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An experimental assessment of measures of mussel settlement: Effects of temporal, procedural and spatial variations

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A R T I C L E I N F O

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A B S T R A C T

Much research has focused on linking larval abundance and dispersal data to observed patterns of settlement. Consequently, measures of settlement have become increasingly important in benthic marine ecology and in understanding benthic-pelagic linkages. Potentially, measures could be confounded by complex settlement behaviors and physical variables that may impact on the abundance of larvae. The effects of timing or duration of deployment and data standardization (to a mussel per day rate) on measures of mussel settlement made using standardized artificial units of habitat (Tuffies™) were tested in three seven day trials. In addition, variations in methodological deployment procedure and position on the shore were assessed. The day of deployment and duration of sampling had species- and size-specific effects on measures of mussel settlement. The abundance of settlers of large (>500 μm) *Perna canaliculus* was highly variable over short temporal scales (one day), and longer deployment durations indicated significant peaks and falls in the number of settlers per Tuffy over seven days. By contrast, the abundance of small (<500 μm) *Xenostrobus pulex* increased linearly and measures taken over longer time-periods well reflected overall settlement. These data suggest that samples should, where possible, be sorted into species and size-classes because different settlement patterns may mask underlying settlement processes.

1. Introduction

The majority of benthic marine invertebrates have a pelagic larval phase and the potential to disperse widely. Settlement is the process by which planktonic larvae transition from the water column to the benthic environment. This is critical stage in the life history of a benthic organism and represents the juncture between wide to limited dispersal, and larval to adult life histories. Benthic ecologists have long recognized the importance of the link between larval distributions and community dynamics and function (Gaines and Roughgarden, 1985; Menge, 1978; Menge, 1991; Thorson, 1950; Underwood and Fairweather, 1989). More recently, the rise of "supply-side ecology" (sensu Lewin, 1986), has resulted in an increased emphasis on the role of larval processes in determining community structure (Menge, 1992; Menge, 2000; see Pineda et al., 2010 for a review). Thus, measures of settlement used to quantify the transition between pelagic and benthic habitats have become fundamental in studies of supply-side ecology.

Artificial units of habitat (hereafter AUHs, Underwood and Chapman, 2006) are routinely used to measure the settlement of larvae and post-larvae (King et al., 1990; Menge et al., 1997; Navarrete et al., 2008) due to their relative ease of use and because each unit is standard in surface area, color, texture and weight, and can be easily replicated (King et al., 1990; Menge et al., 1994). Most AUHs used for quantifying mussel settlement are variations on the same themes: fibrous plastic mesh or pads (used for pot-scrubbing) or filamentous nylon ropes (used in the aquaculture industry for mussel culture), the surface complexities of which superficially mimic those of the filamentous algae onto which competent larvae settle (Menge, 1992). The use of AUHs has facilitated many comparative studies of settlement (Table 1) at spatial scales ranging from tens of meters (e.g., Porri et al., 2008) to between hemispheres (Navarrete et al., 2008; Rilov et al., 2008) and generated time series that range from days (Dudas et al., 2009a) to many years (e.g., Menge et al., 2011). The duration of AUH deployment is highly variable among studies (Table 1) ranging from 1 day (Dudas et al., 2009b; Porri et al., 2008) to over a month (Navarrete et al., 2002; Reaugh-Flower et al., 2010). Data from AUHs have been used to address a variety of ecological questions most frequently concerning variations in settlement among sites (e.g., Broitman et al., 2008; Navarrete et al., 2008; Rilov and Schiel, 2011) or as proxies for offshore larval conditions (e.g., Rilov et al., 2008; Table 1). Given the ubiquity of AUHs and their fundamental role in quantifying key processes, it is pertinent to ask how variations in their deployment affect measures taken with such devices.

Assessments of quantification methods have largely focused on sessile species (e.g., ascidians, barnacles) that permanently attach on

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Table 1

Examples of variation among studies that used artificial units of habitat (AUHs).

Authors	Year	Region	Research focus	AUHs used	Source	Species	n	Duration of study	Duration of deployments	Standardization	Sites	Shore height/depth	Spatial array
Arribas et al.	2015	Argentina	Spatial variation in recruitment and adult densities	Tuffies	S, T, M	*Brachidontes rodriguezii*, *B. purpuratus* - pooled	4	Feb. 2010–Aug. 2011	34–120 days	Mussels/m^2 × 10^3	8 (within 4 locations)	I (mid)	1–3 m
Bownes and McQuaid	2009	South Africa	Habitat segregation between native and invasive mussels	Pot-scourers	T, S	*Perna perna*, *Mytilus galloprovincialis*, *Choromytilus meridionalis*	3	Jul. 2000–Jul. 2001 & Mar. 2003	1 month, 6 days, 1 day	Mussels/30 days	4 (within 2 locations)	3 zones	~1 m
Broitman et al.	2008	USA	Spatial and temporal patterns of recruitment	Tuffies	S, T	*Mytilus* spp.	5–8	Jan 1997–Dec 2004	~1 month	Mussels/AUH/day	26 (over 750 km)	I (mid)	n.s.
Cáceres- Martínez et al.	1994	Spain	Settlement and post-larvae behavior	Nylon ropes	T, S	*Mytilus galloprovincialis*	2	~2 years	1 month	Mussels/AUH	4	S 1 m	2 rafts per site
Denny et al.	2004	USA	Quantifying spatial and temporal scales of 15 variables	Tuffies	S, T	*Mytilus* sp.	14	May 1999–Jun. 2000	30 days	Mussels/AUH/month	1	I (1.6 m above MLLW)	103 positions, 1.72 m apart
Demello and Phillips	2011	New Zealand	Recruitment variation parallels shifts in community structure	Tuffies	S, T	*Perna canaliculus*, *Xenostrobus pulex* - differentiated *Mytilus galloprovincialis*, *Aulacomya maoriana* - pooled	5	Feb. 2003–Mar. 2005	~1 month	Mussels/AUH/day	2	I (mid)	> 5 m apart
Dudas et al.	2009a	USA	Linking larval and settler abundance	Tuffies	S, T, M	*Mytilus* spp.	5	17 to 27 Aug. 2005	1 day	None	2 (160 m apart)	S (1 & 5 m), I (mid)	n.s.
Johnson and Geller	2006	USA	Larval settlement adult population relationships	Scotch-Brite pads	T, S	*Mytilus trossulus*, *M. californianus*	40	Mar. 2002–Feb. 2003	~12 days/month	Mussels/cm^2/week	3	I	n.s.
Le Corre et al.	2013	Canada	Differentiating roles of primary and secondary settlers	Tuffies	T, S	*Mytilus* spp	8	~3 months in 2007 & 2008	7 or 14 days	n.s.	3		n.s.
Menge et al.	1999	New Zealand	Top-down and bottom-up community regulations	Tuffies	S, T	*Perna canaliculus*, *Mytilus galloprovincialis*, *Aulacomya maoriana*	5	Nov. 1994–April 1995	1 month	Mussels/day	4 (within 2 locations)	I (mid, low)	n.s.
Menge et al.	2004	USA	Testing model predictions along an upwelling gradient	Tuffies	S, T	*Mytilus* spp.	5–8	Apr. 1999–Jun. 2001	1 month	n.s.	14 (over 1300 km)	I	n.s.
Menge et al.	2011	USA	Potential impact of climate change	Tuffies	S, T	*Mytilus trossulus*, *M. californianus*	5	1983–present	1 month	Mussels/AUH/day	6	I (mid, low)	n.s.
Navarrete et al.	2002	Chile	Temporal variation in relation to El Niño	Tuffies	T, S	*Perumytilus purpuratus*, *Semimytilus algosus*, *Brachidontes granulata*	5	1997–2000	25–70 days	Mussels/AUH/day	14 (over 900 km)	I (mid)	Along < ;50 m
Navarrete et al.	2005	Chile	Meso- and regional-scale spatial variation	Pot-scourers	S, T	*Brachiodontes purpuratus*	n.s.	72 months	25–70 days	Mussels/AUH/day	14 (over 900 km)	I (mid)	n.s.
Navarrete et al.	2008	Chile & USA	Interhemispheric comparisons of	Tuffies	S, T	*Mytilus californianus*, *M. trossulus*; *Perumytilus purpuratus*,	5–8	1997–2005	~1 month	Mussels/AUH/day	32 (16 /hemisphere)	I (mid)	3–20 m

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