Effects of natural and anthropogenic disturbance on polychaete worm tubes and age-0 flatfish distribution

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ABSTRACT: Tubes of the ampharetid polychaete *Sabellides sibirica* are a prominent yet spatially variable habitat feature in shallow-water flatfish nurseries around Kodiak, Alaska, USA. Juvenile flatfish associate with the edges of worm tube regions but seldom use the dense 'turf-like' worm beds that sometimes form on the bottom in the late summer. The present study used a fine-scale analysis (2 to 3 m) to examine how juvenile flatfish distribution changed with worm tube heterogeneity, i.e. density and patchiness. Using a video sled, 8 transect lines (~250 m each) were repeatedly surveyed from late summer to mid-winter in a worm tube region of Pillar Creek Cove, half of which were experimentally disturbed using simulated trawl gear. Results indicated that juvenile flatfish (mainly northern rock sole *Lepidopsetta polyxystra*) increasingly use patches of bare substrate as worm tube densities increase. However, the simulated trawl disturbance resulted in a unique kind of patchiness, typified by long, thin exposed regions of bare substrate referred to as 'combing'. Unlike natural patches, evidence of combing disappeared 2.5 mo after the initial disturbance, whereas natural patches persisted throughout the entire study. Flatfish abundance increased in trawl-disturbed worm tube beds for only a short period (2 d), possibly due to episodic foraging opportunities rather than physical changes in habitat. These results indicate that worm tube habitat is provisionally resilient to disturbance, and its heterogeneity (density, patchiness, and patch type) is an important component of habitat quality for juvenile flatfish in Alaska.

KEY WORDS: Coastal habitats · Benthic recovery · Patchiness · Habitat heterogeneity · Northern rock sole

INTRODUCTION

Complex seafloor habitats such as sedimentary bedforms and emergent epifauna have been linked to the distribution, growth, and survival of many demersal fish species. For juvenile fishes, complex habitats serve an important nursery function by providing refuge from predators (e.g. Gregory & Anderson 1997, Scharf et al. 2006). However, for juvenile flatfishes, nursery habitats have generally been identified on the basis of sediment type (Gibson 1994, Stoner et al. 2007), likely because flatfish have the ability to bury and use adaptive coloration as effective means of reducing predation (Ryer et al. 2008). As such, flatfish are perceived to be resilient to benthic habitat disturbance resulting from fishing activity or storm events (Kaiser & Ramsay 1997). However, recent evidence points to the strong role of emergent

habitat features in shaping juvenile flatfish distributions of Pacific halibut *Hippoglossus stenolepsis* and northern rock sole *Lepidopsetta polyxystra* (Stoner & Titgen 2003, Ryer et al. 2004) as well as plaice *Pleuronectes platessa* (Pihl et al. 2005, Rabaut et al. 2007). However, in subtidal regions, the importance of emergent habitat on processes in fish nursery areas is poorly understood, likely because the cost and logistic challenges necessitate the use of remotely operated vehicles (ROVs) and submersibles to assess such habitat features (Malatesta & Auster 1999, Diaz et al. 2003, Stoner et al. 2007, Ryer et al. 2010). Therefore, much of our understanding of habitat processes for flatfish is based on coarser scales (e.g. trawl surveys) and abiotic factors such as temperature, salinity, depth, and bottom hardness.

Alaska currently supports some of the largest commercial flatfish fisheries, and many of the target species are highly abundant in subtidal coastal areas (10 to 30 m) during summer and fall (Norcross & Mueter 1999, Stoner et al. 2007). In Kodiak, Alaska, USA, several of these nursery areas have been the focus of process-based studies of habitat function on growth and survival in age-0 juvenile rock sole and halibut (e.g. Hurst et al. 2010, Ryer et al. 2010). Although there is no structure-forming vegetation in nursery areas, Stoner et al. (2007) found that worm tubes (later identified as *Sabellides sibirica*; C. H. Ryer et al. unpubl.) were significantly correlated with age-0 rock sole distributions within and across nursery areas. Associations between worm tubes and juvenile fish have also been reported in the Atlantic (Diaz et al. 2003, Rabaut et al. 2007, 2010). Annual summer habitat surveys in the Kodiak region indicate that *Sabellides sibirica* varies spatially and temporally, from sparse to often extensive, dense 'turf' regions that completely obscure the bottom sediment. Flatfish are disassociated from dense worm tube habitat, possibly because it interferes with the burial/settling capabilities of juvenile flatfish (Stoner et al. 2007, C. H. Ryer et al. unpubl.). However, flatfish are highly abundant along the edges of dense worm tube regions, suggesting that worm tube heterogeneity may be an important functional component of habitat quality for these fish. It has been suggested that similar processes are important in the Eastern Atlantic, where worm tubes *Lanice conchilega* form patchy 'reefs' in nursery areas for *Pleuronectes platessa* and sole *Solea solea* (Rees et al. 2005, Rabaut et al. 2010).

In the present study, we examined worm tube heterogeneity on flatfish distribution, hypothesizing that seasonal disturbance, both natural and anthropogenic, would affect the way juvenile flatfish associate with worm tube areas. As such, we measured fish–habitat associations both at finer scales (2 to 3 m) and later in the year (fall and winter) than other studies from the same region (e.g. Stoner et al. 2007, Ryer et al. 2010, C. H. Ryer et al. unpubl.). We focused on 3 sub-components in our analysis. First, we examined how flatfish abundance and worm tube heterogeneity (abundance, extent, and patchiness) changed naturally from August to January, a period of time with increased storm activity and after the May–August survey periods used in our earlier studies (Stoner et al. 2007, Ryer et al. 2010, C. H. Ryer et al. unpubl.). Second, we examined whether disturbing worm tube beds early in the season (using a simulated trawl) affected habitat heterogeneity and overall flatfish abundance compared to undisturbed transects. Finally, we examined what effect, if any, fine-scale worm tube heterogeneity had on the flatfish distributions. These results are discussed in the broader context of nursery function for flatfish in the Gulf of Alaska.

MATERIALS AND METHODS

Study site

Field work was conducted in the coastal water embayment of Pillar Creek Cove (57° 49' N, 152° 25' W), Kodiak Island, Alaska, USA (Fig. 1). This cove is considered to be a summer nursery area for age-0 rock sole and Pacific halibut, and has been the focal area for habitat and growth studies for these species (Hurst & Abookire 2006, Ryer et al. 2007, 2010, Stoner et al. 2007). The study region is approximately 30 ha, and has a gently sloping sandy bottom with 0.6 km between 5 and 30 m mean low low water (MLLW) depth contours. Summer salinities and water temperature range from 30 to 32 and 6 to 11°C, respectively.

Towed camera assessment

Video surveys of age-0 flatfish and worm tubes were conducted using a towed camera sled (Spencer et al. 2005). Briefly, the sled was towed by a 9 m vessel at an average speed of 60 cm s^{-1} along the bottom. The camera sled was equipped with a lightweight tickler chain that ran along the surface of the benthos, causing flatfish to flush from the bottom. Fish were enumerated and worm tube habitats were classified via playback of video acquired from a camera
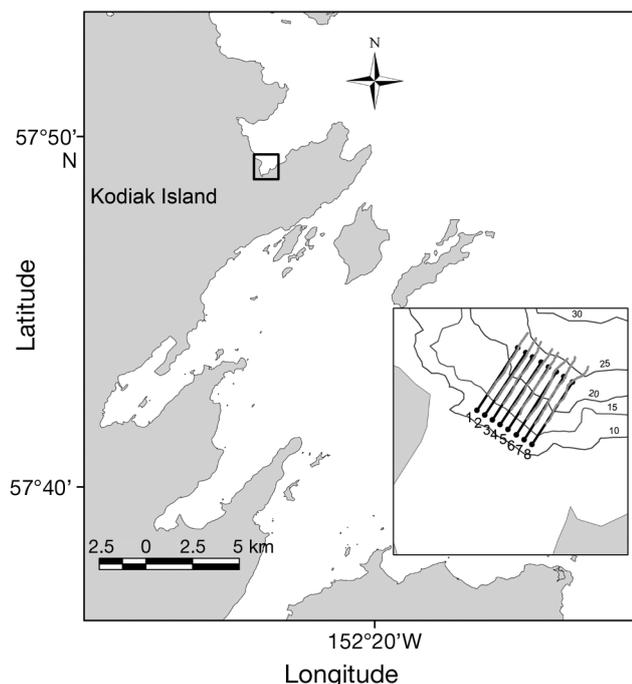
Fig. 1. Pillar Creek Cove, Kodiak Island, Alaska, USA. Eight 250 m transects repeatedly sampled by camera sled, late August 2008 to January 2009, are indicated (black line). Actual boat tracks using September 2008 sampling data as an example are also shown (gray line)

set at an angle of 35° below horizontal. Repeated sled deployment along the same transect line indicated that the tickler chain was not noticeably affecting the benthos or dislodging worm tubes. With typical summer/fall water clarity around Kodiak, a viewer was able to quantify habitat and fish ~3.2 m ahead of the sled during video playback. Earlier work in the area using an identical sled indicated that >95% of the age-0 flatfish were northern rock sole, with the remaining species being Pacific halibut and English sole (Stoner et al. 2007, Ryer et al. 2010). Spatial data and dynamic tow speeds were collected by concurrently re-corded GPS positions aboard the vessel.

The camera sled was deployed along 8 transects that ran across depth strata perpendicular to the shoreline at Pillar Creek Cove (Fig. 1). Each transect was ~250 m long and spanned a depth range of 10 to 30 m (MLLW) to cover the extent of the worm tube bed. Camera sled surveys were performed 9 times over

each transect from August 30, 2008, to March 20, 2009 (see Table 1 for dates and survey effort). How-ever, the video records after January were excluded from the analysis due to poor visibility. Each survey was completed in 2.5 to 3.0 h, and data (recorded video, GPS; Table 2) were sent back to the Hatfield Marine Science Center (Newport, OR) for video ana-lysis and post-processing (see Spencer et al. 2005).

Experimental disturbance

After the initial August 30 survey of the 8 tran-sects with the camera sled, 4 of the 8 transects (hereafter referred to as 'disturbed lines') were sub-jected to a series of simulated trawl footrope incor-porating heavy chain (1.25 cm link thickness) and trawl doors from September 5 to 7 (Fig. 1). The dis-turbed lines were initially exposed to two 250 m passes with a trawl footrope incorporating 12 cm rubber discs, and again 2 d later with 2 passes of a heavy chain with the trawl doors. The disturbance was designed to mimic the bottom contact charac-teristics of flatfish trawls typically utilized in the nearshore flatfish fishery in Kodiak. Video observa-tions of the impact revealed strong evidence of footrope gear contacting and affecting habitat on the disturbed lines. Four hours following the last simulated trawl disturbance, all sites were surveyed using a small 2 m beam trawl and the camera sled (i.e. day 0 post-disturbance in Table 1). The beam trawl was used primarily to identify flatfish species present around the time of the disturbance, but despite having relatively low mass, it was only used once during the experiment to minimize potential effects of repeated disturbance.

Table 1. Timing and survey effort used to measure flatfish densities and worm tube (*Sabellides sibirica*) characteristics. Time period refers to the days before or after the disturbance. YOY: young-of-the-year

Survey date (yyyy/mm/dd)	Time period (d)	Gear used	No. of video intervals analyzed	Mean YOY flatfish density (fish m^{-2})	Mean worm tube index
2008/08/30	−9	Camera sled	999	0.14	3.3
2008/09/08	0	Camera sled and beam trawl	778	0.13	3.0
2008/09/10	2	Camera sled	770	0.10	3.0
2008/09/14	6	Camera sled	734	0.10	2.8
2008/10/16	38	Camera sled	713	0.09	2.9
2008/11/17	70	Camera sled	690	0.11	2.6
2009/01/27	141	Camera sled	791	0.07	1.6

Table 2. Data sources and variables used to characterize habitat and fish densities

Variable	Source of information	Description	Range of values
Depth (m)	Depth-sounder	Water depth (m) recorded each 5 s and rounded to nearest 25 cm depth bin	10–31
Position	GPS	Latitude-longitude recorded each 5 s	
Age-0 flatfish density visual (fish m^{-2})	Video record	Number of age-0 flatfish recorded each 5 s interval divided by the transect distance surveyed	0–2.46
Age-0 flatfish density collected (fish 200 m^{-2})	Beam trawl	Number of age-0 flatfish collected in trawl divided by total swept area	12–80
Worm tube density	Video record	Worm tubes (height >2 cm) created by *S. sibirica*, scored 0–5 (1: patchy, low-density presence; and 5: dense, total coverage of the bottom)	0–5
Worm tube patchiness	Video record	Areas of bare substrate in worm tube regions, scored 0–2 (1: patches 0.01–0.04 m^2; and 2: patches 0.05–0.15 m^2)	0–2
Worm tube combing	Video record	Worm tube regions marked by parallel, bare channels resulting from towed gear, scored 0–1 (1: >50% of the visual area affected)	0–1

Video processing and analysis

Both polychaete worm tube charac-teristics and density of age-0 flatfish were scored by the same observer dur-ing video playback (Table 2). Data were scored at 5 s intervals, typically repre-senting 2.0 to 2.5 m distance along the bottom. Polychaete abundance was scored on a 6-point scale (0 to 5, with 0 representing worm absence, and 5 rep-resenting a contiguous 'worm turf'; Stoner et al. 2007, our Fig. 2). Two addi-tional variables, patchiness and comb-ing, were recorded to describe the degree and nature of how worm tubes covered the bottom (Fig. 2). Patchiness (scale of 0 to 2) described the degree to which worm tubes were interspersed with areas of exposed benthos, the result of either natural or anthropogenic disturbance. A patchiness score of 1 in-dicated patches of 0.01 to 0.04 m^2, and 2 indicated patches of 0.05 to 0.15 m^2. *A priori*, we expected worm tube patchi-ness to be more common at lowest worm tube densities, since they are patchy by definition from prior studies (Stoner et al. 2007, C. H. Ryer et al. un-publ). However, patchiness and worm tube density were independent at the finer scale of our analysis, i.e. 2.0 to 2.5 m^2 transect intervals. The worm tube characteristic combing (scale of 0 to 1) described the presence of grooves of exposed substrate amidst worm tubes
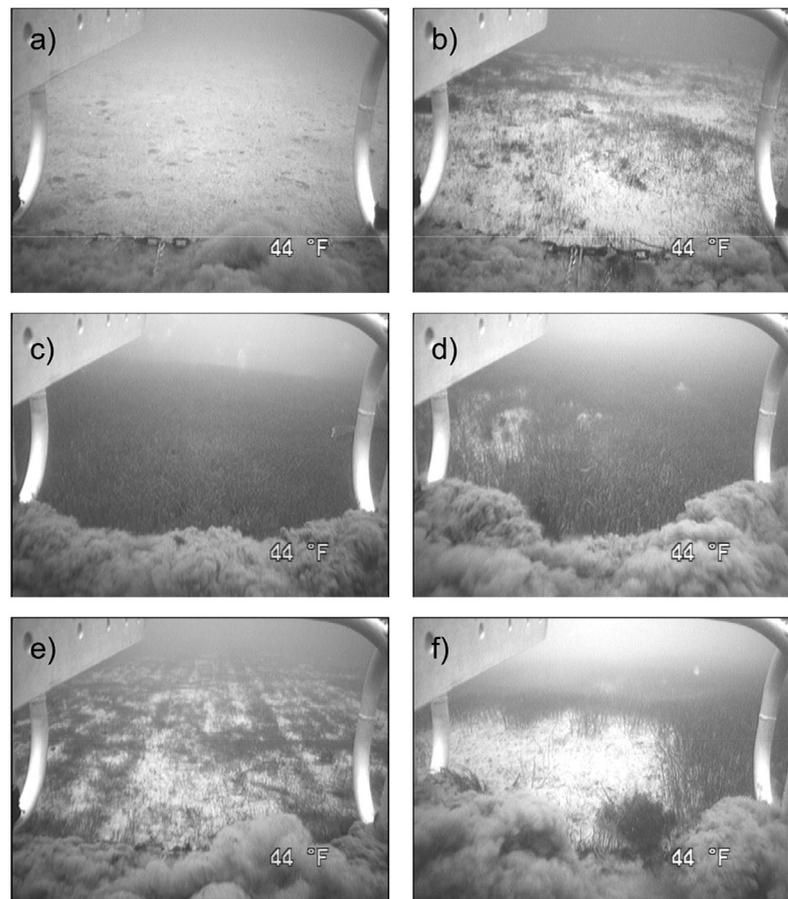

Fig. 2. *Sabellides sibirica*. Still frames from camera sled video of worm tubes depicting various indices of habitat heterogeneity in the field of view: worm tube abundance (WT; scored 0 to 5), patchiness (P; scored 0 to 2), and comb-ing (C; scored 0 to 1). (a) WT = 0, P = 0, C = 0; (b) WT = 2, P = 1, C = 0; (c) WT = 5, P = 0, C = 0; (d) WT = 5, P = 1, C = 0; (e) WT = 3, P = 0, C = 2; and (f) WT = 4, P = 2, C = 0. Note that pictures are examples only. For analytical purposes, habitat characteristics and fish abundance are scored directly from video over a 5 s interval from the tickler chain to ~3.2 m ahead of the sled during play-back. 44°F ≈ 6.7°C

(shown in Fig. 2), and was considered a unique type of worm tube disturbance resulting from towed gear. Worm tube regions were only considered combed (i.e. scored 1) when >50% of the visual area was affected. Combing was scored for all transect lines (control and treatment) since all regions in Pillar Creek Cove were potentially exposed to some prior anthropogenic disturbance. Fish counts were changed to densities by dividing the number of fish counted over the area surveyed in each time period. Intervals were excluded when the tickler chain was not in close contact with the bottom or the view was obscured by low visibility (<30 cm) and/or algae. These protocols resulted in a total of 4798 transect segments (intervals) available for analysis following video processing. Segments were binned into 1 m depth intervals and averaged prior to analysis.

Statistical analysis

We assumed that all counts of fish from each segment were independent for the purposes of the analysis. An examination of frequency histograms on fish density and worm tube indices indicated that data conformed to a Poisson distribution, necessitating the use of a generalized linear model with a logit data link (GLZM; SPSS 10.0). For GLZM analysis, worm tube data were multiplied by 2, incremented by 1 to remove zeros, then rounded to generate integer values. This resulted in an approximate doubling of the integer value range. Our analysis was broken up into a series of components based on the GLZM (Components 1 to 3) to examine natural seasonality, disturbance, and worm tube–flatfish links separately. The first series of analyses (Component 1) was restricted to just the control sites to characterize the natural changes in worm tube characteristics and fish density from August to January. Separate models were run on worm abundance and patchiness using depth, sampling period, and transect line as independent variables. Combing was considered too rare in the control sites to be considered relevant for similar analyses in this model construct. A second series of analyses (Component 2) was used to determine if there was a relative change in worm tube habitat and fish densities as a result of the disturbance. Separate GLZMs were run for worm tube indices (density, patchiness, combing) and fish density. Independent variables in each model included sampling period, treatment (control or disturbed line), transect line (nested within the treatment term of the model), and depth (as a covariate). Data were further analyzed by

sampling period if there was significant interaction to determine the duration of the measured effect.

The final analysis (Component 3) focused on examining the links between worm tube characteristics and flatfish densities. Data were analyzed using the expanded worm indices as independent variables (density, patchiness, and combing, but with a subset of pooled data based on results from the above models). Specifically, data were excluded from the model in sampling periods where flatfish abundance significantly deviated from prior sampling periods, naturally and independent of habitat changes (e.g. emigration out of the nursery region; Component 1), or by way of the trawl disturbance (Component 2). Data were also excluded where worm tubes were entirely absent, as both patchiness and combing are dependent on the presence of some worm tubes. The first model excluded combing as an independent variable since it was relatively rare in the control transect lines. However, a second model, which used only the post-trawl treatment lines, examined worm tube abundance, patchiness, and combing in a full-factorial GLZM.

RESULTS

Model 1: seasonal changes in worm tubes and flatfish

Worm tube characteristics changed naturally over the course of the season. Worm tube abundance decreased throughout the season, but disproportionately faster at shallower depths, as indicated by the significant interaction between sampling period and depth (GLZM: $\chi^2_{[65]} = 90.84$, p = 0.019). For example, the 17 to 20 m depth region was a transitional region to the worm tube bed in late August (mean = 1.5 ± 0.11 worm tube density), whereas the same depth region was relatively devoid of worm tubes in January (mean = 0.1 ± 0.01 worm tube density; Fig. 3). Not surprisingly, worm tube patchiness was also depth-dependent, given that worm tubes were absent in the shallowest regions of the line transects. Patchiness notably increased from late August to early September, then remained constant until it decreased in January as worm tubes became less abundant (GLZM: $\chi^2_{[6]} = 15.43$, p = 0.017; Fig. 3).

Model 2: trawl effects on worm tubes and flatfish

Neither worm tube abundance or patchiness changed significantly as the result of the simulated
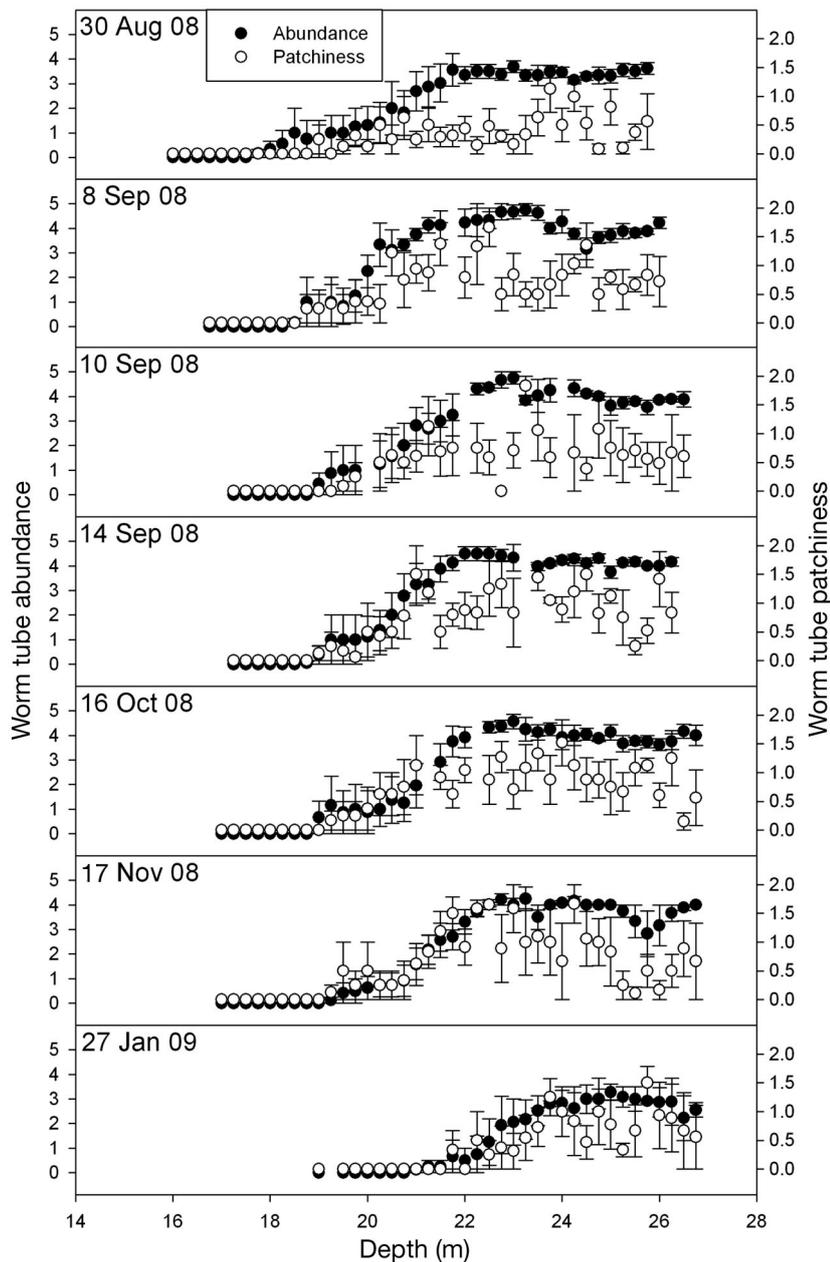
Fig. 3. *Sabellides sibirica*. Natural seasonal changes in worm tube abundance and patchiness indices by depth (see Fig. 2 legend for index values). Data are based on averages of index values ± 1 SE at 25 cm depth bin for individual transects at control sites only (trawl disturbance transects not included)

flatfish abundance (GLZM: $\chi^2_{[6]}$ = 282.98, p < 0.001). These interactions indicate that the trawl had some measureable effect on these response variables, but did not remain constant over the duration of the experimental period. Therefore, further analyses of these response variables (combing, habitat impact, and fish density) were conducted for each sampling period to determine when there was a significant effect of disturbance. These results were compared with the same model runs for worm tube abundance and patchiness for comparative purposes, and are shown in Table 3. As expected, there were no significant differences in any of the response variables between trawled and control lines prior to the deployment of the simulated trawl (Time period −9; August 30, 2008). However, there was a significant increase in worm tube combing immediately following the disturbance (Time period 0; September 8, 2008), which lasted through October 16, 2008 (Time period 38; Table 3, Fig. 4). This was coupled with an increase in flatfish density following the disturbance (Time period 0) in the disturbed transect lines, but was no longer evident in subsequent sampling times (Time periods 2 to 6 [Time period 7 was not analyzed due to poor visibility]; Table 3, Fig. 4). The analysis of beam trawl data following the disturbance (Time period 0) also detected a significant 2- to 4-fold increase in the abundance of flatfish in the disturbed transects (ANOVA: $F_{1,6}$ = 11.22; p = 0.015). Of all the age-0 flatfish sampled, >95% were identified as northern rock sole.

Model 3: worm tube effects on flatfish abundance

The model of patchiness and worm tube abundance indicated a significant interaction between worm abundance and patchiness in the analysis of flatfish density using the combined control and treatment line data (GLZM: $\chi^2_{[29]}$ = 329.38, p < 0.001). Flatfish density initially increased with the presence of

trawl (GLZM — abundance: $\chi^2_{[1]}$ = 0.27, p = 0.609; patchiness: $\chi^2_{[1]}$ = 0.13, p = 0.812). However, a significant interaction was detected between sampling period and line treatment for both worm tube combing and habitat impact indices (GLZM — combing: $\chi^2_{[6]}$ = 12.27, p = 0.041; habitat impact: $\chi^2_{[6]}$ = 13.253, p = 0.039). The model also showed a significant interaction between treatment and sampling period for

Table 3. Generalized linear model with a logit data link (GLZM) analyzing the effects of a simulated trawl disturbance on worm tube (*Sabellides sibirica*) characteristics (see Table 2) and age-0 flatfish density. Time period refers to the days before or after the disturbance. df = 1 for all parameters

Parameter	Time period	χ^2	p
Worm tube abundance	−9	1.41	0.235
	0	0.80	0.375
	2	0.08	0.780
	6	0.01	0.944
	38	0.78	0.377
	70	0.02	0.878
	141	0.19	0.660
Worm tube patchiness	−9	0.01	0.945
	0	0.01	0.930
	2	0.04	0.848
	6	0.05	0.827
	38	0.63	0.428
	70	0.14	0.704
	141	1.30	0.255
Worm tube combing	−9	0.01	0.950
	0	5.07	0.024
	2	8.02	0.005
	6	7.91	0.005
	38	4.34	0.037
	70	0.00	1.000
	141	0.00	1.000
Flatfish density	−9	0.03	0.866
	0	16.37	<0.001
	2	0.17	0.680
	6	2.76	0.096
	38	1.48	0.224
	70	2.19	0.139
	141	0.07	0.797

low worm tube abundance, but steadily declined as worm tube abundance increased. At the same time, flatfish were more likely to be associated with patches as worm tube abundance increased. In the analysis including combing, this resulted in a significant 3-way interaction (GLZM: $\chi^2_{[10]}$ = 105.69, p < 0.001). Combing appeared to attract flatfish with increasing worm tube abundance (at worm tube level 4; see Fig. 2, Table 2), but to a lesser degree than open patches. Combing was also not observed in the highest density worm tube habitat (level 5), and was consequently not examined statistically in the model.

A finer-scale analysis of worm tube heterogeneity, using the original scored data at 2 to 3 m² transect resolution, illustrated the differences in the worm abundance × heterogeneity interaction on flatfish density across the various scores of habitat heterogeneity (uniform, patch 1, patch 2, combs; Fig. 5). No

form of worm tube heterogeneity had an effect on flatfish distribution at low worm tube densities. However, as worm tube abundance increased, the relative density of flatfish increased in regions with bare patches, albeit more so in regions with large patches than small and combed patches (Fig. 5).

DISCUSSION

Polychaete worm tubes remained a prominent habitat feature throughout the duration of the present study, and it was clear that their distribution, density, and heterogeneity were important aspects of habitat quality for age-0 juvenile flatfish. The link between worm tubes and juvenile flatfish in Pillar Creek Cove was first detected by Stoner et al. (2007) using general additive models (GAMs) examining a broad suite of habitat variables in coastal flatfish nurseries in Kodiak at relatively coarser scales (20 to 30 m transect intervals). Using an expanded multi-year dataset and a finer-scale analysis (~7 to 10 m transect intervals), C. H. Ryer et al. (unpubl.) found that juvenile flatfish strongly associated with the edges of worm tube beds, which in turn controlled the annual centralized depth distribution of the population. At the scale of the present study (~2 to 3 m transect intervals), we showed that juvenile flatfish can use high-density worm tube areas, provided that patches of bare sediment are present. At lower worm tube densities, these patches were not preferentially used, likely because juvenile flatfish were able to settle on bottom sediment without the presence of completely bare regions. However, heterogeneity was more important with increasing worm tube abundance, especially in the large patches where flatfish density was 2 to 4 times higher than other dense worm regions. These results further support the idea that associations between juvenile flatfish and worm tubes are conditional and scale-dependent (Diaz et al. 2003, Rabaut et al. 2010).

Functionally, polychaete worm tube heterogeneity may be analogous to better-studied seagrass systems. Seagrass beds in temperate regions also cycle through an annual growth and dieback period that can result in a variety of complex structural arrangements, ranging from sparse patches to dense meadows (Orth et al. 1984). While seagrass is generally considered a refuge and food habitat for juvenile fish (e.g. Levin et al. 1997, Linehan et al. 2001), high stem densities can impede foraging efficiency (Stoner 1982) and anti-predator behavior such as schooling and predator awareness (Laurel & Brown 2006).
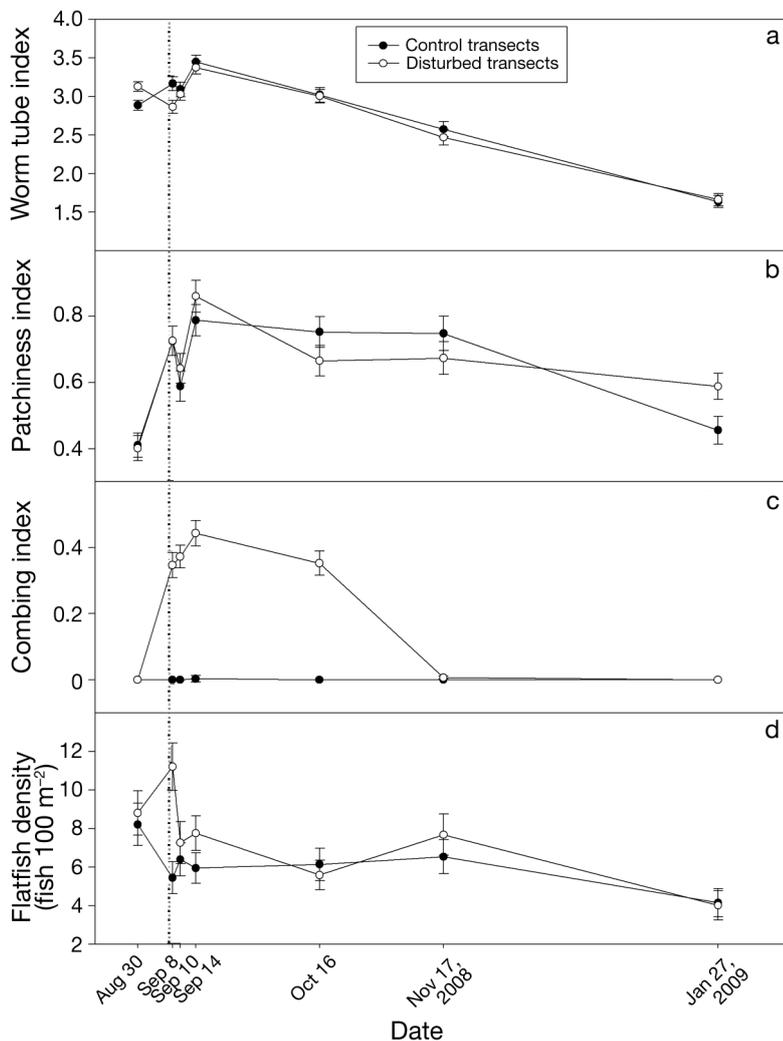
Fig. 4. Changes in (a) worm tube (*Sabellides sibirica*) abundance, (b) patchiness, (c) combing, and (d) flatfish density. Data are plotted separately for trawled (n = 4) and non-trawled (n = 4) transect lines. Trawl disturbance was conducted from September 5 to 7, 2008

near the bottom, thereby eliminating the need to hide in dense worm tube regions where the flatfish's burial capability and escape behavior are reduced (Ryer et al. 2004, C. H. Ryer unpubl. data). In addition, worm tubes and seagrass are similar in that they tend to be more productive than neighboring bare regions (Orth et al. 1984, Levin et al. 1997, Rabaut et al. 2007, Van Hoey et al. 2008, C. H. Ryer & S. C. Jewett unpubl. data). One notable difference is that juvenile rock sole can directly consume worm tubes (B. Knoth unpubl. data), whereas the trophic links between fish and seagrass habitat are indirect (Copeman et al. 2009).

Prior to the present study, our understanding of worm tube habitat was based on annual summer sampling (May to August) in Pillar Creek Cove and adjacent embayments. These surveys demonstrated that worm tubes are routinely found in Pillar Creek Cove, but their extent is highly variable year-to-year (Stoner et al. 2007, C. H. Ryer et al. unpubl.). The majority of worm tubes in May are assumed to be newly recruited because they were smaller (1 to 2 cm) than worm tubes observed in August (~8 cm; C. H. Ryer et al. unpbul., the present study). However, the occasional presence of long worm tubes in May suggests that overwintering can occur, possibly depending on the wave energy experienced from winter to early spring. We observed some evidence of natural cycling and senescence of worm tubes beginning in January when the shoreward edge of the worm tube zone was deeper and overall worm tube density was less. The shallower regions of the study area (12 to 18 m) were always devoid of worm tubes, likely due to increased instability and resuspension of substrates at these depths (Ryer et al. 2010). However, we noted that sand waves occasionally extended deeper than 30 m, suggesting that worm tube beds are also subject to significant amounts of wave energy and may play a role in sediment retention. Interestingly, patchiness did not increase in late fall or early winter despite the corresponding reductions in density and extent of worm tubes. It is possible that patchiness is determined during the larval recruitment period or by
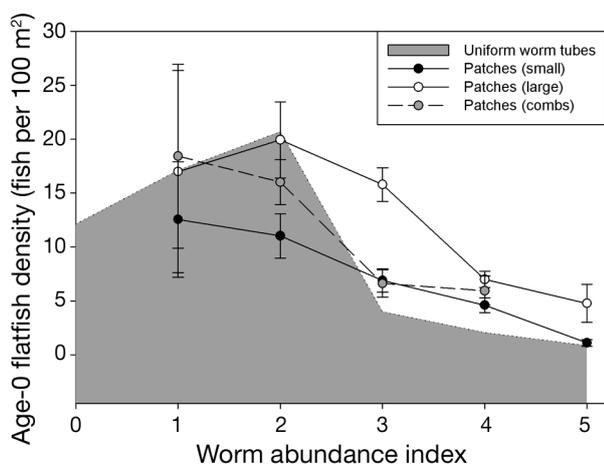
Juvenile fish may therefore spend the majority of time in edge and open patch areas (Laurel et al. 2003, Gorman et al. 2009), restricting movement into seagrass to times when predation risk is significantly elevated (Laurel & Brown 2006). Therefore, the broad-scale relationship between fish abundance and seagrass biomass is often parabolic in nature, with intermediate levels being more utilized compared to bare areas or extensive meadows (Fonseca & Bell 1998, Wells 2002, Thistle et al. 2010). Similar relationships were found in the present study, but they may be restricted to small flatfish, because worm tubes are much shorter than seagrass stems and habitat-edge associations are restricted to 2 dimensions. At these smaller scales, worm tubes can still conceal age-0 flatfish from cruising predators

Fig. 5. Average flatfish density (±1 SE) by worm tube (*Sabellides sibirica*) abundance in uniform worm tube habitat and patchy worm tube habitat (small, large, and combed patches of bare substrate). Data are based on 8 video transects (~250 m each, sampled at ~2 to 3 m² transect intervals) sampled multiple times (n = 7). Four transect lines were exposed to a simulated trawl disturbance from September 5 to 7, 2008

subsequent natural disturbance in late winter and early spring.

Multiple studies have demonstrated the negative effects of fisheries-related trawling on biodiversity, species richness, and fish abundance (e.g. Auster et al. 1996, Kaiser & Spencer 1996, Stainsbury et al. 1997, Freese et al. 1999), and arguably, these studies have largely shaped our impressions of habitat disturbance in soft-bottomed marine systems. However, the majority of such studies have been conducted in low-energy, offshore shelf regions or in sensitive habitats with low recovery rates, e.g. deepwater coral regions (Auster & Langton 1999). It is clear that coastal worm tube habitat can recover from brief instances of trawl disturbance, which in the present study was ~2.5 mo after the initial disturbance. Rapid recovery and resilience to anthropogenic disturbance has also been shown for *Lanice conchilega* worm tubes in intertidal regions (Rabaut et al. 2008). Nearshore worm tubes may have evolved increased resiliency to disturbance from routine seasonal exposure to wind-driven wave energy and the worms' ability to quickly retreat into their tubes (Bergman & Hup 1992). However, it is important to note that the disturbance in the trawled transects was characterized by narrow patches of exposed substrate (combs) rather than patches that occur naturally. Habitat recovery rates are ultimately determined by the magnitude and type of disturbance and the mechanism(s) of habitat recolonization (seasonality, repro-

ductive strategy, dispersal; Dernie et al. 2003). The life history of *Sabellides sibirica* is poorly understood, but preliminary lab experiments indicate that 10 to 15% of 'unrooted' worm tubes reattach to the substrate within 48 h of being dislodged (C. H. Ryer & B. J. Laurel unpubl. data). Another ampharetid polychaete worm tube, *Asabellides oculata*, produces 'crawl-away' larvae with very limited dispersal potential (R. Diaz pers. comm.). Such limited dispersal mechanisms would facilitate self-recruitment and recolonization by *S. sibirica* in regions undergoing natural seasonality and moderate disturbance, possibly explaining why the presence of worm tubes is more consistently found in some embayments than others (Stoner et al. 2007). However, without a consistent supply of outside sources of worm tube larvae, large-scale disturbances (e.g. near-complete worm tube elimination) could potentially affect an embayment for many years. Therefore, the worm tube recovery rates measured in the present study should be considered highly provisional.

The effects of the disturbance on the remaining benthic community were not measured, but the rapid increase in juvenile flatfish following the disturbance suggests that there was likely a brief increase in prey items for these fish. Trawl-disturbed benthos can rapidly lead to a change in benthic invertebrate populations, often characterized by small organisms with opportunistic life histories (Levinton 1982). These short-term changes, along with exposing benthic prey (Ramsay & Kaiser 1998), likely lead to increased foraging and scavenging behavior for fish species following trawl disturbance (Kaiser & Spencer 1994, Carlson et al. 1997). Juvenile flatfish returned to predisturbance densities 2 d after the disturbance, suggesting that infaunal prey species were momentarily brought to the surface. Interestingly, in an earlier field study, age-0 juvenile rock sole decreased in abundance following habitat enhancement (shell debris), likely because the enhancement attracted older conspecifics (age 1+), which are considered predators (Ryer et al. 2007). Larger flatfish were not commonly observed in the present study, but it is possible that age-0 flatfish were able to use the worm tubes as refuge while increasing their foraging opportunities.

In conclusion, ampharetid polychaete tubes remained a prominent habitat feature throughout the study, and it is clear that the heterogeneity of worm tube habitat is an important component of habitat quality for age-0 juvenile flatfish. Juvenile flatfish appear to seek open sediment patches in worm tube beds only at high worm tube densities. However, this

pattern was restricted to large, naturally occurring patches, as the increased patchiness resulting from the simulated trawl (combing) and small patches did not attract juvenile flatfish in the same manner. The notable increase in flatfish following the trawl was not linked to the areas of disturbance, but rather to the transect region as a whole, possibly due to increased foraging opportunities resulting from the disturbed benthos. These qualitative components of worm tube habitat should be considered alongside large-scale effects of worm tubes (e.g. interannual abundance, depth distribution; C. H. Ryer et al. unpubl.) on distribution and abundance patterns of juvenile flatfish in coastal nurseries.

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