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Larval settlement can explain the adult distribution of *Mytilus californianus* Conrad but not of *M. galloprovincialis* Lamarck or *M. trossulus* Gould in Moss Landing, central California: Evidence from genetic identification of spat

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Abstract

We investigated the spatial distribution of adult and newly settled mussels (*Mytilus galloprovincialis* Lamarck, *Mytilus trossulus* Gould and *Mytilus californianus* Conrad) on the shore at Moss Landing, California to test the hypothesis that adult distributions are a result of settlement patterns. Adult *M. californianus* were most abundant on a wave-exposed rocky jetty and adults of Blue mussels (*M. trossulus* and *M. galloprovincialis*) were more abundant inside the protected Moss Landing harbor. Using taxon-specific polymerase chain reactions, we monitored recruitment during continuous 1–2 week intervals on fibrous scrubbing pads for 12 months in 2002–2003. All mussel species settled in greatest numbers on the exposed jetty, and Blue mussels settled in greater numbers there than did *M. californianus*. Because Blue mussels settled abundantly where their adults were rare, post-settlement mortality appeared to be the strongest influence on adult distribution. In contrast, *M. californianus* settled mostly in their adult habitat.

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1. Introduction

Recently, considerable attention has been given to oceanographic processes that affect larval transport and survivorship and thereby influence the supply of larvae available for settlement (Roughgarden et al., 1991; Largier, 2000; Wing et al., 2003). This in turn can regulate the intensity of den-

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sity-dependent adult interactions (Connolly and Roughgarden, 1998; Menge, 2000; Morgan, 2001). Although oceanographic processes deliver larvae to the shore on a regional or landscape scale, larval behaviors are important for actual patterns of settlement (Morgan, 2001). Early research concluded that larval behaviors such as microhabitat preferences, delayed metamorphosis, and decreased discrimination among settlement sites by older larvae were all important for adult distributional patterns (Thorson, 1950; Meadows and Campbell, 1972; Scheltema, 1974; Crisp, 1976). Adults of two species of sessile invertebrates may compete if their larvae are delivered to shore synchronously and settle together in high densities (for example, Connell, 1961), but larval behaviors may result in habitat-level differences in settlement, precluding co-settlement and subsequent competition (Grosberg, 1982). As a consequence, competitive exclusion and differential settlement can produce the same adult distributional patterns, and it is important to consider both possibilities.

The differences in adult distribution of mussels provide an example. Harger (1968, 1972) studied competition between two species of mussels, *Mytilus galloprovincialis* Lamarck [misidentified as *Mytilus edulis* L. (see Geller, 1999)] and *Mytilus californianus* Conrad in southern California. *M. galloprovincialis* was abundant in protected habitats such as harbors, while *M. californianus* dominated wave-exposed rocky communities. Harger (1968, 1972) elegantly demonstrated that *M. galloprovincialis* was an effective competitor in harbors, crawling over and smothering *M. californianus*. *M. californianus*, in turn, is well known as a dominant spatial competitor on exposed shores (Paine, 1966, 1974; Suchanek, 1981). Thus, a plausible hypothesis is that mussels settle widely and that competitive interactions determine adult distributions. However, the observation that *M. galloprovincialis* can smother *M. californianus* in an experimental setting does not demonstrate that this occurs naturally. Possibly, mussels settle widely but die quickly in physiologically inhospitable habitats, producing different adult distributions (Heath et al., 1996). Another plausible hypothesis is that the two species settle differentially in protected and exposed habitats. In this study, we addressed the distribution of mussels in protected and exposed habitats in central

California with specific attention to patterns of settlement.

We compared settlement patterns of *M. californianus*, *Mytilus trossulus* Gould, and *M. galloprovincialis* to the well-established adult distributional patterns described above, which we verified for our sites. Adult abundance and larval settlement were measured in three areas on an exposure gradient to test the hypothesis that adult distributions arise primarily from selective larval settlement rather than post-settlement mortality.

2. Materials and methods

2.1. Species studied

Three large-bodied species of mussels inhabit the central coast of California: the California mussel, *M. californianus*, primarily found in exposed rocky intertidal areas, and two species in the *M. edulis* species complex: *M. trossulus* and the invasive Blue mussel from the Mediterranean Sea, *M. galloprovincialis* (Soot-Ryen, 1955; McDonald and Koehn, 1988; McDonald et al., 1991; Koehn, 1991; Geller et al., 1994; Suchanek et al., 1997). In California, adult *M. trossulus* and *M. galloprovincialis* primarily inhabit protected bays and harbors. Hybridization occurs at locations where species of the *M. edulis* complex are sympatric but genetic differences persists where they are allopatric (McDonald et al., 1991; Gosling, 1992; Rawson et al., 1999).

2.2. Study sites

This study was conducted at Moss Landing in Monterey Bay, California, a harbor at the mouth of Elkhorn Slough, an ocean dominated estuary. Three areas were selected for qualitative differences in wave exposure. They were the ocean-facing end of a rock jetty at the entrance to Moss Landing Harbor (exposed site), the inner jetty channel (intermediate area), and Moss Landing Harbor (protected area). Temperatures that fluctuate tidally and seasonally (13–23 °C) cycles, and large amounts of suspended sediment characterize seawater conditions in Moss Landing Harbor and Elkhorn Slough. In addition, the

harbor site is more prone to changes in salinity due to the input of the Salinas River (Elkhorn Slough Foundation, unpublished data). The rock jetty provides exposed, rocky intertidal habitat that is subjected to frequent high wave action. The jetty channel provides rocky intertidal habitat with moderate wave exposure and mixing of slough and open ocean waters. These conditions collectively create an environment “intermediate” to the exposed shore and protected harbor (W. Broenkow and L. Breaker, in manuscript). Mussels were found on rock surfaces in the exposed and intermediate sites, and on wood piling in the protected site.

2.3. Adult mussel distributions

Adult mussels were sampled at all three sites with a 1 m² quadrat using 10 random points of contact (RPC). The RPC was used to randomly select mussels for identification and measurement of size. The intertidal shoreline was divided into upper (+1 to +2 m) and lower zones (0 to +1 m). Quadrats were placed at ten randomly chosen positions along a 50-m transect in each zone at each site. Adults contacting or nearest to random points within the quadrat were measured with calipers to the nearest millimeter and identified according to the criteria of (Smith and Carlton, 1975) as *M. californianus* or *M. “edulis”* (that is, *M. galloprovincialis* or *M. trossulus*; see above). Mussels were absent from the channel site with the exception of few in rock crevices in the upper zone; the RPC method was not used there and, instead, all mussels within quadrats were identified and measured.

2.4. Identification of larvae in plankton

We used the polymerase chain reaction (PCR) to generate differently sized fragments of the female mitochondrial cytochrome *b* gene to determine the presence or absence of larvae of each species in the plankton samples. Plankton tows were done in March 2002 within the harbor and channel of Moss Landing. The waters adjacent to the exposed site were not sampled due to large swell. Three 100 m long qualitative tows (~5 km h⁻¹) were conducted in each area with a 0.5-m diameter net with 83- μ m mesh size. Mussel veligers in these samples were identified by

their general size and shape (Martel et al., 1999) and were sorted into groups of 10 and 100 veligers. These larvae were incubated for 15 min at 95 °C in 100 μ l water to prepare PCR templates. A first round of PCR amplification was performed using universal primers UCytb151F (TGRGGRGCNACYGTWATYACTAA) and UCytb270R (AANAGGAARTAYCAYTCNG-GYTG) (Merritt et al., 1998). A 2- μ l aliquot of template was used in 20 μ l reactions containing 1 \times PCR buffer (Qiagen), 200 μ M dNTP, 10 pmol of each primer, and 0.5 units Hotstar™ Taq polymerase (Qiagen). Amplification was performed in a PTC-100 thermal cycler (MJ Research). Thermal cycling conditions were 95 °C for 15 min followed by 4 cycles of 94 °C for 1 min, 40 °C for 1 min, a 64 s ramp to 72 °C, and 72 °C for 2 min, then 35 cycles of 94 °C for 1 min, 45 °C for 2 min, and 72 °C for 2 min, and final incubation of 72 °C for 7 min. Products from first round PCR were then used as template for second round PCR using the reaction mix described above with the forward primer Ucytb151F, and a pool of three species-specific reverse primers (*M. californianus*: Mcali190r, TTCGTGTA AAAAGAAAA-GATGAAG; *M. galloprovincialis*: Mgallo 258r, AAACATAACCAAAGAGGTCCTTA; *M. trossulus*: Mtross326r AATAGTTTAAATGATTCCTAACAG). Expected product sizes (base pairs) are indicated in the name of each species-specific primer. Thermal cycling conditions were 35 cycles of 94 °C for 1 min, 51 °C for 1 min, 72 °C for 2 min, followed by 72 °C for 8 min. Positive controls with DNA templates from identified adult mussels (samples from Suchanek et al., 1997) confirmed the specificity of primers, and negative controls (no added template) indicated that amplifications were not contaminated.

2.5. Larval settlement

Flat green 60 cm² Scotch Brite™ pads were used as settling substrata rather than commonly used bulbous Tuffly™ Pads to avoid the possibility of passive ensnarement of juvenile mussels instead of actual recruitment (Caceres-Martinez et al., 1999). Based on results of a pilot study in March 2002, we deployed 40 pads for an average of 12 days each month from March 2002 to February 2003 at each study site. At the end of each sampling interval, pads were retrieved from the field and stored individually in plastic bags

for transport. On average, ten recruitment pads were lost per month at the jetty and channel sites.

2.6. Molecular identification of spat

To facilitate byssal thread detachment, juvenile mussels were extracted from individual pads by soaking them in a 10% solution of commercial bleach for 5 min (Ramirez and Caceres-Martinez, 1999). Individually, pads were then rinsed with fresh water and detached mussels were counted and stored in 1.5 ml centrifuge tubes containing 70% ethanol.

We used a PCR-based method different from that described above for plankton tows to distinguish *M. galloprovincialis*, *M. trossulus*, and *M. californianus* juveniles. We found PCR of the ITS 1 region to be more robust than for cytochrome *b* and thus better suited for routine amplification of individual juvenile mussels. This method utilized size differences in the first internal transcribed spacer (ITS 1) region of the ribosomal cistron in these species (modified from Martel et al., 1999). *M. galloprovincialis* and *M. trossulus* are not readily distinguished by this method, but both are easily distinguished from *M. californianus*. Thus, we report abundances of Blue (*M. galloprovincialis* and *M. trossulus*) and California (*M. californianus*) mussels.

Eighty-eight juvenile mussels per site per month were evenly taken from the set of pads within sites, but randomly chosen from within pads. The number of pads recovered from each site varied due to losses. Mussels stored in 70% EtOH were rehydrated for 15 min in autoclaved Nanopure® water and then moved individually in 2 µl water into wells of a 96 well PCR plate containing 200 µl of 20 mM Tris, pH 8.4, 50 mM KCl, 10 mg/ml Proteinase-K buffer, 5 µl/ml Tween-20, and water (Li and Hedgecock, 1998). Mussels were then incubated at 56 °C for 3 h, then 95 °C for 30 min, and stored at 4 °C.

PCR was used to amplify ITS 1 using a forward primer: (5'TTGATTACGTCCCTGCCCTTT 3') from Martel et al. (1999) sited in 3' end of the ribosomal 18S gene and a newly designed reverse primer (5'AGTGATCCACCGCATAGAGTAGT 3') sited in the 5.8S ribosomal gene. Predicted products for California mussels were about 550 base pairs long

and for Blue mussels were about 600 base pairs long. A 2-µl aliquot of template was used in 10 µl reactions as described above. Cycling parameters were 30 cycles of 94 °C for 30 s, 56 °C for 30 s, and 72 °C for 1 min. Positive controls for PCR used adult genomic DNA isolated from gill tissue using DNAzol (Molecular Research Center): these PCR products were used both for size comparisons and as evidence of successful PCR. Negative control reactions, containing no template, also were performed for every batch of juveniles identified to ensure there was no contaminating template in PCR set-ups. PCR products were electrophoresed on 1.5% agarose gels stained with ethidium bromide and visualized with UV light.

A blind validation test was performed to ensure PCR products were correctly identified on gels. DNA was extracted and amplified from tissue samples from ten adults of each species using the same protocol as juveniles. Shells were kept as vouchers for morphological species identification. Amplification products were loaded onto an agarose gel in a randomized pattern unknown to the scorer (SBJ). All mussels were correctly identified.

2.7. Statistical analyses

The absolute number of settlers for each species (or species group) was estimated as the proportion of Blue or California mussels from each pad as identified by PCR (that is, out of the 88 that were processed on each sampling date) multiplied by the total number of settler on that pad. Monthly averages were then calculated from these data and used as replicates for analysis of variance (ANOVA). Harbor samples were excluded from an ANOVA testing species specific patterns due to lack of California mussel settlement: a model-I two-factor (species and site) ANOVA was used to test for differences in settlement by California and Blue mussels on the two remaining sites. A model-I, one-factor ANOVA was used to test for differences in Blue mussel settlement among all sites (α -level=0.05). A one-sample Kolmogorov-Smirnov test showed data were not normally distributed for species proportions and average sizes of juveniles and adults. We found no transformation to normalize data. However, ANOVA is robust to non-normality (Zar, 1998), so analyses were performed

despite this violation. Assumptions of equal variances (Cochran's test $P > 0.05$), and independence were met.

3. Results

3.1. Identification of larvae in plankton samples

Positive amplification using species-specific PCR primers indicated the presence of larvae all three species in plankton tows of slough and channel waters in March 2002 (Table 1).

3.2. Adult distributions

M. californianus mussels were the dominant species found on the jetty and the majority were 1–3 cm in length in the upper zone and 2–4 cm in length in the lower zone. Only a few Blue mussels, 1–2 cm in length, were found in the upper and lower zones of

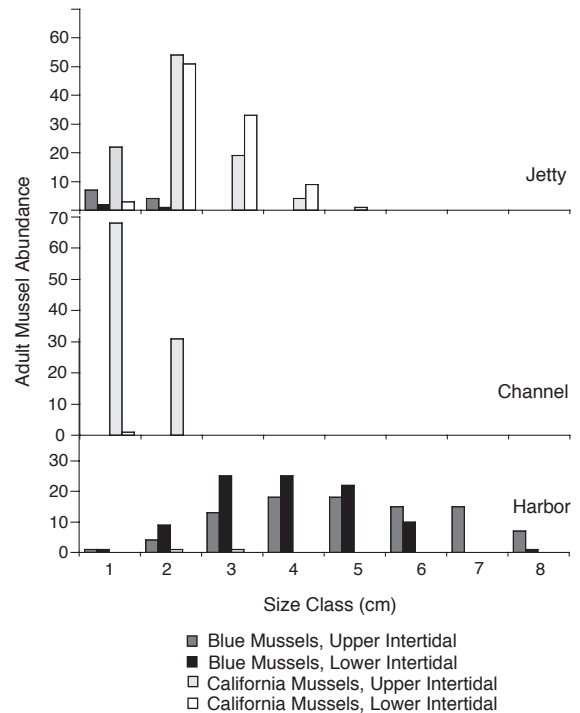


Fig. 1. Size frequency distributions for adult Blue (*M. galloprovincialis* and *M. trossulus*) and California (*M. californianus*) mussels in lower (0 m to +1 m tide) and upper intertidal zones (+1 m to +2 m tide). Mussels were absent from the lower tidal level of the channel site.

Table 1
PCR identification of *Mytilus* larvae from plankton tows in March 2002

Location		Species		
		<i>M. californianus</i>	<i>M. trossulus</i>	<i>M. galloprovincialis</i>
<i>Channel</i>				
Tow 1	10 Larvae	✓	✓	✓
	100 Larvae	✓	✓	✓
Tow 2	10 Larvae	✓	✓	✓
	100 Larvae	✓	✓	✓
Tow 3	10 Larvae	✓	✓	0
	100 Larvae	✓	✓	0
<i>Harbor</i>				
Tow 1	10 Larvae	✓	✓	0
	100 Larvae	✓	✓	✓
Tow 2	10 Larvae	✓	✓	0
	100 Larvae	✓	✓	✓
Tow 3	10 Larvae	✓	✓	0
	100 Larvae	✓	✓	0

Mussel larvae from plankton tows in Moss Landing Harbor and the channel of Moss Landing Harbor were pooled into groups of 10 and 100. DNA was isolated from each pool of larvae, and assayed by PCR for the presence of three species of *Mytilus* (see text). ✓ denotes positive amplification (=species present) of the species-specific mitochondrial cytochrome *b* PCR product and 0 signifies no amplification (=species absent).

the jetty (Fig. 1a). At the channel site, no mussels were found living in the lower zone, and *M. californianus* in the upper zone were small (≤ 1 cm) (Fig. 1b).

Blue mussels dominated mussel populations in the harbor, with only two small California mussels found in the upper zone. On average, adult Blue mussels from the upper zone in the Harbor were smaller than those in lower zone, but all mussels from this site were larger than those at the other sites (Fig. 1c).

3.3. Temporal settlement pattern

Settlement of mussel larvae occurred during the entire year but varied temporally at all sites (Fig. 2). Settlement was high from late spring (May) through early fall (November) and was low during winter months. All settlement pads for the channel and jetty were lost in December 2002 during a large

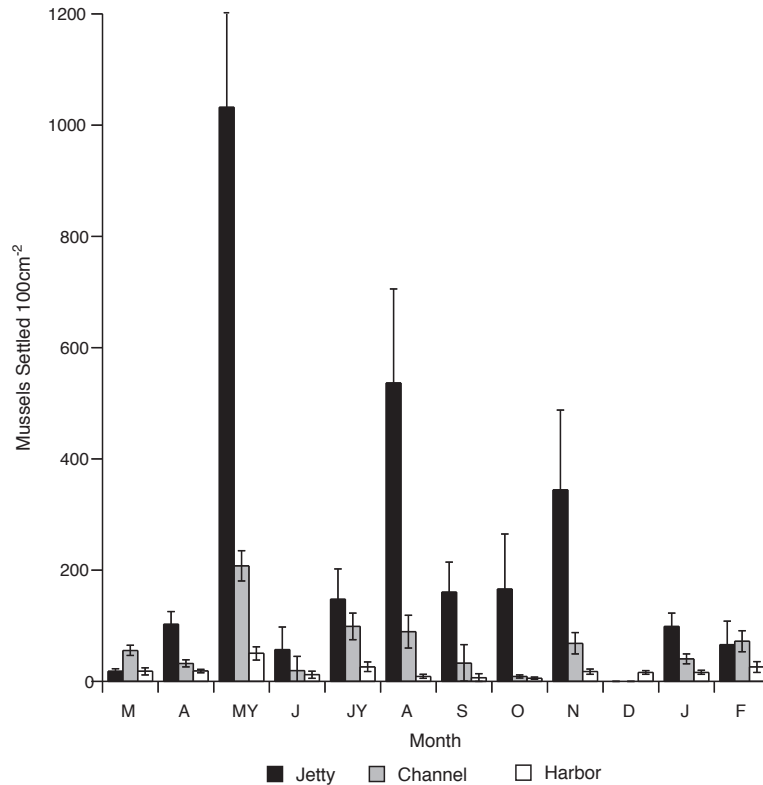


Fig. 2. Total settlement of mussels (*M. galloprovincialis*, *M. trossulus*, and *M. californianus*) (monthly mean of settlers $100 \text{ cm}^{-2} \text{ week}^{-1} \pm \text{S.E.}$) settling on 60 cm^2 recruitment pads at three sites with different wave exposure levels (jetty > channel > harbor) between March 2002 and February 2003.

storm. There were large pulses of settlement in May, August, and November 2002 at all sites. Settlement rates on the jetty were generally higher than the channel and harbor during late spring and summer months, ranging from 0.01 to $1.8 \text{ settlers cm}^{-2} \text{ week}^{-1}$. Settlement in the channel was intermediate with settlement rates ranging from 0.01 to $0.75 \text{ settlers cm}^{-2} \text{ week}^{-1}$. Settlement in the harbor was low throughout the year, ranging from 0.01 to $0.1 \text{ settlers cm}^{-2} \text{ week}^{-1}$.

3.4. Settlement by Blue and California mussels

The ratio of Blue and California mussels settling on the jetty and channel did not significantly differ. However, the absolute rate of settlement on the jetty and channel differed, with more mussels settled on the jetty than at the channel site (Table 2a; Fig. 3). The harbor site was excluded from these analyses because

settlement was very low: most of the few settlers there were Blue mussels, and California mussel settlers were rare or absent in all months.

Table 2

ANOVA testing for (A) differences in average monthly settlement rate of mussel species groups (Blue or California mussels) on the jetty and channel, and (B) differences in average monthly settlement rate of Blue mussels at three sites

Source of variation	Sum of squares	df	F	P
<i>A</i>				
Species group	1928.651	1	1.812	0.187
Site	801.128	1	4.363	0.044*
Site \times Species group	770.171	1	1.742	0.195
Error	15913.770	36	442.049	
<i>B</i>				
Site	30.199	2	68.559	<0.001*
Error	107.038	486		

* Indicates significance at $\alpha=0.05$.

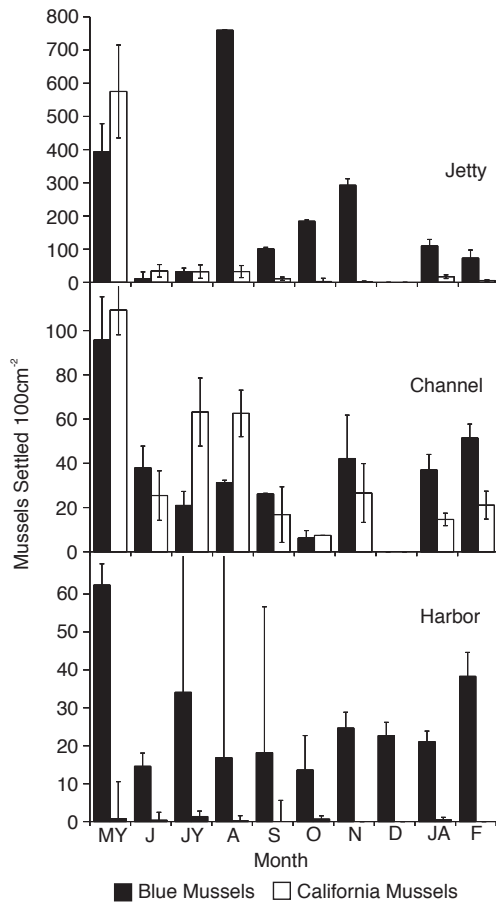


Fig. 3. Settlement rate (monthly mean of settlers $100\text{ cm}^{-2}\text{ week}^{-1} \pm \text{S.E.}$) of Blue mussels (*M. galloprovincialis* and *M. trossulus*) and California (*M. californianus*) mussels at three sites with different wave exposure levels (jetty>channel>harbor) between May 2002 and February 2003.

Blue mussel settlement was observed at all sites, with the jetty site having significantly higher rates of settlement (Table 2b). In most months, newly settled spat of Blue mussels outnumbered those of California mussels (Fig. 3).

4. Discussion

The distribution of adult mussels in Moss Landing was broadly similar to previous descriptions for California: we found adult *M. californianus* almost exclusively in wave-exposed areas (exposed and intermediate sites), while larger (>2 cm) *M. gallopro-*

vincialis and *M. trossulus* were exclusively found in the protected site (Harger, 1968; Suchanek, 1978). This was the expected pattern that led to our initial question: is this difference in distribution a result of settlement patterns, or might post-settlement processes be responsible?

We found that settlement of *M. californianus* differed among sites, with almost no settlement in the protected harbor. However, a single day's plankton sampling in March 2002 revealed the presence of *M. californianus* in harbor waters. While this limited sampling clearly does not demonstrate continued transport of *M. californianus* larvae into Moss Landing Harbor, it is consistent with ongoing studies that show massive influx of Monterey Bay water into Elkhorn Slough with daily tidal cycles (W. Broenkow and L. Breaker, in manuscript). It is reasonable to assume that *M. californianus* larvae are indeed regularly transported into Elkhorn Slough and Moss Landing Harbor when they are present in Monterey Bay waters. In a study concurrent to ours at nearby sites in Moss Landing Harbor, settlement of *M. californianus* was observed at low rates on pier pilings and docks (Braby, 2004). However, we found no evidence for settlement or empty shells of juvenile *M. californianus* that might suggest juvenile mortality following settlement. Our results were also similar to those of Heath et al. (1996) who also did not find settlement of *M. californianus* in protected sites near exposed coastal areas. Although Blue mussels are thought to displace California mussels from protected sites (Harger, 1968, 1972; Suchanek, 1985), any mechanism involving competition requires that both species settle in sufficiently high numbers to produce mixed aggregations and space limitation. Our results reveal that this condition did not occur in 2002–2003 at the site we studied in Moss Landing.

The failure of *M. californianus* to settle in Moss Landing Harbor was not due to unsuitable substrata, as they did settle on identical fibrous pads in the exposed site. Alternatively, perhaps appropriate settlement cues, such as might be produced from beds of adult conspecifics, were missing (Petraitis, 1978; Suchanek, 1978, 1981). However, larvae of *M. californianus* settled on adults of *M. trossulus* when given the choice of conspecific adults, algae or *M. trossulus* adults in a study in Oregon, (Petersen, 1984). Although *M. galloprovincialis* has not been

similarly tested as a settlement substrate for *M. californianus*, it does not appear that *M. californianus* can be entirely dependent on cues from adult conspecifics for settlement.

From our observations, it appears that *M. californianus* are transported through and settle on the rock jetty at the entry to Elkhorn Slough, yet fail to settle once inside. Because larval supply and substrate conditions do not provide compelling explanations for this failure, we speculate that the absence of settlement of *M. californianus* in the protected harbor environments may be a result of sensitivity of larvae or juveniles to temperature and salinity fluctuation (Young, 1941; Lutz and Kennish, 1992; Heath et al., 1996; Helmuth, 1999). Conversely, Blue mussels are more tolerant of extreme environmental stresses such as desiccation, changes in salinity, and thermal stress than are California mussels (Seed, 1969; Harger, 1972). Elkhorn Slough and Moss Landing Harbor have higher average monthly temperatures than open coastal waters of Monterey Bay (Elkhorn Slough Foundation and Monterey Bay Aquarium Research Institute, unpublished data). Possibly, *M. californianus* larvae suffer high rates of mortality once advected inside the harbor or Elkhorn Slough, while Blue mussels are less affected. If so, effective larval supply can be limited not by transport but instead by environmental conditions.

In contrast to *M. californianus*, Blue mussels (*M. trossulus* and *M. galloprovincialis* in unknown proportions) settled in all three sites, with greatest numbers at the exposed site. This result contrasts the distribution of adult Blue mussels, which were small and rare on the outer shore in this and previous studies in California (Harger, 1972; Connolly and Roughgarden, 1998). This pattern of settlement was also observed on wave exposed sites on the west coast of Canada, where juvenile *M. trossulus* outnumbered juvenile *M. californianus* (Heath et al., 1996). In the northeast Pacific, *M. trossulus* naturally co-occurs with *M. californianus* on outer shores, where it is found in patches within or in a fringe above beds of *M. californianus* beds (Suchanek, 1981; Emmett et al., 1987). Many Blue mussels in our study are likely *M. galloprovincialis*, an introduced species (Suchanek et al., 1997; C. Braby, pers. com.). In its native habitat, *M. galloprovincialis* may occur in wave-exposed areas, and it also does so in some non-native

areas (Hammond and Griffiths, 2004). It appears that Blue mussel larvae are not generally averse to settlement in high-energy environments.

We conclude that the absence of adult Blue mussels from exposed and semi-exposed environments in Moss Landing is not due to a deficiency in the supply or physiological condition of their larvae. We consider explanations involving post-settlement processes as more plausible. One hypothesis is competition with *M. californianus*. As adults, *M. californianus* can crush Blue mussels in exposed rocky intertidal areas (Seed and Suchanek, 1992). However, we did not find evidence of crushing on settlement pads or on unmanipulated substrata. Remnant byssal threads on the rock jetty, however, were observed throughout the study period, indicating previous occupation of mussels on the jetty. We do not know the species to which these byssal threads belonged. However, Blue mussels, with thinner byssal threads and thinner shells, are known to be more susceptible to heavy wave shock and rocky intertidal predators than *M. californianus* (Bell and Gosline, 1997). For example, on exposed Washington shores, *M. trossulus* settle in algal turfs, but compete poorly with barnacles and *M. californianus* (Wootton, 2001; Sanford et al., 2003). In Moss Landing, the absence of large Blue mussels from the exposed site may be due directly to physical factors, such as removal by waves, or by interspecific interactions. If patterns of settlement in 2002–2003 do not differ from those over longer time frames, some post-settlement process must result in the absence of adults on exposed sites.

5. Conclusion

In Moss Landing, Blue mussel settlement may be opportunistic on hard substrata, and adult distributions would then reflect post-settlement processes. The most striking evidence for this was the high number of Blue mussel settlers in the wave-exposed site, outnumbering *M. californianus* settlers. Most of these Blue mussel juveniles apparently died rather quickly, as very few small adults were observed at the exposed site. In contrast, differential settlement as we observed in 2002–2003 was a sufficient mechanism to produce the distribution of adult *M. californianus*, and post-settlement competition with Blue mussels need not be

evoked: we saw no settlement of *M. californianus* to the protected harbor site where adult Blue mussels were abundant. However, from identification of larvae in plankton, we have limited evidence of the delivery of *M. californianus* to the harbor site. We emphasize that larval transport is necessary for but does not ensure settlement. Settlement depends on transport together with larval condition and habitat characteristics that influence settlement behavior.

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