

LETTER

Water flow drives biodiversity by mediating rarity in marine benthic communities

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Abstract

In aquatic ecosystems, water flow mediates the delivery of reproductive propagules, competition and predation, each of which may have contrasting effects on biodiversity. Here, we show that water flow has a net positive effect on the biodiversity of benthic invertebrate communities in three biogeographic regions. In Palau and Alaska, flow velocity predicted 55–91% of the variance in species richness in natural communities. In experimental communities in Alaska and Maine, enhanced water flow treatments resulted in higher levels of species density (+56%) and richness (+74%), which were predicted by the abundance of locally rare species. Additionally, the richness of recruitment was higher in experimentally enhanced flows (+46%). Thus, the data suggest that flow drives diversity by mediating the delivery of rare species in multiple biogeographic regions. Consequently, flow velocity should be included in future developments of diversity theory and conservation strategy.

Keywords

Biodiversity, flow, metacommunities, rarity, recruitment, species density, species diversity, species pools, species richness.

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INTRODUCTION

There is a compelling need to understand the forces that shape the large-scale patterns of biological diversity. In both marine and terrestrial systems, increased levels of biodiversity result in increased ecosystem productivity and stability (Hooper *et al.* 2005; Worm *et al.* 2006). Until the mechanisms that generate and maintain biodiversity are more fully understood, it will be difficult to predict the resilience of communities to anthropogenic impacts and thereby achieve success in conservation efforts.

At small scales in both marine and terrestrial communities, decades of experiments have shown that competition (Connell 1961; Harpole & Tilman 2007), predation (Paine 1966; Chase *et al.* 2002), positive interactions (Callaway *et al.* 2002; Bruno *et al.* 2003), productivity (Hawkins *et al.* 2003; Witman *et al.* 2008) and the temporal variability and magnitude of disturbance (Dayton 1971; Collins 1987), can regulate the diversity of communities. Because local communities are a subset of larger scale ecological systems, large-scale processes such as the dispersal of reproductive propagules (McEuen & Curran 2004; Levin 2006) are also known to have substantial effects on local community diversity. Moreover, many terrestrial and marine communities appear open to immigration (Foster *et al.* 2004; Witman *et al.* 2004; Starzomski *et al.* 2008). Consequently, the delivery of reproductive propagules (immigrants, larvae, asexual buds) is likely to play an important driving role in determining community diversity, invasibility and stability in many systems (Tilman 1997; Lee & Bruno 2009).

Assuming reproductive propagules in marine environments are well mixed at small scales and water movement controls their dispersal (Eckman 1983), propagule delivery increases with water flow. Consequently, although flow should increase the species richness of propagules available to local sites, it will also augment recruitment (Gaines & Bertness 1992) and growth rates (Sanford *et al.* 1994), which may lead to competitive exclusion and a reduction of diversity. Moreover, as water flow has also been shown to mediate productivity (Patterson *et al.* 1991), competition (Kim & Lasker 1997), community structure (Leonard *et al.* 1998) and larval settlement (Abelson & Denny 1997), the expected influence of increased flow on local species richness and species density is not clear. Recent work in mesocosms, however, has suggested that propagule supply may control the diversity of a marine grazer community (Lee & Bruno 2009). Additionally, although flow was not experimentally manipulated, and many other variables differed among sites, observational studies of invertebrates in mountain streams (Hawkins *et al.* 1982) and octocorals on coral reefs (Fabricius & De'ath 2008) have shown that local diversity may increase with flow velocity.

In this study, we used a combination of observational and experimental methods to investigate the effect of water flow on the species richness of benthic invertebrate communities. Specifically, we surveyed rock wall sites in Palau and Alaska, and experimentally manipulated water flow at sites in Alaska and Maine to address two hypotheses across biogeographic regions and spatial scales: (1) increased water flow velocities lead to increased local species density and species richness and (2) water flow generates increased species richness by promoting the increased recruitment of rare species. In all communities examined in three biogeographic regions, increased water flow resulted in an increase in community richness and diversity, a result mediated by the delivery of locally rare species. As such, our results suggest that the positive effects of flow on diversity are widespread and should be incorporated into diversity theory and conservation efforts.

MATERIAL AND METHODS

Diversity surveys

To determine if flow influences diversity, benthic invertebrate communities on vertical walls were photographically sampled at six sites in Palau in November 1998 (Witman *et al.* 2004) and four sites in Alaska in September 2008 (Table S1 in Supporting Information). At each site, 24–73 high-resolution photographs of quadrats (0.25 m²) were taken at a depth of 10–15 m. Quadrats were sampled at random locations along replicate transects stretched horizontally across vertical rock wall habitats as in Witman *et al.* (2004). The spatial scale of the local community sampled for species richness was *c.* 30–120 m long horizontal span of vertical rock wall habitat. Species identifications were generally possible for species > 0.5 mm, and were made in consultation with taxonomic experts, by referring to voucher specimens, and comparing species to photo libraries. Where positive identification was not possible, a descriptive name was assigned and referenced among occurrences for consistency as in Witman *et al.* (2004).

To determine flow rates at sites in Alaska, we deployed an S4 current meter (InterOcean Systems, San Diego, CA, USA) that measured flow every 10 min for a minimum of 30 days. In Palau, flow was estimated by the dissolution of plaster blocks: one block was attached to the wall (Thompson & Glenn 1994) at each site for 1 week in November 1998. Dissolution was calculated as loss in mass per day.

Enhancer design and construction

To hold larval pool and flow environment constant, water flow must be manipulated experimentally. To enhance flow while minimizing flow separation and turbulence, flow enhancers were designed, modelled and tested in a flume at Brown University. Each flow enhancer provided a total of six settlement plates (10 × 10 cm) in both ambient and enhanced flow regimes (Fig. 1). We deployed four flow enhancers, constructed of aluminium framing and polycarbonate panelling with stainless steel hardware, at each of four sites in May 2006 and May 2007. Flow enhancers were deployed in Alaska at Kachemak Bay at Seldovia and Jakolof Bay; in Maine, enhancers were deployed in York Harbor and at Fort Foster, Kittery (Table S1). Regions were chosen for logistical reasons, and sites were treated as a random factor to test for generalities. Deployment at all sites occurred 1 m below mean low water for a minimum duration of 45 weeks (maximum 104 weeks), aligned so that flow was driven by bidirectional tidal flux.

External diversity controls

To ensure that experimental artefacts were not affecting diversity in the flow enhancers, settlement plates were installed on rock walls at four sites in Alaska (the sites used for diversity surveys; Table S1). In early June 2007, 10 clearings 30 cm × 30 cm were made by scraping all visible benthic organisms from the rock wall using wire brushes. In the centre of each clearing, 10 × 10 cm settlement plates identical to those used in flow enhancers were deployed.

Flow measurement at experimental sites

For each replicate, average water flow was estimated by combining flow measurements at two scales: whole site and within each enhancer. Site-level flow was measured for

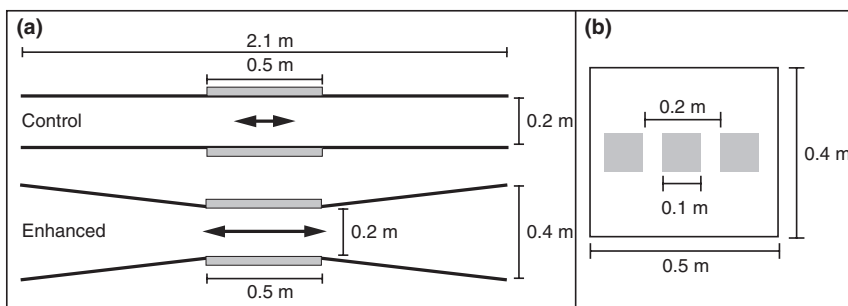


Figure 1 Schematic of flow enhancers. (a) Top-view schematic representation of enhanced and control flow treatments. Solid lines indicate channel walls; panels containing settlement plates, indicated by grey rectangles, slide vertically for removal from the apparatus. Arrows indicate direction and relative magnitude of water flow. All replicates were aligned with prevailing currents and attached to pilings at a depth of 1 m below mean low water. (b) Frontal view of a removable panel. Three 10 × 10 cm settlement plates were attached to each panel (two per flow treatment), for a total of six settlement plates per treatment per replicate.

30 days at 10-min intervals by S4 current meters. Concurrent flow measurements were recorded with an Acoustic Doppler Velocimeter (ADV; Sontek, San Diego, CA, USA) recording at 10 Hz. At each site, flow through all flow enhancers was quantified over six periods (three ebbing and three flooding tides). In each flow enhancer during each measurement period, the following procedure was replicated three times: flow was measured for 1 min in the control treatment, and then for 1 min in the enhanced treatment.

Flow measurement data (ADV and S4) were matched in time, and a regression of flow velocity at the settlement plate (ADV data) against site flow velocity (S4 data, flow in-line with enhancers) was constructed for both flow treatments in all enhancers (all $P < 0.01$, all $r^2 > 0.75$). Using these equations, average water velocity was estimated for all replicates over a 30-day period (Fig. S1).

To test for effects of turbulence on response variables, ADV data were separated according to the Reynolds decomposition: $u = \bar{u} + u'$, where instantaneous velocity (u) is the sum of average velocity (\bar{u}) and an instantaneous velocity fluctuation (u'). For each 1 min measurement, a ratio of turbulence intensity ($|u'|/\bar{u}$) to average velocity was constructed.

Sampling methods

In the 2006 deployment, high-resolution (10 megapixel; Canon G7 camera (Canon USA, Lake Success, NY, USA) in an Ikelite underwater housing (Ikelite, Indianapolis, IN, USA) digital photographs were taken at 5 and 10 weeks post-deployment at all sites ($n = 24$ settlement plates per flow treatment per site). Due to corrosion, replicates were lost beginning 10 weeks after deployment. Photos were taken at 15 weeks in York ($n = 24$) and Kittery ($n = 12$), and 20 weeks in York ($n = 18$) and Seldovia ($n = 24$). At 20 weeks, the experiment was removed from the water at all sites except Seldovia, where sampling occurred at 45, 50, 59, 74, 89 and 104 weeks post-deployment ($n = 18$ for all). For the 2007 deployment, a change in fasteners reduced corrosion, and high-resolution photographs (12.1 megapixel; Canon G9 camera in an Ikelite housing) were taken at 5, 10, 15, 30 and 45 weeks post-deployment at all sites ($n = 24$ for all). After 40 weeks of deployment, high-resolution photographic sampling was conducted at the external diversity control sites in Alaska. This sampling was concurrent to the 45 week sampling of flow enhancers at nearby sites.

Species in all 1804 photographs were identified to the lowest taxonomic classification possible, and the basal area of all species on each plate was determined using ImageJ (Rasband 2008). Species identifications, generally possible for species > 0.5 mm, were made in consultation with taxonomic experts, by referring to voucher specimens, and comparing species to photo libraries. Where positive identification was not possible, a descriptive name was assigned and referenced among occurrences for consistency. Using species abundance data, we calculated the number of species per settlement plate (hereafter species density) and species richness for all plates within the experimental site (hereafter local species richness). Using photos from consecutive sampling periods, the growth rate of solitary barnacles (those not surrounded by conspecifics), average basal area summed across all species (aggregate growth of the community), recruitment area and the species richness of newly recruited species (i.e. species not on the plate at the previous time step) was determined.

Data analysis and statistics

We used ordinary least squares (OLS) regression to estimate the effect of water flow on species richness for natural communities in Alaska. As flow rates were estimated by dissolution methods in Palau, we used major axis (MA) regression (Legendre & Legendre 1998).

To avoid underestimating local richness, the Chao2 estimator of species richness was used and standard errors computed (Chao 1989). The Chao index estimates the number of the species not present in the collection of photographs and adds them to observed species richness. By doing so, it provides a better estimate of true species richness for small numbers of samples than simply reporting the number of observed species (i.e. S_{obs}), and has relatively low bias and high accuracy when compared to other richness estimators (Magurran 2004; Walther & Moore 2005). As there are no replicates at the level of 'site' for species richness, standard errors of the Chao2 estimates between enhanced and control flow were compared within site and time.

Within site and time, sample sizes used to create the Chao2 estimator varied from 24 to 12 (see the Sampling methods section for details). Because the performance of richness estimators is sensitive to sample size (e.g. Magurran 2004; Walther & Moore 2005), S_{obs} was also calculated for all sites and times. In all cases with respect to the effect of flow on richness, the results of Chao2 estimation and S_{obs} were identical. As such, values of S_{obs} are not presented.

To compare the species richness of treatments within the flow enhancer and external control sites, sample-based rarefaction was used to control for unequal sample sizes ($n = 24$ in flow enhancers, $n = 10$ at external control sites).

Linear mixed effects (LME) models (Pinheiro & Bates 2000) were used to test for the effects of flow treatment on the ratio of turbulence intensity to average velocity. Using the data from settlement plates, we used LME models to test for effects of time (fixed), water flow treatment (fixed), site (random), enhancer (within site, random), side of enhancer (within enhancer, random) and left to right position (within side of enhancer, random) on: species density, the diversity and area of immigrating species, and growth rates (of both individual barnacles and whole communities). All random terms were modelled as a function of time. To test for the significance of individual terms in LME models, nested models were constructed and likelihood-ratio (LR) tests compared model fits using maximum likelihood (fixed effects) or restricted maximum likelihood (random effects) (Pinheiro & Bates 2000).

As comparisons of changes to species density between flow treatments could not be made at the level of the settlement plate, we used MA regression to estimate the relationship between increased numbers of rare species present in enhanced flow treatments and the observed increase in species density with enhanced flow. To estimate the relationship between the increased number of singletons and doubletons present in enhanced flow with the corresponding enhancement in species richness, we used OLS regression.

All underlying assumptions of statistical tests were met, following log transformation where appropriate. All analyses were conducted in R version 2.8.1 (R Development Core Team 2008) and all null hypotheses were rejected for $P < 0.05$.

RESULTS

Natural communities

The species richness of the six benthic invertebrate communities sampled in Palau (Table S1) was high, ranging from 117 to 291 species (Witman *et al.* 2004; Fig. 2). These communities were dominated by sponges, Cnidarians (especially scleractinian corals and octocorals) and Ascidians, although members of nearly all sessile invertebrate phyla were also present. The species richness observed on four Alaskan rock wall communities was considerably lower, ranging in richness from 50 to 71 species (Fig. 2), and characterized by barnacles, bryozoans and hydrozoans, interspersed with dense aggregations of the anemone *Metridium senile*.

In both Palau and Alaska, regressions indicate a strong positive relationship between flow rates and local species richness, with flow explaining 55 and 91% of the variance in richness in Palau and Alaska, respectively (Fig. 2). In Alaska, species richness

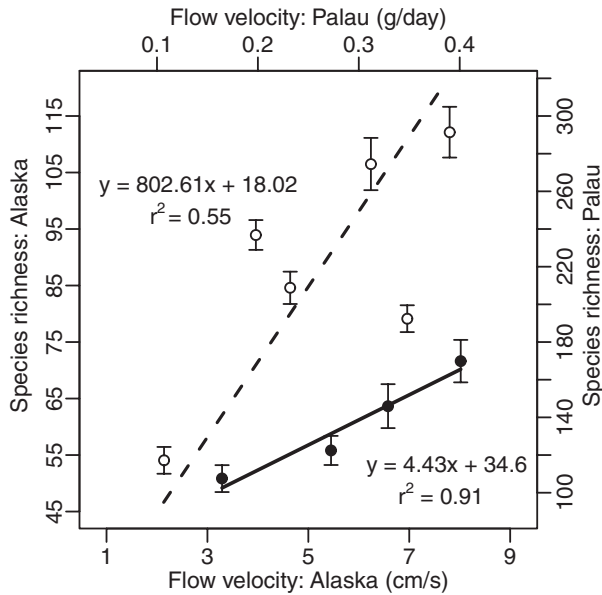


Figure 2 Flow increases the diversity of natural communities. Local species richness (Chao2 ± SEM) of subtidal benthic invertebrate communities significantly increases with flow velocity in Alaska (●) and Palau (○) (Alaska: OLS regression, $P = 0.02$; Palau: MA regression, $P = 0.04$). Flow was determined by an S4 current meter in Alaska and the dissolution of plaster blocks in Palau.

increased by an average of 4.4 species for each 1 cm s^{-1} increase in flow velocity between 3 and 8 cm s^{-1} ; such a comparison in Palau is not possible, due to the use of plaster flow blocks to measure relative flow rates.

Experimental communities

Flow

Mean ambient flow rates at the four experimental sites varied from 5 to 33 cm s^{-1} , with flow rates at Jakolof < Seldovia < Kittery < York. At all sites, flow through the enhanced treatment was significantly faster than flow through the control treatment, with an average increase of 55% (Figure S1). We tested for differences in the ratio of turbulence to flow velocity among sites and flow treatments but found none (LR test: $\chi^2 = 4.68$, $P = 0.09$; Table S2).

Species density and richness

Open space on settlement plates decreased rapidly at all sites in both 2006 and 2007 deployments. Early settlement was dominated in Alaska by the barnacle *Semibalanus balanoides*, and in Maine by the hydrozoan *Ectopleura larynx*. In both years, sessile invertebrates covered > 70% of all settlement plates and > 90% of the vast majority of plates by 15 weeks. Importantly, the settlement substrate did not appear to limit the ability of a diverse suite of invertebrates to settle: a minimum of six sessile invertebrate phyla (Porifera, Cnidaria, Mollusca, Annelida, Arthropoda, Bryozoa and Chordata) was observed at all survey sites within 15 weeks of deployment. Moreover, with the exception of bryozoans on barnacle tests, no three-dimensional settlement was observed.

Experimental results show that increasing water flow increases species density in benthic invertebrate communities. At all sites and times, average species density (i.e. number of species per settlement plate) was higher in enhanced flow than in control flow, with an average increase of 69% in 2006 (LR test: $\chi^2 = 361.60$, $P < 0.01$; Figure S3; Table S3) and 46% in 2007 (LR test: $\chi^2 = 379.38$, $P < 0.01$; Fig. 3; Table S3). In both 2006 and 2007, the absolute difference in species density between enhanced and control flow treatments increased with time until at least 15 weeks at all sites. Thereafter, the absolute difference in species density remained relatively constant with an average of 3.3 additional species on settlement plates in enhanced flow at 30 and 45 weeks (Fig. 3; Figure S3).

Species richness was higher in the enhanced flow treatment at all sites and sampling periods, with an average increase of 74% over richness in the control treatment (Fig. 4; Figure S4). This difference in species richness between flow treatments was maintained for over 45 weeks at all sites (2007 deployment) and over 100 weeks during the 2006 deployment at Seldovia (Fig. 4; Figure S4). The absolute difference in species richness between enhanced and control flow treatments was greatest at Jakolof (Fig. 4;

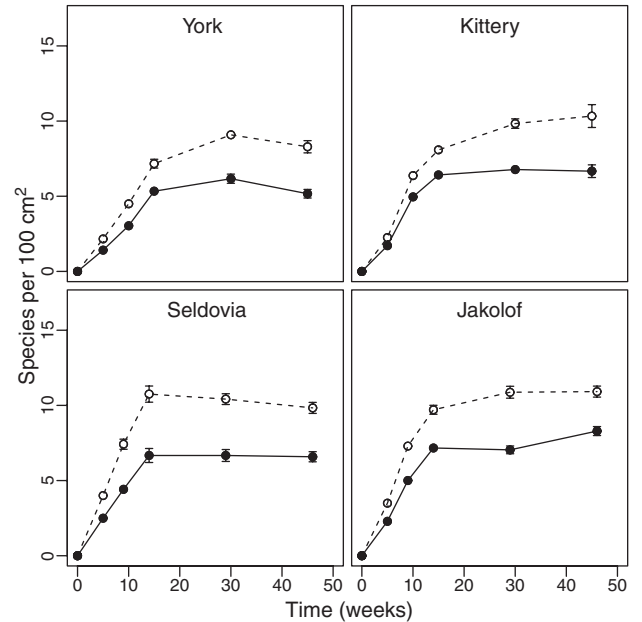


Figure 3 Species density increases with flow. Species density (average number of species per $100 \text{ cm}^2 \pm \text{SEM}$) was higher on settlement plates exposed to enhanced (○) flow than on plates exposed to control (●) flow treatments at sites in Maine (York, Kittery) and Alaska (Seldovia, Jakolof) in 2007. Effects of site, flow treatment and time are statistically significant. All $n = 24$. Statistical results are shown in Table S3.

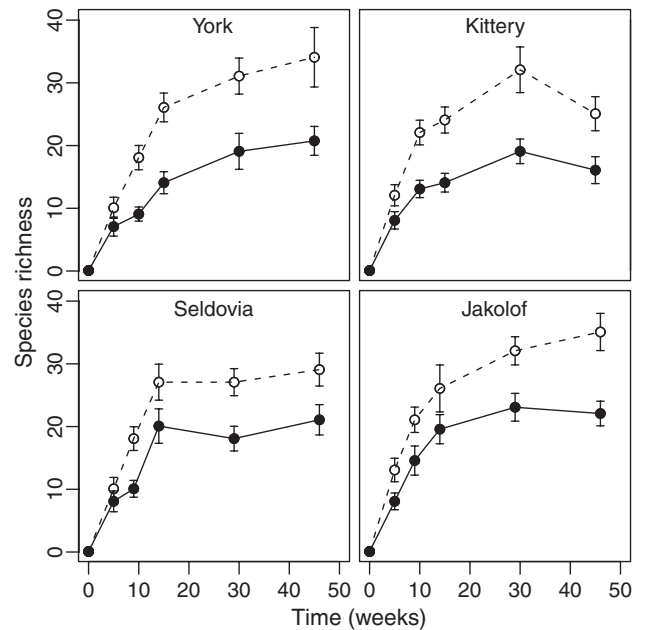


Figure 4 Local species richness increases with flow. Local species richness (Chao2 ± SEM) on settlement plates exposed to enhanced flow (○) was higher than on settlement plates exposed to control flow (●) at sites in Maine (York, Kittery) and Alaska (Seldovia, Jakolof). Error bars represent standard errors of the mean number of species added, and overlap on only two occasions: 5 weeks at York and 5 weeks at Seldovia. All $n = 24$.

Figure S4), the site with the slowest flow velocity (Figure S1), suggesting that the relative influence of increased flow is greatest at sites with low flow rates.

After 45 weeks of community development, species density on settlement plates within the control flow treatment of flow enhancers at Seldovia and Jakolof was 6.6 ± 0.3 and 8.3 ± 0.3 species per 100 cm^2 , respectively (Figure S2). These values fell within the range of species densities on settlement plates deployed on nearby rock walls

after 40 weeks (range: 6.3 ± 0.3 to 8.7 ± 0.8 species per 100 cm^2 ; Figure S2). Likewise, rarefied local species richness of control flow settlement plates (for $n = 10$ settlement plates) within flow enhancers (Seldovia: 22.1 ± 2.4 ; Jakolof: 23.2 ± 2.0) fell within the range observed on settlement plates deployed on rock walls (range: 19–28 species) (Figure S2).

Growth and recruitment

There was no difference in aggregate community growth rates between control and enhanced flow treatments (LR test: $\chi^2 = 1.00$, $P = 0.61$; Table S4), despite observing higher individual growth rate in the enhanced flow treatment for barnacles (LR test: $\chi^2 = 17.91$, $P < 0.01$; Table S4). Additionally, with the exception of short-term saturation caused by the hydrozoan *E. larynx* in Maine (week 5 in 2006, week 10 in 2007), complete plate coverage did not occur. Instead, minimal free space (normally $3.0\text{--}5.0 \text{ cm}^2$) was available, which allowed recruitment to occur between all sampling periods.

To test the hypothesis that differences in species richness resulted from differential recruitment between flow treatments, we calculated the number of species recruiting into open space on all plates at all sampling periods, correcting for available free space. At all sites and times, the richness of recruiting species was greater in enhanced flows than in control flows (Fig. 5). Averaged across all sampling periods and sites, recruitment was 46% more speciose in the enhanced flow treatment than in the control flow treatment (LR test: $\chi^2 = 213.36$, $P < 0.01$; Fig. 5; Table S5).

Rare species and richness

In both Alaska and Maine, rare species accounted for a substantial proportion of observed diversity. Across sites during the 2007 deployment of flow enhancers, singleton and doubleton species (i.e. those species that appeared on only one or two settlement plates) accounted for an average of 20.8 ± 2.3 and $28.8 \pm 1.6\%$ (average \pm SEM) of species richness on control and enhanced flow settlement plates, respectively.

To test the hypothesis that species density and richness increased with the number of rare species, we regressed the difference in species density and richness between flow treatments (i.e. enhanced – control) against the difference in (a) the average number of rare species (defined as $< 3\%$ cover) and (b) the increase in the number of singleton and doubleton species, between flow treatments (Fig. 6). Increased numbers of rare species in enhanced flow explained 38 and 47% of the variance in species density and richness, respectively (Fig. 6). Notably, the estimated slope of the regression line in both cases is within error of 1.0.

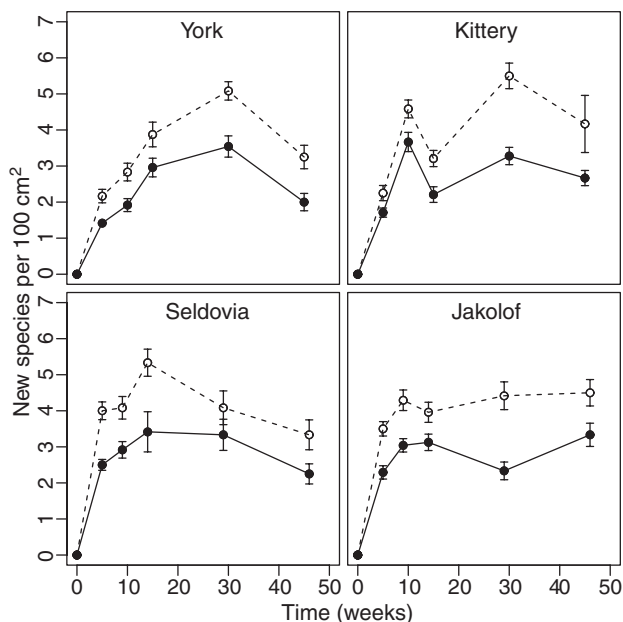


Figure 5 Species richness of recruits increases with flow. The species richness of newly recruited invertebrate species (average number per plate \pm SEM) was higher on plates exposed to enhanced flow (○) than on plates exposed to control (●) flow treatments at sites in Maine (York, Kittery) and Alaska (Seldovia, Jakolof) in 2007. Effects of flow treatment, site, the interaction of site and flow treatment, and time are statistically significant. All $n = 24$. Statistical results are shown in Table S4.

DISCUSSION

Patterns of community diversity

Our results indicate that the assembly and maintenance of diversity within epifaunal invertebrate communities is strongly affected by flow. Across observational sites and experimental deployments, communities exposed to higher flow exhibited higher species density and richness values. As such, the data support our hypothesis that increased flow rates lead to increased levels of community diversity that are stable through time.

Survey results from Palau and Alaska strongly suggest that increased flow leads to an increase in the number of species found in the local community (Fig. 2). Moreover, the predictive power of flow on species richness was strong, with water velocity explaining 55 and 91% of the variability among sites in Palau and Alaska, respectively. Like previous observations of invertebrate communities in mountain streams (Hawkins *et al.* 1982) and octocorals on coral reefs (Fabricius & De'ath 2008), these surveys provide compelling evidence that flow is positively related to the species richness of natural benthic invertebrate communities. However, they cannot indicate causation, mechanism, nor the speed at which these patterns may become apparent in nature. Moreover, our inability to adequately replicate within-site flow measurements in Palau allows for ambiguity. Our experimental data, however, provide strong evidence that flow plays a direct and important role in determining the local species richness of benthic invertebrate communities, and establishes the mechanisms involved.

Experimental data demonstrate that flow velocity is a vitally important determinant of species richness. As both species density (+56%) and species richness (+74%) were greater in enhanced flow treatments at all of our sites, for both the 2006 and 2007 experimental deployments, the effect of flow on diversity appears to be strong and repeatable in space and time (Figs 3 and 4; Figures S3 and S4). Moreover, because species density and richness values observed within the control flow treatment at sites in Alaska were within the range of values observed on settlement plates deployed on nearby rock walls (Figure S2), these results do not appear to be the result of experimental artefacts that decrease diversity under low flow conditions.

In addition to being repeatable in space and time, our data indicate that the effect of flow on diversity is robust across multiple spatial scales. First, the effect is robust among sites: site-level species richness scaled linearly with flow rate within both Palau and Alaska (Fig. 2). Second, the effect of flow on species richness is robust within sites: at all four experimental sites, species richness in experimentally enhanced flow was higher than species richness in control flow (Fig. 4; Figure S4). Third, the effect is robust at the scale of species interactions: within sites (and flow enhancer within site), average species densities on $10 \text{ cm} \times 10 \text{ cm}$ plots were higher in enhanced flow than in control flow (Fig. 3). As such, the effects of flow on diversity are measurable from the scale of settlement plates (centimetres) to sites within a region (kilometres).

The effect of flow on biodiversity is also manifested in three biogeographic regions and across a wide range of flow velocities. As the effect of flow on diversity was manifested in regions with high (Palau), moderate (Alaska) and low (Maine) species pools (Witman *et al.* 2004), the positive relationship between flow velocity and diversity appears robust to global variation in regional species pools. Finally, although species richness is likely to decrease beyond some threshold flow velocity because of difficulty settling (Abelson & Denny 1997; Jonsson *et al.* 2004) or feeding (Eckman & Duggins 1993; Johnson & Sebens 1993), such a point was not reached at any of our sites. Peak flow rates (during spring tides) in excess of 50 cm s^{-1} at experimental sites in Maine and survey sites in Alaska did not appear to have a negative impact on species richness. Consequently, the evidence that flow plays an important role in determining the diversity of benthic marine communities is compelling: the effect is repeatable in time, occurs in observational and experimental data, is robust across spatial scales, the richness of regional species pools, and is visible across wide range of flow velocities.

Mechanism

To determine the mechanism behind our observations, we measured aggregate growth of all species within experimental communities, and the growth rate of solitary barnacles (i.e. those not surrounded by conspecifics). Despite the fact that the individual growth rate of barnacles was higher in the enhanced flow treatment (Leonard *et al.* 1998), as was the frequency of barnacle hummocking (Bertness *et al.* 1998), aggregate community growth rates between flow treatments was not different. This suggests that competition within species may be higher than competition among species within these communities (Connell 1983), and/or that the growth rates of species did not respond uniformly to increases in flow rates (Eckman & Duggins 1993). In either case, the data do not support the hypothesis that differential growth rates (Huston 1979) or competitive exclusion (Connell 1961) created differences in diversity between flow treatments.

During all sampling periods, the richness of species recruiting onto experimental plates was higher, by an average of 46% across all sites and times. Consequently, our data support the hypothesis that the positive relationship observed between water flow and species density and richness (Figs 3 and 4; Figures S3 and S4) is the result of an

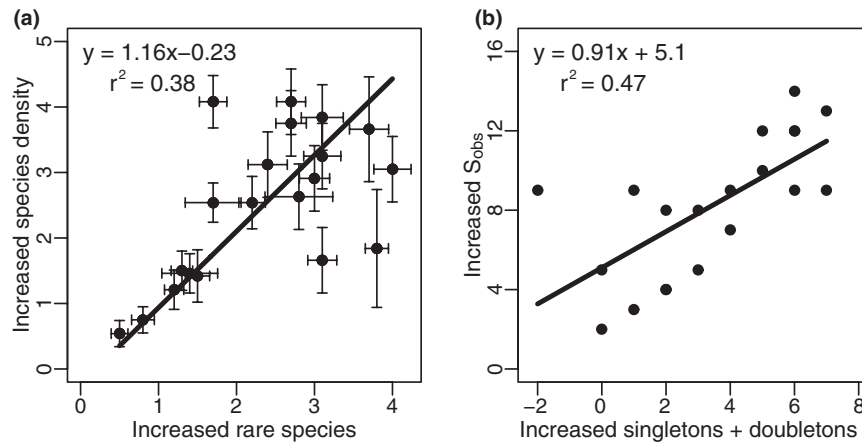


Figure 6 Effects of rarity on total species density and richness. Differences in total species density and richness between flow treatments (i.e. enhanced flow – control flow) are predicted by the difference in rare species density and richness. (a) An increase in the average number of rare species (< 3% cover) present in enhanced flow treatments (\pm SEM) predicted increased average species density (\pm SEM) (MA regression, $n = 20$, $P < 0.01$). (b) Using another measure of rarity, the increase in the number of singletons and doubletons in enhanced flow treatments predicts increases in observed species richness (OLS regression, $n = 20$, $P < 0.01$).

increased number of species recruiting in enhanced flow (Fig. 5). Moreover, because the species density of recruits was higher in the enhanced flow treatment at all sites and times (Fig. 5), it is likely that the increased richness observed with increased levels of flow is stable through time, a prediction consistent with both survey observations (Fig. 2), and experimental results at one site through 100 weeks (Figures S3 and S4).

In both Alaska and Maine, singleton and doubleton species accounted for a substantial proportion of observed diversity. As the majority of species in ecological communities are rare (Preston 1948; Magurran 2004), we hypothesized that species density and richness increase with flow because of an increase in the number of rare species. At the scale of both settlement plates and site, an increase in the number of rare species present in the sample led to an increase in species observed, at a rate within error of 1 : 1 (Fig. 6). As such, our results strongly suggest that increasing flow velocity results in increased recruitment rate of species (Fig. 5), generating greater species density (Fig. 3; Figure S3) and richness (Fig. 4; Figure S4). As such, the delivery of propagules by flow may provide a mechanism for the observation that the species richness of benthic communities and recruits is tightly correlated (Smith & Witman 1999). Moreover, our observations are consistent with modelling results which have shown that increasing immigration rates increase diversity by disproportionately increasing the number of rare species present in a community (Zillio & Condit 2007).

Although our data indicate that flow drives marine benthic diversity by increasing the recruitment rate of rare species, determining why this is so requires further study. One possibility is that rare marine epifaunal species may be poor dispersers, as observed in rare species from other systems (Gaston 1994). If this is correct, the relative abundance of rare species in enhanced flows may be explained by increased passive dispersal. By increasing dispersal distance, flow would increase the dispersal range size of rare species, and thereby increase connectivity among distant sites within the meta-community. As such, high flow areas may be analogous to landscape corridors that connect fragmented terrestrial habitat. Such corridors have been shown to increase native species richness at large scales (Damschen *et al.* 2006). However, because of the paucity of data on dispersal distances of marine epifaunal invertebrate species (Levin 2006), particularly for rare species, further research is required to test this hypothesis.

Our results have several important implications for ecological theory and conservation. First, the data support the hypothesis that local diversity is commonly open to enrichment from a diverse pool of propagules at some spatial scale larger than that of the local habitat (Harrison & Cornell 2008). Flow-driven propagule dispersal may be a mechanism to link local sites to the regional species pool. Second, while 'supply sided' thinking has been incorporated into population biology within species (Hughes *et al.* 2000), our results underscore the need for investigations of the supply sided influences of flow on the assembly, maintenance and resilience of diversity in local and meta-communities (Leibold *et al.* 2004). Third, as the richness of both resident and recruiting species increased with water velocity, flow may serve as a reliable indicator of areas susceptible to species invasion.

Because it has been strongly linked to the ability of ecosystems to provide a suite of ecosystem services (Hooper *et al.* 2005; Worm *et al.* 2006), one of the most urgent needs in ecology is to develop a better understanding of the processes that regulate biodiversity. With experiments and surveys in three different biogeographic regions, we have shown that the diversity of marine communities is strongly related to water flow through increased recruitment rate of rare species. As such, our data provide a fundamental contribution to understand the forces that shape patterns of aquatic diversity in space and time. As flow velocity has a large influence on species richness

and density, it should be considered in future developments of diversity theory. Moreover, as it is easily measured it should be incorporated into the implementation of conservation practice.

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SUPPORTING INFORMATION

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

- Figure S1** Average flow rates in enhancers.
- Figure S2** Species density and local species richness on settlement plates deployed on rock walls and within the control flow treatment of experimental flow enhancers.
- Figure S3** Species densities within flow enhancers in 2006.
- Figure S4** Species richness within flow enhancers in 2006.
- Table S1** Names and locations of all study sites.
- Table S2** Effects of flow on turbulence.
- Table S3** Effects of flow on species density.
- Table S4** Effects of flow on growth rates.
- Table S5** Effects of flow on the species richness of recruitment.

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