and nearly equally so at the Patch Reef site (90%) and the SE site (95%; Fig. 5, bottom). In contrast, water column attacks by *A. aspera* were site dependent: nearly twice as often at the Patch Reef site (65%) than at the SE site (37%; Fig. 5, bottom). A two-way analysis of variance of arcsine transformed proportions showed that a greater proportion of attacks were in the water column for *A. spinosa* than *A. aspera* (ANOVA: $F_{1,32} = 51.61$, $P < 0.01$). There was also a significant site × species interaction, driven by the decline in the proportion of water column attacks for *A. aspera* at the SE site relative to the Patch Reef site. Additional one-way ANOVAs to test for site effects on a species by species basis showed that *A. aspera* attacked in the water column significantly more at the Patch Reef site than at the SE site (ANOVA: $F_{1,15} = 6.75$, $P = 0.02$). There was no difference between sites in the proportion of attacks in the water column for *A. spinosa* (ANOVA: $F_{1,17} = 0.63$, $P = 0.44$).

For *A. aspera*, the proportion of attacks in the water column (pooled for both sites) was negatively correlated with $H_s$ ($r = -0.79$, $P = 0.004$). *A. spinosa* showed no such relationship for pooled data ($r = 0.08$, $P = 0.76$). At the highest significant wave heights recorded for each species during video observation, 21% of *A. aspera* attacks were in the water column ($H_s = 0.96$ m) and 93% of *A. spinosa* darts were in the water column ($H_s = 1.62$ m).

Analysis of variance with Tukey's pairwise comparisons of attack distances revealed significant differences between species (Fig. 6). *A. spinosa* attacked prey at greater distances than did *A. aspera* regardless of site or direction of attack (Fig. 6; ANOVA: $F_{1,47} = 8.38$, $P = 0.006$). No other class variables (site or attack direction) or interactions were significant in the ANOVA model.

### Plankton sampling

The abundance of possible food items for each fish species was examined at the Patch Reef and SE sites (Fig. 7). For each taxon of zooplankton analyzed, there were consistent trends in abundance with species or site. However, only the calanoid and harpacticoid copepods showed any statistically significant differences. Calanoid copepods were more abundant at the Patch Reef site than at the SE site. Harpacticoid copepods were equally abundant at the Patch Reef and SE sites, but there were significantly higher abundances at the *A. aspera* shelters than at *A. spinosa* shelters. The species × site interaction was also significant, reflecting the greater relative abundance of harpacticoid copepods at the SE site.

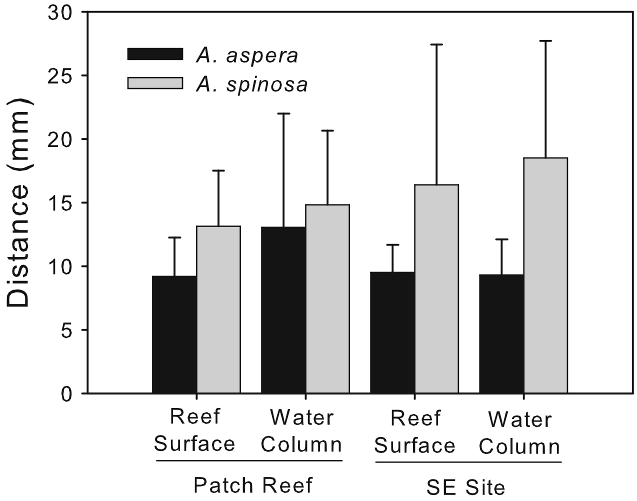

**Fig. 6** Results of quantitative video observations of tube blennies at two field sites exhibiting low wave conditions (Patch Reef) and high wave conditions (SE site). Attack distance is measured as the maximum distance traveled by the fish from its shelter during the attack. *Error bars* indicate 1 SD

## Discussion

The interaction of ocean currents and waves with the complex three-dimensional structure of a coral reef generates a full spectrum of hydrodynamic microhabitats that can influence a range of physiological and ecological processes (Trager et al. 1994; Sebens et al. 1998; Williams and Carpenter 1998; Gardella and Edmunds 2001; Hearn et al. 2001). This series of field studies shows that two species of tube blennies are vertically segregated on the reef, which causes them to experience differing flow conditions. Moreover, behavioral observations support the hypothesis that the flow conditions experienced within each microhabitat are consistent with diet, feeding performance, and feeding strategy employed by the two species.

The blennies in this study were vertically segregated within each site such that roughhead blennies (*A. aspera*) occupy shelters that are 0.5–1.3 m deeper and are associated with topographically low features relative to spinyhead blennies (*A. spinosa*). Boundary layer theory predicts that *A. spinosa* would experience faster, more turbulent flows than *A. aspera* based on their vertical positions (e.g., Shashar et al. 1996). However, because water flow on these reefs was wind-wave driven, water motion varied proportionally with $H_s$ and inversely with depth (Denny 1988). It follows, then, that differences in flow experienced by the two species will depend on site depth and wave conditions.

Figure 8 depicts a conceptual model of how wave-induced flows are experienced by blennies within each site as a function of wave height. The distribution of blennies is shown at right in the figure and is consistent with the vertical segregation of the species at our field sites (Table 1). Within a given site, at low $H_s$ wave energy is relatively weak and produces only modest flows at all depths with corresponding mild velocity gradients (Figs. 2, 3, 4). Thus, there are minimal or no differences in flow speed or turbulence between the two species within a site at low $H_s$ (Figs. 2, 3). At moderate $H_s$, substantial amounts of kinetic energy are transported to mid and deeper depths and produce a strong gradient in flow (Figs. 2, 3, 4). Under such conditions, one would expect to see (and this study demonstrates) differences in flow conditions for organisms living at different heights above the bottom within a site (Figs. 2, 3). Finally, at high $H_s$ enough kinetic energy is transported to the bottom to thin the BBL such that the vertical gradient in flow conditions is again diminished (Figs. 2, 3, 4).

The particular $H_s$ that produces maximal vertical gradients in flow will vary with site and depth. Shallower sites will be “saturated” with wave energy at relatively low $H_s$,

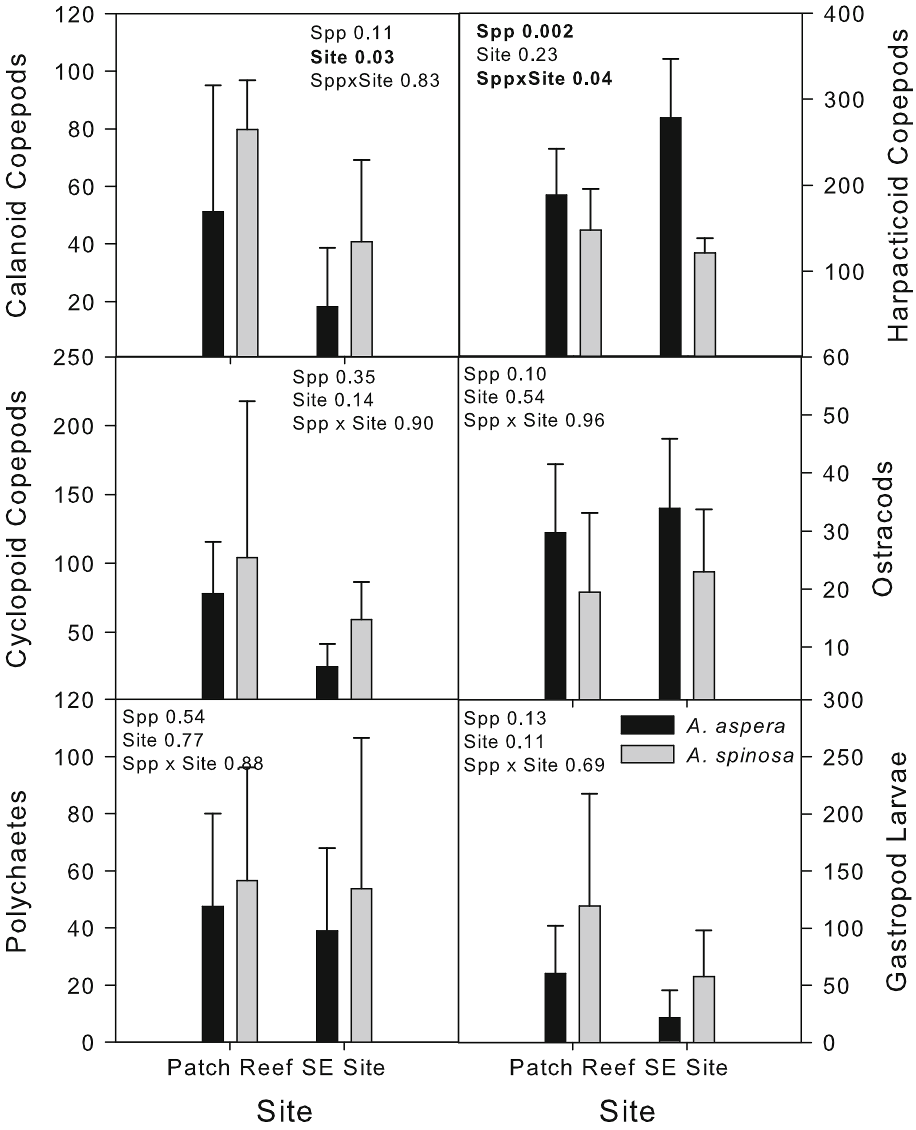

**Fig. 7** Density (number per m$^3$) of plankton collected from the location of tube blenny shelters at two field sites exhibiting low wave conditions (Patch Reef) and high wave conditions (SE site). $N = 4$ for each site and species combination. $P$ values indicate results of two-way analysis of variance comparing plankton density between sites and species. *Error bars* indicate 1 SD

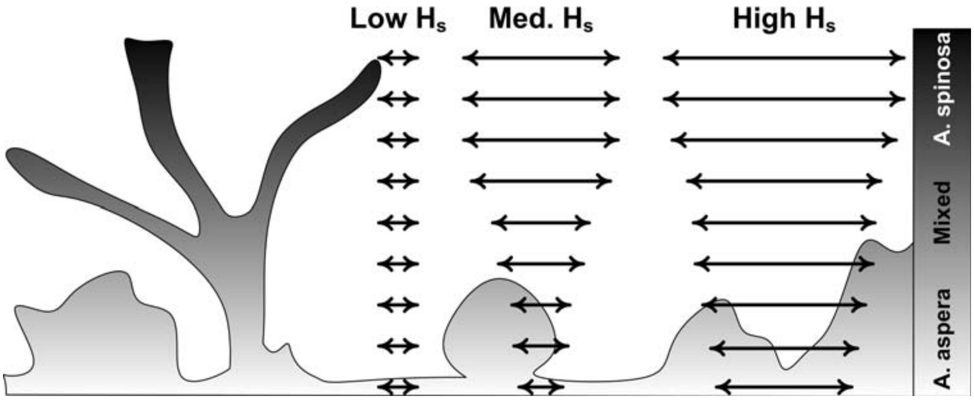

**Fig. 8** Diagrammatic representation of tube blenny distribution within the field sites and flow conditions experienced by tube blennies at low, medium, and high significant wave heights

while larger waves are needed to produce maximal gradients at deeper sites. For example, at the Patch Reef site there were significant differences in mean flow speeds between species at low to intermediate $H_s$ (<0.4 m; Fig. 2). When $H_s$ increased at this site to a modest 0.5 m, differences in flow speed between the two species disappeared due to a thin BBL (Figs. 2, 4). In contrast, at the deeper and more exposed sites (NW and SE), significant differences in flow experienced by to the two species were noted primarily when $H_s$ was relatively large (Figs. 2, 3). For example, at the NW site, mean flow speed and TKE were different for the two species for $H_s > 0.6$ m, while at the SE site differences between the species were most pronounced at $H_s > 1.0$ m and $H_s < 1.4$ m.

A strong interaction between site depth, wave height, and vertical gradients in flow was also suggested by the synoptic measurements obtained in this study using a bottom-mounted current profiler. These measurements showed mild flow speed gradients to a height of 2 m above the seafloor at all sites under all wave conditions (Fig. 4). However, flow speeds at 3.0 and 4.0 m above the bottom were up to two times higher than those at 0.4 m. Maximal vertical gradients in flow speed were found at $H_s$ that varied with site according to depth (Fig. 4). For example, maximal gradients were found at $H_s = 0.1$ m for the shallow Patch Reef, whereas maximal gradients were found at $H_s = 0.9$ for the NW and SE sites, which had similar deeper depths (Table 1, Fig. 4). This finding is expected given the strong attenuation of wave energy with increasing depth. These data also show that within each site, the most frequently encountered waves are those that produce maximal vertical gradients in flow (Fig. 4) and produce the greatest differences in flow conditions experienced by *A. aspera* and *A. spinosa* (Figs. 2, 3). These complementary results from short-term point measurements of flow at blenny shelters and longer-term reef-scale flow measurements suggest a strong link between blenny distribution, flow microhabitats at the shelter, and reef-scale hydrodynamic processes.

The conceptual model (see Fig. 8) provides a mechanistic explanation for why these two species experience differing flow conditions but does not answer why the two species are vertically segregated. This explanation may be found in their foraging behavior and (perhaps) food availability. The video studies demonstrate species-specific patterns of feeding that can be interpreted as a response to hydrodynamic conditions. While both species forage at similar rates, *A. spinosa* forages almost exclusively in the water column and ventures further from their shelters than *A. aspera*. This may indicate a preference for planktonic over benthic prey items (see also Clarke et al. 2009), and it may indicate that this species is a stronger swimmer capable of foraging under more energetic conditions (see also Fulton et al. 2005). Moreover, the field observations show that *A. aspera* reduces exposure to high flows by decreasing the proportion of darts toward the water column (64% in the relatively quiet conditions of the Patch Reef versus 36% in the more energetic conditions of the SE site). A greater foraging ability under high flow conditions for *A. spinosa* and avoidance of high flow by *A. aspera* are further supported by laboratory experiments in which *A. spinosa* foraged over a large proportion of the wave cycle, whereas *A. aspera* restricted foraging to just before slack currents at wave reversal (Clarke et al. 2009). Robinson et al. (2007) similarly showed that escape responses of calanoid copepods were diminished by faster flow speeds and greater turbulence. Thus, *A. spinosa* may be better able to exploit this food resource with more aggressive foraging (e.g., Clarke et al. 2005) at locations with higher flow.

Spatial segregation of the blennies may also result from availability of particular food items at their shelters. The pump samples showed significant differences in plankton abundance between tube blenny species only for harpacticoid copepods that were more abundant at the *A. aspera* shelters, suggesting a benthic food pool for those fish. Other generalities may be inferred from these data that are consistent with benthic versus pelagic food pools for the two species. For example, both harpacticoid copepods and ostracods are likely of benthic origin and showed higher abundances at *A. aspera* shelters. In contrast, fully planktonic forms (calanoid copepods, cyclopoid copepods, polychaetes, and gastropod larvae) were more abundant at *A. spinosa* sites. While these patterns are suggestive, the variation in densities between samples makes interpretation difficult and may eclipse any real biological meaning. Rather, it is suggested that *A. spinosa*, by virtue of its more aggressive feeding behavior, is better suited to exploit topographically high shelters that experience faster flows (and thus higher flux of plankton given equal concentrations) and conditions that interfere with copepod escape responses (e.g., Robinson et al. 2007).

Finally, the role of blenny behavior in driving vertical segregation of the species should be noted. Clarke (1989) has shown that the vertical distribution of these tube blennies results from competitive interactions among the blennies for preferred higher locations. The measurements in this study show that the height above the bottom of shelters occupied by *A. spinosa* was constant at all three sites, but that *A. aspera* resided in higher shelters on the Patch Reef than at the SE or NW sites. The shelter height for *A. spinosa* is fixed by its occupation of the highest available shelters, which are similar (erect coral skeletons) at all three sites. The maximum height of *A. aspera* shelters is set by both competition with *A. spinosa* and hydrodynamic conditions. At SE and NW sites, it is proposed that competition with *A. spinosa* and some aspects of the hydrodynamic environment (flow speed, turbulence, food flux, feeding performance, etc.) prevent *A. aspera* from moving to higher shelters. At the Patch Reef site, *A. aspera* was able to occupy shelters at 0.5 m (vs. 0.25 m at the other sites) due to relaxation of competition (e.g., due to higher abundance of calanoid copepods) and/or more benign flow conditions. Thus, these data support a strong interaction between the physical (flow, $H_s$) and biological (feeding, competition) processes that drive tube blenny distribution.

The present study has provided a mechanistic explanation of the distribution and flow conditions experienced by planktivorous tube blennies at three sites within Glovers Reef, Belize. The resulting conceptual model captures the relevant physical ($H_s$, depth, flow speed, turbulence) and biological components (feeding strategy, food availability) of this system and accounts for between site variation (e.g., shelter heights of *A. aspera*) as well as the focal within site patterns. However, the present study was geographically limited and the data used to generate the conceptual model are descriptive in nature. Further efforts, therefore, are needed to test the generality of the model at other reef sites and to experimentally test the links between flow and blenny feeding under controlled hydrodynamic conditions. Such an experimental examination of blenny feeding is provided by Clarke et al. (2009).

**Acknowledgments** We would like to thank the lab managers and staff at the Middle Cay Field Station for their expert help, especially our boatmen and dive masters Elmar Avila, Cardinal Andrews, Faygon Villanuevia, and Randolph Nunez. Field support was provided by Carly Gaebe, Benjamin Kessler, and Jora Ehrlich. This work was authorized by a research permit from the Belize Fisheries Department, Ministry of Agriculture and Fisheries, and the University of Texas Institutional Animal Care and Use Committee permit number 04113007. Funding was provided by National Science Foundation Awards OCE-0324724, OCE-0324413, and OCE-0324694/0715271. This paper is contribution number 1488 of the University of Texas Marine Science Institute and publication number 30 of the Wildlife Conservation Society's Glovers Reef Research Station.

## References

Bellwood DR, Wainwright PC (2001) Locomotion in labrid fishes: implications for habitat use and cross-shelf biogeography on the Great Barrier Reef. Coral Reefs 20:139–150

Clarke RD (1989) Population fluctuation, competition and microhabitat distribution of two species of tube blennies, *Acanthemblemaria* (Teleostei: Chaenopsidae). Bull Mar Sci 44:1174–1185

Clarke RD (1992) Effects of microhabitat and metabolic rate on food intake, growth and fecundity of two competing coral reef fishes. Coral Reefs 11:199–205

Clarke RD (1994) Habitat partitioning by chaenopsid blennies in Belize and the Virgin Islands. Copeia 1994:398–405

Clarke RD (1996) Population shifts in two competing fish species on a degrading coral reef. Mar Ecol Prog Ser 137:51–58

Clarke RD (1999) Diets and metabolic rates of four Caribbean tube blennies, genus *Acanthemblemaria* (Teleostei: Chaenopsidae). Bull Mar Sci 65:185–199

Clarke RD, Buskey EJ, Marsden KC (2005) Effects of water motion and prey behavior on zooplankton capture by two coral reef fishes. Mar Biol 146:1145–1155

Clarke RD, Finelli CM, Buskey EJ (2009) Water flow controls distributions and feeding behavior of two co-occurring coral reef fishes: II: Laboratory measurements. Coral Reefs. doi:10.1007/s00338-009-0479-7

Denny MW (1988) Biology and the mechanics of the wave-swept environment. Princeton University Press, Princeton, NJ

Depczynski M, Bellwood DR (2005) Wave energy and spatial variability in community structure of small cryptic coral reef fishes. Mar Ecol Prog Ser 303:283–293

Forrester GE (1991) Social rank, individual size and group composition as determinants of food consumption by humbug damselfish, *Dascyllus aruanus*. Animal Behavior 42:701–711

Fulton CJ, Bellwood DR (2005) Wave induced water motion and the functional implications for coral reef fish assemblages. Limnol and Oceanogr 50:255–264

Fulton CJ, Bellwood DR, Wainwright PC (2005) Wave energy and swimming performance shape coral reef fish assemblages. Proc R Soc B 272:827–832

Gardella DJ, Edmunds PJ (2001) The effect of flow and morphology on boundary layers in the scleractinians *Dichocoenia stokesii* (Milne-Edwards and Haime) and *Stephanocoenia michilini* (Milne-Edwards and Haime). J Exp Mar Biol Ecol 256:279–289

Genin A, Yahel G, Reidenbach MA, Monismith SG, Koseff JR (2002) Intense benthic grazing on phytoplankton in coral reef revealed using the control volume approach. Oceanography 15:90–96

Gischler E, Hudson JH (1998) Holocene development of three isolated carbonate platforms, Belize, Central America. Mar Geol 144:333–347

Glynn PW (1973) Ecology of a Caribbean coral reef. The *Porites* reef-flat biotope: Part II. Plankton community with evidence for depletion. Mar Biol 22:1–21

Hamner WM, Carleton JH (1979) Copepod swarms: attributes and role in coral reef ecosystems. Limnol and Oceanogr 24:1–14

Hamner WM, Jones MS, Carleton JH, Hauri IR, Williams DM (1988) Zooplankton, planktivorous fish, and water currents on a windward reef face: Great Barrier Reef, Australia. Bull Mar Sci 42:459–479

Hearn CJ, Atkinson MJ, Falter JL (2001) A physical derivation of nutrient-uptake rates in coral reefs: effects of roughness and waves. Coral Reefs 20:347–356

Heidelberg KB, Sebens KP, Purcell JE (2004) Composition and sources of near reef zooplankton on a Jamaican forereef along with implications for coral feeding. Coral Reefs 23:263–276

Hobson ES (1991) Trophic relationships of fishes specialized to feed on zooplankters above coral reefs. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, San Diego, CA, pp 69–95

Johansen JL, Bellwood DR, Fulton CJ (2008) Coral reef fishes exploit flow refuges in high-flow habitats. Mar Ecol Prog Ser 360:219–226

Madin J, Black KP, Connolly SR (2006) Scaling water motion on coral reefs: from regional to organismal scales. Coral Reefs 25:635–644

Motro R, Ayalon I, Genin A (2005) Near-bottom depletion of zooplankton over coral reefs: III: vertical gradient of predation pressure. Coral Reefs 24:95–98

Robinson HE, Finelli CM, Buskey EJ (2007) The turbulent lives of copepods: laboratory flume studies of how flow over a coral reef affects their ability to detect and evade predators. Mar Ecol Prog Ser 349:171–181

Roy AG, Biron P, de Serres B (1996) On the necessity of applying a rotation to instantaneous velocity measurements in river flows. Earth Surface Process Landf 21:817–827

Sebens KP, Maney EJ Jr, Witting J (1992) A portable dive operated plankton sampler for near-substratum use. American Academy of Underwater Sciences.

Sebens KP, Grace SP, Helmuth B, Maney EJ, Miles JS (1998) Water flow and prey capture by three scleractinian corals, *Madracis mirabilis, Montastrea cavernosa* and *Porites porites,* in a field enclosure. Mar Biol 131:347–360

Shashar N, Kinane S, Jokiel PL, Patterson MR (1996) Hydromechanical boundary layers over a coral reef. J Exp Mar Biol Ecol 199:17–28

Smith-Vaniz WF, Palacio FJ (1974) Atlantic fishes of the genus *Acanthemblemaria* with description of three new species and comments on Pacific specis (Clinidae: Chaenopsinae). Proc Acad Nat Sci Phila 125:197–224

Trager G, Achituv Y, Genin A (1994) Effects of prey escape ability, flow speed, and predator feeding mode on zooplankton capture by barnacles. Mar Biol 120:251–259

Vogel S (1994) Life in moving fluids. Princeton University Press, Princeton, NJ (467)

Williams SL, Carpenter RC (1998) Effects of unidirectional and oscillatory water flow on nitrogen fixation (acetylene reduction) in coral reef algal turfs, Kaneohe Bay, Hawaii. J Exp Mar Biol Ecol 226:293–316

Yahel G, Post AF, Fabricius K, Marie D, Vaulot D, Genin A (1998) Phytoplankton distribution and grazing near coral reefs. Limnol and Oceanogr 43:551–563

Yahel R, Yahel G, Genin A (2005) Near-bottom depletion of zooplankton over coral reefs: I: diurnal dynamics and size distribution. Coral Reefs 24:75–86

Zar JH (1984) Biostatistical Analysis. Prentice Hall, Englewood Cliffs