EXPERIMENTAL EFFECTS OF BLACK BRANT HERBIVORY AND FECAL ADDITION ON THE EELGRASS ANIMAL COMMUNITY IN HUMBOLDT BAY, CALIFORNIA, USA

By

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ABSTRACT

Experimental effects of black brant herbivory and fecal addition on the eelgrass animal community in Humboldt Bay, California, USA

Adam J. Frimodig

Seagrass beds are productive, structurally complex ecosystems that support an abundant and diverse assemblage of animals. Although light is clearly important to seagrass productivity, grazers also alter this aspect of plant communities. Grazers may indirectly affect the associated animal community but this perspective has not been rigorously examined in temperate western North American seagrass beds. My thesis objective was to experimentally examine the effects of Pacific black brant geese (*Branta bernicla nigricans*) grazing and fecal addition on the abundances and sizes of the animals within an eelgrass (*Zostera marina*) bed of Humboldt Bay, CA (40º 43.1' N, 124º 13.3' W). *In situ* brant simulations were used to investigate the effects of different treatments (clipping, fecal addition, the combination of both at "intermediate" and "intense" levels, and brant exclusion) on the abundances and sizes of the animals within the *Z. marina* community. Animal treatment responses were only compared when *Z. marina* vegetation structure (shoot density, shoot length) significantly differed among treatments. By including covariates like climate and water quality variables, as well as distance of a treatment from channels, this study also identified the recruitment and environmental conditions that favor the development of a positive or negative relationship between animal abundance and size versus *Z. marina* complexity. For example, large interannual

variation in juvenile Dungeness crab (*Cancer magister*) abundance was attributed to warmer water current structure changes during 2005, and may have therefore delivered fewer megalopae to Humboldt Bay. Similarly, the effects of fish predation may have equalized the abundance and distribution of small *Z. marina* invertebrates, such as caprellid and gammarid amphipods and bay isopod (*Idotea resecata*), and thus prevented a relationship with vegetation structure from developing. Following the effects of climate on recruitment and fish predation, brant induced changes to the vegetation structure did affect animal abundances and sizes, but responses were species-specific. The abundance of Taylor's sea hare (*Phyllaplysia taylori*) increased when a maximum number of shoots were created by intermediate levels of brant grazing, and both the abundance and size of *P. taylori* decreased in response to shorter shoots created by intense levels of brant grazing. Other animal responses responded negatively to brant induced changes to the vegetation structure. For example, *I. resecata* were smaller when shoots were more dense and longer, and they were larger when shoots were less dense and shorter. Lastly, the abundances and sizes of some animals were significantly different among brant simulation treatments, but animal differences did not parallel the brant induced changes to the vegetation. Therefore, brant induced changes to the structural complexity of *Z. marina* affect both the abundance and size of the associated animal community under a limited set of circumstances.

ACKNOWLEDGEMENTS

My thesis constituted part of a larger project which included the eelgrass productivity response to the grazing and fecal fertilization by black brant geese. The entire project was fully supported by California Sea Grant (Project #: R/CS-189). Drs. Frank Shaughnessy and Jeff Black were Principal Investigators (PIs) and Wildlife graduate student, Susannah Ferson, and I were Research Trainees.

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space; and David Hull who permitted the temporary placement of literally thousands of PVC pipes in the bay.

This study consisted of an enormous amount of field work including months of set-up and take-down before and after the 3-4 month experiments in both 2004 and 2005. Over 50 people, mostly undergraduate and graduate students from Humboldt State University (HSU) and College of the Redwoods took part in the field work. These people were willing to get out on the water before sunrise, slog through mudflats on their hands and knees using boogieboards, and even handle brant geese stools! For that, I am truly grateful. A special thanks goes out to the following people who spent an exceptional amount of time in the field: Braden Hogan, Chris West, Michelle Koury, Emily Bjerre, Julia Frahnet-Nornbeck, Samantha Treu, Scott Ohman, Tammy Branston, Dave Topolewski, Greg Roberts, Marisa Alvarado, Brett Leonard, Asa Spade, James Carey, Jordan Muir, Skip Shoemaker, and Abby Boyd. In particular, Ryan "Squatch" Murdoff, Steve Spain, and Christine Caurant were my "go-to crew" who I could always count on and somehow managed to keep the group morale high through both long days and harsh weather. There were also a handful of people that worked a substantial amount of hours in the lab including Courtney Herman, Samantha Vincent, Russ Enriquez, Jessie Oliver, and Bill Mikolay. I cannot thank each of you enough!

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INTRODUCTION

Seagrass beds are sheltered and physically complex ecosystems that support an abundant and diverse assemblage of aquatic animals, many of which are commercially important (Orth and Heck 1980, Pollard 1984, Thayer et al. 1984a, Bell et al. 1987, Heck et al. 1989, Short et al. 2001, Heck et al. 2003). They are recognized for their high productivity, refuge, nursery, recruitment and sediment stabilization functions within bays, estuaries and lagoons around the world (Orth 1977, Leber 1985, Bell and Westoby 1986a, b, c, Thom and Albright 1990, Fonseca 1992, Perkins-Visser et al. 1996, Boström and Bonsdorff 2000, Williams and Heck 2001, Heck et al. 2003, Koch et al. 2006). Seagrasses and epiphytic algae are the major primary producers (Williams and Heck 2001, Borowitzka et al. 2006), and the nutrients and energy they bring into the system can follow either detritus or grazer based pathways (Perkins-Visser et al. 1996, Cebrián et al. 1997, Valentine et al. 1997, 2000, Duffy and Harvilicz 2001, Moore et al. 2004). The detritus pathway is emphasized in the literature in part because grazers of seagrasses have been lost or greatly reduced in abundance (Domning 2001, Valentine and Duffy 2006). However, there are still locations where herbivores such as waterfowl, urchins, limpets, green turtles and dugongs feed on seagrasses (Baldwin and Lovvorn 1994, Clausen 1994, Preen 1995, Fox 1996, Zimmerman et al. 1996, Madsen 1998, Valentine and Heck 1999, Valentine and Duffy 2006), and invertebrate mesograzers of epiphytic algae are common (Orth and van Montfrans 1984, Borum 1987, Klumpp et al. 1992, Fong et al. 2000, Williams and Heck 2001, Borowitzka et al. 2006).

Refuge, nursery, recruitment and sediment stabilization functions of seagrass beds depend in part on their vegetation complexity, which in turn is affected by factors affecting seagrass productivity. Seagrass beds provide a structurally complex habitat which is used by animals as a refuge from predators (Heck and Orth 1980, Orth et al. 1984, Irlandi 1994, Heck and Orth 2006). For example, seagrass blades provide cover for amphipods and polychaetes by reducing fish predation (Heck and Orth 1980). Similarly, predation on the hard clam (*Mercenaria mercenaria*) in seagrass beds of Back Sound, North Carolina appears to be influenced by belowground biomass and shoot density (Irlandi 1994). The nursery function of seagrass beds occurs because of the cover and trophic support they provide to the ecosystem. Many studies have found that both the survival and growth rates of juvenile animals is enhanced in seagrass beds compared to nearby unvegetated areas (Peterson 1982, Heck and Thoman 1984, Thayer et al. 1984a, Pohle et al. 1991, Heck et al. 1995, Irlandi 1996, Perkins-Visser et al. 1996, Irlandi 1997, Heck et al. 2003). For example, juvenile bay scallops (*Argopecten irradians*) avoid predatory crabs by attaching their byssal threads to seagrass blades at a distance of 20-35 cm above the substrate (Pohle et al. 1991).

Seagrass beds also function as a stable environment for small animals because they slow down the water velocity which consequently enhances sediment accumulation and both invertebrate and algal recruitment (Fonseca 1992, Borowitzka et al. 2006, Koch et al. 2006). In addition to their leaf canopy effects on water motion, seagrass beds have a dense, matted root system that stabilizes the soft bottom and is capable of withstanding storms as severe as hurricanes (Nybakken 2001). Field experiments have shown that

seagrass beds absorb wave disturbance thus decreasing the risk of dislodgement of blue mussels, *Mytilus edulis* L. (Reusch and Chapman 1995). Seagrass beds also serve as a filter by trapping and binding sediments therefore improving the overall water quality (Rasmussen 1977, Fonseca 1992).

Most efforts to conserve seagrass bed functions have focused on bottom-up effects that regulate these communities since seagrass grazers may not be abundant and the effects of suspended sediments and nutrient loading on light extinction can be conspicuous (Williams and Heck 2001, Valentine and Duffy 2006). However, a variety of seagrass grazers still exist and the populations of some, such as waterfowl, are stable. These grazers have both immediate and delayed effects on the vegetation complexity of the bed (Belsky 1986, Valentine et al. 1997, Cebrián et al. 1998, Valentine et al. 2000). Immediate effects range from the removal of leaf epidermal cells, partial to entire leaves, to both the removal of above and below ground portions of the plant (Williams and Ruckleshaus 1993, Clausen 1994, Preen 1995, Zimmerman et al. 1996, Valentine et al. 1997, 2000, Moore 2002, Moore and Black 2006a). Delayed effects on complexity may depend on fecal matter returned to the system by the grazer (Wotton and Malmqvist 2001, Croll et al. 2005), and whether enough photosynthetic tissue and shoot meristems have been left intact to permit seagrass compensation or even overcompensation. Overcompensation is the term used to describe the capacity of grazed grass to be more productive than ungrazed grass (Belsky 1986, Belsky et al. 1993) and compensation refers to the response of grazed grass which results in no net difference from ungrazed grass (Gurevitch et al. 2006). Top-down effects of seagrass grazers therefore potentially

affect seagrass ecosystem functions by altering both the productivity as well as the structure of seagrasses (Thayer et al. 1984b, Zieman et al. 1984, Belsky 1986, Clausen 1994, Valentine and Heck 1997, Cebrián et al. 1998, Valentine and Heck 2000, Williams and Heck 2001, Valentine and Duffy 2006).

The objective of the present study is to experimentally determine the effects of eelgrass (*Zostera marina*) grazing by the Pacific black brant geese (*Branta bernicla nigricans*) on the abundance and size of the smaller fish and invertebrates in a *Z. marina* bed in Humboldt Bay, California. Both the immediate and delayed effects of brant on *Z. marina* vegetation complexity (Ferson 2007) could indirectly affect the animal community in the bed. While secondary productivity and the composition of the animal community in bay *Z. marina* beds has probably been affected by an accelerated rate of suspended sediments arriving in the bay since the mid to late 1800's, the indirect effects of brant on animals may also have substantial effects on these animals (Shaughnessy et al. 2007). In the Pacific Northwest, brant geese consume almost exclusively *Z. marina* (Reed et al. 1998, Moore et al. 2004, Ward et al. 2005) and, historically, they occurred in Humboldt Bay throughout the year (Moore and Black 2006b). Brant presently arrive in the bay during November on their northward migration and leave by late May, with the largest number of birds (~ 17,000) occurring during March, and a total of 80,000 birds over the year (Lee et al. 2007). They forage for 8-12 hours each day while floating, and each bird removes 300 g dry weight of *Z. marina* leaves per day with a preference for the three youngest most nitrogen rich leaves, leaving the shoot apical meristems intact (Moore 2002, Moore and Black 2006a). Brant therefore have an immediate effect on *Z.*

marina vegetation structure by opening up the canopy of leaves. In Humboldt Bay they also have a delayed effect on this structure by inducing *Z. marina* overcompensation (Ferson 2007).

How should the abundance and size of seagrass fauna change in response to alterations to the complexity of seagrass vegetation? Bell and Westoby (1986b) proposed a model stating that larval recruits settling from the plankton into seagrass beds may simply be a function of active habitat selection. They also proposed an alternative "settle and stay" model stating that juveniles settle in the first seagrass bed they encounter, regardless of complexity, and stay there for several months (Bell et al. 1987, Worthington et al. 1992, Hannan and Williams 1998, Upston and Booth 2003). Post-settlement relationships between the animal community and seagrass beds may then develop because vegetation structure provides animals with refuges from predation (Heck and Orth 1980, Orth et al. 1984, Heck and Crowder 1991, Orth 1992, Williams and Heck 2001, Heck and Orth 2006), increased food availability (Connolly 1994, Perkins-Visser et al. 1996, Connolly 1997, Boström et al. 2002), or active habitat selection (Leber 1985, Bell and Westoby 1986c, Edgar and Robertson 1992, Halliday 1995, Levin et al. 1997). However, this relationship may develop only at a small spatial scale (i.e. within a single seagrass bed) (Bell and Westoby 1986b, Worthington et al. 1992, Jenkins et al. 2002), and such relationships are species-specific (Heck and Orth 1980, Bell and Westoby 1986a, b, Heck et al. 1995, Horinouchi et al. 1999, Boström and Bonsdorff 2000, Guidetti and Bussotti 2002, Hovel et al. 2002, Nakaoka 2005, Sirota and Hovel 2006). Furthermore, disturbances such as storm events or overwhelming recruitment may mask

the relationship between animals and vegetation structure (Bell and Westoby 1986b, Orth 1992, Jenkins et al. 1996, 1997, Tolan et al. 1997, Boström and Bonsdorff 2000, Koch et al. 2006), and fish predation pressure may influence whether or not animals develop a relationship with vegetation structure (Stoner 1979, Stoner 1980, Orth et al. 1984, Connolly 1994, Levin 1994, Tayasu et al. 1996, Adams et al. 2004). Thus, while brant potentially have a large effect on *Z. marina* productivity and structure, there has been limited success in predicting either how particular types of species or functional groups should respond to seagrass complexity, or the recruitment and environmental circumstances necessary for that relationship to develop.

Based on this previous work, this experimental study tests the hypothesis that animal abundance and size will differ in response to brant induced changes to *Z. marina* vegetation structure. By including covariates like distance of a treatment from the bay entrance, as well as climate and water variables, this study will identify the recruitment and environmental circumstances that favor the development of a positive or negative relationship between animal abundance and size versus *Z. marina* complexity. The present study measured animal responses at the same time and using the same field experiment as Ferson (2007).

METHODS

Site description

Humboldt Bay is a protected embayment located in northern California and consists of Arcata Bay at its north end (sometimes called North Bay), Central Bay and South Bay (Figure 1). *Zostera marina* covers 1,037 ha in Arcata Bay, 52 ha in Central Bay, and 801 ha in South Bay (Schlosser et al. *accepted*). Although there is less *Z. marina* area in South Bay, the population there is significantly denser than the *Z. marina* population in Arcata Bay (Tennant 2006). The dense *Z. marina* beds of South Bay are among the most important locations of *Z. marina* growth in the Pacific Northwest (Phillips 1984) and support ~ 60% of the brant population in Humboldt Bay (Henry 1980, Moore et al. 2004). The experimental site in South Bay (40º 43.1' N, 124º 13.3' W) was located in an extensive, continuous *Z. marina* bed occurring at an elevation of ~ -0.076 m MLLW, ~ 11 m from the nearest channel (Hookton Channel), and its north end was ~ 3400 m from the mouth of Entrance Channel (Figure 2). Epiphytic algae and clumps of drift macroalgae (mostly *Rhizoclonium riparium* and *Ulva californica*) are interspersed in the *Z. marina* and the site is characterized by fine-grained (silty-clay) sediments (Barnhart et al. 1992).

While the same treatments were designed to test for both immediate effects of brant on *Z. marina* growth and their delayed effects on the associated animal community, only the methods relevant to the design and animal responses are presented herein. Ferson (2007) describe the methods relevant to the *Z. marina* response. The first

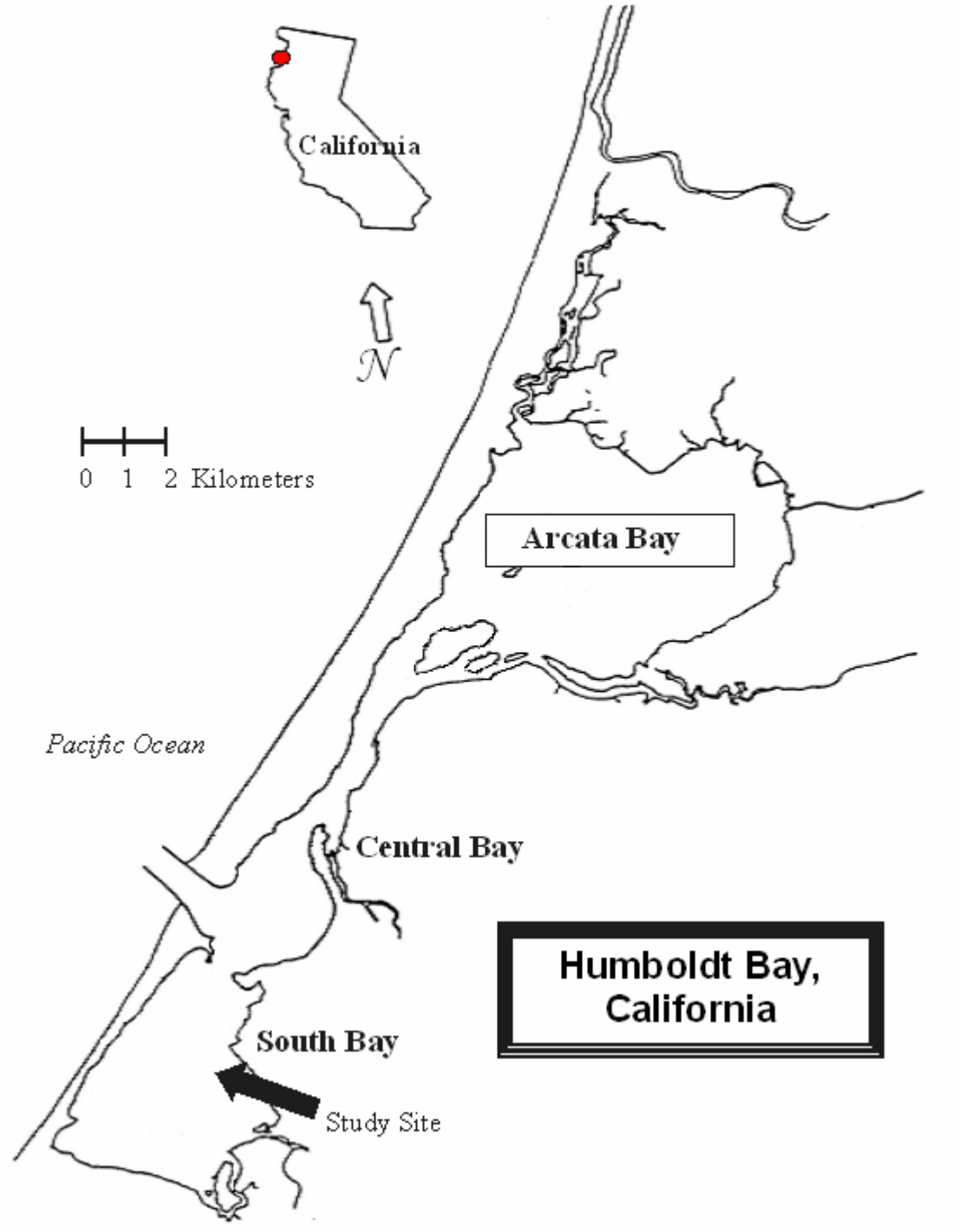

Figure 1. Map of Humboldt Bay, California. The study site was located in South Bay designated by the arrow (40º 43.1' N, 124º 13.3' W). Map modified from Barnhart et al. (1992).

Figure 2. Aerial view of South Bay showing *Z. marina* coverage and major channels. Darker portions are *Z. marina* beds. The study site is shown in a solid yellow line indicated by the red arrow in a continuous *Z. marina* bed situated alongside of Hookton Channel. Image was obtained from HSU CICORE.

experiment, in year one (2004), was designed to determine which brant activity, intermediate fecal addition, intermediate grazing, or both, affect *Z. marina* and associated animal responses, whereas the experiment in year two (2005) built upon results from 2004 and compared *Z. marina* and animal responses to intermediate and intense levels of brant clipping and fecal addition simulations.

Year 1 (2004) Experiment

A randomized block design was used in year one where each block contained one replicate of each of four treatments, and each block was separated by 9.0 m (Figure 3). There were six sample times and six replicate blocks were sacrificed each time (Table 1). Blocks were randomly assigned to one of the six sample times. Each block was also designed to maximize independence among the four treatments it contained; there was a 2.0 m buffer area between each treatment and a 1.0 m buffer between each treatment and the outside of each block (Figure 3). The four treatments, each being 2.25 m^2, were randomly positioned within each block and were: (1) grazer exclusion; no fecal addition + no *Z. marina* clipping, (2) intermediate fecal addition, (3) intermediate clipping, and (4) intermediate fecal addition and clipping. Edges compared to the interior portions of seagrass beds attract fish (Heck and Orth 1980) as well as support higher densities of smaller invertebrate species (Orth 1977, Bologna and Heck 2002, Barberá-Cebrián et al. 2002, Tanner 2005). Thus, our patch size ensured that animal sampling techniques were describing a grazed (clipped) habitat as opposed to an edge habitat. To discourage actual brant grazing, each block was surrounded by PVC pipes (3.0 m high) inserted into the mud at 0.8 m increments to exclude brant. This technique was successful during pilot

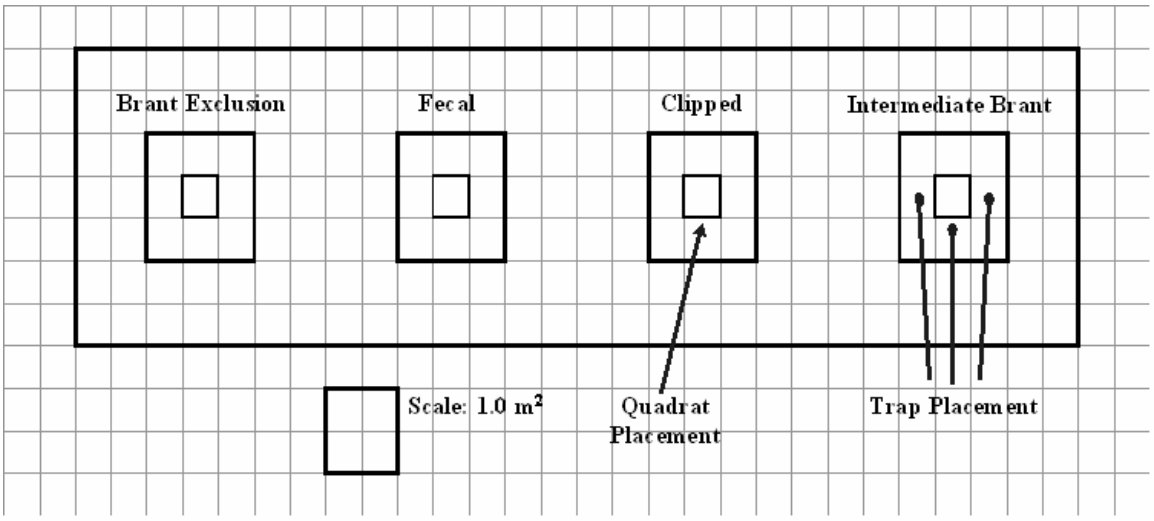

Figure 3. Diagram of one block (14.0 m x 3.5 m) and the arrangement of each treatment (1.5 m^2) for 2004. The entire block was surrounded by PVC poles placed at 0.8 m increments. A total of 36 blocks were arranged alongside Hookton Channel in South Bay.

Table 1. Timeline for experimental setup, brant manipulations and sampling periods in 2004 and 2005.

	Year 1 (2004)	Year 2 (2005)
Set up PVC plots	December - January	January
1st Fecal + Clip manipulation	March 13 - March 17	March 29 - April 1
2nd Fecal + Clip manipulation	April 7 - April 9	April 10 - April 13
1st sampling period (Time 1)	April 20 - April 23	April 25 - April 28
2nd sampling period (Time 2)	May 5 - May 9	May 10 - May 13
3rd sampling period (Time 3)	May 19 - May 23	May 26 - May 29
4th sampling period (Time 4)	June 3 - June 6	June 23 - June 26
5th sampling period (Time 5)	June 17 - June 20	
6th sampling period (Time 6)	July 16 - July 19	

studies in Humboldt Bay (S. Ferson, personal communication) and in the present study. Brant do not graze within the blocks apparently because they prefer open water for an escape response.

The first treatment was the exclusion treatment that was free of any manipulation (Brant Exclusion). The second treatment consisted of clipping *Z. marina* (Clipped) to a height mimicking an intermediate level of brant grazing. The same areas within each treatment were clipped on two different dates since brant typically return to regraze the tender, more nutritious, regrowth of shoots (Moore 2002). All of the shoots in each treatment were cut to 0.45 m in height in order to approximate two visitations by a foraging flock of geese, and the average length of grazed leaves (evident from the concave bite) was 0.45 m. The two applications of these treatments occurred from March 13-17 and April 7-9 when brant populations are at their peak (Table 1, Moore 2002). The third treatment was only an intermediate level of fecal addition (Fecal) on the same two occasions. Brant excrete a stool about every five minutes. Since they do this about 12 times each hour and there are about two geese per 1.0 m^2, then 24 stool additions (~ 117.5 g) were commensurate to one hour of brant activity for a population of intermediate size. Brant fecal material was collected at a nearby roost site in South Bay (Lee et al. 2004). Since brant fecal matter is loose, half was divided into 25 clumps and pressed 2 cm into the mud in a grid-like fashion and the other half was mixed together in a 591 milliliter bottle filled with seawater and evenly spread over the treatment as a liquid solution when little to no water was over the *Z. marina*. The fourth treatment received both intermediate clipping and fecal matter as described above (Intermediate Brant). In

order to minimize damage to the study site and to the treatments, most of the work was accomplished either from extra thick boogieboards set at the treatment edge or from floating kayaks. Movement among treatments within a block was done by first moving out of the block into the buffer zone.

Response Variables

Fish and invertebrates were counted and their lengths measured to the nearest millimeter during each of the six sample periods (Table 2 and 3). Animals were chosen based on their lifestyle traits (i.e. nektonic, epifaunal, and infaunal), relative small size, and management concern. They were identified to the lowest taxon possible (Miller and Lea 1972, Smith and Carlton 1975, Fritsche and Cavanagh 1995). Crabs were counted and carapace width measured using a caliper, whereas every shrimp was measured from the tip of the rostrum to the end of the telson using a ruler; lengths of all isopods, annelids, bivalves and gastropods were also measured using a ruler. All fish were counted and total lengths were measured using a ruler. Amphipods and brittle stars were only counted because they were uniformly small and/or difficult to accurately size. Clams were enumerated and measured in shell length using a caliper.

Sampling Techniques

Five sampling techniques were used to quantify animal responses within each treatment, including three kinds of traps as well as quadrat sampling and belowground sieving (Table 2 and 3). Each trap was located toward the center of each treatment in

Table 2. Types of animals and total individuals collected with each sampling technique. Animals were collected from April - July 2004. Shown below in boxes are animals that were analyzed by grouping multiple sampling techniques.

	Minnow trap	Plexiglass tray	Tuffy trap	Quadrat	Sediment core	Σ
Fishes						
Apodichthys flavidus	5	0	0	0	0	5
Aulorhynchus flavidus	2	2	0	0	0	4
Embiotocidae (Family)	36	2	0	0	0	38
Enophrys bison	1	0	0	0	0	1
Gasterosteus aculeatus *	157	2	0	0	0	159
Hexagrammos decagrammus	3	0	0	0	0	3
Lepidogobius lepidus	17	2	0	0	0	19
Leptocottus armatus *	54	1	0	0	0	55
Ophiodon elongatus	1	0	0	0	0	1
Pholis ornata *	60	40	31	0	0	131
Parophrys vetulus	14	0	0	0	0	14
Sebastes caurinus	2	0	0	0	0	2
Sebastes melanops	26	0	0	0	0	26
Syngnathus leptorhynchus	8	2	0	0	0	10
Crustaceans						
Calanoida (Order)	0	0	1	0	0	1
Cancer antennarius	1	3	1	1	0	6
Cancer gracilis	0	5	0	0	0	5
Cancer magister *	110	245	33	8	17	413
Cancer productus	1	5	0	0	1	7
Caprellidea (Suborder) *	8	3	142	209	0	362
Crangon franciscorum *	334	16	2	0	3	355
Cumacea (Order)	0	0	3	0	0	3
Gammaridea (Suborder) *	0	0	1217	0	0	1217
Gnorimosphaeroma spp.	0	1	24	10	0	35
Hemigrapsus nudus	1	10	0	0	11	22
Hemigrapsus oregonensis	0	2	0	0	0	2
Heptacarpus spp. *	1385	1576	8	1	0	2970
Hippolytidae (unknown)	1	0	0	0	0	1
Idotea resecata *	79	37	22	719	3	860

Pugettia producta	1	0	0	0	0	1
Gastropods						
Aeolida papillosa	1	0	3	0	0	4
Archidoris montereyensis	1	0	0	0	0	1
Hermissenda crassicornis	1	3	2	0	0	6
Lacuna variegata	3	3	6	26	0	38
Phyllaplysia taylori *	4	18	2	2139	5	2168
Bivalves						
Clinocardium nuttallii *	0	0	0	0	56	56
Macoma nasuta *	0	0	0	0	353	353
Mytilus spp.*	0	0	0	58	0	58
Tresus nuttallii	0	0	0	0	1	1
Annelids						
Phyllodocida (Order) *	8	45	16	0	0	69
Echinoderms						
Amphiodia occidentalis *	0	21	22	6	0	49
Total	2326	2044	1535	3177	450	9531

* Animals abundant enough to be considered for analyses.

Table 3. Types of animals and total individuals collected with each sampling technique. Animals were collected from April - June 2005. Shown below in boxes are animals that were analyzed by grouping multiple sampling techniques.

	Minnow trap	Plexiglass tray	Tuffy trap	Quadrat	Sediment core	Σ
Fishes						
Aulorhynchus flavidus	1	0	0	0	0	1
Gasterosteus aculeatus *	75	0	0	0	0	75
Lepidogobius lepidus	4	0	0	0	0	4
Leptocottus armatus *	40	0	0	0	0	40
Parophrys vetulus	1	0	0	0	0	1
Pholis ornata *	64	42	12	0	2	120
Sebastes melanops	1	0	0	0	0	1
Syngnathus leptorhynchus	3	0	0	1	0	4
Crustaceans						
Cancer antennarius	2	0	0	0	0	2
Cancer magister	4	15	1	0	1	21
Cancer productus	0	1	0	0	0	1
Caprellidea (Suborder) *	41	42	1671	4686	0	6440
Crangon franciscorum *	123	2	0	1	3	129
Crangon styloristris	0	1	0	0	0	1
Gammaridea (Suborder) *	0	0	1650	0	0	1650
Gnorimosphaeroma spp. *	1	0	16	25	0	41
Hemigrapsus nudus	6	9	0	0	4	19
Heptacarpus spp. *	334	682	5	0	1	1022
Idotea resecata *	2	1	11	470	0	484
Pinnixia franciscana	0	1	0	0	2	3
Gastropods						
Hermissenda crassicornis	1	3	0	0	0	4
Lacuna variegata	0	0	7	5	0	12
Phyllaplysia taylori *	2	2	0	193	0	197
Bivalves						
Clinocardium nuttallii *	0	0	0	0	43	43
Macoma nasuta *	0	0	0	0	213	213
Mytilus spp.	1	0	0	3	0	4
Annelids						

Phyllodocida (Order) *	14	28	29	0	0	71
Echinoderms						
Amphiodia occidentalis	0	9	3	0	0	12
Total	720	838	3405	5384	269	10615

* Animals abundant enough to be considered for analyses.

order to minimize edge effects, but also to avoid the exact center of each treatment where *Z. marina* growth was being assessed (Figure 4). The abundance and size of smaller animals living in the water column, such as amphipods and isopods, was determined by using tuffy traps. Each of the latter consisted of two 0.5 mm mesh pads (0.305 m x 0.305 m) rolled around a short PVC pipe and fastened with two zip-ties. One tuffy trap was pushed down within each treatment until the bottom of the mesh was flush with the substrate for two tidal cycles (48 hours). Upon collection, the mesh pads were gently removed from the PVC pipe and placed directly into a labeled, sealed bag. The animals were then transferred to the Humboldt State University Telonicher Marine Laboratory, removed from the mesh pads and immediately fixed in 10% buffered Formalin for a week, then fixed in 70% Ethanol for 2-3 days. Individuals were enumerated, measured, and identified to the lowest taxon possible using a dissecting microscope.

Plexiglass trays (0.305 m x 0.305 m x 0.102 m deep) filled with mostly intact oyster shell halves (~ 1525 g / tray) were placed in treatment areas for the same two tidal cycles (48 hours) in order to quantify the number and size of juvenile crabs as well as *Heptacarpus* and *Crangon* shrimp among other animals. Juvenile crabs and shrimp used the shells as a refuge from sculpin predation. Each tray was pushed down ~ 1.0 cm into the substrate and held in place by short PVC pipes positioned on each side of the tray. Upon collection, each tray was placed in a labeled, sealed bag and taken to shore. The animals from each tray were immediately sorted by hand and anesthetized in MS 222 solution and placed in another set of labeled, sealed bags. They were then transferred to

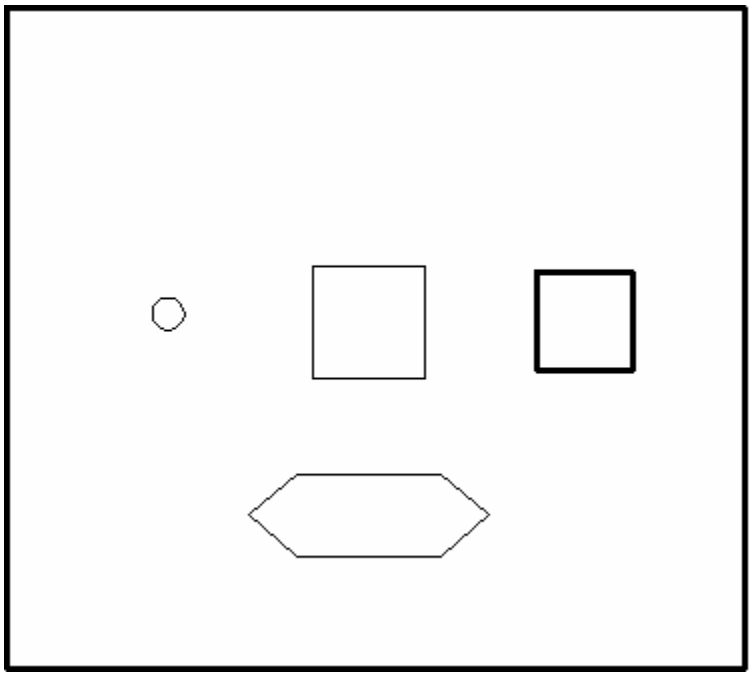

Figure 4. Example treatment area showing trap and quadrat placement in both 2004 and 2005. Traps were set in the *Z. marina* bed for 48 hours before collection. Quadrats (center square) were placed in the center of each treatment, and tuffy traps (circle), plexiglass trays (darkened square), and minnow traps (hexagon) were placed on respective sides of the quadrat as shown above. Scale = 2.25 m^2 for 2004 and 9.0 m^2 for 2005.

the laboratory and immediately fixed in 10% buffered Formalin for a week, then transferred to 70% Ethanol for 2-3 days and then identified.

The number and size of crabs, shrimp, fish, and other animals were also assessed by using minnow traps that had a small mesh size (3.17 mm) and each end had a round entrance of 2.0 cm in diameter. The bottom of the minnow trap was also lined with oyster shell fragments (~ 1525 g). These trap dimensions were chosen to exclude larger cannibalistic crabs. Two short PVC pipes were attached to each side of a minnow trap and pushed into the substrate until the bottom of the minnow trap was flush with the substrate for two tidal cycles (48 hours). The animals were hand sorted and preserved as for tray trapped animals.

Quadrats (0.25 x 0.25 m) were placed in the center of each treatment in order to enumerate epifauna (Figure 4). All of the shoots within the quadrat were clipped with scissors at the level of the mud, transferred to sealed bags, and frozen. Samples were later sorted in the laboratory in order to quantify *Z. marina* shoot density and shoot length, epiphyte loads, as well as the number and size of the opisthobranch, Taylor's Sea Hare (*Phyllaplysia taylori*), and any other important epifaunal mesograzers such as the bay isopod (*Idotea resecata*) and caprellid amphipods. Shoots were gently rinsed with water while on a 0.5 mm sieve in order to remove sediments and retrieve any animals that fell off. The number of *Z. marina* shoots was counted per 0.0625 m^2 to determine shoot density and each shoot was measured in length from the bottom of the meristem to end of the longest leaf. Shoot length, sometimes referred to as canopy height or shoot height, was determined as the average length of all shoots per 0.0625 m^2.

Following the removal of shoots in the field from the quadrat within each treatment, a standard 39 ounce coffee can (16.5 cm high, 15.3 cm diameter) was used as a sediment core to assess belowground infauna. The mud was transferred to a plastic tub and this step was repeated until all of the mud within the quadrat down to the can depth was removed. The larger infauna, which was mostly bivalves, were separated from the mud using a 5.0 mm sieve, then frozen for subsequent measurements. Belowground infauna was only collected in the first and last sampling periods of both years because they were not expected to respond rapidly to treatments.

Epiphyte loads (mg dry wt cm^{-2}), which were primarily diatoms, were determined from three *Z. marina* shoots randomly selected out of all the shoots that were collected within each quadrat. Sample shoots for epiphytic determinations in this study each contained two to six leaves and both sides of each leaf were scraped for epiphytes using a razor blade. The removed epiphytes were placed on pre-weighed pieces of aluminum foil and dried to constant weight (mg) in an oven at 95°F for 24 hours. Scraped leaves were placed onto the white surface of a photo stand and photographed using a digital camera that was mounted at a fixed height. Leaf images were contrasted in black and separated from the white surface using Image J (National Institute of Health) spatial analysis software. Image J was then used to calculate the leaf surface areas (cm^2). Epiphyte loads were calculated as mg dry wt cm^{-2} by grouping the three shoots per treatment and dividing the total epiphyte weight (sum of all leaves) by the total leaf area (sum of all leaves).

Year 2 (2005) Experimental Design

The effects of intermediate and intense brant herbivory and fecal addition on the abundance and size of animals in a *Z. marina* bed were the focus in the second year of the study. The Brant Exclusion and Intermediate Brant treatments were repeated this year, but three changes were made to the experimental design (Figure 5). The first was to add a new treatment, Intense Brant. The experimental plots were manipulated to mimic the effect of both a medium goose flock that forages for a normal period of time (e.g. 30 min) and a large goose flock foraging for a long period of time (e.g. two hrs). Therefore, the first treatment was again the exclusion treatment that was free of any manipulation (Brant Exclusion). The second treatment (Intermediate Brant) consisted of clipping shoots to ~ 45.0 cm in length and allotting 235 g of brant fecal matter on two occasions separated by two weeks. The third treatment (Intense Brant) consisted of clipping shoots to ~ 15.0 cm in length and allotting 706 g of brant fecal matter on two occasions separated by two weeks. All clipping and fecal stool additions took place during March 29 – April 1 and April 10 –13 of 2005 (Table 1) when the surrounding brant population was at its peak. The second design change in 2005 was to expand the area of all replicates for all treatments to 9.0 m^2. Since the treatments in 2005 were too large for us to manipulate the entire area by leaning over them from their edges, we entered partway into all treatments on the boogieboards. The larger treatments also meant that each block was larger (19.0 m x 5.0 m), and these blocks were placed in the 9.0 m buffer zones from 2004. The last design change was to reduce the number of sample times to four, resulting in a total of 24

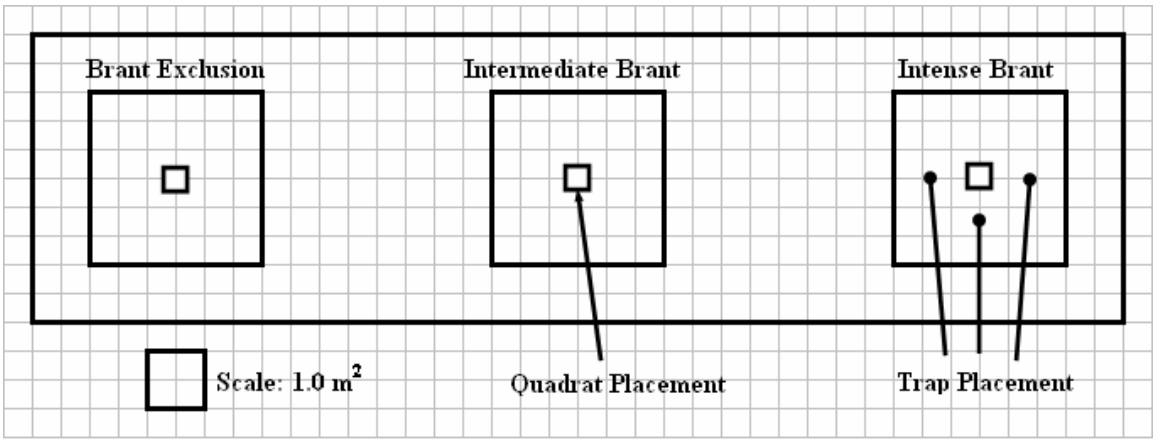

Figure 5. Diagram of one block (19.0 m x 5.0 m) and the arrangement of each treatment (3.0 m^2) for 2005. The entire block was surrounded by PVC poles placed at 0.8 m increments. A total of 24 blocks were arranged alongside Hookton Channel in South Bay.

blocks. The same response variables and trapping techniques used in the first year of the study were also used in the second year.

Covariates

The distance of each treatment within a block from Entrance Channel and Hookton Channel (Figure 2) was recorded in order to more accurately assess treatment effects; elevation was not used as a covariate as all treatments were located from 0.15 m to –0.18 m MLLW. Distances from channels were determined by using the GPS interactive map operated by the Center for Integrative Coastal Observation, Research and Education (CICORE) and Humboldt State University (HSU). The timing of these experiments in the context of the El Niño Southern Oscillation (ENSO) was described by water temperature data recorded by a CA Sea Grant water temperature data logger (StowAway TidbiT Temp Logger) located along the Eureka waterfront in central Humboldt Bay. Determination of whether or not an ENSO signal in ocean surface temperatures was present in these temperature readings and therefore during the experiments was done by identifying the minimum temperatures during the months of May through August, with the assumption that minimum temperatures during these months were the product of upwelled water rather than air temperatures over the water in the bay (Shaughnessy et al. 2007). The daily minimum water temperatures were further reduced by determining the mean of all the daily minimum temperatures from each month. Precipitation, wind, and turbidity data were used to examine other potential shifts in climate conditions that could change the relationship between animals and *Z. marina* complexity. Total monthly precipitation was recorded by the National Weather Service

on Woodley Island, in Humboldt Bay. Hourly wind speed data were obtained from the Eureka weather buoy operated by NOAA (#46022), which is located 31 km West-Southwest of Eureka. Turbidity data were obtained from the Yellow Springs Instruments sonde (mo 6600) located in the central part of Humboldt Bay and operated by the CICORE and Humboldt State University (HSU). Mean daily values were calculated for the hourly wind data collected by NOAA and the 15 minute turbidity data collected by CICORE.

Statistical Treatments

Some animal species were collected entirely with one sampling technique but the majority of the most abundant animal species were collected with multiple techniques. For many species, data from multiple sampling techniques was grouped in order to more accurately assess treatment effects (Table 2 and 3). Descriptive statistics were compiled using SYSTAT 10 in order to produce graphics which were performed with SigmaPlot 2000. Since the objective of this study was to determine if animal abundance and size differed when the *Z. marina* vegetation differed among treatments, animal treatment responses were compared when *Z. marina* vegetation structure differed among treatments according to Ferson (2007). These *Z. marina* differences were found to occur in two structural forms: (1) shoot density which was significantly different among treatments in the third and sixth sampling periods of 2004, as well as the third sampling period of 2005; and (2) shoot height which was significantly different among treatments for every sampling period in 2005 except the second one (Table 4, Figure 6). Aboveground biomass was considered, but it was only relevant in 2004 for one sampling period and

Table 4. Time periods when *Z. marina* structural components differed significantly among treatments during both years of the experiment (see Ferson 2007).

Eelgrass Structural Component	2004	2005
Shoot Density	T3, T6	T3
Shoot Length	none	T1, T3, T4
Aboveground Biomass	T6	T1, T3, T4
Belowground Biomass	T4	none
Leaf Growth Rate	none	T2, T3*

* Indicates significant differences for leaves # 2 - 4

T1 (Time 1): 4/22/04 and 4/27/05

T2: 5/8/04 and 5/12/05

T3: 5/22/04 and 5/28/05

T4: 6/5/04 and 6/25/05

T5: 6/19/04

T6: 7/18/04

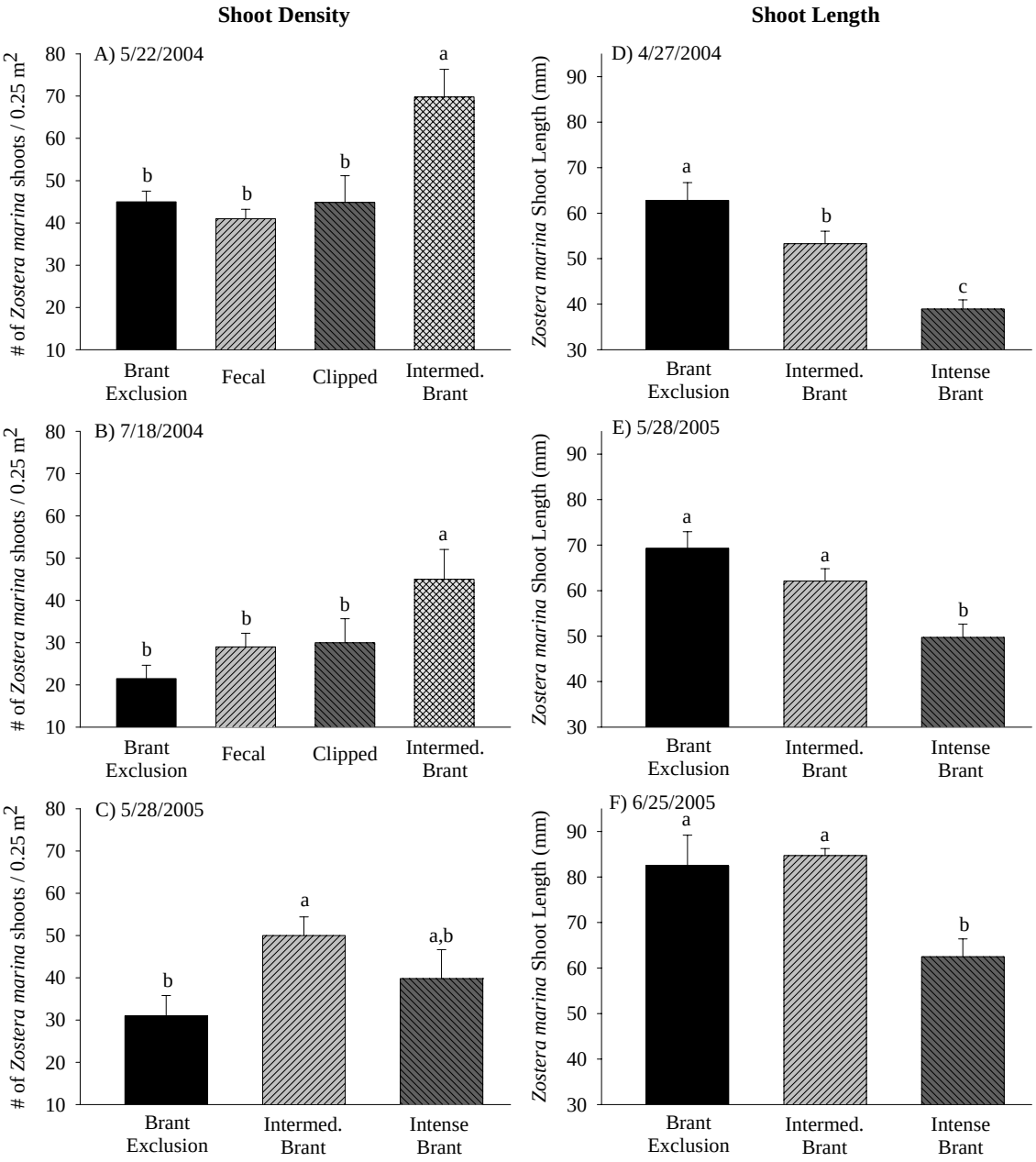

Figure 6. (A) *Zostera marina* shoot density per 0.25 m^2 collected April 22, 2004; (B) July 18, 2004; and (C) May 28, 2005. (D) *Z. marina* mean shoot length (mm) collected April 27, 2005; (E) May 28, 2005; and (F) June 25, 2005. Error bars are ± 1 SE. Treatments that are significantly different from each other are denoted by lower case letters above each bar from Fisher's LSD multiple comparison tests. Data is from Ferson (2007).

was redundant on length and density measures during 2005. Belowground biomass of *Z. marina* was also considered, but it was found to only be relevant in a sampling period when clams were not collected. Therefore, analyses were limited to only those species that were numerically abundant (Table 2 and 3) and the only times examined were those when shoot density and/or shoot length differences occurred among treatments.

Animal abundance and size responses were compared with analysis of covariance (ANCOVA, $\alpha = 0.05$) in Number Cruncher Statistical System (NCSS, Hintze 2004) software. A repeated measures analysis was not used because different blocks were sacrificed each time. Scatter plots were used to check for equality of slopes (i.e. regression lines are reasonably parallel) and linearity between treatments and covariates in each group. Normality assumptions were checked with probability plots and equal variances were checked with Bartlett's test (NCSS procedure: Equality of Covariance). Transformations (e.g. log, square root) were used when data did not meet normality and equal variance assumptions (Underwood 1997). Transformations were seldom needed for animal size analyses; however, data were frequently non-normal for animal abundance analyses, in which case transformations were used only if normality was improved. Although rare for some abundance analyses, the variance remained heterogeneous, but not too extremely different, after transformation attempts. I used ANOVA in these cases as it is fairly robust to deviations from homogeneity of variance when sample sizes are equal (Underwood 1997).

Treatment was the main effect in each ANCOVA analysis and was considered significant at $p = 0.05$; but marginal significance (from 0.05 to 0.10) was also noted as for

other manipulative experiments where power is problematic (Bell and Westoby 1986a, Bell and Westoby 1987). Covariates were distance from Entrance Channel and distance from Hookton Channel. Covariates were retained in the model if their p-value was < 0.10 in order to reduce the effects of confounding variables. For many animal comparisons, covariates were not significant, in which case a 1-way ANOVA was used. Normality assumptions were checked with probability plots and a modified-Levene equal-variance test was also used to check for unequal variances. For every significant result, a Fisher's Least Significant Difference multiple comparison procedure was also used (Carmer and Swanson 1973).

RESULTS

The overall number of animal species and their abundances collected during the two years of the study was quite different. In 2004, a total of 9,531 individual animals and 41 different species were collected during six periods from late April through mid-July (Table 2). In 2005, 10,615 animals representing 28 species were collected during four periods from late April through late June (Table 3). Although more individual animals were collected in 2005, caprellid and gammarid amphipods were the only two animal groups with greater abundances compared to 2004. The abundance of caprellids alone constituted 61% of the total animals collected in 2005. However, the abundance of most species was markedly higher in 2004. For example, there was a 20 fold greater number of Dungeness crabs (*Cancer magister*) in 2004 than 2005, and similarly, blue mussels (*Mytilus* spp.), were more than 14 times more abundant during 2004.

In order to determine if brant induced changes to vegetation structure affected species abundances and their sizes, treatment effects on the latter were only analyzed when shoot density or shoot length differences existed among treatments (Table 4). Figures convey two types of information; whether abundances and sizes of particular animal species significantly differed among treatments, and whether those differences were paralleled by treatment differences in shoot density or shoot length (Figure 6). Some animals never differed among treatments, others did but did not parallel differences in vegetation structure, and some animals changed in abundance or size as the *Zostera marina* structure changed. In many cases, the covariates of distance from Hookton

Channel, or distance from Entrance Channel, were as important as treatments in explaining animal variation.

Phyllaplysia taylori

On 5/22/2004, *P. taylori* abundance was significantly higher in the Intermediate Brant treatment, which is also the treatment with the highest density of *Z. marina* shoots (Table 5, Figure 6A, 7A). The number of *P. taylori* in the Intermediate Brant treatment was higher than for the Clipped and Fecal treatments and lowest in the Fecal treatment, and significantly different from the Intermediate Brant and Brant Exclusion treatments. The distance these treatments were from Hookton Channel was a marginally significant covariate for *P. taylori* abundance and the relationship was positive (Table 5). *P. taylori* size, however, responded differently from abundance and was significantly higher in the Fecal than in the Intermediate Brant and Clipped treatments, and lowest in the Clipped and significantly different from the Fecal and Brant Exclusion treatments (Figure 7B). Distance from Entrance Channel was significant and positive. In contrast to 2004, *P. taylori* abundance and size on 5/28/2005 did not differ among treatments (Table 5, Figure 7C and 7D) although shoot densities did (Figure 6C).

In addition to shoot densities, *P. taylori* abundance and size responded to some of the shoot length differences, which only occurred during the 2005 treatments. *Z. marina* lengths on 4/27/2005 were highest in the Brant Exclusion treatment, lowest in the Intense Brant treatment, and each treatment was significantly different from both of the other 2005 treatments (Figure 6D). Similarly, *P. taylori* abundance was significantly lower in the Intense Brant treatment compared to every other treatment, but the Intermediate Brant

Table 5. ANCOVA statistical output for animal abundance and size responses in time periods when *Z. marina* shoot density and shoot length were significantly different among treatments. The relationship between covariate and animal abundance or size is described by either a positive (+) or negative (–) sign.

Taxon	Eelgrass Form	Date	Response Variable	DF	F-ratio	P-value
Phyllaplysia taylori	Shoot Density	5/22/04	Abundance	3	4.03	0.022**
			Hookton Channel (+)	1	3.02	0.097*
		5/22/04	Size	3	4.18	0.006***
			Entrance Channel (+)	1	15.49	0.000***
		5/28/05	Abundance	2	0.87	0.437
		5/28/05	Size	2	1.59	0.216
	Shoot Length	4/27/05	Abundance	2	4.72	0.027**
			Entrance Channel (–)	1	3.68	0.076*
		4/27/05	Size	2	1.69	0.196
		5/28/05	Abundance	2	0.87	0.437
		5/28/05	Size	2	1.59	0.216
		6/25/05	Abundance	2	7.29	0.010**
			Entrance Channel (+)	1	5.17	0.044**
		6/25/05	Size	2	5.00	0.013**
Epiphyte Load	Shoot Density	5/22/04	Weight	3	2.47	0.091*
		7/18/04	Weight	3	0.20	0.895
			Hookton Channel (–)	1	5.28	0.034**
		5/28/05	Weight	2	0.94	0.413
	Shoot Length	4/27/05	Weight	2	5.33	0.018**
		5/28/05	Weight	2	0.94	0.413
		6/25/05	Weight	2	3.21	0.080*
Caprellidea spp.	Shoot Density	5/22/04	Abundance	3	0.56	0.649
		7/18/04	Abundance	3	0.08	0.969

Caprellidea cont.			Hookton Channel (–)	1	6.64	0.018**
		5/28/05	Abundance	2	0.85	0.446
	Shoot Length	4/27/05	Abundance	2	3.73	0.053*
			Entrance Channel (–)	1	4.19	0.061*
			Hookton Channel (–)	1	4.37	0.057*
		5/28/05	Abundance	2	0.85	0.446
		6/25/05	Abundance	2	2.86	0.098*
			Hookton Channel (–)	1	6.37	0.028**
Gammaridea spp.	Shoot Density	5/22/04	Abundance	3	0.46	0.714
			Entrance Channel (–)	1	4.13	0.056*
		7/18/04	Abundance	3	2.39	0.120
			Hookton Channel (+)	1	3.33	0.084*
		5/28/05	Abundance	2	0.45	0.648
			Entrance Channel (–)	1	4.21	0.059*
	Shoot Length	4/27/05	Abundance	2	2.86	0.091*
			Entrance Channel (–)	1	4.09	0.063*
		5/28/05	Abundance	2	0.45	0.648
			Entrance Channel (–)	1	4.21	0.059*
		6/25/05	Abundance	2	4.10	0.044**
Idotea resecata	Shoot Density	5/22/04	Abundance	3	0.50	0.684
		5/22/04	Size	3	1.79	0.157
			Entrance Channel (+)	1	11.39	0.001***
		7/18/04	Abundance	3	0.58	0.638
			Hookton Channel (–)	1	6.63	0.019**
		7/18/04	Size	3	6.66	0.000***
		5/28/05	Abundance	2	1.82	0.197
		5/28/05	Size	2	3.59	0.040**
	Shoot Length	5/28/05	Abundance	2	1.82	0.197

I. resecata cont.		5/28/05	Size	2	3.59	0.040**
		6/25/05	Abundance	2	10.28	0.003***
		6/25/05	Size	2	0.15	0.860
Heptacarpus spp.	Shoot Density	5/22/04	Abundance	3	0.77	0.522
		5/22/04	Size	3	2.73	0.045**
		7/18/04	Abundance	3	0.10	0.960
		7/18/04	Size	3	0.58	0.631
			Entrance Channel (–)	1	5.68	0.019**
		5/28/05	Abundance	2	0.48	0.627
		5/28/05	Size	2	0.85	0.429
			Entrance Channel (+)	1	6.03	0.015**
	Shoot Length	4/27/05	Abundance	2	2.44	0.121
		4/27/05	Size	2	1.55	0.214
			Entrance Channel (–)	1	4.60	0.033**
		5/28/05	Abundance	2	0.48	0.627
		5/28/05	Size	2	0.85	0.429
			Entrance Channel (+)	1	6.03	0.015**
		6/25/05	Abundance	2	7.74	0.008***
			Hookton Channel (+)	1	5.51	0.039**
		6/25/05	Size	2	1.82	0.166
Cancer magister	Shoot Density	5/22/04	Abundance	3	0.72	0.549
			Size	3	4.36	0.006***
Pholis ornata	Shoot Density	5/22/04	Abundance	3	2.26	0.115
			Entrance Channel (–)	1	10.70	0.004***
		5/22/04	Size	3	2.38	0.093*
			Hookton Channel (+)	1	4.79	0.038**
		5/28/05	Abundance	2	0.71	0.505
		5/28/05	Size	2	3.07	0.067*

P. ornata cont.	Shoot Length	4/27/05	Abundance	2	0.48	0.626
		4/27/05	Size	2	1.14	0.338
		5/28/05	Abundance	2	0.71	0.505
		5/28/05	Size	2	3.07	0.067*
		6/25/05	Abundance	2	1.24	0.323
		6/25/05	Size	2	0.30	0.742
			Entrance Channel (+)	1	3.56	0.071*

*** = $p < 0.01$
** = $p < 0.05$
* = $p < 0.10$

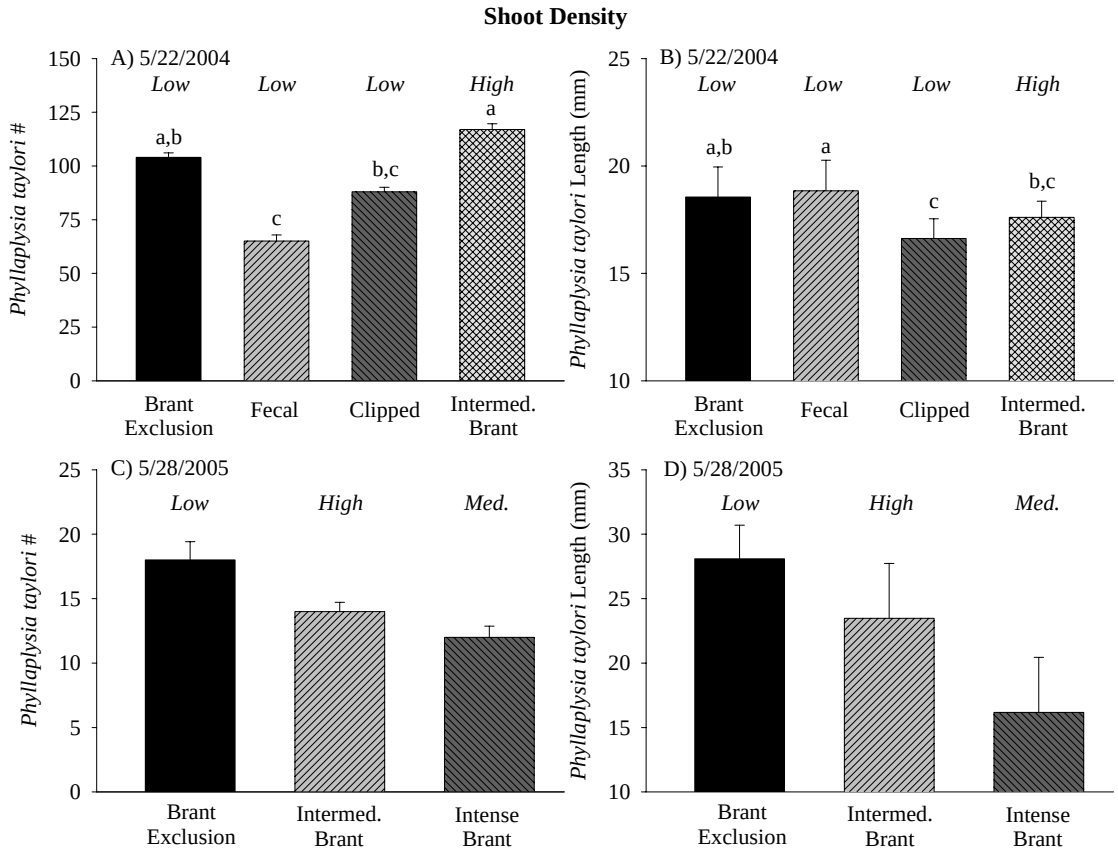

Figure 7. (A) *Phyllaplysia taylori* mean abundance and (B) size (mean length) collected May 22, 2004; and (C) abundance and (D) size collected May 28, 2005 in response to shoot density. Error bars are ± 1 SE. Treatments that are significantly different from each other are denoted by lower case letters above each bar from Fisher's LSD multiple comparison tests. Relative *Z. marina* shoot density (Low, Medium, High) is indicated in italics above each treatment bar.

and Brant Exclusion treatments were not different from each other (Figure 8A), and distance from Entrance Channel was marginally significant and positive. *P. taylori* size, however, was not different among treatments (Figure 8B). On 5/28/2005, *P. taylori* abundance and size did not differ among treatments (Figure 8C and 8D) although shoot lengths did (Figure 6E). On 6/25/2005, *Z. marina* lengths were significantly lower in the Intense Brant treatment compared to both of the other treatments (Figure 6F), which was paralleled by significantly lower *P. taylori* abundance in the Intense Brant treatment compared to both of the other treatments (Figure 8E). Distance from Entrance Channel was significant and positive. Similarly, on 6/25/2005, *P. taylori* was significantly smaller in the Intense Brant treatment compared to both of the other treatments (Figure 8F).

Epiphyte Load

Epiphyte load was used as a response variable because they constitute a large portion of the diet of epifaunal invertebrates such as *P. taylori*, *Idotea resecata*, and amphipods. Epiphyte load in 2004 ranged from 0.018 to 0.059 mg cm^{-2} and was substantially lower compared to epiphyte load in 2005 which ranged from 0.627 to 4.135 mg cm^{-2}.

Epiphyte load in 2004 was significantly higher in the Fecal than in the Clipped treatments on 5/22/04 (Figure 9A), but did not differ among treatments on 7/18/04 (Figure 9B); distance from Hookton Channel was significant and negative. During 2005, epiphyte load was significantly lower in the Intense Brant treatment compared to both of the other treatments on 4/27/05 (Figure 9D). Epiphyte load was not different among

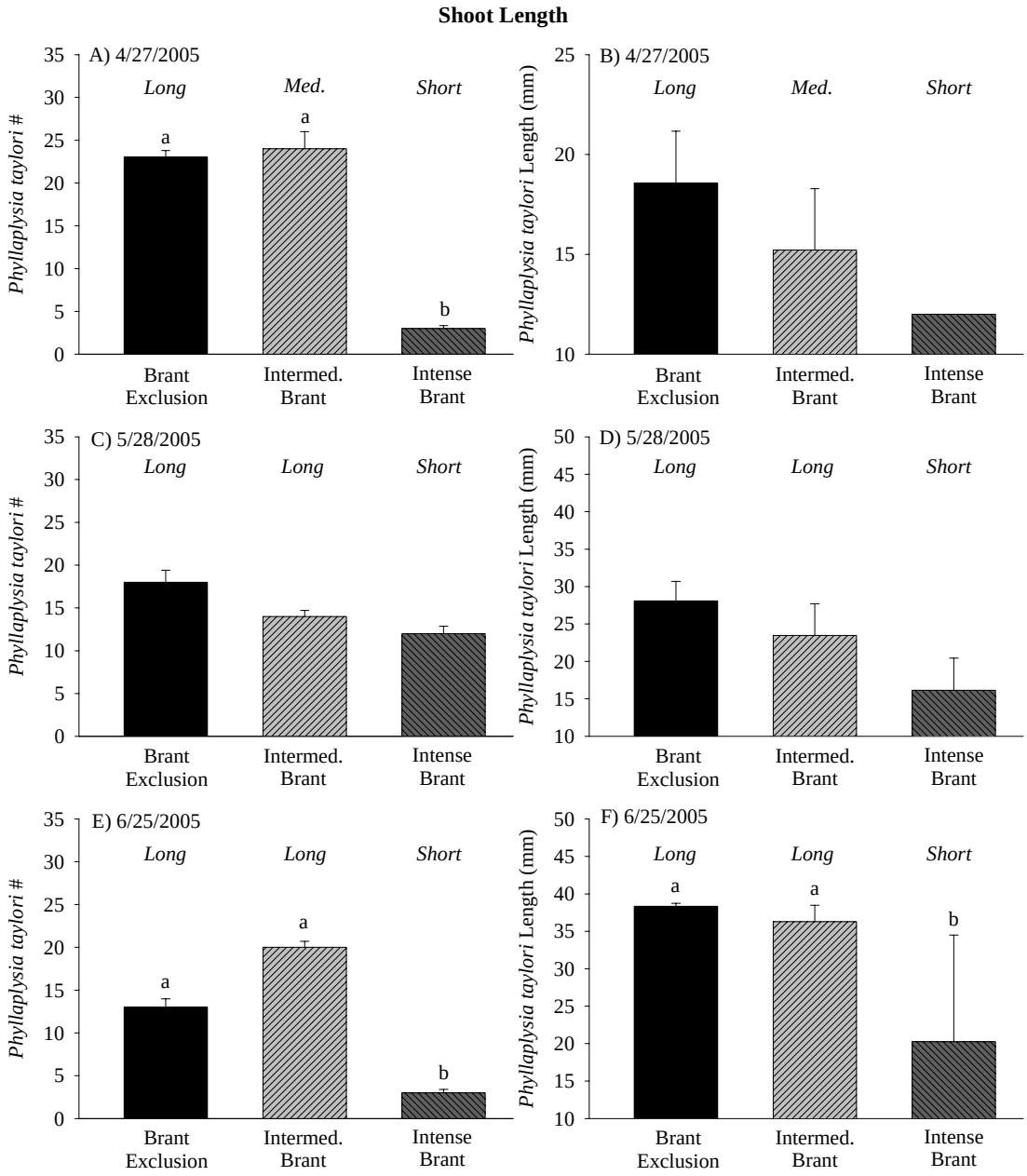

Figure 8. (A) *Phyllaplysia taylori* mean abundance and (B) size (mean length) collected April 27, 2005; (C) abundance and (D) size collected May 28, 2005; and (E) abundance and (F) size collected June 25, 2005 in response to shoot length. Error bars are ± 1 SE. Treatments that are significantly different from each other are denoted by lower case letters above each bar from Fisher's LSD multiple comparison tests. Relative *Z. marina* shoot length (Short, Medium, Long) is indicated in italics above each treatment bar.

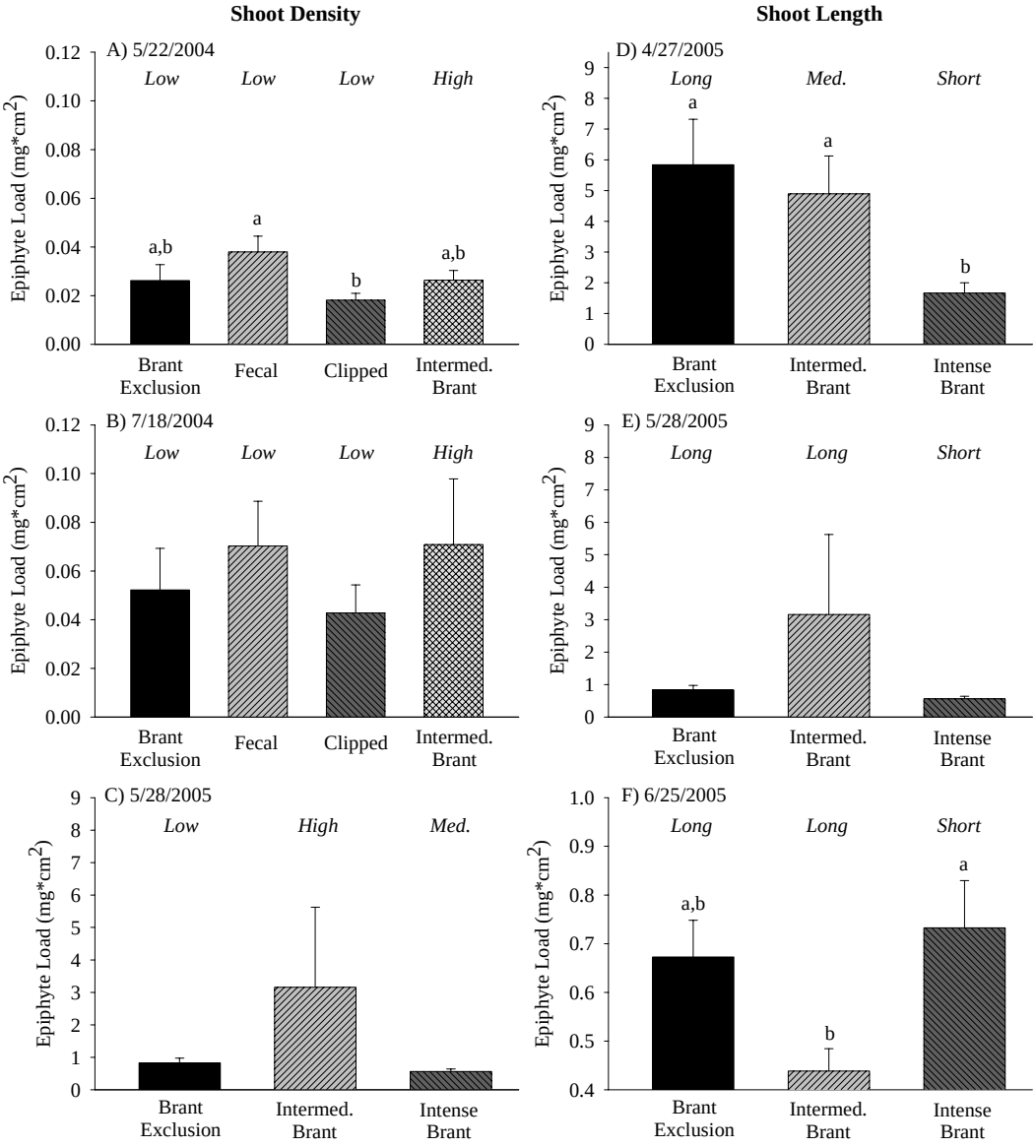

Figure 9. (A) Epiphyte load collected May 22, 2004; (B) July 18, 2004; and (C) May 28, 2005 in response to shoot density. (D) Epiphyte load collected April 27, 2005; (E) May 28, 2005; and (F) June 25, 2005 in response to shoot length. Error bars are ± 1 SE. Treatments that are significantly different from each other are denoted by lower case letters above each bar from Fisher's LSD multiple comparison tests. Relative *Z. marina* shoot density and shoot length is indicated in italics above each treatment bar.

treatments on 5/28/05 and significantly higher in the Intense Brant treatment than in the Intermediate Brant treatment on 6/25/05 (Figure 9E and 9F).

Amphipods

Caprellid and gammarid abundance never differed among treatments (Figure 10A – 10F) even when shoot densities did during 2004 and one sampling period in 2005. However, distance from Hookton Channel was significant and negative for caprellid abundance, and marginally significant and positive for gammarid abundance on 7/18/2004. Additionally, distance from Entrance Channel was marginally significant and negative for gammarid abundance on 5/22/2004 and 5/28/2005 (Table 5, Figure 10D, 10B and 10F).

Amphipod abundances responded differently to some of the shoot length differences among treatments during 2005. *Z. marina* differences on 4/27/2005, which were highest in the Brant Exclusion treatment, were not paralleled by caprellid or gammarid abundances. Caprellid abundance was significantly lower in the Brant Exclusion treatment compared to both of the other 2005 treatments (Figure 11A), however, gammarid abundance was significantly higher in the Intense Brant treatment than in the Brant Exclusion treatment (Figure 11B). Both distance from Entrance Channel and Hookton Channel were significant and negative for caprellid abundance, and distance from Entrance Channel was marginally significant and negative for gammarid abundance on 4/27/2005. On 5/28/2005, caprellid and gammarid abundance did not differ among treatments (Figure 11C and 11D) even when shoot lengths did. Distance from Entrance Channel was marginally significant and negative for gammarid

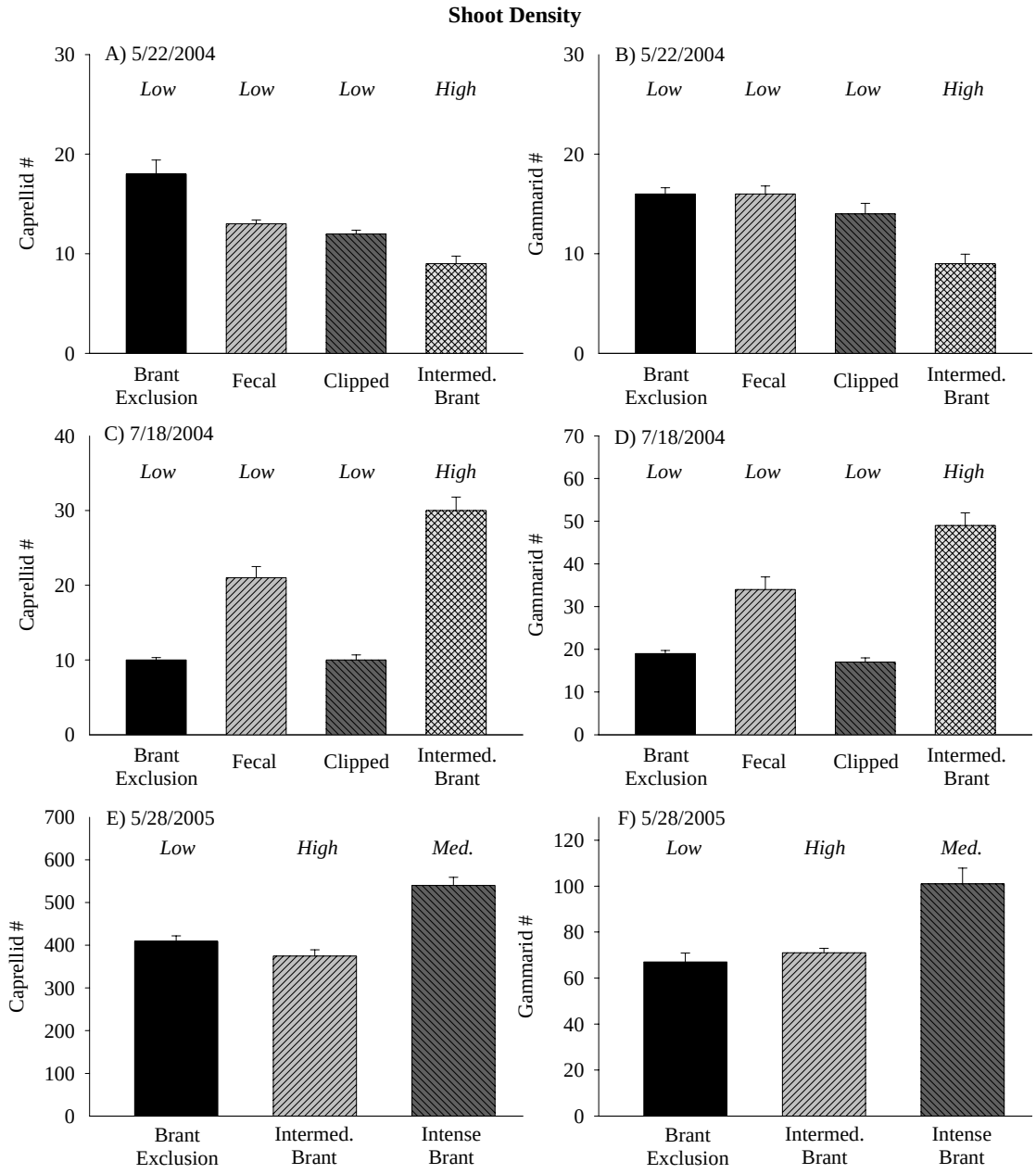

Figure 10. (A) Caprellid and (B) gammarid mean abundance collected May 22, 2004; (C) caprellid and (D) gammarid mean abundance collected July 18, 2004; and (E) caprellid and (F) gammarid mean abundance collected May 28, 2005 in response to shoot density. Error bars are ± 1 SE. Treatments that are significantly different from each other are denoted by lower case letters above each bar from Fisher's LSD multiple comparison tests. Relative *Z. marina* shoot density is indicated in italics above each treatment bar.

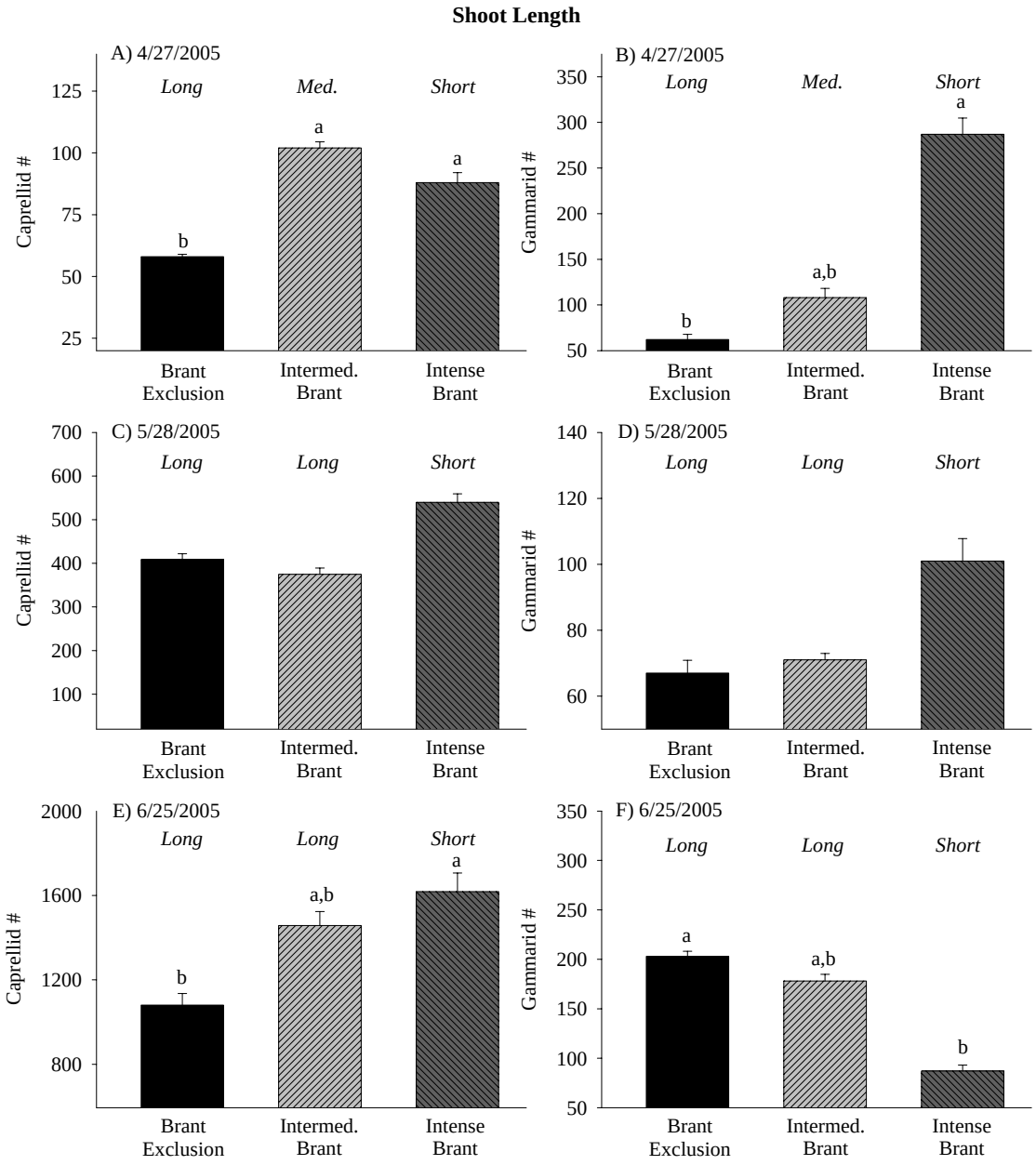

Figure 11. (A) Caprellid and (B) gammarid mean abundance collected April 27, 2005; (C) caprellid and (D) gammarid mean abundance collected May 28, 2005; and (E) caprellid and (F) gammarid mean abundance collected June 25, 2005 in response to shoot length. Error bars are ± 1 SE. Treatments that are significantly different from each other are denoted by lower case letters above each bar from Fisher's LSD multiple comparison tests. Relative *Z. marina* shoot length is indicated in italics above each treatment bar.

abundance. *Z. marina* differences on 6/25/2005, which were lowest in the Intense Brant treatment, were not paralleled by caprellid abundance. Caprellid abundance was significantly higher in the Intense Brant treatment but only compared to the Brant Exclusion treatment (Figure 11E). Distance from Hookton Channel was significant and negative for caprellid abundance. Gammarid abundance, however, did parallel *Z. marina* lengths by being significantly lower in the Intense Brant but only compared to the Brant Exclusion (Figure 11F).

Idotea resecata

I. resecata did sometimes differ among treatments, but these differences did not correspond to changes in shoot density. *I. resecata* abundance and size did not differ among treatments on 5/22/2004 (Figure 12A and 12B) despite differences in shoot density; distance from Entrance Channel was significant and positive for *I. resecata* size. The same lack of correspondence occurred for *I. resecata* abundance on 7/18/2004 (Figure 12C), although the distance from Hookton Channel was the significant covariate at this time and the relationship was negative. *I. resecata* size, however, responded differently from abundance and was significantly larger in the Clipped treatment compared to the Brant Exclusion and Intermediate Brant treatments; and significantly smaller in the Fecal treatment compared to every other 2004 treatment (Figure 12D). The next year, on 5/28/2005, *I. resecata* abundance did not differ among treatments (Figure 12E) but *I. resecata* was significantly larger in the Brant Exclusion treatment compared to the Intermediate Brant treatment (Figure 12F).

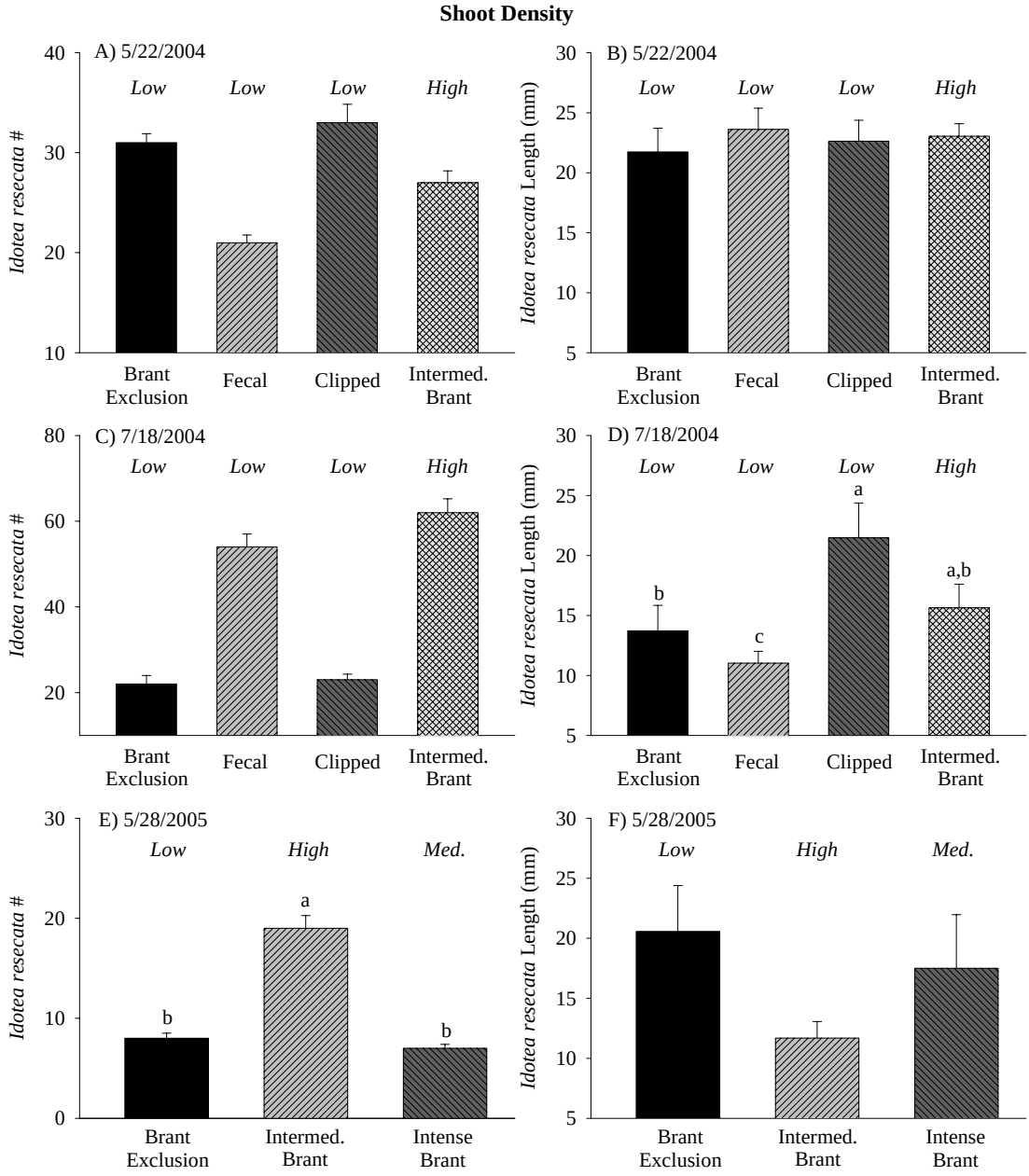

Figure 12. (A) *Idotea resecata* mean abundance and (B) size (mean length) collected May 22, 2004; (C) abundance and (D) size collected July 18, 2004; and (E) abundance and (F) size collected May 28, 2005 in response to shoot density. Error bars are ± 1 SE. Treatments that are significantly different from each other are denoted by lower case letters above each bar from Fisher's LSD multiple comparison tests. Relative *Z. marina* shoot density is indicated in italics above each treatment bar.

I. resecata abundance and size responded similarly to shoot length differences among treatments as they did to shoot density. *Z. marina* length on 5/28/2005 was significantly lower in the Intense Brant treatment compared to both of the other treatments, but *I. resecata* abundance did not differ among treatments (Figure 13A). *I. resecata* size, however, was significantly larger in the Brant Exclusion treatment compared to the Intermediate Brant treatment (Figure 13B). On 6/25/2005, *Z. marina* lengths were significantly lower in the Intense Brant compared to both of the other treatments, which was paralleled by *I. resecata* abundance (Figure 13C). *I. resecata* size, however, was not different among treatments (Figure 13D). There was also a vast difference in both the abundance and size of *I. resecata* between the last two sampling periods of 2005. There was also nearly a 12 fold greater number of animals on 6/25/2005 compared to 5/28/2005 and average size was much smaller on 6/25/2005 at 11.68 (± 0.38 SE) compared to 20.57 mm (± 3.82 SE) on 5/28/2005.

Heptacarpus spp.

Broken-back shrimp (*Heptacarpus* spp.) abundance did not differ among treatments (Figure 14A) during 5/22/04 even when shoot densities did, but animal size did parallel *Z. marina* densities by being significantly larger in the Intermediate Brant compared to the Clipped and Brant Exclusion treatments, but not different from the Fecal treatment (Figure 14B). On both 7/18/2004 and 5/28/2005, neither *Heptacarpus* abundance nor size differed among treatments (Figure 14C – 14F) even when shoot

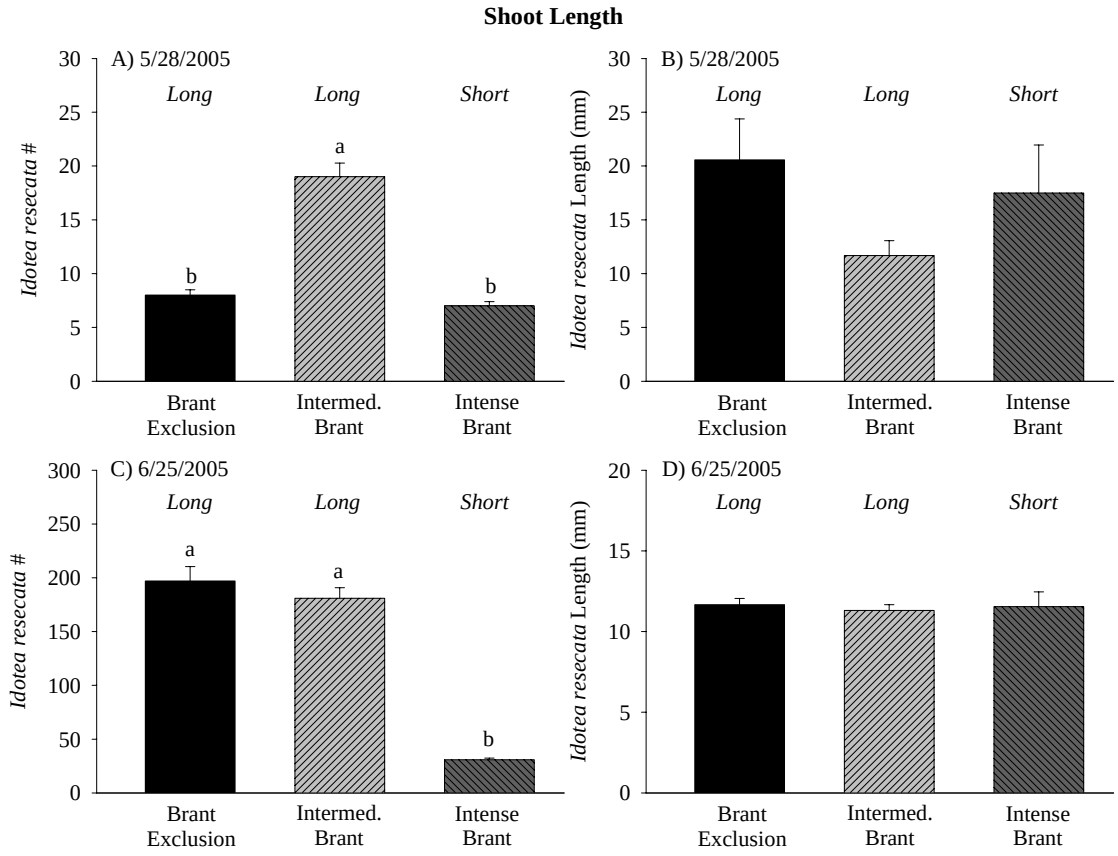

Figure 13. (A) *Idotea resecata* mean abundance and (B) size (mean length) collected May 28, 2005; (C) abundance and (D) size collected June 25, 2005 in response to shoot length. Error bars are ± 1 SE. Treatments that are significantly different from each other are denoted by lower case letters above each bar from Fisher's LSD multiple comparison tests. Relative *Z. marina* shoot length is indicated in italics above each treatment bar.

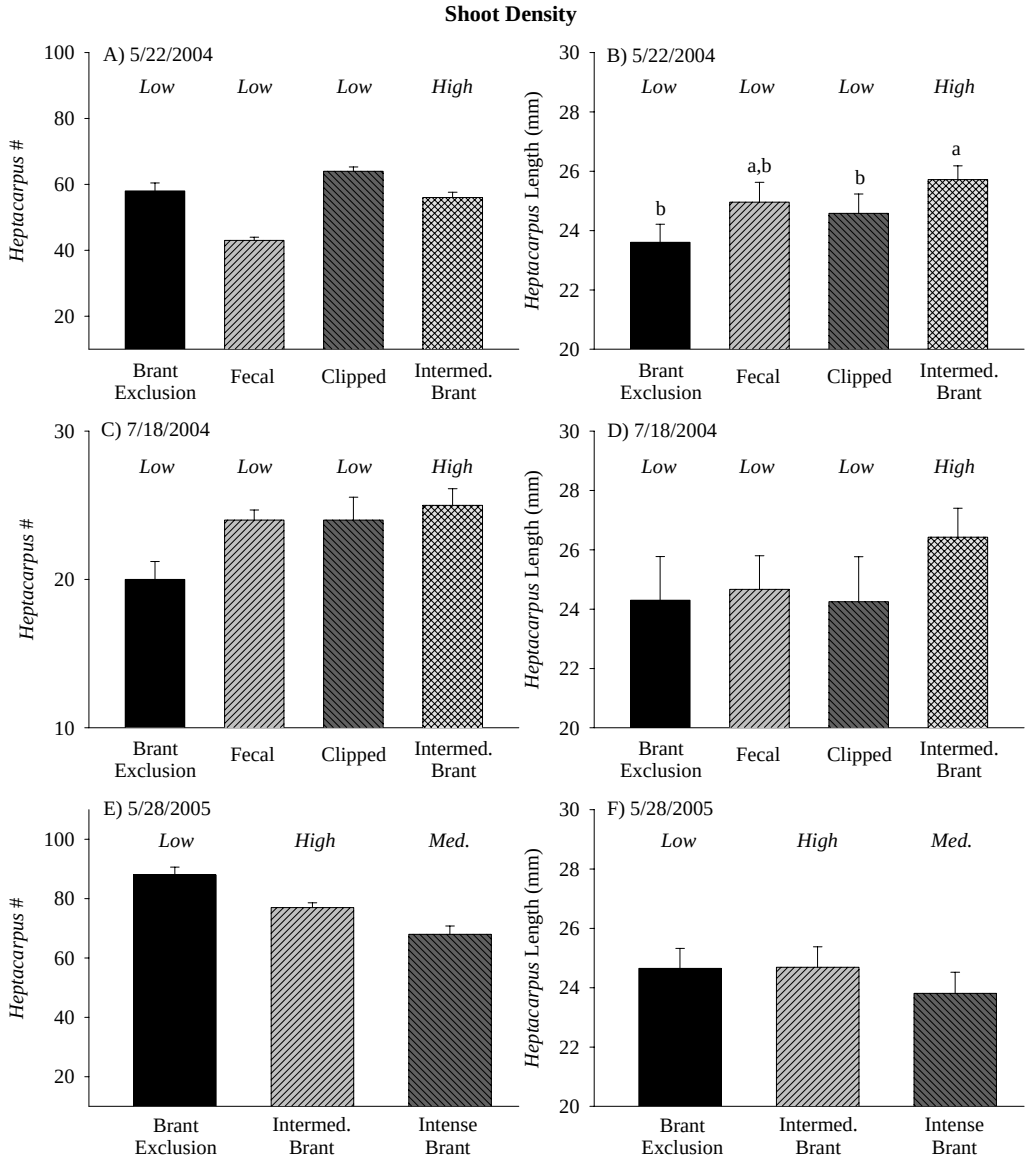

Figure 14. (A) *Heptacarpus* mean abundance and (B) size (mean length) collected May 22, 2004; (C) abundance and (D) size collected July 18, 2004; and (E) abundance and (F) size collected May 28, 2005 in response to shoot density. Error bars are ± 1 SE. Treatments that are significantly different from each other are denoted by lower case letters above each bar from Fisher's LSD multiple comparison tests.Relative *Z. marina* shoot density is indicated in italics above each treatment bar.

densities did. Distance from Entrance Channel was significant and negative for *Heptacarpus* size on 7/18/2004; and also significant, but positive on 5/28/2005.

Heptacarpus rarely responded to shoot length differences among treatments. On both 4/27/2005 and 5/28/2005, neither *Heptacarpus* abundance nor size differed when shoot lengths did (Figure 15A – 15D). Distance from Entrance Channel was significant for *Heptacarpus* size on both of these dates, but the relationship was negative on 4/27/2005 and positive on 5/28/2005. On 6/25/2005, *Z. marina* lengths were significantly lower in the Intense Brant treatment compared to both of the other treatments, which was paralleled by significantly lower *Heptacarpus* abundance in the Intense Brant treatment compared to both of the other treatments (Figure 15E). Distance from Hookton Channel was significant and positive. *Heptacarpus* size, however, was not different among treatments (Figure 15F).

Cancer magister

Z. marina density on 5/22/2004 was significantly higher in the Intermediate Brant treatment compared to every other 2004 treatment, but *C. magister* abundance did not differ among treatments (Figure 16A). *C. magister* size also did not parallel shoot densities, however, there were significantly smaller *C. magister* in the Clipped treatment compared to every other treatment (Figure 16B). *C. magister* was not numerically abundant enough to perform an analysis on 7/18/2004 or any of the sampling periods during 2005 in response to shoot length.

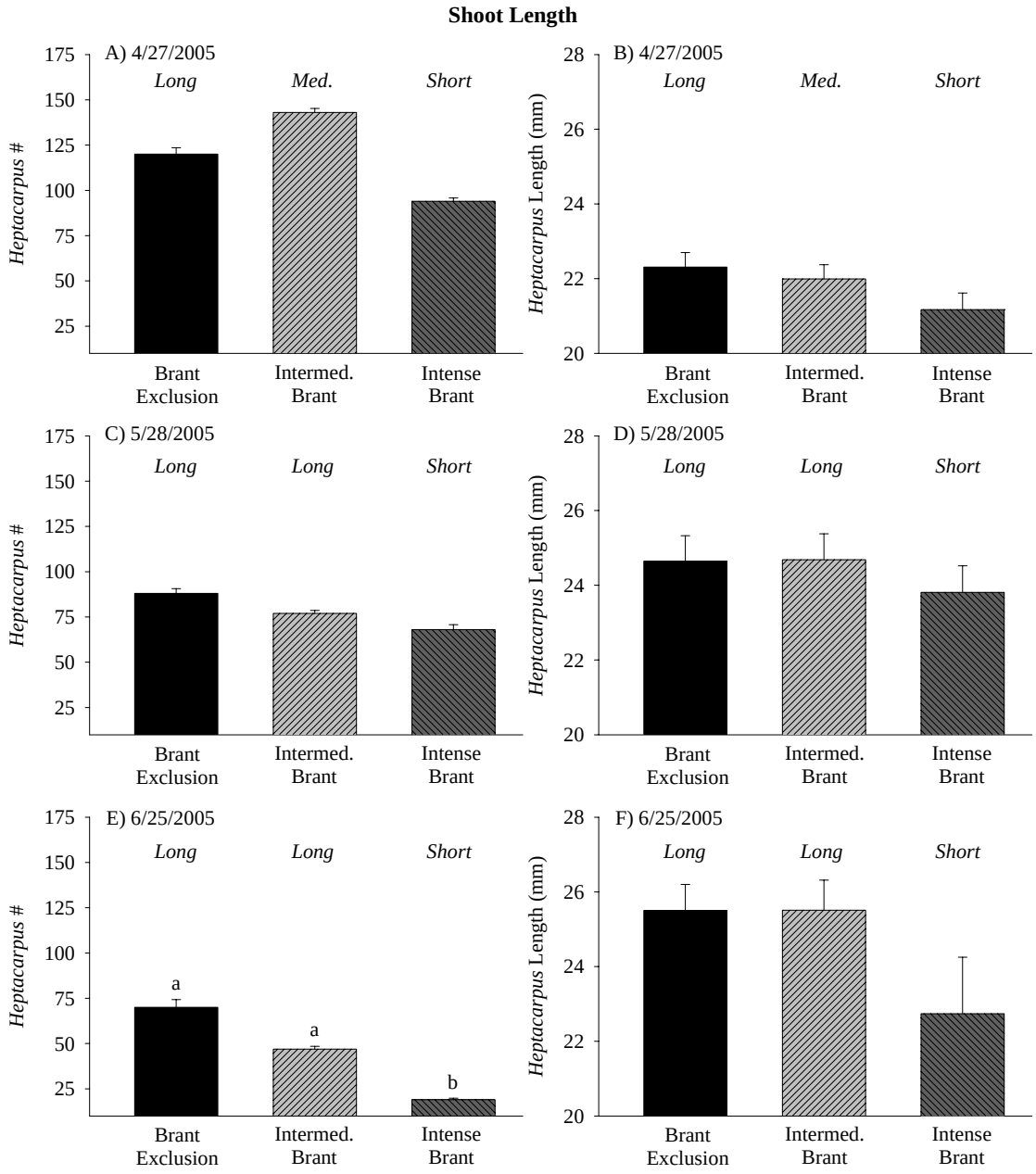

Figure 15. (A) Heptacarpus mean abundance and (B) size (mean length) collected April 27, 2005; (C) abundance and (D) size collected May 28, 2005; and (E) abundance and (F) size collected June 25, 2005 in response to shoot length. Error bars are ± 1 SE. Treatments that are significantly different from each other are denoted by lower case letters above each bar from Fisher's LSD multiple comparison tests. Relative Z. marina shoot length is indicated in italics above each treatment bar.

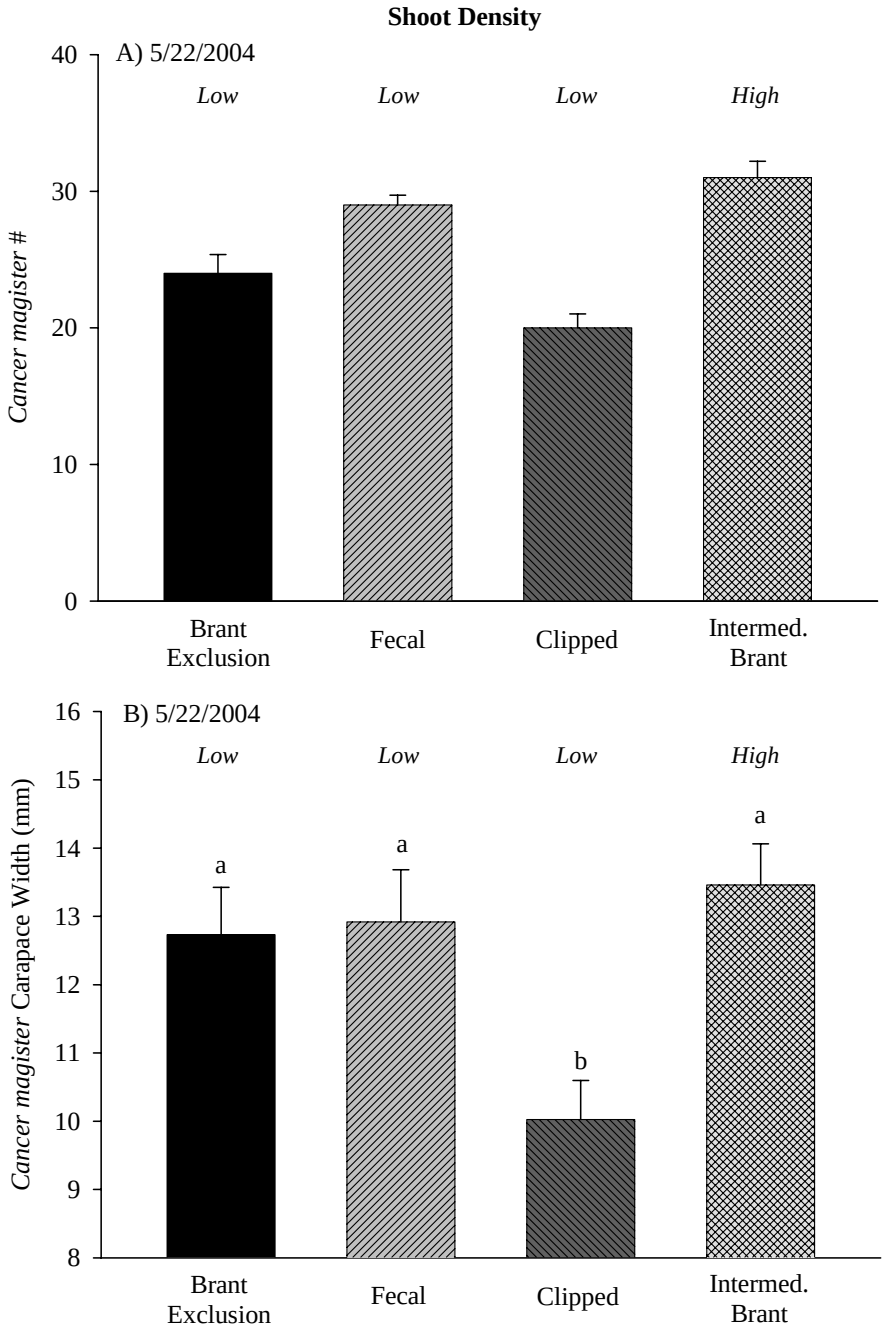

Figure 16. (A) *Cancer magister* mean abundance and (B) size (mean carapace width) collected May 22, 2004 in response to shoot density. Error bars are ± 1 SE. Treatments that are significantly different from each other are denoted by lower case letters above each bar from Fisher's LSD multiple comparison tests. Relative *Z. marina* shoot density is indicated in italics above each treatment bar.

Fishes

Total fish abundance reached its peak in late May of both years and was made up mostly by three fish species including three-spined stickleback (*Gasterosteus aculeatus*), saddleback gunnel (*Pholis ornata*), and Pacific staghorn sculpin (*Leptocottus armatus*), and abundances of these three species were not significantly different among treatments at any time in either year of the study. Additionally, the abundances of other fish species were markedly higher in 2004. For example, there were 38 juvenile surfperch (Embiotocidae spp.) collected in 2004 and zero in 2005; 26 black rockfish (*Sebastes melanops*) in 2004 and one in 2005; 19 bay goby (*Lepidogobius lepidus*) in 2004 and four in 2005, and 14 english sole (*Parophrys vetulus*) in 2004 and one in 2005 (Tables 2 and 3).

P. ornata abundance did not differ among treatments on 5/22/2004 (Figure 17A) even when shoot densities did, but distance from Entrance Channel was significant and negative. *P. ornata* size, however, did parallel shoot densities by being significantly larger in the Intermediate Brant treatment than in the Fecal and Brant Exclusion treatments, but not different from the Clipped treatment (Figure 17B); distance from Hookton Channel was significant and positive. During 2005, *P. ornata* abundance was not different among treatments (Figure 17C) when shoot densities varied, but animal size paralleled shoot densities by being significantly larger in the Intermediate Brant than in the Brant Exclusion (Figure 17D).

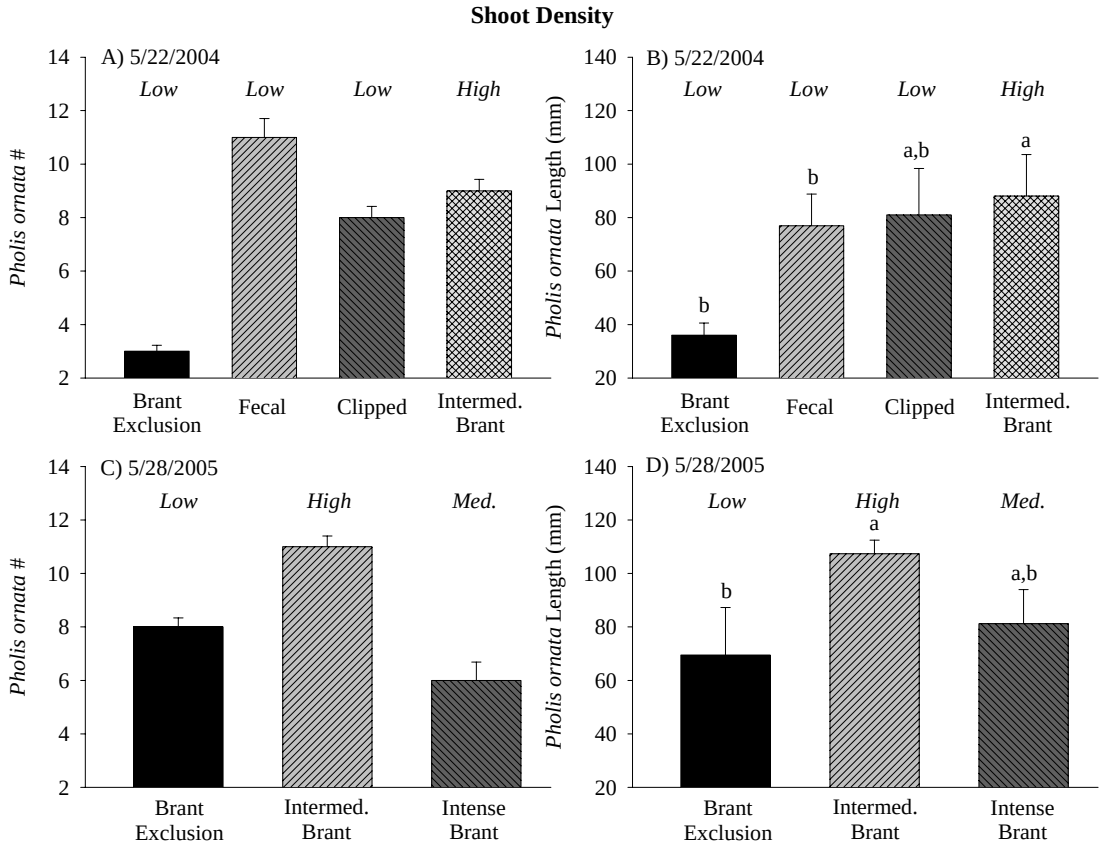

Figure 17. (A) *Pholis ornata* mean abundance and (B) size (mean length) collected May 22, 2004; and (C) abundance and (D) size collected May 28, 2005 in response to shoot density. Error bars are ± 1 SE. Treatments that are significantly different from each other are denoted by lower case letters above each bar from Fisher's LSD multiple comparison tests. Relative *Z. marina* shoot density is indicated in italics above each treatment bar.

On 4/27/2005, neither *P. ornata* abundance nor size differed among treatments (Figure 18A and 18B) although shoot lengths did. On 5/28/2005, when brant affected shoot lengths, *P. ornata* abundance was not affected. While there were significant differences in animal size among treatments on this date, they did not parallel shoot length differences (Figure 18C and 18D). On 6/25/2005, neither *P. ornata* abundance nor size differed among treatments (Figure 18E and 18F) although shoot lengths did. Distance from Entrance Channel was marginally significant and positive for *P. ornata* size (Table 5).

Other Factors Affecting Animal Responses

There was a substantial amount of interannual variation that occurred among animal abundance and species composition (Table 2 and 3), however brant populations in South Bay were nearly equal between both years of this study (E. Bjerre, S. Ferson, and J. Black, unpublished data) suggesting that other factors need to be taken into consideration. Therefore, mechanisms that could affect animal distribution and size other than brant induced changes to the vegetation were examined. Climate variables were used to understand why apparent differences in recruitment and fish predation occurred each year.

In order to understand if there was a change in currents delivering recruits to Humboldt Bay during 2004 and 2005, the minimum water temperatures entering the bay during the summer months were examined in order to detect the oceanic temperature signal within the bay. Water temperatures were high in 1998, dropped to a minimum

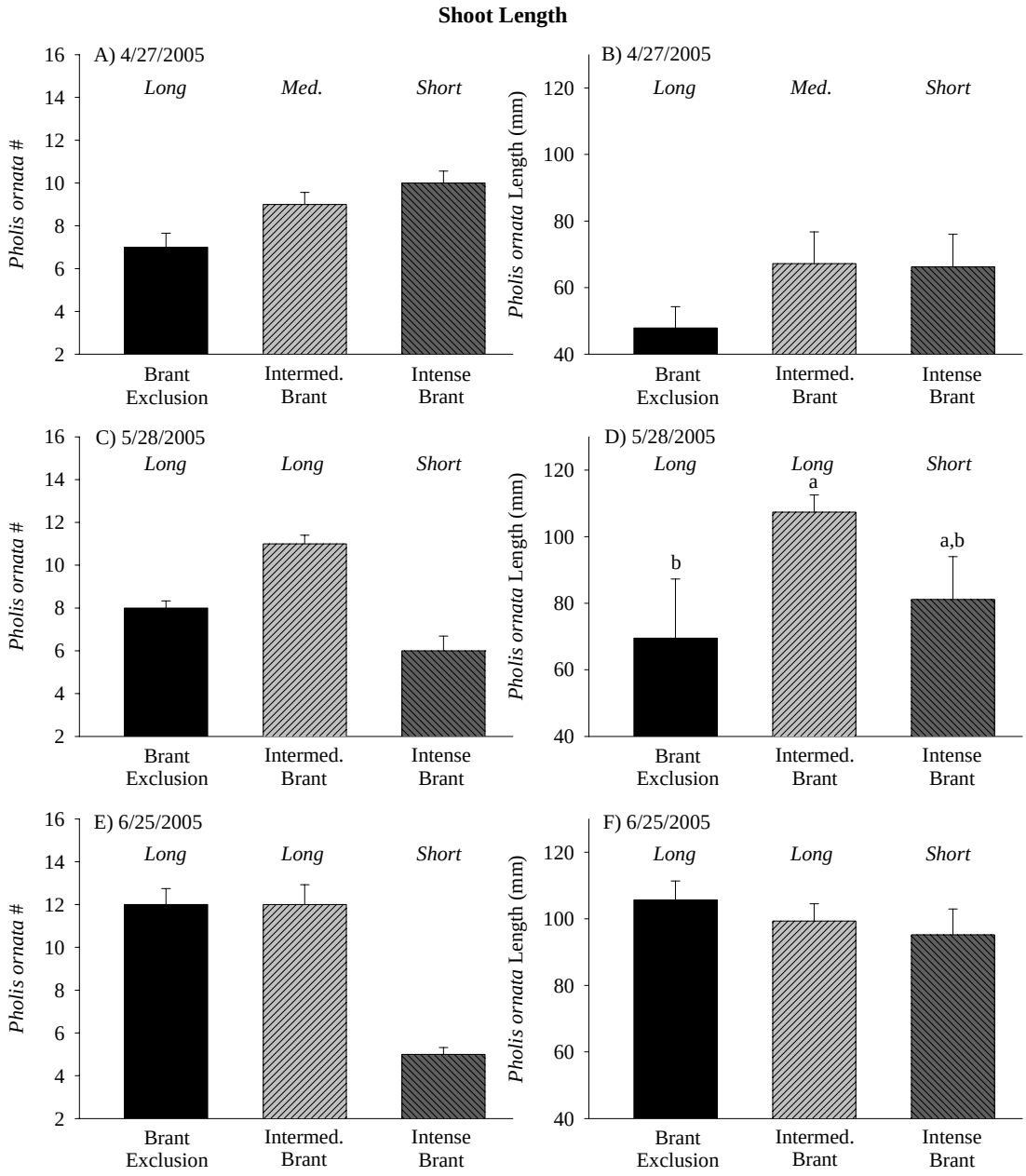

Figure 18. (A) *Pholis ornata* mean abundance and (B) size (mean length) collected April 27, 2005; (C) abundance and (D) size collected May 28, 2005; and (E) abundance and (F) size collected June 25, 2005 in response to shoot length. Error bars are ± 1 SE. Treatments that are significantly different from each other are denoted by lower case letters above each bar from Fisher's LSD multiple comparison tests. Relative *Z. marina* shoot length is indicated in italics above each treatment bar.

level by 2000, and were high again by 2003, characteristic of a complete El Niño Southern Oscillation (ENSO) cycle. Water temperatures fell about a half degree from 2003 to 2004, the latter being the year of the first experiment, and instead of continuing to drop in temperature to the La Niña minimum, temperatures came up about a quarter of a degree during 2005 (Figure 19). In addition to the change in current structure indicated by water temperature changes and its implications for recruitment into the bay, increases in water temperature are accompanied by increases in wind speed, precipitation, and turbidity, all of which could directly affect animals already in the bay. The latter three variables were almost twice as high in 2005 as 2004 (Figures 20, 21, and 22). There was a much greater amount and diversity of fish in the bay in 2004 than 2005 (Tables 2 and 3). As the total number of fish increased during 2004, the number of invertebrates decreased (Figure 23). Additionally, as the total number of fish decreased towards the end of the experiment, the number of invertebrates increased.

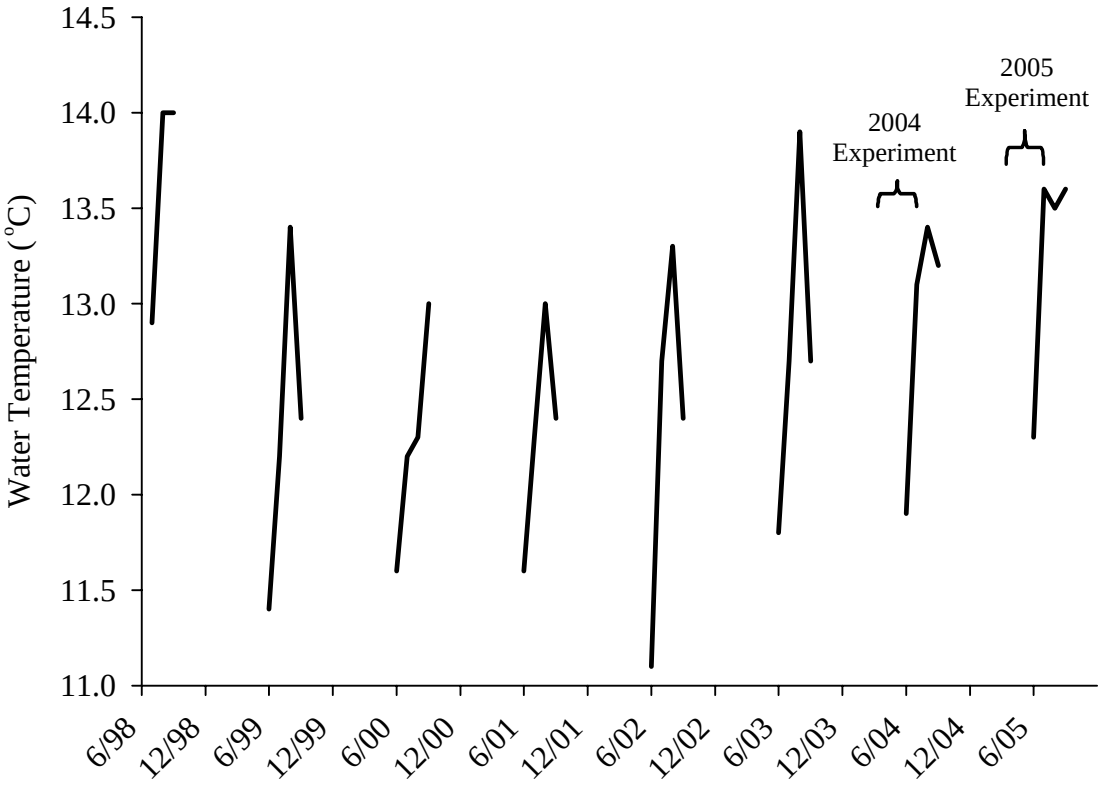

Figure 19. Mean of daily minimum temperatures (ºC) recorded by a data logger (StowAway TidbiT Submersible Temperature Logger) located along the Eureka waterfront in central Humboldt Bay during summer months from 1998 through 2005. The brackets indicate when each experiment was run.

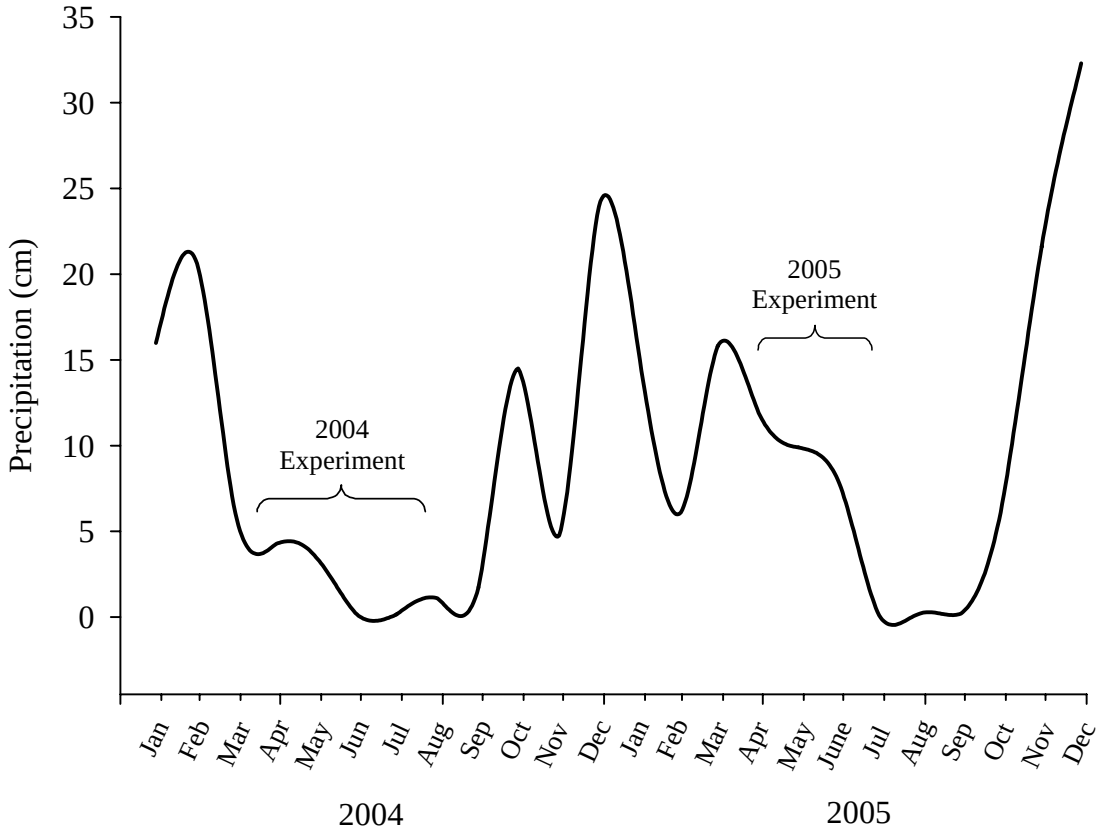

Figure 20. Total monthly precipitation (cm) from January 2004 – December 2005 recorded by the National Weather Service on Woodley Island in Humboldt Bay. The brackets indicate when each experiment was run.

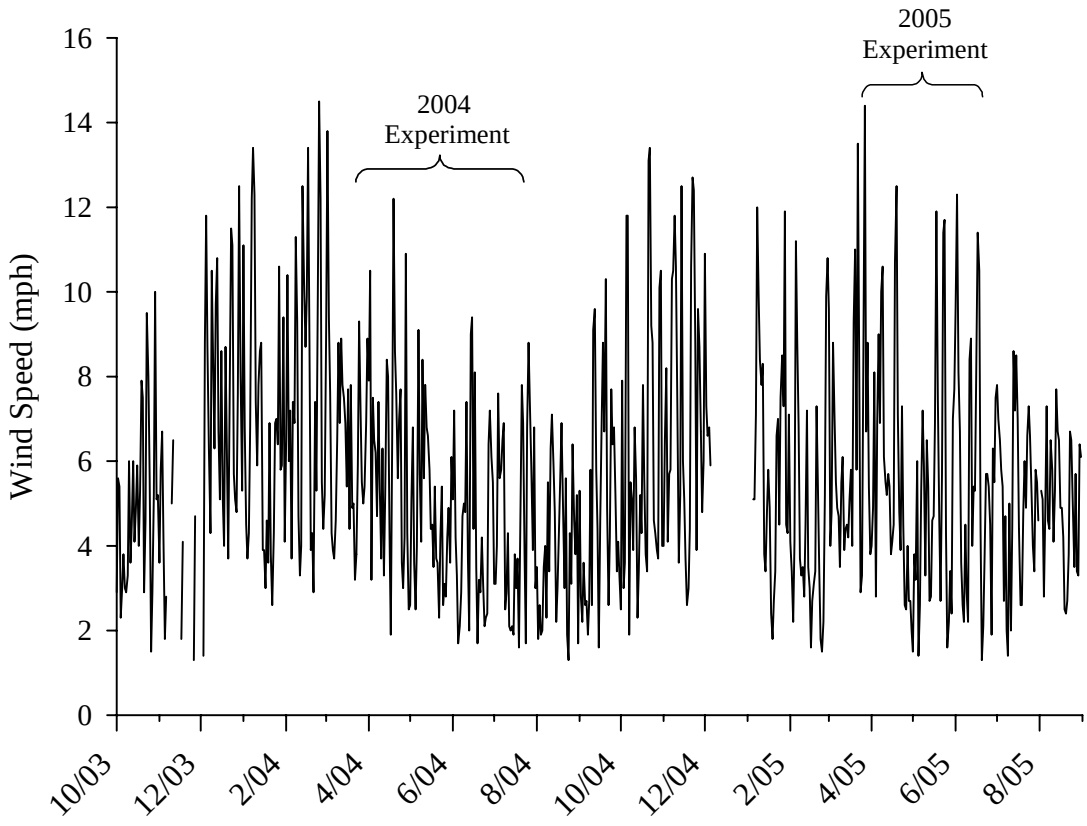

Figure 21. Hourly wind speed (mph) recorded from October 2003 – September 2005 by the Eureka weather buoy operated by NOAA (#46022), which is located 31 km West-Southwest of Eureka. The brackets indicate when each experiment was run.

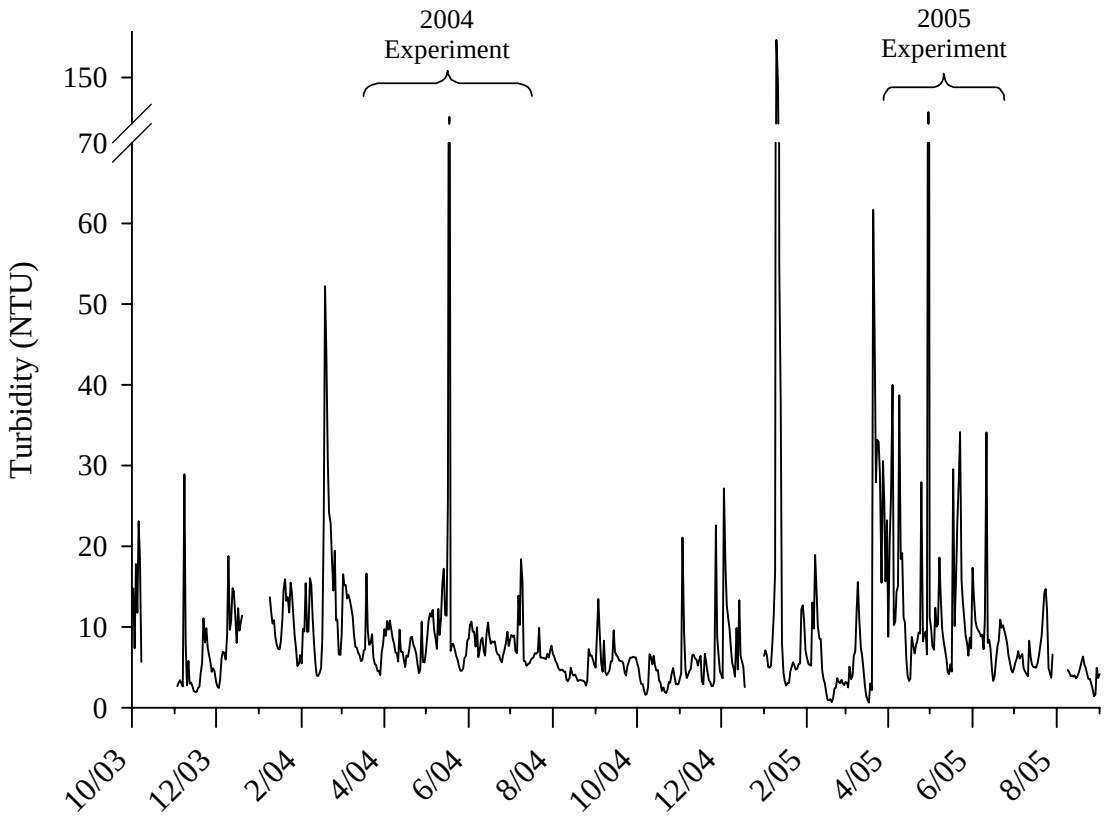

Figure 22. Mean daily turbidity (NTU) values from October 2003 – September 2005 recorded by the Yellow Springs Instruments sonde (mo 6600) located in the central part of Humboldt Bay and operated by CICORE. The brackets indicate when each experiment was run.

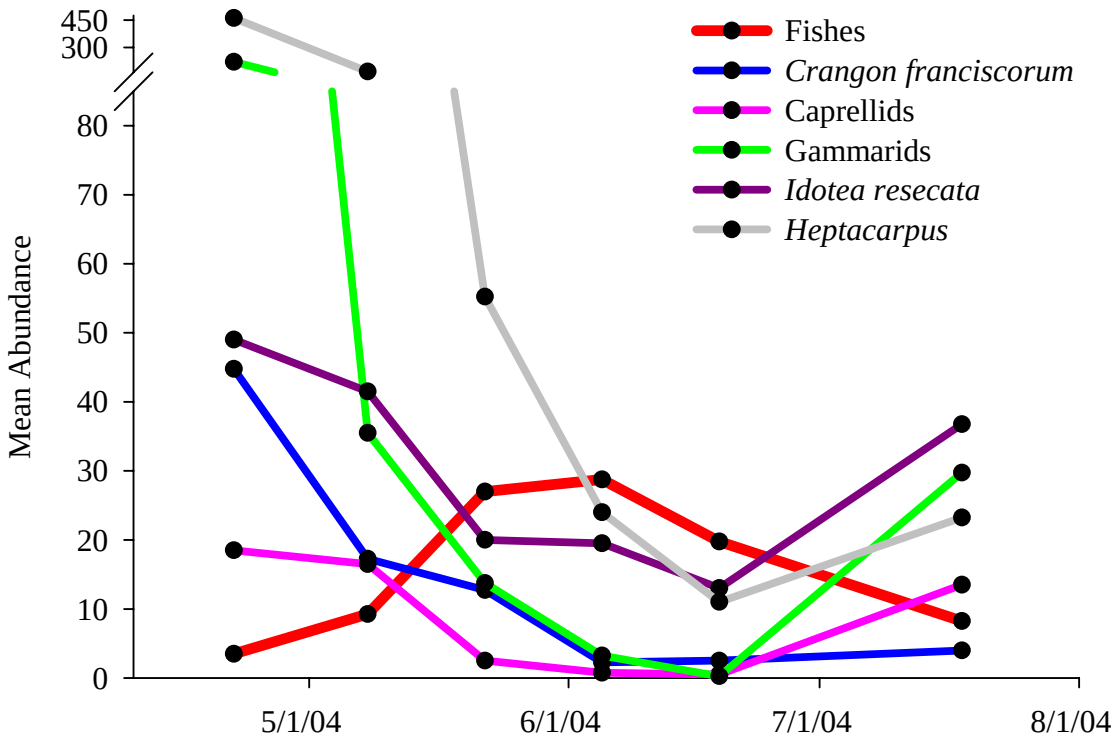

Figure 23. Relationship between the mean abundances of total fish and fish prey taxa collected April – July 2004.

DISCUSSION

Seagrass ecologists and managers are generally focused on bottom-up mechanisms that affect seagrass distribution and abundance, primarily nutrient and sediment loading and their effects on light. However, top-down mechanisms may also play an important role in shaping the assemblage and function of seagrass ecosystems (Valentine and Heck 1999, Williams and Heck 2001, Valentine and Duffy 2006). Few studies have examined the grazing effects of large herbivores (i.e. dugongs, urchins, and conchs) on seagrass and the associated animal residents (Stoner et al. 1995, Rose et al. 1999, Nakaoka et al. 2002), only one study in the past ten years has examined the top-down effects of grazers on western North American *Z. marina* beds (Zimmerman et al. 1996), and no study has examined waterfowl grazing effects on *Z. marina* and the associated animal community. Brant are abundant in Humboldt Bay from December until April and are major grazers that selectively feed on the youngest, innermost leaves of *Z. marina* shoots (Moore and Black 2006a, b). Their grazing has an immediate effect on *Z. marina* vegetation structure by opening up the canopy of leaves and a delayed effect on this structure by inducing *Z. marina* overcompensation (Ferson 2007). My study examined how the abundance and size of small animals living within a *Z. marina* bed respond to these brant induced *Z. marina* structural changes. The hypothesis that animal abundances and sizes would differ in response to brant induced changes to *Z. marina* vegetation structure was not consistently supported in this study because they either did not respond to vegetation changes, or they did parallel vegetation changes but

only under a particular set of conditions. Some of these conditions were identified in this study. Brant induced changes to the structural complexity of the *Z. marina* bed may affect the distribution and abundance of animals, but their effects are secondary in importance to the effects of recruitment and fish predation, and the latter are in turn affected by physical processes.

Recruitment may have been more influential than brant induced changes to the vegetation structure for many of the animals in this study. Most notably, there was nearly a 20 fold greater number of juvenile Dungeness crab (*Cancer magister*) collected in 2004 compared to 2005. I attribute this particular annual change in abundance to the altered warmer water current structure during 2005 that may have delivered fewer megalopae to Humboldt Bay. *C. magister* megalopae are assisted by currents in their transport from offshore areas into shallow estuaries and bays (Emmett et al. 1991).

The distribution of other animals, such as caprellid and gammarid amphipods and to a lesser extent, *Idotea resecata*, also appeared to have been more strongly influenced by recruitment. The species composition and abundance of macroinvertebrates and fish in seagrass beds is influenced by distance from the mouth of the estuary (Bell and Westoby 1986c) and location within the bay, which may affect recruitment to the seagrass bed (Jenkins et al. 1998, Raposa and Oviatt 2000, Hovel et al. 2002). The two covariates used in this study, the distance a treatment replicate was from Entrance Channel, and the distance a treatment replicate was from the edge of Hookton Channel, were significant in 8 of the 12 analyses for caprellids and gammarids with more individuals being found closer to each channel. This spatial distribution of the

amphipods in combination with the planktonic larval stages in their life histories suggest that patterns of dispersal have a large effect on the distribution and abundance of settled amphipods. The influence of distance from channels was not as evident for *I. resecata*, but nonetheless, distances were highly significant on two occasions. Additionally, when shoot densities were different among treatments, the abundances of caprellids and gammarids were not. Although caprellid and gammarid abundances were sometimes different among treatments in response to shoot length differences among treatments, the differences did not parallel the changes in shoot length. This evidence indicates that amphipods did not discriminate between differences in structural complexity, which is consistent with the "settle and stay" hypothesis (Bell and Westoby 1986b, Bell et al. 1987, Worthington et al. 1992, Hannan and Williams 1998, Upston and Booth 2003).

The effects of brant induced changes to the vegetation structure on the abundance and size of *Z. marina* bed invertebrates may also be less important compared to the effects of apparent fish predation. In 2004, there was a negative relationship between the number of small invertebrates and total fish, suggesting that invertebrates such as amphipods, *I. resecata*, and shrimp species, are prey for fishes in the bay. Fishes are known to consume a similar group of invertebrates in other studies conducted in seagrass studies (Stoner 1983, Caine 1989, Connolly 1997), and in Humboldt Bay, the diets of two common rockfish (*Sebastes melanops* and *S. caurinus*) and one surfperch (*Hyperprosopon argenteum*) consist largely of amphipods (R. Studebaker, unpublished data; Moring 1984 respectively). Peak fish numbers in 2004 occurred towards the end of May at the same time that the simulated intermediate level of brant grazing and fecal

addition resulted in a maximum density of *Z. marina* shoots (Ferson 2007). If *Z. marina* complexity was more important than predation I would have expected small invertebrate abundances to be increased in treatments with the greatest amount of structure available as a refuge from predation (Heck and Orth 1980, Orth et al. 1984, Heck and Crowder 1991, Orth 1992, Williams and Heck 2001, Heck and Orth 2006), but this was not the case. In fact, the abundance and size of nearly all the major invertebrate prey species did not respond to changes to the vegetation structure at this time. Since the abundances of every fish species examined in this study were also not different among treatments at this time, the effects of fish predation may have equalized the abundance and distribution of small invertebrates and thus masked a relationship with vegetation structure from developing.

Weather related changes in physical processes may be why the effects of apparent fish predation on invertebrates were so much greater during 2004 than 2005. There was a greater abundance (nearly three fold) and diversity (nearly two fold) of fish in the bay in 2004 than 2005. The combined abundances of juvenile surfperch (Embiotocidae spp.), black rockfish (*S. melanops*), bay goby (*Lepidogobius lepidus*) and english sole (*Parophrys vetulus*) represented 20.7% and 3.5% of the fish composition respectively in 2004 and 2005. The greater precipitation, turbidity and winds, with the latter potentially generating higher wind waves (Koch et al. 2006), could have either prevented fish from recruiting into the bed during 2005 and resident fish may have avoided the bed due to all the shallow water disturbance. Seagrass beds can attenuate waves up to a particular

threshold of hydrodynamic force at which point the waves start eroding the bed (Koch et al. 2006) and presumably remove animals or prevent them from entering the bed.

Following the effects of recruitment and fish predation on the larger spatial and temporal scales of animal abundance and size in this study, brant induced changes to the vegetation structure did affect animal abundances and sizes. Individual habitat characteristics, such as shoot density, shoot length and shoot surface area, have been shown to influence faunal density and diversity in other seagrass habitats (Hovel and Lipcius 2001, Parker et al. 2001, Jenkins et al. 2002, Sirota and Hovel 2006). I would expect this to be the case especially for animals that have coevolved with *Z. marina* like the opisthobranch, *Phyllaplysia taylori*, which does not have a planktonic larval stage in its life history. *P. taylori* is a mesograzer that consumes epiphytic algae and spends nearly its entire life cycle attached to *Z. marina* (Beeman 1968, Keiser 2004, Shaughnessy et al. 2007). Consistently more and larger *P. taylori* were found when shoots were longer, and less and smaller *P. taylori* occurred when shoots were shorter. Additionally, on one occasion, more *P. taylori* were found when shoot density was greatest. Epiphyte loads also responded to brant induced structural changes by initially being higher when shoots were longer. However, two months later, epiphyte loads were lowest in the treatment with the longest shoots. The latter treatment was also accompanied by the greatest number of *P. taylori*, suggesting they may have the ability to reduce epiphyte loads considerably. Mesograzers have the ability to regulate epiphyte biomass (van Montfrans et al. 1984, Hootsman and Vermaat 1985, Williams and Ruckleshaus 1993, Nelson 1997, Schanz et al. 2002, Hily et al. 2004). *P. taylori*

abundance was negatively correlated with *Z. marina* epiphyte loads in Humboldt Bay, and when *P. taylori* was experimentally excluded from *Z. marina* leaves the latter hold more epiphytes (Keiser 2004, Shaughnessy et al. 2007). Intermediate levels of brant grazing resulted in the maximum number of shoots, whereas intense levels result in shorter shoot lengths (Ferson 2007). The abundance of *P. taylori* therefore increased when a maximum number of shoots were created by intermediate levels of brant grazing, and both the abundance and size of *P. taylori* decreased in response to shorter shoots created by intense levels of brant grazing. This relationship occurs because of the greater leaf surface area that results from either an increase in shoot density, shoot length, or both (Parker et al. 2001, Sirota and Hovel 2006). Even with an animal such as *P. taylori* where a close relationship between brant induced changes to the vegetation and animal abundance would be expected, it is notable that the unfavorable climate conditions in 2005 probably caused an 11 fold decrease in abundance relative to 2004.

Positive relationships were also found between brant induced structural changes and both saddleback gunnel (*Pholis ornata*) and *Heptacarpus* spp., although they were not as consistent as for *P. taylori*. Larger *P. ornata* were found when shoot density was higher and when shoots were longer. Similarly, *Heptacarpus* size increased in response to the maximum number of shoots, and there were always fewer and smaller *Heptacarpus* when shoots were shorter. These results are consistent with other studies in which increasing amounts of vegetation result in an increase in the abundance and/or size of the associated animal community (Heck and Orth 1980, Orth et al. 1984, Irlandi 1994, 1997, Mattila et al. 1999, Boström and Bonsdorff 2000, Hughes et al. 2002, Wyda et al. 2002).

The abundance and size of other animals in response to brant induced changes to the vegetation structure were not always positive. In fact, the size of *I. resecata* and abundances of caprellids and gammarids responded negatively to brant induced changes to the vegetation structure although these responses occurred less frequently. *I. resecata* were smaller when shoots were more dense and longer, and they were larger when shoots were less dense and shorter. Similarly, both caprellid and gammarid abundances were highest when shoot lengths were shortest. These results are consistent with other studies in which the abundance and/or size of similar animals decreased with an increase in the physical complexity of seagrasses (Bell and Westoby 1986b, Harrison 1987, Bostrom and Bonsdorff 2000). Therefore, the present study agrees with others that have demonstrated that the relationship between the animal community and the structural complexity of *Z. marina* appears to be species-specific (Heck and Orth 1980, Bell and Westoby 1986a, b, Heck et al. 1995, Horinouchi et al. 1999, Bostrom and Bonsdorff 2000, Guidetti and Bussotti 2002, Hovel et al. 2002, Nakaoka 2005, Sirota and Hovel 2006).

There were a number of examples where the abundance and size of an animal did significantly differ among the brant simulation treatments, but animal differences among the treatments did not parallel the brant induced changes to the vegetation. For example, the abundances of caprellids and gammarids were consistently higher in treatments where fecal addition was added. Additionally, fewer and smaller *C. magister* were found only when *Z. marina* was clipped, but the addition of fecal matter may have offset the negative effects of clipping. The role of fecal matter in aquatic environments has rarely been considered, despite the fact that it can be very abundant in aquatic habitats (Wotton and

Malmqvist 2001). Seabird guano represents a repackaging of available organic matter, and in the Alaskan Aleutian archipelago, the transfer of nutrients by seabirds from the ocean to land is vital for plant productivity and nutrient flow to higher trophic levels (Croll et al. 2005). Although a small portion of fecal matter is lost from surface waters, it is likely that all the dissolved organic matter is retained within the photic zone (Wotton and Malmqvist 2001). It is therefore reasonable to expect that fecal addition may represent increased food availability for detritivorous animals such as caprellids, gammarids, and *C. magister*.

Differences among treatments that do not parallel brant induced changes to the vegetation structure may also be explained by other mechanisms not examined in this study. For example, interspecific competition has been found to influence the habitat selection of fishes (Hixon 1980, Schofield 2003), while other animals have been shown to actively select habitat (Leber 1985, Bell and Westoby 1986c, Edgar and Robertson 1992, Halliday 1995, Levin et al. 1997).

Summary

The hypothesis that animal abundances and sizes would differ in response to brant induced changes to *Z. marina* vegetation structure was not consistently supported. The abundances and sizes of some animals did parallel vegetation changes, but only under a limited set of circumstances. Other factors, such as recruitment and fish predation, were more influential than brant induced changes to the vegetation structure for many of the animals in this study. Nevertheless, following the effects of climate on recruitment and fish predation, some animals developed either a positive or negative relationship with the

brant induced structural changes to the vegetation. For example, the abundance of *P. taylori* increased when a maximum number of shoots were created by intermediate levels of brant grazing, and both the abundance and size of *P. taylori* decreased in response to shorter shoots created by intense levels of brant grazing. However, other animals responded negatively to brant induced changes to the vegetation structure. For example, *I. resecata* were smaller when shoots were more dense and longer, and they were larger when shoots were less dense and shorter. Additionally, some animals did not develop a relationship with the brant induced changes to the vegetation structure. For example, the abundances of caprellids and gammards did significantly differ among the brant simulation treatments, but they did not parallel the brant induced changes to the vegetation and were instead increased in treatments where fecal addition was added. Therefore, the relationship between the animal community and the structural complexity of *Z. marina* appears to be species-specific.

Limitations and Suggestions for Future Research

Several aspects of this study could be improved for future research. First, more top-down effects might have occurred if brant manipulations spanned the entire brant season, instead of the two manipulations used in the experiments of this study. Second, more top-down effects might have occurred in 2004 if our treatment clearing sizes were as large as they were in 2005. Treatment sizes in 2004 were 2.25 m^2 and may have been too small of a habitat area for animals to respond to (especially for highly mobile species) when compared to the much larger 9.0 m^2 treatment areas in 2005. For example, Eggleston et al. (1998) showed that decapods were maximally abundant in 4.0 m^2

experimental patches. Third, the types of trapping techniques used in this study targeted mostly smaller, juvenile animals. Thus, future research should include the top-down effects on larger animals. Fourth, statistical power problems were an issue with a number of animal analyses. Unfortunately, increasing the number of replicates and sample sizes for a study of this magnitude would be extremely labor-intensive and difficult to accomplish under this experimental design. Lastly, it would be interesting to examine the effects of brant grazing and fecal addition on the animal community at a landscape scale (as defined in Bell et al. 2006) in order to evaluate whether or not similar results of grazer effects within a single *Z. marina* bed (as in this study) can be applied to a landscape scale.

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Appendix A. Summary of total abundance, mean size, and ranges of both for every animal collected during six sampling periods from April 22, 2004 – July 18, 2004.

Taxon	Total Abundance	Abundance Range	Mean size (mm)	Size range (mm)
Aeolida papillosa	4	0 - 1		
Amphiodia occidentalis	49	0 - 17		
Apodichthys flavidus	5	0 - 1	62.00	45 - 73
Archidoris montereyensis	1			
Aulorhynchus flavidus	4	0 - 1	67.25	32 - 136
Calanoida spp.	1			
Cancer antennarius	6	0 - 2	37.02	8 - 85
Cancer gracilis	5	0 - 1	41.51	24 - 82
Cancer magister	413	2 - 125	11.63	3 - 34
Cancer productus	7	0 - 3	55.18	15 - 111
Caprellidea spp.	362	2 - 111		
Clinocardium nuttallii	58	24 - 32	37.26	4 - 66
Crangon franciscorum	355	12 - 183	36.91	9 - 76
Cumacea spp.	3	0 - 1		
Enophrys bison	1		32.00	32
Embiotocidae spp.	38	0 - 24	43.58	37 - 66
Gammaridea spp.	1217	1 - 887		
Gasterosteus aculeatus	159	0 - 65	66.57	46 - 76
Gnorimosphaeroma spp.	35	0 - 7		
Hemigrapsus nudus	22	1 - 5	10.72	6 - 16
Hemigrapsus oregonensis	2	0 - 2	16.18	10 - 23
Heptacarpus spp.	2970	44 - 1843	25.27	6 - 45
Hermissenda crassicornis	6	0 - 2		
Hexagrammos decagrammus	3	0 - 2	65.67	51 - 82
Hippolytidae (unknown spp.)	1		27.00	27
Idotea resecata	860	63 - 227	20.69	3 - 47

Lacuna variegata	38	0 - 10		
Lepidogobius lepidus	17	0 - 8	93.35	17 - 115
Leptocottus armatus	55	0 - 19	84.76	31 - 115
Macoma nasuta	353	159 - 194	32.16	6 - 58
Mytilus spp.	58	1 - 24	10.33	3 - 26
Ophiodon elongatus	1		135.00	135
Parophrys vetulus	14	0 - 8	50.00	36 - 63
Pholis ornata	131	1 - 46	69.17	20 - 160
Phyllaplysia taylori	2168	4 - 750	16.57	4 - 42
Phyllodocida spp.	69	0 - 31		
Pugettia producta	1		5.37	5.37
Sebastes caurinus	2	0 - 2	63.00	62 - 64
Sebastes melanops	26	0 - 25	50.23	40 - 56
Syngnathus leptorhynchus	10	0 - 3	119.30	40 - 231
Tresus nuttallii	1		65.75	65.75

Appendix B. Summary of total abundance, mean size, and ranges of both for every animal collected during four sampling periods from April 27, 2005 – June 25, 2005.

Taxon	Total Abundance	Abundance Range	Mean size (mm)	Size range (mm)
Amphiodia occidentalis	12	1 - 4		
Aulorhynchus flavidus	1		58.00	58
Cancer antennarius	2	0 - 1	17.84	13 - 22
Cancer magister	21	0 - 8	7.84	3 - 12
Cancer productus	1		7.47	7.47
Caprellidea spp.	6440	248 - 4156		
Clinocardium nuttallii	43	9 - 34	42.76	7 - 64
Crangon franciscorum	129	10 - 54	38.40	18 - 66
Crangon styloristris	1		31.00	31
Gammaridea spp.	1650	239 - 486		
Gasterosteus aculeatus	75	0 - 46	67.18	57 - 76
Gnorimosphaeroma spp.	41	5 - 22		
Hemigrapsus nudus	19	1 - 4	10.09	4 - 19
Heptacarpus spp.	1022	136 - 357	23.79	10 - 35
Hermissenda crassicornis	4	0 - 2	9.50	6 - 13
Idotea resecata	484	17 - 409	12.70	3 - 52
Lacuna variegata	12	0 - 3		
Lepidogobius lepidus	4	0 - 2	93.35	68 - 112
Leptocottus armatus	40	2 - 18	82.55	50 - 100
Macoma nasuta	213	91 - 122	34.18	12 - 47
Mytilus spp.	4	0 - 1	6.33	3 - 11
Parophrys vetulus	1		53.00	53
Pholis ornata	120	25 - 40	87.13	32 - 139
Phyllaplysia taylori	197	36 - 63	23.93	3 - 55
Phyllodocida spp.	71	7 - 17		

Pinnixia franciscana	3	0 - 2	10.23	8 - 14
Sebastes melanops	1		51.00	51
Syngnathus leptorhynchus	4	0 - 2	157.50	59 - 232