

Habitat and bathymetry influence the landscape-scale distribution and abundance of drift macrophytes and associated invertebrates

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Abstract

We used a remotely operated vehicle to investigate landscape-scale patterns of subtidal drift material and invertebrates within a 60-km² marine basin in Washington State. Specifically, we quantified the distribution and abundance of drift macrophytes (seaweed and seagrass) and four macroinvertebrate species across depth and habitat type to depths of 170 m. Drift macrophytes were present on 97% of all video segments deeper than 30 m, with large drift piles particularly associated with low-angle habitats at depths exceeding 70 m. Two commercially harvested species (*Strongylocentrotus franciscanus* and *Pandalus platyceros*) that feed directly on drift material appear to be distributed in space (depth and substrate type) so as to maximize access to drift macrophyte food resources, according to their respective feeding modes. Basin shape and depth drive the landscape-scale distribution of drift material and indirectly the consumers that feed on it. The export of large amounts of detritus derived from nearshore macrophyte production into deep-water habitats likely fuels extensive secondary production in these aphotic zones.

Nearshore macrophyte production contributes a substantial amount of carbon to high-latitude marine ecosystems. Much of this production is exported as macroscopic detritus (i.e., drift) to adjacent deeper, aphotic habitats (Mann 1988; Okey 2003). Despite the absence of endogenous carbon sources, these deep subtidal environments (DSE) often support considerable secondary productivity (Vetter 1995; Vetter and Dayton 1999; Britton-Simmons et al. 2009) and are a key source of commercial fisheries worldwide (Food and Agriculture Organization 2007). However, subtidal population and process-focused studies are typically constrained to depths accessible by divers and to relatively small spatial scales. In the present study, we examined the landscape-scale distribution and abundance of drift macrophytes and select invertebrates within the San Juan Archipelago (SJA), a 60-km² marine basin, in Washington State.

Subtidal drift macrophytes in our system are produced by a diverse assemblage of nearshore seaweeds and seagrasses that diminish in abundance below 18 m and become rare by 23-m depth (Britton-Simmons et al. 2009) due to light limitation. Most subtidal drift biomass is contributed by kelps (order Laminariales) with substantial contributions also made by orders Fucales and Desmarestiales. Seagrasses (mostly *Zostera marina*) are present in the drift but contribute relatively little to biomass (Britton-Simmons et al. 2009). Drift material is an excellent food resource since it tends to have elevated levels of nitrogen (Mann 1988) and diminished levels of defensive chemicals (Duggins and Eckman 1997). This resource could be important for driving marine secondary productivity in

DSE, but we know little about its distribution among depths and habitat types within DSE. Moreover, we need key information about where this material is distributed relative to the taxa that could be using it (Suchanek et al. 1985; Vetter and Dayton 1999; Okey 2003). Recent evidence suggests that trophic linkages between drift sources and recipient species can operate at kilometer scales (Kirkman and Kendrick 1997; Vanderklift and Wernberg 2008), highlighting the importance of a landscape approach to this phenomenon.

Like many marine animals, several commercially important species in our system have very large vertical distributions that span both photic and aphotic (DSE) zones and a wide range of habitat types. For example, red urchins (*Strongylocentrotus franciscanus*), which are harvested in Washington State (Pfister and Bradbury 1996), can be found from depths of 2–200 m (pers. obs.). Harvesting of red urchins is accomplished by divers primarily at depths of 15 m or less, but the deep fraction of the population shows no diminished fecundity (Britton-Simmons et al. 2009) and probably contributes substantially to the larval pool that repopulates all depths. The trophic ecology of red urchins has been studied in this region for decades (Vadas 1968), yet virtually everything we know about this animal comes from shallow depths. Likewise, little is known about the distribution and trophic ecology of most other organisms in DSE.

The subtidal zone in the SJA is a heterogeneous mosaic of habitat types including rocky and soft sediment substrates of varying slopes. Different substrates are likely indicative of different hydrodynamic regimes (e.g., mud will not persist in high-current areas) and are occupied by different species (Gogina and Zettler 2010); they may also vary in the availability of drift material. The focal invertebrates in our study represent distinct feeding modes that could use drift directly (herbivorous sea urchins) or

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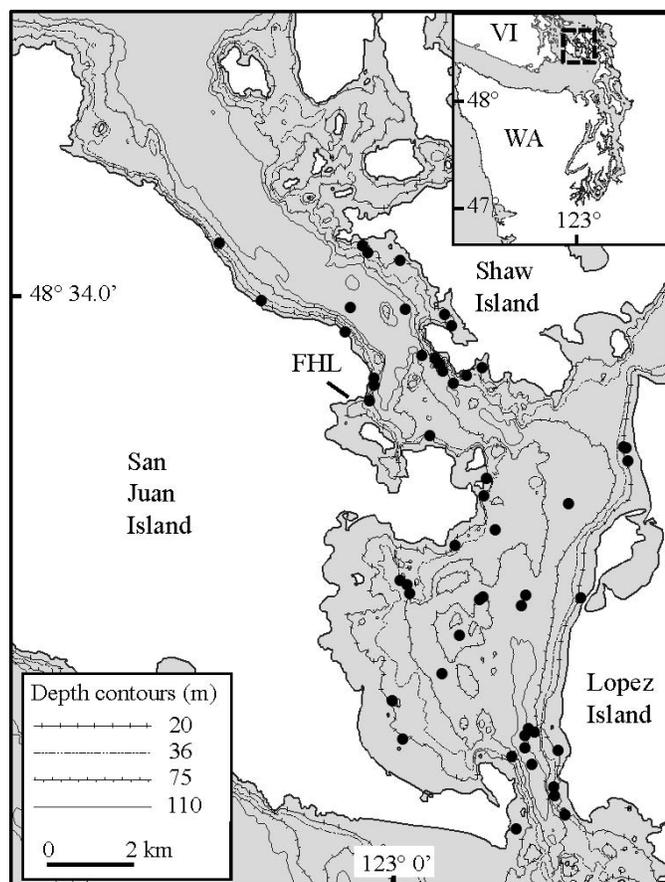


Fig. 1. Map of San Juan Channel, Washington, with bathymetric depth contours. ROV transects were conducted at locations marked by black dots. Large-scale inset shows location of San Juan Islands between Vancouver Island (VI), Canada, and mainland Washington State (WA). FHL, Friday Harbor Laboratories.

indirectly (detritivorous prawns and sea cucumbers and carnivorous sea stars). Three of the four species we studied are commercially harvested. The associations of these consumer taxa with drift material have not previously been investigated at the scale of our study.

Although macrophyte-derived carbon exists in a size continuum ranging from dissolved organic matter to entire thalli, the focus of our study is the larger macroscopic fraction. We used remotely operated vehicle (ROV) surveys to study the patterns of distribution (down to 170-m depth and in different habitat types) and abundance of these four invertebrate species with (1) depth, (2) habitat type, and (3) each other.

Methods

Description of study area—The SJA is an inland sea in the northern part of the Puget Trough (Fig. 1). The area is protected from outer coast swells; storm waves can be important during fall and winter, but their effect is localized in space and time (Eckman et al. 2003; K. Britton-Simmons and H. Stewart unpubl.) and restricted to the shallowest depths in this study (< 20 m; Eckman et al.

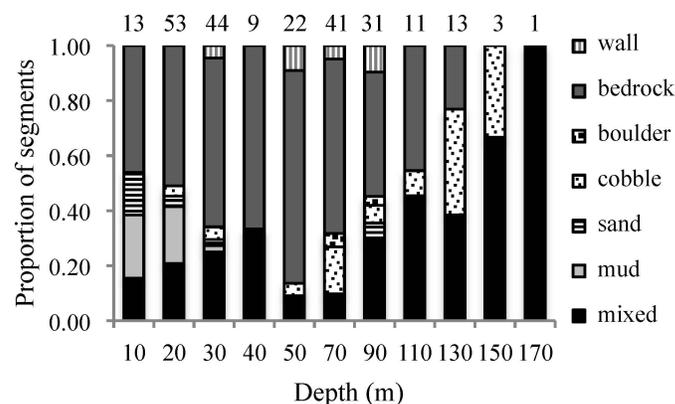


Fig. 2. Distribution of ROV video segments across depth and habitat type. Numbers above each bar are the number of replicates in each depth bin. Total replicates for invertebrates is 241, total number of macrophyte replicates is 130 (drift macrophytes were not counted in the 10-, 20-, and 30-m-depth bins).

2003). The oceanography of the basin is well studied but complex (see review by Thomson 1994); the dominant hydrodynamic forces are tidally generated currents that occur at all depths and can exceed 100 cm s^{-1} (Eckman et al. 2003; Britton-Simmons et al. 2008) and surface freshwater discharge from the Fraser River in Canada. This current-dominated study region is representative of hundreds of miles of similar inland marine waterways in the northeastern Pacific.

The marine basins of the SJA (Fig. 1) are bathymetrically complex. Channels are fairly steep sided, often with vertical or sloped bedrock in shallow waters transitioning to unconsolidated substrate types at depth (Fig. 2). Habitat types are diverse and include mud, sand, cobble, boulder, bedrock, rock wall, and mixed-substrate bottom types (Fig. 2). The focal survey area (San Juan Channel) was selected based on the availability of high-resolution bathymetric habitat maps for this region (G. Greene unpubl.). Detailed maps were used to randomly select sites that covered a broad spatial area and represented all available habitat types seen in prior ROV and dredge surveys (Pacunski et al. 2008).

Acquisition of ROV video in field—Surveys from 4- to 131-m depth were conducted between 30 September and 20 October 2004 using a Deep Ocean Engineering Phantom HD2+2 ROV (Pacunski et al. 2008). The ROV was equipped with six thrusters and a Sony EVI-330 high-resolution color zoom camera with tilt capability. Camera angle was fixed at 45° during surveys, optimizing seafloor coverage while providing the driver with an adequate view. Two 15-mW red lasers (DeepSea Power and Light) aligned at a separation distance of 10 cm were mounted on top of the camera housing to provide a reference scale that was used to estimate object sizes and field of view width during video analysis. Light was supplied by two 250-W floodlights (DeepSea Power and Light).

The ROV pilot received heading ($\pm 1^\circ$) and depth ($\pm 0.65 \text{ m}$) information from a fluxgate compass and pressure

sensor within the ROV housing. The georeferenced position of the ROV was calculated with Hypack[®] Max navigational software linked to a Wide Area Augmentation System-enabled Northstar 952 differential global positioning system and KVH Industries Azimuth[®] 1000 digital fluxgate compass. The ROV was tethered to the support vessel via a 240-m-long, 32-conductor, neutrally buoyant tether that provided power, control, video, and data transmission between the ROV and the control console. Video data were recorded to digital Hi-8 videotape for subsequent analysis. Time, date, and calculated ROV global positioning system (GPS) location were imprinted on the video footage using a Pisces Design video-text overlay system.

On transects conducted at depths less than 30 m, the ROV tether was hand managed from the deck of the boat. For deeper transects, the ROV tether ran from the deck, down a cable to a 185-kg clump weight suspended below the vessel and maintained several meters above the bottom. In this arrangement, the ROV was free to explore the substratum within a fixed radius (determined by the amount of tether) of the clump weight, and the vessel followed the ROV from above as it swam the transect. See Pacunski et al. (2008) for further technical details on ROV equipment and survey protocol.

Analysis of ROV video—Each site ($n = 61$; Fig. 1) was surveyed with one video transect. Preliminary examination of a subset of the videos showed that one transect often encompassed several depths and habitat types. To account for this variation, we further subdivided each transect into analysis units (segments) that were uniform in terms of predefined depth zone and habitat-type characteristics (e.g., Fig. 2). Numbers of replicate segments per transect ranged from 1 to 11. Within the shallow zone, where light attenuation is rapid (Britton-Simmons 2004) and benthic community composition varies with depth (Neushel 1967; Britton-Simmons et al. 2009), we binned depth at 10 m intervals (Fig. 2). That interval was increased to 20-m intervals below 50 m, which is well below the photic zone (~ 30 m) in this system. We identified seven habitat types that could be reliably identified on ROV video footage (Fig. 2): rock wall (vertical), bedrock (various angles but not vertical), boulder, cobble, sand, mud, and mixed (gravel, sand, and shell hash).

Prior to quantitative analysis, each ROV video was briefly previewed at high speed to quickly identify in advance where the habitat or depth changes (and therefore segment boundaries) occurred. Segment lengths were not uniform, as a transition in either depth bin or habitat type triggered the creation of a new segment. All video analysis was done by one person to minimize sampling error. Within each segment, the viewer collected data on the numbers of pieces (*see below*) of drift macrophytes and counts of individuals of select invertebrate species (hereafter referred to by genus only): *S. franciscanus* (red urchin, herbivore or detritivore), *Parastichopus californicus* (sea cucumber, detritivore or deposit feeder), and *Pycnopodia helianthodes* (sea star, predator). *Pandalus platyceros* (spot prawn, detritivore) were assessed on a semiquantitative

scale (absent, present [≤ 25 per segment], common [> 25]) because individual enumeration was not feasible.

Red laser dots on video footage allowed the viewer to assess the size of macrophyte detritus. We subdivided macroalgal drift into two size categories: large (> 0.25 m²) vs. small (25 cm² $\leq X < 0.25$ m²) pieces. Pieces smaller than 25 cm² could not be seen reliably. All *Z. marina* detritus 25 cm in length (~ 25 cm²) or larger was counted. Assuming an average blade width of 1 cm (*S. Wyllie-Echeverria* pers. comm.), the smallest *Z. marina* blade counted is approximately equal in area to the smallest algal detritus counted. In some discrete locations on the ROV video footage, there were large quantities of macrophyte detritus, often with many pieces piled on top of one another so that it was not possible to accurately count them. We operationally defined these locations as drift piles and recorded their number and GPS coordinates.

During video analysis, the viewer used the scale lasers to measure the width of field of view once per minute. The average of these width measurements within a segment was multiplied by the segment length to calculate total segment area. Segment length was determined from the tracking data acquired by the navigation software and smoothed in ArcView geographic information system (GIS) Software. Segment lengths were taken directly from ROV GPS track lines using ArcView GIS software where possible. Persistent problems with the Trackpoint acoustic tracking system resulted in bad or missing ROV GPS position information on some transects. For those, the GPS track line of the vessel was used as a proxy for the ROV track line when calculating segment lengths. Because the ROV sampling methodology employed in this study keeps the ROV in close proximity to the vessel, the ROV track line should be very similar to that of the vessel.

ROV footage that did not meet minimum quality standards was not analyzed. This included video where the ROV was not moving in a straight line, when the ROV was changing depth rapidly, and when visibility was too poor to see target organisms.

Slope angle analysis—To further understand landscape-scale bathymetric influences on the density and distribution of drift macrophytes in our study area, we conducted bathymetric survey transects within a GIS framework (ESRI ArcMAP). We selected 20 random latitude start points within the bounds of our ROV survey area, 10 each on the eastern and western San Juan Channel shorelines. Bathymetric transects ran perpendicularly from the shore to the deepest point of the channel directly offshore. On each transect, we recorded the surface (straight line) distance between each 10-m isobath and used the arctan function to estimate slope angle between each isobath.

Statistical analyses—To test for associations of drift types and invertebrate densities with each other and with depth, we employed parametric statistics (linear and polynomial regressions) where possible but Spearman rank correlation tests when normality could not be achieved even after transformation (arcsin-square root for proportions and ln for counts). We tested for differences of drift

type among benthic habitat types with a two-way analysis of variance (ANOVA). To analyze the relationships of individual invertebrate species with habitat types, the large number of zeros precluded the use of ANOVA; in those instances, we used Kruskal–Wallis nonparametric tests (with post hoc test as described by Zar [1999]). The categorical densities of *Pandalus* were analyzed with contingency tests to examine patterns with depth and habitat type.

Results

The use of ROV technology allowed unprecedented access to deep SJA habitats but imposed some constraints. Juvenile (< 5 cm) invertebrates are difficult to find even during SCUBA surveys (pers. obs.) and are not reliably visible on ROV footage. In addition, in shallow water (< 30 m), “prostrate” kelps (primarily *Agarum* and *Saccharina*) are abundant (Britton-Simmons et al. 2009), obscuring small invertebrates on the substrate beneath them. Thus, our analysis is constrained to adults (> 5 cm) of the invertebrate taxa we studied, and our invertebrate counts in the shallowest depth bins (10, 20, and 30 m) may underestimate actual population sizes. The living kelps also made it impossible to differentiate attached from drift macroalgae; thus, drift was not quantified in transects shallower than 30 m.

Habitat—The distribution of segments across depths indicates some variation in sampling effort among depths (Fig. 2) but is generally representative of the distribution of habitat within San Juan Channel. Both shallow, photic environments (≤ 30 m) and deep subtidal environments (> 30 m) were sampled intensively (Fig. 2). The dominant habitat types in this system change with depth with a transition from rocky to unconsolidated bottom types (Fig. 2). Sand was uncommon at all depths, and mud was seen only in shallower depths, in areas presumably protected from tidal currents.

Analysis of bathymetry within our study area suggested a depth-related pattern of slope angle (Fig. 3c). In the seaweed zone (< 25 m), slope angle was typically shallow (< 10°). Intermediate depths were marked by steeper (but more variable) slopes. At depths of 80–110 m, the basin slope angle decreases, indicating a shelflike area at this depth that was present consistently across sites, then steepens again toward the bottom of the channel (Fig. 3c).

Macrophytes—One or more pieces of drift material were present on 97% (124/130) of segments greater than 30-m depth (Fig. 3a). Second-order polynomial regression models best fit the relationships between depth and each of the three macrophyte categories (seagrass, small seaweed drift, large seaweed drift). The plots and model fits were virtually identical for all three macrophyte types (Table 1). Additionally, the densities of seaweed and seagrass drift were strongly linearly correlated, suggesting that the distribution of both drift types is driven by the same processes ($r^2 = 0.69$, $p < 10^{-4}$, $n = 130$). Therefore, we combined the three drift types for all subsequent analyses involving depth.

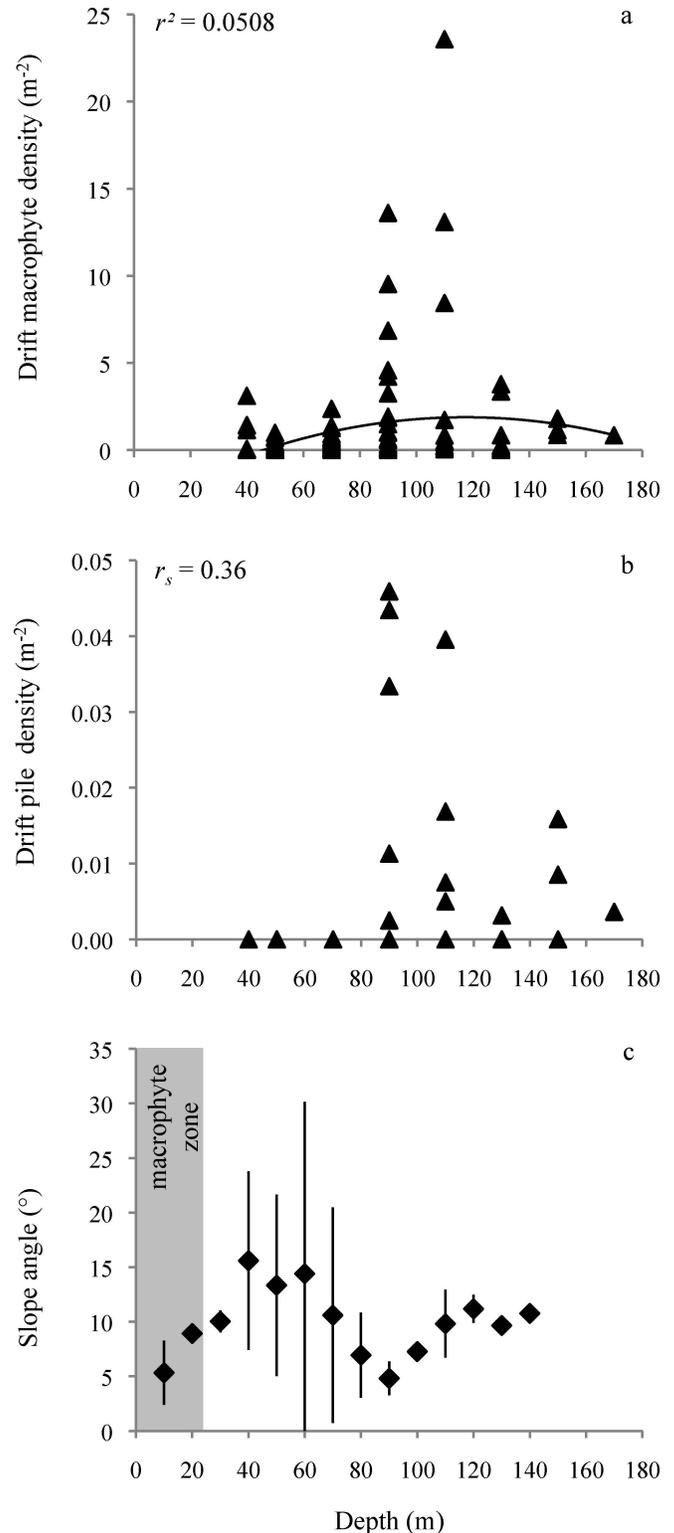


Fig. 3. (a) Drift macrophyte density. The curve indicates the best-fit polynomial regression, $r^2 = 0.051$. (b) Drift pile density. r_s is the Spearman rank correlation between density and depth. (c) Mean basin slope angle as a function of depth. Shaded region of (c) indicates depths at which attached seaweeds and seagrasses are found (means ± 1 SD).

Table 1. Composition of subtidal macrophyte drift material. Data from all ROV video segments are combined ($n = 130$). Regression values are derived from polynomial curves and untransformed data.

Category	No. pieces	Proportion*	Mean density (m^{-2})	Regression with depth (r^2, p)
Seagrass (<i>Zostera marina</i>)†	6976	0.29	0.43	0.04, 0.06
Small seaweed‡	16,743	0.69	0.77	0.05, 0.04
Large seaweed§	664	0.03	0.04	0.05, 0.04
Total	24,383		1.11	0.05, 0.04

* Do not sum to 1.0 because of rounding error.

† > 25 cm in length.

‡ $25 \text{ cm}^2 \leq X < 0.25 \text{ m}^2$.

§ > 0.25 m^2 .

There was a statistically significant relationship between total drift macrophyte density and depth, but the model explains very little variation in macrophyte density ($r^2 = 0.05$, $p = 0.04$, $n = 130$; Fig. 3a).

Most of the drift material was seaweed derived (72% of 24,383 total pieces; Table 1), but sites at the mouth of large bays containing substantial seagrass populations (e.g., Friday Harbor, Griffin Bay) did tend to have proportionally more seagrass detritus than other sites. Ninety-six percent of all seaweed drift was small pieces, and that fraction did not vary with depth (arcsin-square root transformed, $r^2 = 0.01$, $p > 0.2$, $n = 120$). Finally, although the percentage of segments that contained drift was consistently high across depths (range = 88–100%), there was a tendency for this percentage to increase with depth (arcsin-square root transformed, $r^2 = 0.56$, $p = 0.03$, $n = 9$). There was also a positive relationship between depth and the density of drift piles (Spearman rank correlation, $r_s = 0.36$, $p < 10^{-4}$, $n = 130$; Fig. 3b). Drift piles were especially abundant at depths between 70 and 110 m, which is a relatively flat region of this basin (Fig. 3c).

We examined the relationship between drift type (seagrass, large seaweed, small seaweed) and habitat type using a two-way ANOVA. Sand habitat occurred in only two segments below 30 m and was therefore excluded. We found a drift type \times substrate type interaction ($F_{8,369} = 4.84$, $p < 10^{-4}$), indicating that the distribution of drift among habitat types varied among macrophyte types. One-way ANOVA and Student's t post hoc analyses performed on each drift macrophyte type separately indicated two clear patterns: drift density was consistently higher in the mixed-substrate habitat (11/12 post hoc pairwise comparisons), and drift density did not vary significantly among the remaining habitat types in the analysis (bedrock, boulder, cobble, wall; 18/18 post hoc comparisons not significant). These overall patterns are illustrated in the combined plot of all drift types (Fig. 4a).

Invertebrates—Densities of three of the four invertebrates we counted showed relationships with depth. *Strongylocentrotus* (7325 individuals) were present on 46% of segments, and their density was negatively correlated with depth (Spearman rank correlation, $r_s = -0.21$, $p < 10^{-3}$, $n = 241$; Fig. 5a). *Parastichopus* (2590 individuals) were found on 70% of segments and also declined in abundance with depth (Spearman rank corre-

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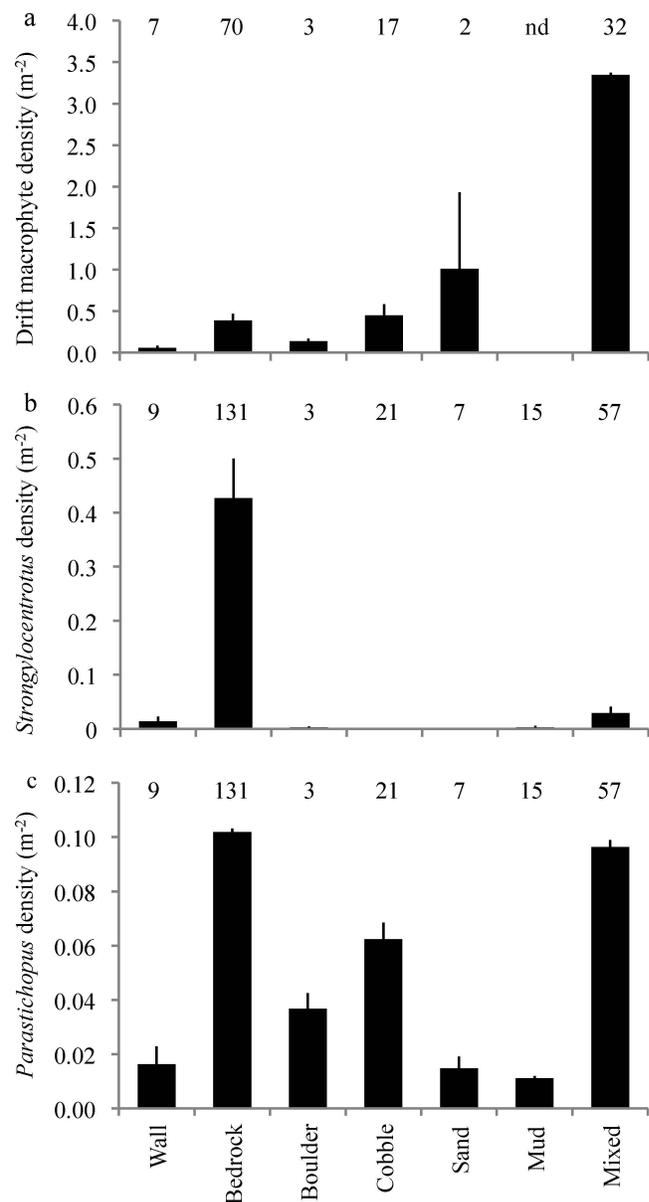


Fig. 4. (a) Distribution of drift macrophytes, (b) *Strongylocentrotus franciscanus*, and (c) *Parastichopus californicus* across different habitat types. Numbers above bars indicate replicates. nd, no data.

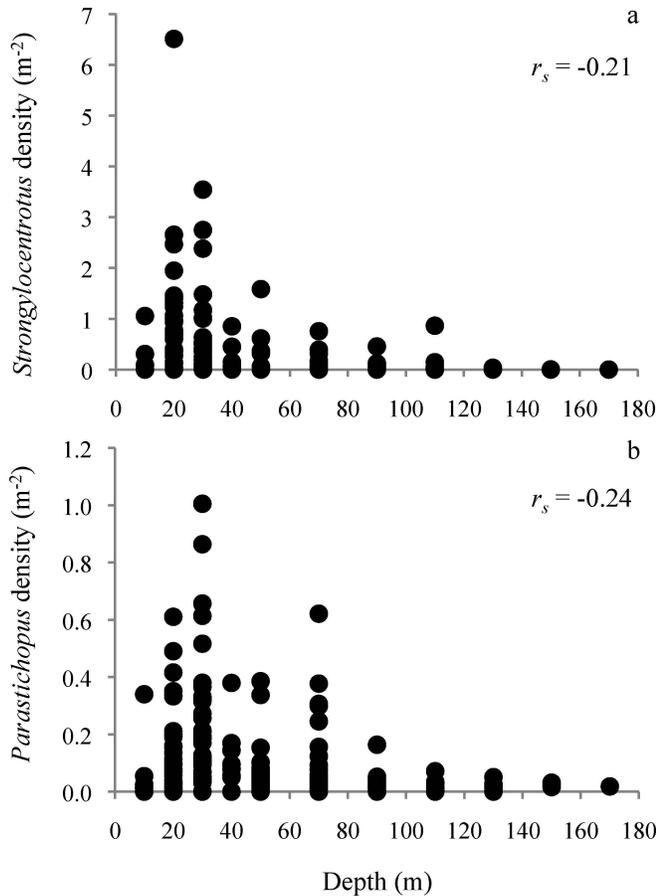


Fig. 5. (a) *Strongylocentrotus franciscanus* and (b) *Parastichopus californicus* density as a function of depth.

tion, $r_s = -0.24$, $p < 10^{-3}$, $n = 241$; Fig. 5b). *Pycnopodia* (261 individuals) occurred on 33% of transects and showed no relationship with depth (Spearman rank correlation, $r_s = -0.07$, $p = 0.28$, $n = 241$). *Pandalus* (spot prawn) were present on only 18% of segments and only at deeper depths (Fig. 6). A contingency test indicated that shrimp abun-

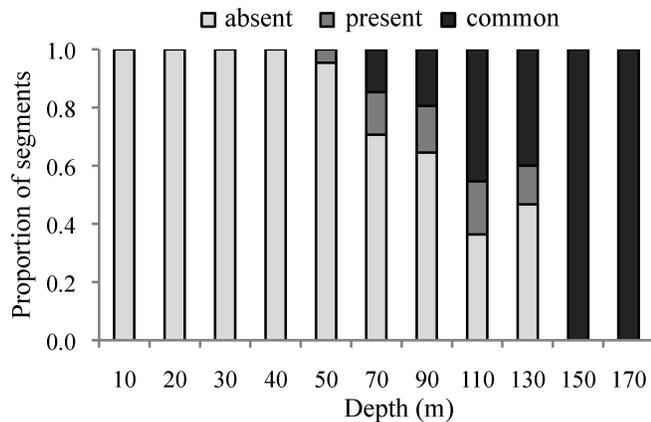


Fig. 6. Abundance of the spot prawn *Pandalus platyceros* across depth. “Present” indicates that 25 or fewer *P. platyceros* were present on the video segment. “Common” indicates more than 25 *P. platyceros* per segment.

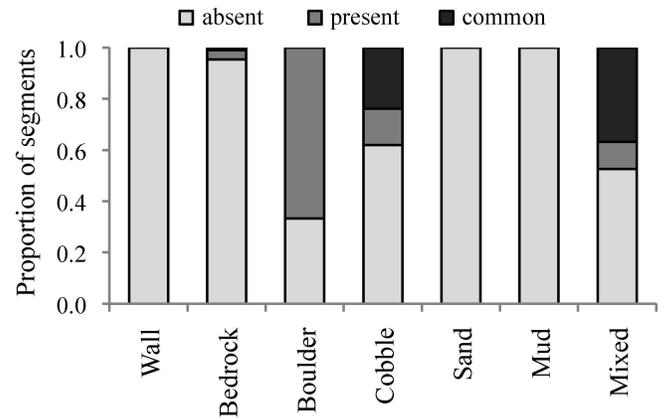


Fig. 7. Abundance of the spot prawn *Pandalus platyceros* in different habitat types.

dance was depth dependent ($\chi^2 = 104.5$, $p < 10^{-4}$, $n = 243$).

There were considerable differences among species in their habitat associations. *Strongylocentrotus* density varied among habitat types (Kruskal–Wallis, $\chi^2_6 = 66.4$, $p < 10^{-4}$; Fig. 4b), and nonparametric post hoc comparisons showed that density was higher on bedrock than on wall, cobble, sand, mud, and mixed habitat ($p < 0.05$ in each case). However, the difference between *Strongylocentrotus* density on bedrock and boulder habitats was not statistically significant ($p > 0.05$), probably because the boulder habitat had only $n = 3$ replicate segments, nor were any of the remaining pairwise comparisons. There was some evidence that *Parastichopus* density varied among habitat types (Kruskal–Wallis, $\chi^2_6 = 18.5$, $p < 0.005$; Fig. 4c), but none of the post hoc comparisons revealed significant differences ($p > 0.05$ in all cases). There was no variation in *Pycnopodia* density among habitat types (Kruskal–Wallis, $\chi^2_6 = 10.0$, $p = 0.12$). *Pandalus* were present in only four habitat types and were common only on cobble and mixed habitats (Fig. 7). A contingency test indicated that shrimp abundance was habitat dependent ($\chi^2 = 88.6$, $p < 10^{-4}$, $n = 243$).

Associations—The invertebrate species in our study varied in their association with drift material. Neither *Strongylocentrotus* (Spearman rank correlation, $r_s = 0.02$, $p = 0.79$, $n = 130$) nor *Parastichopus* ($r_s = 0.04$, $p = 0.67$, $n = 130$) density was correlated with total drift macrophyte density. There was a positive association between *Pycnopodia* and drift density ($r_s = 0.21$, $p = 0.02$, $n = 130$). For *Pandalus*, segments with prawns present (see Methods) had on average 37% more drift than segments with no prawns; segments where prawns were common had seven to nine times more drift than those where prawns were absent or just present (Fig. 8; one-way ANOVA, $F_{2,127} = 29.4$, $p < 10^{-4}$, $p < 0.05$ for all post hoc comparisons). Invertebrates were not clearly associated with each other; *Strongylocentrotus* and *Parastichopus* were not correlated with each other, and neither was correlated with *Pycnopodia* density ($p > 0.2$ in all cases).

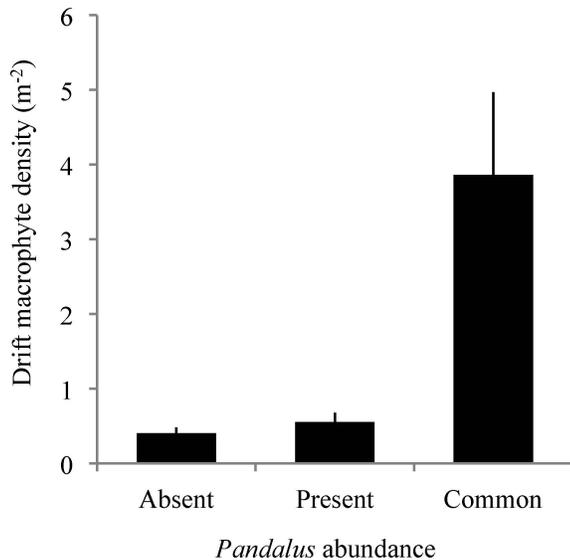


Fig. 8. Drift macrophyte density in segments where *Pandalus platyceros* was absent, present, and common (means \pm 1 SE).

Discussion

Drift macrophytes were ubiquitous in DSE, present on 97% of all video segments where they could be distinguished from attached thalli. Both drift macrophyte density and drift pile density varied significantly with depth (Fig. 3), although depth explained very little variation in the former. In areas shallower than 70 m, drift piles were absent, and drift pieces occurred at low densities. For both response variables, large drift accumulations begin appearing abruptly in the 90-m-depth bin (Fig. 3). We suggest that basin shape and hydrodynamics can account for this distinctive depth-related pattern (Riegl et al. 2005; Kotta et al. 2008). Drift macrophytes are produced at depths of approximately 25 m or less (Neushul 1967; Britton-Simmons et al. 2009). The fraction of macrophyte-derived detritus that is negatively buoyant will have a tendency to sink but will also be transported laterally and repeatedly deposited and resuspended by tidal currents (Biber 2007; Canal-Verges et al. 2010; pers. obs.). Habitats just below the photic zone typically are relatively steep sided and unlikely to accumulate drift material (Fig. 3c). However, habitats in the vicinity of 90 m are spatially invariant in their low slope angle, indicating that relatively flat shelflike areas are common in San Juan Channel at these depths. Our data suggest that these low-angle habitats are key places where drift material accumulates. Similarly, basin depressions and similar features have been recognized as important for trapping drift (Kotta et al. 2008). Dense drift patches are relatively rare, and many flat areas in the deep subtidal have little drift, implying that other factors, such as local hydrodynamics (Kopecky and Dunton 2006), may determine which low-angle shelves concentrate drift material.

To the extent that drift pieces act like passively drifting particles, their nonuniform distribution among habitat types might reflect covarying differences in hydrodynamic

regime (Bell and Hall 1997). For example, within DSE, drift was more abundant in mixed habitat (Fig. 4a), which probably reflects the depositional hydrodynamic regime that created it (mixed habitat includes variable quantities of fine sediment and sand). Mixed habitats tend to have relatively low slope angles, and they were more common at depth, which complicates interpretation of the drift-habitat data. The other clearly depositional habitat, mud, was surveyed only in shallow depths (Fig. 2), where drift could not be quantified. This influence of hydrodynamic regime on spatial distribution of drift macrophytes has been suggested in other systems (Biber 1997; Kopecky and Dunton 2006; Biber 2007), indicating that it may be a general phenomenon.

ROV video surveys provide a snapshot look at the amount of drift present at one moment in time. In ongoing research, we are investigating the temporal patterns of drift abundance at DSE sites from this study that had high and low drift abundance. However, based on hundreds of diver-hours in this system, we know that drift material is highly dynamic. It is constantly being resuspended, transported, and redeposited as current speed and direction change (Holmquist 1997; Biber 2007). The amount of drift on the seafloor at any given moment is essentially an instantaneous net standing stock of drift material that is dependent on the recent net local retention (Witman et al. 2004). For logistical reasons, ROV surveys are timed to coincide with slack or low current intervals, when more drift is typically settled on the seafloor. Therefore, our drift data are best interpreted as a sort of maximum net early autumn standing stock.

Drift seaweeds dominated the macrophytes within DSE (72% of 24,383 pieces); sites with substantial seagrass drift were typically only within or adjacent to bays containing large *Z. marina* beds. Given that the average mass of a seaweed drift fragment is more than 20 times the mass of the average seagrass drift fragment (K. Britton-Simmons and H. Stewart unpubl.), it is likely that seaweed detritus overwhelmingly dominates the drift biomass at all sites, even those where seagrass made up a large fraction of the total drift pieces. Seagrass blades have gas-filled lacunae that make them positively buoyant, so they are common in drift mats at the sea surface. Seagrass detritus may get exported far from its production site as it drifts at the surface for some unknown period of time until it degrades enough to sink.

There was variation among the four invertebrate species in our study in their distributions with respect to depth and habitat type. The sea star *Pycnopodia* was the only species that showed no pattern with either variable, as also suggested by Shivji et al. (1983). This generalist predator occurred at relatively low densities in all videos, and there was no evidence that *Pycnopodia* influenced the distribution of either *Parastichopus* or *Strongylocentrotus*. Both these potential prey species have rapid and effective escape responses to *Pycnopodia* (Mauzey et al. 1968; Moitza and Phillips 1979; Cameron and Fankboner 1989), so neither is commonly consumed in the field (Mauzey et al. 1968; Duggins 1983; Shivji et al. 1983).

Strongylocentrotus density declined with depth (Figs. 2, 5a), consistent with the availability of their preferred bedrock substrate type (Fig. 4b). Adult urchins move little locally, preferring to feed by capturing drift algae from the water column (Duggins 1981; Britton-Simmons et al. 2009), and the capture of this material is positively correlated with current velocity (K. Britton-Simmons and H. Stewart unpubl.). High current habitats with low standing biomass of drift can still have substantial fluxes of drift material through them (Biber 2007). The strong *Strongylocentrotus*–bedrock association therefore makes sense given that drift capture rates would be elevated in exposed bedrock habitats because these are typically present in higher current areas (where unconsolidated sediments are carried away). Bedrock also provides urchins with better substrate for attachment. *Strongylocentrotus* were rare in mixed habitat (Fig. 4b) where drift accumulation was highest (Fig. 4a) and were not associated with drift piles on the video footage (A. Rhoades pers. obs.). A logical interpretation of these data is that red urchins select habitat on the basis of drift flux rather than drift standing stock.

Despite an anecdotal report to the contrary (DaSilva et al. 1986), we found that *Parastichopus* was common on bedrock and present on all habitat types (Fig. 4c), suggesting that it is relatively insensitive to hydrodynamic regime. It declines in abundance with depth (Fig. 5b; Courtney 1927; Fankboner and Cameron 1985) and was absent below 80 m in our study area both in 1927 (Courtney 1927) and now. Available evidence suggests that during summer, when individuals move randomly up to several meters per day (DaSilva et al. 1986; Cieciel et al. 2009), only shallow (< 15-m depth) individuals are reproductive (Courtney 1927), which some have interpreted as evidence of seasonal migration to shallow areas for spawning (Woodby et al. 1993). Our data indicate that even during fall, when feeding and movement cease (Fankboner and Cameron 1985), most of the *Parastichopus* population is already concentrated at shallow depths. Our work does not address the reason why *Parastichopus* declines with depth, but food limitation has been hypothesized as a cause (Fankboner and Cameron 1985).

Pandalus (spot prawns) were strongly associated with mixed and cobble habitats greater than 50 m deep (Figs. 6, 7) where drift was abundant (Fig. 8). The depth range of *Pandalus* in our study is consistent with previous work in this region (Jamieson and Pritchard 1988). This species is a generalist scavenger that could be feeding directly on drift algae (Rensel and Prentice 1980) or consuming small crustaceans (O'Clair and O'Clair 1998) or other material associated with drift. Consistent with previous work (Rensel and Prentice 1980), our ongoing lab observations clearly indicate that *Pandalus* readily consume a wide range of macroalgal taxa, including fresh and detrital material. Therefore, we hypothesize that the strong association between *Pandalus* and drift is a trophic connection that occurs because the prawns aggregate to deeper habitats where macrophyte detritus is concentrated by currents.

Overall, the patterns of response of invertebrates to depth and habitat type were species specific. The two species (*Strongylocentrotus* and *Pandalus*) that are known

to feed directly on drift material appear to be distributed within DSE so as to maximize access to drift macrophyte food resources, according to their respective feeding modes. Strong, temporally variable tidal currents play a key role in transporting detached macrophytes (K. Britton-Simmons and H. Stewart unpubl.), and deep areas of low slope angle and reduced current likely create sites of detritus accumulation. The supply of such large quantities of biomass from nearshore sites into aphotic subtidal landscapes creates habitats that can support substantial secondary production despite the complete absence of primary production. When consumers of this drift are commercially harvested species, as several are in our region, the role of such spatial subsidies to subtidal trophic webs is particularly important.

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