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Title: Do Settling Mussels (Mytilus spp.) Prefer Macroalgae over Artificial Substrates? A test of Collector Preference along the Oregon Coast

Abstract approved :

Bruce A Menge, PhD

This study investigated whether a device commonly used to measure settlement of mussel larvae for ecological studies, the Tuffy™, functions uniformly whether placed in a bed of filamentous algae or on bare rock. During the summers of 2004 and 2005, the number of mussel larvae settling on Tuffys in patches of the filamentous algae *Endocladia muricata* and *Neorhodomela larix*, known to be natural substrata for settlement of mussels, was shown to be the same as on Tuffys on adjacent patches of bare rock. The data provide no evidence that adjacent filamentous algae affects settlement to Tuffys and support the utility of this technique for measuring the intensity of larval settlement.

Do Settling Mussels (Mytilus spp.) Prefer Macroalgae over Artificial Substrates? A test of Collector Preference along the Oregon Coast

by

John Howieson

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APPROVED:

Major Professor, representing Zoology

Chair of the Department of Zoology

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

John Howieson, Author

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Do Settling Mussels (Mytilus spp.) Prefer Macroalgae over Artificial Substrates? A test of Collector Preference along the Oregon Coast

CHAPTER 1

GENERAL INTRODUCTION

Mussels of the family Mytilidae are dominant species in many exposed rocky shore communities within the temperate zone worldwide (Suchanek 1986). Mussels dominate space in many intertidal habitats, serve as a principal prey of many predator species (Whitman et al. 2003, Lappalainen et al. 2005,) and as habitat for numerous others (Durr and Wah 2004). As a consequence, mussels have long been a focus of study of community ecology. *Mytilus* is the most diverse and the most widely distributed genus of the Family Mytilidae. Along the US west coast, mussels (*Mytilus* spp.) dominate space in the middle intertidal zone on wave exposed rocky shores (Ricketts et al. 1985, Jamieson et al. 1999, Menge et al. 2004) . In the northeastern Pacific region the range of marine mussels extends from Baja California to southeastern Alaska (Jamieson et al. 1999). Both *Mytilus californianus* and *Mytilus trossulus* occupy the wave exposed coasts north of San Francisco (McDonald and Koehn 1988, Gosling 1992). *Mytilus trossulus* can also tolerate calmer waters occurring in protected bays and estuaries (Harger 1968).

Mussels are dioecious and free spawning, producing a veliger larva. This stage typically feeds in the plankton for one to four weeks and, upon settlement, matures into a pediveliger which is capable of metamorphosing (Carriker 1961).

Mussel larvae become competent to settle at approximately 250 µm shell length but can delay settlement to 400 µm if a suitable substrate is not available (Bayne 1965). Settlement may occur either directly to a site where development through plantigrade and juvenile stages occurs or in two phases, if the initial site proves unsuitable in which case the larva can detach and enter a second planktonic phase, the bysso-pelagic stage (Bayne 1964). During this second planktonic stage, movement in the water column is facilitated by secretion of a long thin byssal thread that increases the drag of currents (Sigurdson et al. 1976, Lane 1985). A third sequence of settlement events, direct primary settlement into established mussel beds has also been described (Petersen 1984). After post-settlement metamorphosis the developing mussel is referred to as a "plantigrade."

Studies of the factors underlying the local distribution and abundance of mussels were initially focused primarily on its post-recruitment interactions with predators and competitors (Paine 1966, Paine 1974, Paine 1984, Menge 1976, Suchanek 1986, Seed 1992). More recently, marine ecologists have turned to consideration of the influence of recruitment and oceanographic processes as initial determinants of mussel bed dynamics (Connolly et al. 2001, Menge 1992, 1994, 1999, Robles and Desharnais 2002, Menge et al. 2004). A valuable tool in such research has been the development of techniques useful in quantifying recruitment to adult habitat. Various artificial media have been used as substrata in studies of mussel recruitment and settlement (Seed 1969b). A recent technique has been the use of the "Tuffy" or plastic mesh ovoid originally developed for use in cleaning dishware (Menge 1992). The Tuffy was selected because it is readily available, uniform in size, easily deployed and removed from the field, and easy to process for removal of settlers in the laboratory. Its plastic fibers are similar in size to the branches of common intertidal filamentous algae especially *Endocladia muricata.* This red filamentous alga has been shown to be a preferred settlement substratum for mussel larvae (Paine 1974, Petersen 1984). The association of newly settled mussel larvae and filamentous seaweed has been observed for over a century (McIntosh 1885) and has subsequently been verified repeatedly (Wieser 1952, Verwey 1952, 1954, Chipperfield 1953).

Efforts to characterize recruitment usually reveal that recruitment of mussels varies widely in space and time (Menge 1992), and much effort has been aimed at attempting to learn the factors underlying this variation (e.g., (Menge et al. 1997, 2003, 2004, Broitman et al. 2005, Navarrete et al. 2005). One issue that has yet to be explored is whether the microhabitat into which Tuffys are deployed has an effect on the number of larvae settling. In a study of settlement preferences, an effect of adjacent algae on recruitment to collectors was demonstrated (Dobretsov and Wahl 2001). They showed greater settlement to monofilament plastic threads suspended one to ten meters over the filamentous seaweed *Cladophora rupestris* than to collectors over Laminarian kelps. In addition they demonstrated effects at a centimeter scale in partitioned boxes containing a sample of an alga and collection plates. The boxes were suspended in the water column under anchored floats. Such experiments would not, however, be possible in water conditions prevalent at our Oregon Coast research sites where the wave forces would preclude the deployment of the devices they described (*ibid.*). It seems unlikely, therefore that their results are applicable in wave-exposed coastal habitats.

It has been suggested that, on the coast of Washington, natural substrata such as *Endocladia muricata* or other foliose algae or the byssal threads of adult mussels could be more attractive to pediveliger larvae as settlement sites than are Tuffys (C.Harley, personal communication). If that were the case, settlement to Tuffys placed on bare rock might be higher than to Tuffys placed close to, for example, *Endocladia*. A short study testing the efficacy of Tuffys on Tatoosh Island found virtually no settlement into Tuffys placed in the field in spring (M. Wonham, personal communication). This lack of settlement to Tuffys coupled with the Dobretsov and Wahl (2001) hypothesis suggested the desirability of evaluating the efficacy of Tuffys as settlement collectors in relation to natural filamentous algal surfaces. The goal of this study was to test the hypothesis that Tuffys exhibit equal efficiency whether on bare rock or within a patch of filamentous seaweed.

CHAPTER 2

Do settling mussels (*Mytilus spp.*) prefer macroalgae over artificial substrates? A test of collector preference along the Oregon Coast

Introduction

The structure of most temperate rocky intertidal communities usually has mussels as a primary component (Suchanek 1986, Gosling 1992). As a consequence, much effort has been focused on determining the factors that underlie the structure and persistence of mussel beds (Paine 1966, 1974, 1984, Dayton 1971, Menge 1976, Menge et al. 1994, 1997, 1999, 2004, Robles and Desharnais 2002). Although early ecological studies of distribution and abundance of mussels focused on interactions with predators and competitors (Paine 1966, 1974, 1984, Menge 1976, Suchanek 1986, Seed 1969b), marine ecologists have more recently considered mussel bed dynamics to be strongly influenced by recruitment and oceanographic processes as well (Roughgarden et al. 1988, Connolly et al. 2001, Menge 1992, Menge et al. 1994, 1999, Robles and Desharnais 2002). To assess whether the factors governing recruitment are oceanographic larval transport mechanisms, the availability of suitable substratum, or post settlement processes such as competition, predation or facilitation, it is, therefore, essential to accurately quantify settlement for ecological studies.

An association between newly settled mussel larvae and filamentous seaweed has been observed for over a century (McIntosh 1885) and has been verified repeatedly (Wieser 1952, Chipperfield 1953, Verwey 1952, 1954). However, sampling of natural substrata to quantify recruitment potentially introduces a number of issues, including heterogeneity among the samples in substratum type or texture, three-dimensional structure of the algae or other settlement substrata, and possible depletion of the abundance of the natural settlement surface. Thus, the observation that larvae of *Mytilus edulis* will attach preferentially to artificial substrata that simulated the filamentous algae (deBlok 1958) was a potentially valuable insight for more rigorous investigation of the processes controlling recruitment of mussels.

Several types of artificial media have been extensively used as collectors of larval mussels in marine biological studies and in aquaculture. The various media used include rubberized hair, yarn, embroidery silk, cotton thread, hemp string, nylon yarn and thread, shag rug, and plastic ribbon (deBlok 1958, Seed 1969b, Davies 1974, Dare 1976, Menge 1978b), panels of Tufnol or Perspex (trade names for plastics), concrete, mortar, wood, and fiberglass (Seed 1969b), polystyrene (Bohle 1971) and ropes (Kautsky 1982, Dare and Edwards 1983). Large numbers of mussels in the early settling stages attach to rubberized hair pad collectors in the field (Davies 1974, Dare 1976, Dare and Edwards 1983). Quantitative data compare numbers of mussels settling on various collectors (deBlok 1958). Pitted or grooved plates and filamentous substrates were preferred to smooth surfaces and the filamentous substrates appear most effective (Bayne 1965). For *Mytilus edulis,* laboratory studies showed a preference by larvae for algae over mussels and bare tiles. Settlement on algal and byssal filaments, but not on scouring pad fibers was reported by Eyster and

Pechenik (1987). In other studies, larvae of *Mytilus edulis* were seen to attach preferentially to artificial substrata that simulated filamentous algae (deBlok 1958).

Only one publication was found to show an effect of nearby algae on recruitment to artificial collectors. Dobresov and Wahl (2001) found that more mussels recruited to monofilament plastic collectors suspended one to ten meters from anchored floats over beds of *Cladophora rupestris* (a filamentous green alga) than to collectors over Laminarian kelps. These effects were also demonstrated on a centimeter scale within boxes partitioned into three compartments. Each space within the partitioned box was open top and bottom and at its center was a mesh bag containing either *Cladophora,* a kelp or a control empty bag. They found that the *Cladophora* collected more and the kelp collected less than the control. However, it is clear that the oceanographic conditions that prevailed in the Dobretsov and Wahl (2001) experiments varied widely from conditions on the Oregon Coast. The wave forces prevailing in Oregon would certainly dislodge any similar experiment. In addition our ocean conditions would almost certainly lead to much greater water flow through the experimental chambers and mixing inside the chambers than prevailed in their experiments.

Although a variety of artificial settlement media have proven to be valuable tools in studies of mussel recruitment (Seed 1969b), they also vary widely in convenience, feasibility for use in turbulent rocky intertidal habitats, cost and availability. In an effort to identify a device that eased some of these issues, Menge (1992) employed the readily available plastic mesh ovoid or “Tuffy™” (SOS Tuffy pads; The Clorox Company, Oakland, CA, USA) originally developed for cleaning dishware. In addition to ease of use and ready availability, this device was selected because its fibers are similar in size to the branches of filamentous algae, especially *Endocladia muricata* and *Neorhodomela larix*, that are preferred settlement media for mussel larvae (Petersen 1984).

Notwithstanding the similarity of Tuffys to some physical attributes of filamentous seaweed, it has been hypothesized that larvae may select natural over artificial settlement sites when both are in close (= a few centimeters) proximity (CDG Harley, personal communication). At Tatoosh Island, Washington, USA a trial use of Tuffys was reported to be a failure since only a few larvae were collected during an entire spring season (M. Wonham com, personal munication). If the effectiveness of the collector varies with its surrounding macroalgae, then its effectiveness as an ecological tool is diminished.

Here I present the results of a study aimed at testing the hypothesis that settlement to Tuffy collectors did not vary with the substrate microhabitat in which the collectors were deployed. To test this hypothesis, I deployed Tuffys to two microhabitats: (1) bare rock with no filamentous algae within 15 cm, and (2) rock substratum covered with filamentous algae.

Materials and Methods

Study Sites

In summer 2004, experiments were set up at two study sites on the Oregon coast. The sites were Strawberry Hill (44º15.3’N, 124º06.7’W) and Fogarty Creek (44º50.1’N, 124º03.7W)(Fig. 2.1). In summer 2005, the experiment with *Endocladia* was repeated and, in addition, a new set of experiments was set up using another prevalent filamentous seaweed, *Neorhodomela larix.*

The two sites were selected because extensive ecological studies have characterized the mussel zones at these sites (Menge et al. 1994, 1997, 2004, Berlow 1997, Navarrete 1996). In addition, extensive work has also been carried out at Boiler Bay, a location with similar physical characteristics approximately 0.5 km south of Fogarty Creek. These studies have shown mussel settlement at Strawberry Hill is often greater than at Boiler Bay and Fogarty Creek 83 km. to the north.

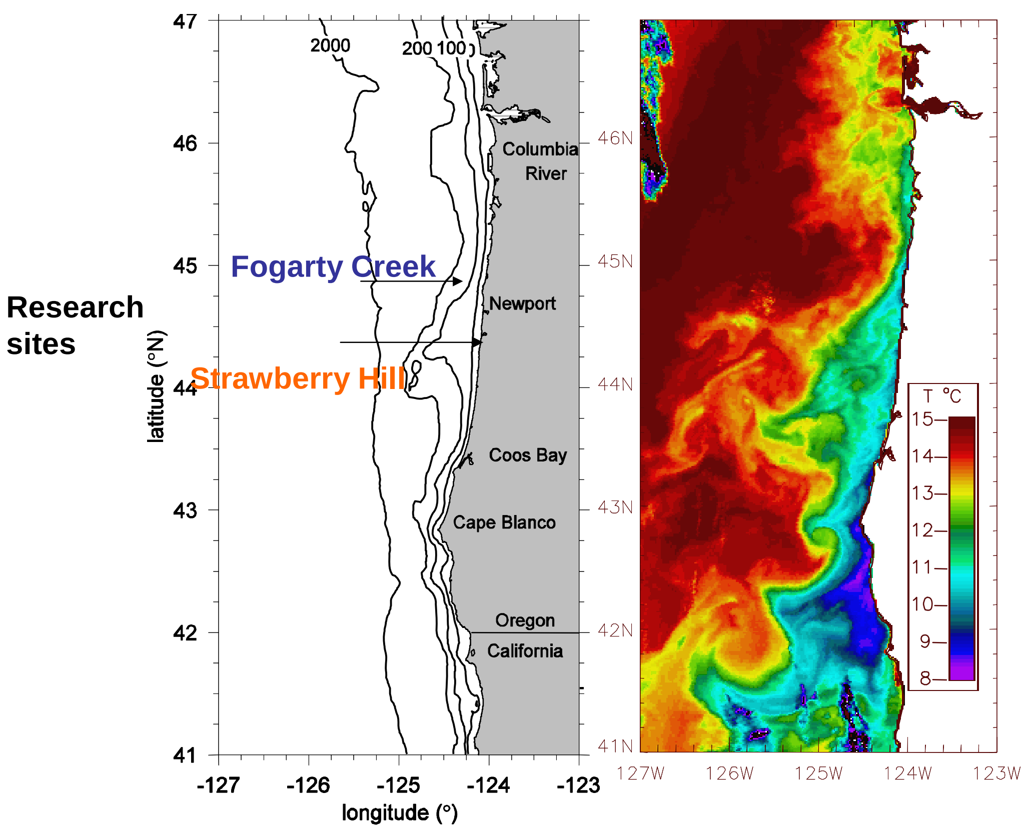

Fig. 2.1. Oregon Coast study sites. The left image is a bathymetry plat revealing that the 100 meter depth line deviates much farther offshore at Strawberry Hill than at Fogarty creek. The right image is a sea surface temperature plat showing the wider band of cool onshore water during upwelling at Strawberry Hill than at Fogarty Creek. This zone of cool surface temperature extending offshore to

approximately the 200 meter depth line indicates stronger upwelling of cool deep water at Strawberry Hill than is seen at Fogarty Creek.

Recruitment Experiment. During summer 2004, each experimental replicate consisted of a pair of plastic mesh ovoids (Tuffys) attached to the substratum with lag screws inserted into wall anchors embedded in the rock (Fig. 2.2). One Tuffy of each pair was anchored to the rock within a bed of *Endocladia muricata*. An adjacent Tuffy was similarly attached in a 30 cm diameter zone from which all macrobiota had been scraped away leaving bare rock. Five replicates were placed in the lower part of the *Endocladia* bed just above the mussel zone at Fogarty Creek and at Strawberry Hill (e.g., Fig. 2.3). Collectors were initially deployed at both sites on July 15, 2004. Five collections of Tuffys from both sites were made during each spring tide thereafter from August 1 to September 30, 2004 (August 1, August 15, September 1, September 15 and September 30). Upon retrieval, the Tuffys were stored at -12º C until they were processed. In the laboratory the mussels were washed from the plastic mesh into a plastic bowl using a jet of water, sieved into 250-500 µm and >500µm samples and counted under a dissecting microscope.

Fig. 2.2 Photograph of a replicate deployment, with the left Tuffy in *Endocladia muricata* turf and the right Tuffy on rock substratum. A smattering of barnacles has settled into the cleared area around the Tuffy on the right.

Fig. 2.3 Fogarty creek 2004: View of Tuffy array at the interface between the lower mussel bed (left) and the upper algal zone (right).

During summer 2005, the experiment comparing collector effectiveness in patches of *Endocladia* to adjacent cleared zones was repeated. A similar array of collectors was deployed. In addition, Tuffys were placed in patches of *Neorhodomela* *larix* and in adjacent cleared 30 cm diameter plots. This arrangement mimicked the design of the *Endocladia* experiment, the only differences being the species of alga and the associated tidal height. Maximum *Neorhodomela* abundance occurs about one meter lower on the shore than that of *Endocladia*. Five replicates of the *Endocladia* experiment were established at each of two sites, Fogarty Creek and Strawberry Hill on July 5. The *Neorhodomela* experiment was begun in the same fashion on July 21. Collection dates for *Endocladia* in 2005 were at each spring tide from July 5 to September 16 (July 5, July 21, August 3, August 19 and September 15). For *Neorhodomela* the collection dates were July 21, August 3, August 19, and September 15. A spring tide occurred on September 3, 2005 but collectors were not exchanged at either site because of unfavorable conditions. As a result, the September 15-17, 2005 collectors had been in place for 2 tide cycles. Storage and counting procedures were the same as those for 2004 collections.

To test the effects of treatment (algal substratum vs. bare rock), site and time on variation in mussel recruitment, I used repeated measures ANOVA. Sphericity tests (Mauchly criterion) indicated that after transformation (*ln* x) the data satisfied the requirement of multivariate normality, so we present unadjusted probabilities. Separate analyses were done for the 2004 experiment and the two (*Endocladia* and *Neorhodomela*) 2005 experiments.

Results

In general, the results indicate that there was no effect of algal proximity on the density of mussel larvae settling into Tuffys. In 2004, the “between subjects” repeated measures results indicated that overall, the number of recruits in algal substratum plots (E plots) was not different from the number in bare rock plots (C plots)(Fig. 2.4, Table 2.1). As has been observed in prior work (Menge 1992, Connolly et al. 2001), recruitment varied between sites through time (Table 2.1; time x site interaction). From inspection of Fig. 2.4, this interaction appears due to the different pattern of increase of recruitment between August and September. At Fogarty Creek, recruitment increased abruptly and stayed high to the end of September while at Strawberry Hill, recruitment increased in early September and then decreased in later September.

In 2004, the univariate and multivariate repeated measures analysis gave contrasting results, suggesting that treatment effects either were (univariate) or were not different (multivariate). In other words, when temporal changes are included in the analysis, it appears that an algal substratum may have affected recruitment. This effect was relatively weak, however ($p = 0.039$), and is contradicted by the more conservative multivariate test ($p = 0.083$).

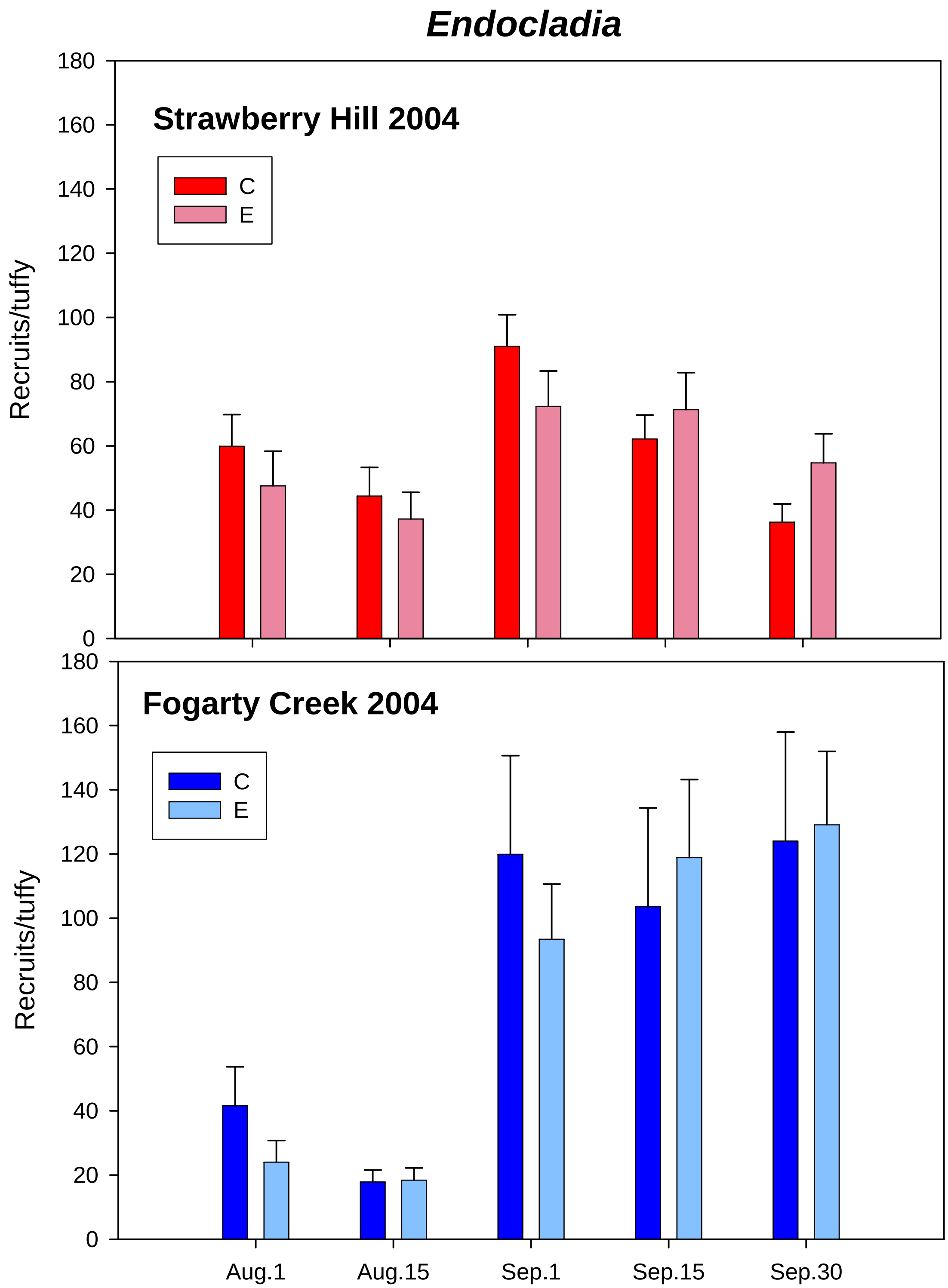

Fig. 2.4. Results of 2004 experiment at Fogarty Creek and Strawberry Hill . C = Tuffy in cleared patch and E = Tuffy in *Endocladia* patch Error bars are one SE.

Table 2.1. Repeated measures analysis of variance on 2004 recruitment experiment. DF = degrees of freedom. Data were transformed (*ln* x) before analysis. Univariate and multivariate probabilities are shown for within subjects results. Test for sphericity (Mauchly criterion) p = 0.247. Significant effects are shown in boldface.						
Effect	DF	Sum of squares	Mean square	F	Univariate p	Multivariate p
Site	1	0.018	0.018	0.03	0.87	
Treatment	1	0.081	0.081	0.12	0.73	
Treatment x site	1	0.098	0.098	0.14	0.71	
Error	14	9.453	0.6752			
Time	4	20.221	5.055	55.19	**<0.0001**	**<0.0001**
Time x site	4	11.415	2.854	31.16	**<0.0001**	**<0.0001**
Time x treatment	4	0.995	0.249	2.71	**0.039**	0.083
Time x treatment x site	4	0.464	0.116	1.27	0.29	0.48
Error	56	5.129	0.092			

In 2005 for *Endocladia*, overall recruitment differed between sites but not between collectors in algal turf vs. collectors on bare rock (Fig. 2.5, Table 2.2). As in 2004, recruitment was lower in August 2005 than in September 2005 at both sites, but the increase at Strawberry Hill in 2005 was much greater than at Fogarty Creek (Table 2.2, univariate time x site interaction).

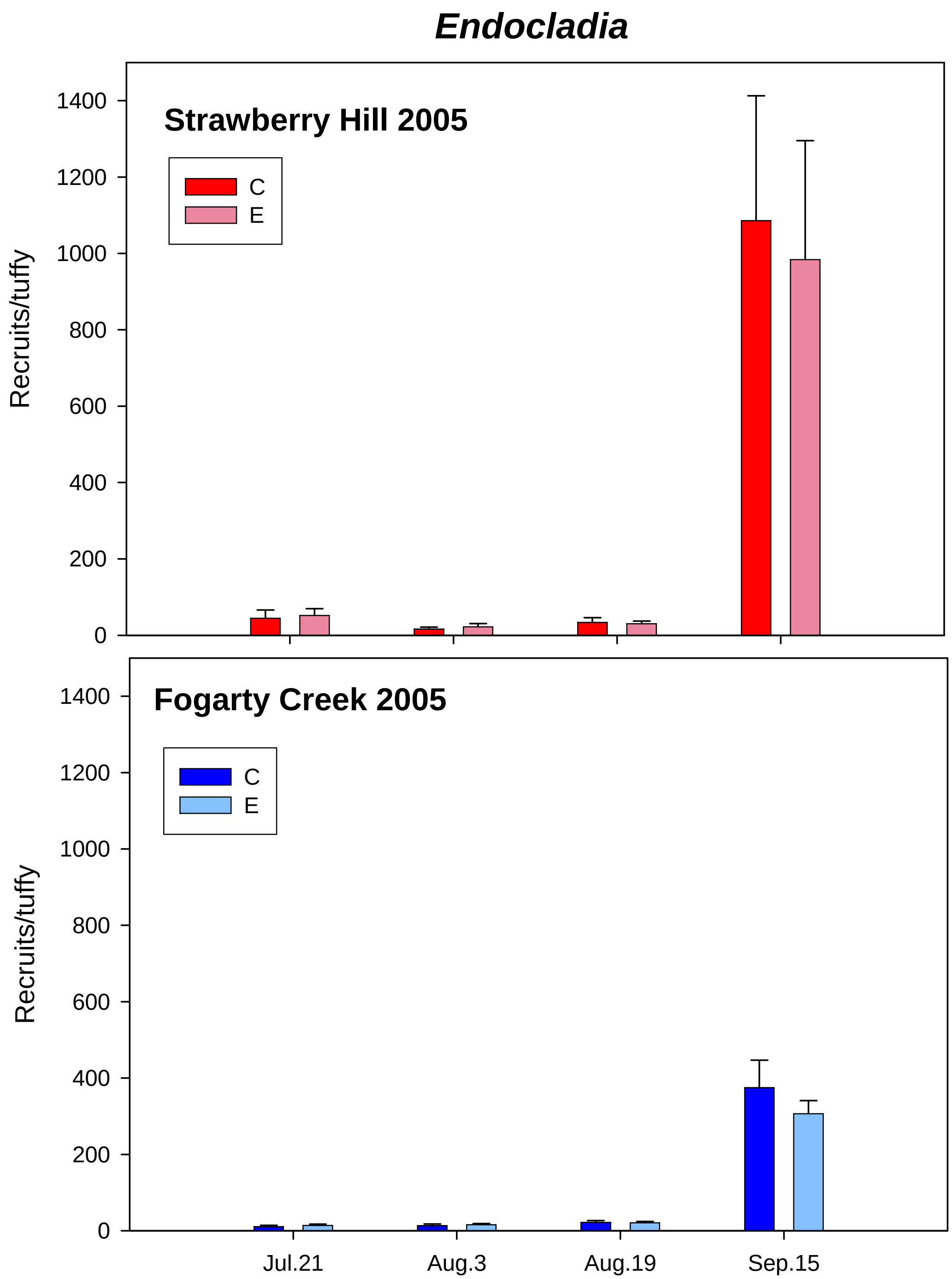

Fig. 2.5. Results of 2005 experiment at Fogarty Creek and Strawberry Hill in *Endocladia*, C= cleared patches, E = *Endocladia* patches.

Variation among collectors was quite high at Strawberry Hill, however (see large 95% confidence intervals in Fig. 2.5), and the more conservative multivariate results suggest that the time x site interaction is marginally significant (Table 2.2).

Table 2.2: Repeated measures analysis of variance of effects of proximity of *Endocladia* (present vs. absent) and site (Fogarty Creek and Strawberry Hill) on recruitment of mussels to collectors in 2005. DF = degrees of freedom. Data were transformed (*ln* x) prior to analysis. Univariate and multivariate probabilities are shown for within subjects tests. Test for sphericity (Mauchly criterion) p = 0.321. Significant p values are shown in bold face.

Effect	DF	Sum of squares	Mean square	F	Univariate p	Multivariate p
Site	1	7.2396	7.2396	5.35	**0.036**	
Treatment	1	0.4771	0.4771	0.35	0.56	
Treatment x site	1	0.1570	0.1570	0.12	0.74	
Error	14	18.9414	1.3530			
Time	3	156.9892	52.3297	227.52	**<.0001**	**<0.0001**
Time x site	3	3.2881	1.0960	4.77	**0.006**	0.064
Time x treatment	3	0.9587	0.3196	1.39	0.26	0.20
Time x treatment x site	3	0.06	0.02	0.09	0.97	0.97
Error	42	9.660	0.230			

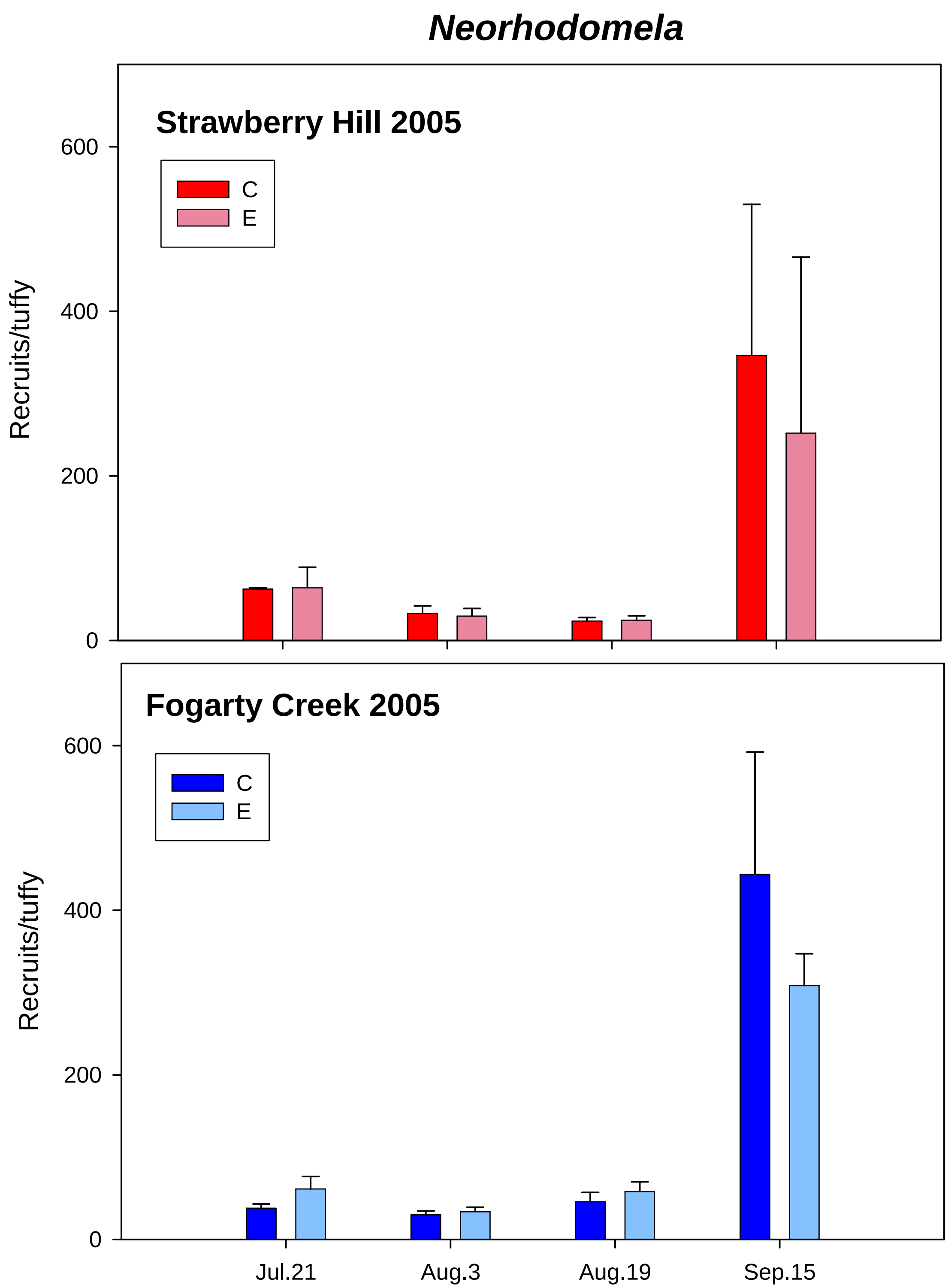

Fig. 2.6. Results of 2005 experiment at Fogarty Creek and at Strawberry Hill in *Neorhodomela.*, C = cleared patches, E = *Neorhodomela* patches.

In 2005, the recruitment of mussels into Tuffys placed in *Neorhodomela* beds did not differ from recruitment into Tuffys placed on bare rock (Fig. 2.6, Table 2.3). As in the other experiments, recruitment varied with time (Table. 2.3), with an increase in recruitment occurring in September 2005 (Fig. 2.6). In contrast to the *Endocladia* results, however, recruitment rates in the *Neorhodomela* experiment did not differ between sites (Fig. 2.6, Table 2.3)

Table 2.3: Repeated measures analysis of variance of effects of proximity of *Neorhodomela* (present vs. absent) and site (Fogarty Creek and Strawberry Hill) on recruitment of mussels to collectors. DF = degrees of freedom. Data were transformed (*ln* x) prior to analysis. Univariate and multivariate probabilities are shown for within subjects tests. Test for sphericity (Mauchly criterion) p = 0.174. Significant p values are shown in bold face.

Effect	DF	Sum of squares	Mean square	F	Univariate p	Multivariate p
Site	1	0.5729	0.5729	1.40	0.26	
Treatment	1	0.0215	0.0215	0.05	0.82	
Treatment x site	1	0.4021	0.4021	0.98	0.35	
Error	10	4.1021	0.4102			
Time	3	33.8732	11.2911	41.62	**<0.0001**	**0.0005**
Time x site	3	1.7462	0.5821	2.15	0.12	0.15
Time x treatment	3	0.8437	0.2812	1.04	0.39	0.42
Time x treatment x site	3	0.0732	0.0244	0.09	0.97	0.98
Error	30	8.1395	0.2713			

In 2005 the recruitment rates did not differ between sites.

Discussion

In this study the data revealed little to no effect of the presence of filamentous algae on recruitment of mussels into collectors at either Fogarty Creek or Strawberry Hill. That is, the number of larvae settling in the Tuffys in the cleared patches was similar to Tuffys in *Endocladia* patches. This pattern was observed in both 2004 and 2005 indicating that the pattern of no effect of presence or absence of *Endocladia* may persist through time. Further, in 2005, similar results were observed for *Endocladia* and *Neorhodomela*, suggesting that differences in the species of filamentous algae that are close to Tuffys are unlikely to influence settlement. *Endocladia muricata* and *Neorhodomela larix* are both favored natural settlement media for mussel larvae (Paine 1974).

In this study, mussel recruitment was higher at Strawberry Hill than at Fogarty Creek. What might be the causes of this difference? Prior studies also detected this pattern, and led to the suggestion that oceanographic conditions might favor higher larval retention in the vicinity of Strawberry Hill than at Fogarty Creek (e.g., Menge et al 1997, 2004). Other possible factors include differing wave exposure or burial by sand. Fogarty Creek is a sloping rocky bench that is exposed to the open ocean close to the northern margin of Boiler Bay. It appears to experience greater wave action than Strawberry Hill where the location of the experiments was to some degree sheltered by large offshore rock outcrops (J. Howieson personal observation). Nevertheless, the wave action at Strawberry Hill was sufficient to loosen and in some cases remove Tuffys that were bolted to the rock, suggesting wave forces can be substantial at Strawberry Hill. In addition, prior measurements using dynamometers have revealed that maximum wave forces are similar between these sites (Menge et al. 1996, P. Halpin unpublished data). As has also been reported earlier (Menge et al. 1994), Strawberry Hill is more subject to influx of sand which, during the last collection on September 15, 2005 buried several Tuffys so that they were irretrievable.

The null hypothesis that mussel recruitment does not differ between Tuffys placed in filamentous algal beds vs. Tuffys placed on bare rock is generally supported by the results of my experiment. The only exception was for *Endocladia* in 2004, where recruitment to Tuffys differed between bare rock and *Endocladia* plots on the last sampling date, 30 September 2004 (repeated measures ANOVA, treatment effect, $p = 0.03$). As noted previously, this result was not significant in the more conservative multivariate analysis (Table 2.1) and was the only case in 13 analyzed sample dates in which a difference was observed. I conclude that settlement of mussel larvae on artificial collectors is not influenced by the proximity of filamentous algae in this system.

It is conceivable that some chemical influence emitted by the algae could act over a distance much greater than 15 centimeters and that such an influence would be missed by the design of this study, thus affecting recruitment on a larger spatial scale, possibly even including site. However considering the great dilution of any chemical gradients exuded by algae that would be expected from the large volume of water washing over the mid intertidal sites, and the complex mixing of different chemicals from the many species of algae and invertebrates that occur in these habitats, any such long distance chemical influence seems unlikely. Nonetheless, this idea cannot be dismissed and might warrant further study.

Based on prior results, the temporal fluctuations in recruitment to Tuffys that I detected in my study was expected (e.g., Connolly et al. 2001). Such variation is possibly related to variable larval supply through time. It could also be related to different physical conditions between sites that may have affected the survival of settlers. In 2004 at Fogarty Creek, the number of recruits increased steadily throughout the summer but at Strawberry Hill peak settlement was in August. During summer 2005 lower counts were again observed during August compared to September. The longer duration of deployment of the collectors harvested in September 2005 due to omission of the first September exchange no doubt accounts for part of the increase, but the average larval count per Tuffy increased from under 100 to approximately 400 per collector suggesting that a doubling of the interval between collections was not the sole factor. These fluctuations of settlement over time have been observed in other systems (Seed 1969a, Menge 2000) and seem mostly attributable to oceanographic factors that either influence the concentration of larvae or the rate of delivery to the intertidal areas. The interplay of factors such as upwelling and downwelling probably influences larval concentrations available for settlement, but the interrelationship of wind and currents to larval concentrations in the water column and thence to fluctuations of settlement remain to be explained.

In this regard 2005 was a unique year. From an oceanographic standpoint the sea temperature was two to 5 degrees warmer than normal (F. Chan et al. personal communication). The upwelling of cold water that usually begins in March or April did not occur until July and no similar lack of upwelling had been observed during the last 50 years (J. Barth et al. personal communication). In Oregon mussel recruitment and phytoplankton concentrations in Oregon were far below the 15 year average until the middle of July, 2005 (B. Menge personal communication), after which most sites rebounded to equal or exceed the norm. Thus, the extreme difference between 2004 and 2005 allows the inference that my results are applicable to a wide range of oceanographic conditions.

My results are inconsistent with the idea that variation in the number of mussels settling into Tuffys is in part driven by whether or not they are in contact with naturally occurring beds of algae that are known to be preferred settlement substrata. Thus, the suggestion that the short-term failure of mussel recruitment into Tuffys on Tatoosh Island might be because settling larvae are drawn instead to the naturally occurring *Endocladia muricata* instead of the artificial Tuffy collectors seems without merit.

Why didn't Tuffys "work" at Tatoosh Island? Further study is clearly necessary, but there are several possibilities that could be examined. First, the time of study on Tatoosh Island might have been either too short or in the wrong season or both. In Oregon, mussel recruitment is highly seasonal, reaching a peak from August to November, with low settlement from December through May or June (Menge 1994, 1997, Connolly et al. 2001). Thus, deploying Tuffys only in spring seems likely to provide misleading results, both about settlement densities and about the efficacy of the Tuffy method. Second, oceanographic conditions at Tatoosh Island are different from those further south along the coast (Hickey 1998), and thus, for example, larval transport patterns may differ greatly between these locations. It is possible, therefore, that the number of mussels arriving onshore at Tatoosh is very low relative to areas along the rest of the Washington and Oregon coasts. Other possibilities include such effects as different methods of deployment, deployment in different zones of the shore, or highly localized effects of stress causing high mortality during deployment.

The results here, in combination with successful use of Tuffys in virtually all other geographic regions in which they have been deployed (e.g., Oregon - Menge et al. 1992, 1994, 1997; New Zealand – Menge et al. 1999, 2003, Rilov et al. unpublished data; Chile - Navarrete et al. 2002, Navarrete et al. 2005; Channel Islands - Broitman et al. 2005; Maine -Leonard et al. 1998; US West coast – Connolly et al. 2001, Menge et al. 2004; South Africa – E. Wieters personal communication) suggests that if recruitment does not occur in Tuffys it is likely due to a lack of available recruits. Further, across these regions, several mussel species have settled into Tuffys, including *Mytilus trossulus, M. galloprovincialis, M. californianus, M. edulis, Perna canaliculus, Xenostrobus pulex, Aulacomya maoriana, Perumytilus purpurpatus, Semimytilus algosus,* and *Brachidontes granulata* (Menge 1992, Menge et al. 1994, 1997, 1999, 2003, 2004, Connolly et al. 2001, Leonard et al. 1998, Navarrete 2005) so species differences also seem unlikely to explain a lack of recruitment. I conclude that Tuffys remain valuable as an ecological tool for the investigation of mussel settlement.

CHAPTER 3

GENERAL CONCLUSIONS

This study supports the use in ecological field studies of the plastic mesh ovoid with the commercial name Tuffy™ as a collector of larval mussels. The concern that the efficiency of this type of collector might be impaired by placement in proximity to the natural settlement media, *Endocladia muricata* and *Neorhodomela larix* is not supported by my data. The observations at two sites on the Oregon Coast, during two years, and with two filamentous algae suggest that the conclusion can be generalized within habitats having similar characteristics. Ancillary observations of settlement intensity differences between the study sites and at different times of year are consistent with previous studies (Menge 1992, 1997, 2004).

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