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Kevin R. Turner

Effects of fish predation on benthic communities in the San Juan Archipelago

Kevin R. Turner

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Reading Committee:

Kenneth P. Sebens, Chair

Megan N. Dethier

Daniel E. Schindler

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Abstract

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Kevin R. Turner

Chair of the Supervisory Committee:
Professor Kenneth P. Sebens
Department of Biology

Predation is a strong driver of community assembly, particularly in marine systems. Rockfish and other large fishes are the dominant predators in the rocky subtidal habitats of the San Juan Archipelago in NW Washington State. Here I examine the consumptive effects of these predatory fishes, beginning with a study of rockfish diet, and following with tests of the direct influence of predation on prey species and the indirect influence on other community members.

In the first chapter I conducted a study of the diet of copper rockfish. Food web models benefit from recent and local data, and in this study I compared my findings with historic diet data from the Salish Sea and other localities along the US West Coast. Additionally, non-lethal methods of diet sampling are necessary to protect depleted rockfish populations, and I successfully used gastric lavage to sample these fish. Copper rockfish from this study fed primarily on shrimp and other demersal crustaceans, and teleosts made up a very small portion of their diet. Compared to previous studies, I found much higher consumption of shrimp and much

lower consumption of teleosts, a difference that is likely due in part to geographic or temporal differences in prey availability.

Given that copper rockfish diet was so dominated by shrimp, in the second chapter I used field experiments and surveys to determine the top-down effect of rockfish and other large demersal fishes on shrimp and other prey species. In three years of predator and prey surveys I found that shrimp abundance was negatively correlated with pooled predator biomass, but not abundance. Small fish and crab abundance were not correlated with predators. In two rounds of experimental exclusion of predatory fishes I found elevated abundance of both shrimp and small fishes in areas protected from predators. Despite this direct effect of predators on their prey, I did not find evidence of an indirect predator influence on the encrusting assemblage in the exclusion experiment.

Trophic cascades are common in temperate marine ecosystems, often mediated by predators consuming urchins and urchins grazing on kelp. The San Juan Archipelago is notable for its lack of both urchin predators and strong grazing pressure from urchins. In the final chapter I looked for evidence of trophic cascades structuring the benthic community in this system. I surveyed the mobile invertebrates and sessile epibenthos at 12 sites within San Juan Channel, and compared these assemblages to predatory fishes to test for co-variance between the groups. Despite some limited evidence of co-variance between the predatory fishes and the other groups, the species involved did not suggest trophic relationships as the causal agent. Instead, predatory fishes may be responding to the biotic habitat provided by benthic organisms. Co-variation between the mobile invertebrates and sessile epibenthos provides supporting evidence of a three-species interaction between urchins, chitons, and social ascidians, and evidence of urchins reducing kelp cover. Finally, I compared these three assemblages to current flow and found

strong evidence of current influencing assemblage composition. Although this benthic community does not appear to be controlled by a fish-initiated trophic cascade, consumptive interactions at lower trophic levels and dependence on abiotic factors play important structuring roles.

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Dedicated to my parents,
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CHAPTER 1

Non-lethal analysis of diet of copper rockfish in the San Juan Archipelago

ABSTRACT — Rockfish populations in the Salish Sea are at historically low levels due to slow population growth rates and a history of overexploitation. Fisheries managers are now attempting to rebuild stocks with a complete fishery closure. Food web models of the Salish Sea depend on current diet data, but lethal methods of diet sampling are not tenable with at-risk rockfish populations. Non-lethal sampling of diets, such as by gastric lavage, had not been tested with rockfish, but can help minimize depletion of the populations for research needs. I used lavage to sample the diet of copper rockfish in San Juan Channel, WA in fall 2010. Copper rockfish fed primarily on caridean shrimp and other demersal crustaceans, and consumed very few teleost prey. Previous studies of copper rockfish diet documented much higher reliance on teleost and non-shrimp crustacean prey. This difference in diets is likely due in part to differing resource availability.

INTRODUCTION

Several species of rockfish are commonly found in the Salish Sea (Puget Sound, the Strait of Juan de Fuca and the Strait of Georgia), including copper (*Sebastes caurinus*), quillback (*S. maliger*), yellowtail (*S. flavidus*), black (*S. melanops*), and Puget Sound (*S. emphaeus*) rockfish. A handful of other species are also sighted occasionally, and a total of at least 27 species have been reported at least once from the Salish Sea (Love et al. 2002, Palsson et al. 2009). Rockfishes are generally long-lived, with some species achieving maximum ages of over 200 years (Munk 2001, Love et al. 2002, Palsson et al. 2009). Species common in the Salish Sea may live as long as 50 (copper and black), 65 (yellowtail), or 100 years (quillback). With this extended longevity comes extended time to maturity, and full sexual maturity may not be reached until an age of 5-15 years (Love et al. 2002, Palsson et al. 2009).

The populations of large-bodied rockfish species, including copper, quillback, black and yellowtail, have been in decline in the Salish Sea for decades (Palsson et al. 2009). Although there was little historic interest in harvesting rockfish, the 1974 Boldt Decision's reduction of allowable recreational and commercial salmon (*Oncorhynchus* spp.) harvest prompted the State of Washington to promote bottom fishing, including the harvest of rockfishes, in an effort to prevent fishing conflicts (Williams et al. 2010). Expanding fishing pressure combined with slow time to maturity, long generation times, and sedentary behavior made rockfishes easily subject to overharvest, and early underestimates of longevity contributed to inaccurate demographic models and harvest allotments (Chilton & Beamish 1982, Palsson et al. 2009, Williams et al. 2010). In response to declining stock assessments, the state instituted restrictions on commercial

gear and sequential reductions in recreational harvest (Palsson et al. 2009, Williams et al. 2010), culminating with the complete closure of rockfish harvest in Puget Sound in 2010 (WAC 2010).

Successful management of fish populations in the Salish Sea depends on adequate data, including demographic information such as abundance, size and age distributions, harvest rates, habitat requirements, and diet. Diet information can be used to aid successful ecosystem-based management (Latour et al. 2003). If diet is known, prey species can be managed so as to maintain a sufficient prey base for particular fish species and populations, or habitats of prey species can be protected if necessary. Additionally, more complete diet information can provide data about temporal variation in fish behavior. Shifts in diet within a year may help explain movement patterns, and shifts in diet over longer time periods may be indicative of larger changes in the ecosystem.

The most abundant species of large rockfish in the San Juan Islands is the copper rockfish. Diet information for copper rockfish exists from throughout its range along the NE Pacific coast, including from California (Prince & Gotshall 1976), Alaska (Rosenthal et al. 1988), and from five studies in inland waters: two from Puget Sound near Seattle, WA (Patten 1973, Hueckel & Buckley 1987), one from Saanich Inlet, BC (Murie 1995), and two from the San Juan Islands, WA (Moulton 1977, Miller et al. 1977).

Fish diet studies frequently rely on excision of the stomach. While this ensures complete evaluation of gut contents (Bowen 1996), it is an undesirable method to use with a declining population. Due to the decline of rockfish in the Salish Sea, including the recent listing of three species on the Endangered Species List as Threatened or Endangered (bocaccio [*S. paucispinus*], yelloweye [*S. ruberrimus*], and canary rockfish [*S. pinniger*]) (NMFS 2010), non-lethal methods would be preferable (Haley 1998). Gastric lavage, flushing stomach contents out through the

mouth with pressurized water, has been used successfully with numerous fish species (Crossman & Hamilton 1978, Kamler & Pope 2001), but never with rockfish.

Our objectives are to provide current information about copper rockfish diet in the San Juan Islands, and to test the utility of gastric lavage as a method for sampling rockfish stomach contents. Because diet items may change in abundance or identity due to the introduction of exotics, local extirpations, or climate change (Heath 2005, Albins & Hixon 2013), it is important to be able to routinely update basic biological knowledge, including diet. Gastric lavage could be used as a tool to periodically resample rockfish diet and update food web models without exposing the population to unnecessary mortality.

METHODS

Study Area

I collected wild copper rockfish from San Juan Channel, in the San Juan Archipelago, a cluster of islands in northwest Washington State (Latitude 48° 33' N, Longitude 123° 00' W) (Figure 1). The San Juan Archipelago is located at the center of the Salish Sea. The majority of collections were from Shady Cove, San Juan Island, and Point George, Shaw Island, two sites near the center of San Juan Channel with abundant rockfish habitat (high relief rock: Palsson et al. 2009), where bottomfishing has been excluded for 20 years (WAC 1998). These sites have high rockfish abundance relative to other sites within San Juan Channel, maximizing my catch

per effort. Laboratory testing took place at the University of Washington's Friday Harbor Laboratories, in Friday Harbor, WA.

Fish collection and handling

I tested the anesthetization and lavage procedures on three copper rockfish individuals in the lab prior to field work. In this preliminary laboratory testing I determined that 100 mg L⁻¹ buffered tricane methanesulfonate (MS-222) in seawater was an adequate dosage to induce rapid anesthetization followed by rapid recovery upon immersion in clean seawater. I inserted a plastic tube into the throat of an anesthetized fish to hold the esophagus open (16-28 mm diameter, depending on the size of the fish). I then inserted the hose of a hand-pumped garden sprayer filled with clean seawater through the center of the larger tube and into the stomach of the fish to flush out stomach contents. Forceps were used to extract larger prey items lodged in the stomach or esophagus. The inserted tubes and forceps used during lavage were adequate to scan the stomach for any food items remaining after flushing with the sprayer.

Following preliminary testing in the laboratory I allowed the three test subjects to recover in large flow-through aquaria for three days. The fish were observed twice daily to monitor for immediate or long-term injury from the procedure. Although the test subjects were provided with unlimited prey (coonstripe shrimp, *Pandalus danae*) of varying sizes, I did not track prey disappearances and I did not directly observe any predation in the lab following the lavage testing.

All rockfish were collected between October and December 2010. I captured fish by angling using barbless hooks to minimize injury to the fish. In an effort to reduce the risk of

barotrauma to the fish, I targeted fish in water shallower than 18 m. Upon hooking a rockfish, it was reeled rapidly and steadily to the surface and placed in an anesthetic solution of 100 mg L⁻¹ MS-222 in seawater, buffered with sodium bicarbonate to ambient pH. Fish remained in the anesthetic until unresponsive to handling, about 5-7 minutes. After lavage, fish were placed in a cooler filled with clean seawater to recover from anesthesia, and then returned to the original capture depth using an inverted weighted basket (Theberge & Parker 2005). I did not observe any mortality or significant injury in the laboratory subjects or in any subjects handled in the field. Although I was unable to track the fish after release, copper rockfish have very high survival rates with hook and line capture followed by recompression at depth (Hannah & Matteson 2007). In total, I captured three copper rockfish for laboratory testing, and 37 rockfish, measuring 235-351 mm total length (TL), to study diet.

Stomach contents were preserved in 95% ethanol and identified in the laboratory to the lowest taxonomic level possible using Kozloff (1996), and Eschmeyer and Herald (1999). I counted the prey items, patted them dry with paper towels, and weighed them. These data were used to calculate frequency of occurrence of diet items (O_i), proportion by number (N_i), and proportion by blotted wet weight (W_i) (Chipps & Garvey 2007).

Statistical analysis

Because copper rockfish are known to shift their diet as they grow, I divided the fish into into two size groups: 200-299 mm ($n = 19$) and 300+ mm ($n = 10$) TL, following Patten's (1973) and Prince & Gotshall's (1976) size divisions (Figs. 2-3), and compared diets between these two groups. I used abundance- and incidence-based species rarefaction (Chao1 and Chao2) to

compare the diet breadth of the two size classes. I also compared individual diet richness, diversity (Shannon-Wiener H'), and abundance between the two size classes using Welch's t-tests.

Previous studies of copper rockfish diet from the Salish Sea, California, and Alaska presented population-level diet data, rather than diet information from individual fish, reducing the number of sample units to one per study. Thus I was unable to perform formal statistical comparisons of prey assemblages between the studies (e.g. MANOVA and similar tests: Chipps & Garvey 2007). Instead I used visual comparisons between studies to explore species-level prey differences by location, time, and collection method. The taxonomic resolution reported by previous studies varied considerably, and I adjusted my taxonomic resolution to match in each comparison. I also used non-metric multidimensional scaling, with Bray-Curtis dissimilarity, to visualize community-level prey assemblages between the studies. I used N_i as the index for comparing between studies in this ordination, as this was the index shared by the majority of studies.

Statistical analyses were performed using the 'fossil' (Vavrek 2015) and 'vegan' (Oksanen et al. 2015) packages in R, v. 3.1.2 (R Core Team 2014).

RESULTS

Twenty-nine of the 37 rockfish I sampled had non-empty stomachs. Demersal crustaceans were the most frequently observed diet item, occurring in 86% of non-empty copper rockfish stomachs (Fig. 3a, Table S1). Shrimp, predominately *P. danae*, but also *P. eous*,

Crangonidae and *Spirontocaris* sp., were the most commonly observed crustacean species. Other demersal crustaceans observed in the rockfish diet were small-bodied crabs: *Scyra acutifrons*, *Lophopanopeus bellus*, *Petrolisthes* spp. and *Glebocarcinus oregonensis*. The next most frequently observed category of prey was teleost fishes (24%). Only two individual teleost prey items were identifiable to species: one *Rhinogobiops nicholsii*, the blackeye goby, and one small *Sebastes* sp. in a separate sample. Other teleost prey were not identifiable, but their size and shape suggest that some of them may have been pelagic fishes such as Pacific sand lance, *Ammodytes hexapterus*, a common prey fish species in the San Juan Islands (Fresh, 1979, Beaudreau and Essington, 2007). Other common prey items were errant polychaete worms (21% occurrence) and gammarid amphipods (10% occurrence).

A total of 116 prey items were collected from all rockfish stomachs. Demersal crustaceans were the most numerically abundant group, composing 65% of all prey items consumed, with shrimp alone accounting for 56% of all prey items (Fig. 3b). Errant polychaetes were the second most common prey item (15%N). Teleost fishes accounted for only 7% of all prey items.

Copper rockfish had between 0.01 and 5.99 g of prey in their stomachs (mean = 1.90 g, median = 1.26 g). Demersal crustaceans were the primary constituent of this mass, accounting for 77% of the total mass consumed (Fig. 3c, Table S1). Shrimp accounted for 59% of total mass consumed, and Teleosts 17%.

All prey species categories except *Sebastes* sp. were observed in the smaller size class (200-299 mm), but the larger fish (300+ mm) consumed fewer species of prey. Large fish were less likely to consume crabs and some species of shrimp (*Spirontocaris* sp. and *P. eous*). The occurrence and abundance of the remaining crustacean prey in large fish diets was similar to that

in the smaller fish: unidentified shrimp (70%O and 38%N in large fish vs. 63%O and 34%N in smaller fish), *P. danae* (20%O and 6%N vs. 21%O and 7%N), and Crangonidae (10%O and 4%N vs. 11%O and 4%N). Mass contribution of *P. danae* was greater in large fish than in smaller fish (38%M vs. 18%M, respectively). There was greater occurrence, abundance and mass contribution of unidentified teleost prey in large fish diets (30%O, 8%N and 20%M in large fish vs. 11%O, 3%N and 4%M in smaller fish). *Sebastes* sp. was only observed in one large copper rockfish stomach, while *Rhinogobiops nicholsii* was only observed in one smaller copper rockfish stomach. Polychaete worms were much more frequent and abundant in large fish diets than in small fish diets (40%O and 29%N vs. 11%O and 4%N, respectively) (Figs. 3d-i).

Collectively, the smaller fish in my study consumed a greater richness of prey items than larger fish did ($S_{\text{obs}} = 18$ and 8, respectively). Although the number of individuals sampled in each size class differed, species rarefaction estimators confirm that smaller fish collectively consumed significantly more different prey types than larger fish (S_{Chao1} 95% confidence interval = 18.9-22.1 and 7.8-8.7, S_{Chao2} 95% CI = 19.0-22.2 and 9.1-15.9, respectively). On an individual basis, fish in both size classes showed comparable diet richness, diversity and number of prey items consumed. Welch's t-tests revealed no significant difference in individual diet richness between smaller and larger fish (average $S = 2.5$ and 2.3, respectively, $t = 0.3999$, $df = 19.41$, $P = 0.69$), Shannon diversity (average $H' = 0.73$ and 0.58, $t = 0.6735$, $df = 18.29$, $P = 0.51$), and number of prey items consumed (average number = 3.6 and 4.8, $t = -0.97$, $df = 14.19$, $P = 0.35$).

Diet comparisons

Several authors (Prince & Gotshall 1976, Moulton 1977, Miller et al. 1977, Rosenthal et al. 1988, Murie 1995) reported numerical abundance for all prey items found in copper rockfish diets. My results showed much higher abundance of shrimp than any of the other studies (Fig. 4-5). Pelagic crustaceans (euphausiids, mysids, leptostracans, and crustacean larvae), gammarid and hyperiid amphipods, cancrid crabs, and pelagic fishes (*Am. hexapterus*, *Allosmerus elongatus*, *Clupea harengus*, *C. pallasii*, and *Engraulis mordax*) all were lower in abundance in my study than in former studies.

Seasonal diet comparison. — Copper rockfish are known to change their feeding habits throughout the course of the year. Murie's (1995) findings showed a transition from numerous pelagic fish in the diet in January-March, towards a diet dominated by pelagic crustaceans through the spring and summer, and finally a demersal and pelagic crustacean diet in the fall. The preponderance of pelagic fishes (all Pacific herring, *C. harengus*) in the winter diet may indicate opportunistic feeding on the large herring runs in the Salish Sea in January-April (Bargmann 1998).

Murie's (1995) was the only study that reported copper rockfish diet information specifically from the fall season, the same time of year my sampling occurred. Comparisons of broad diet categories show that the frequency of occurrence of prey items in the diet of modern copper rockfish in San Juan Channel and individuals from historic studies in Saanich Inlet are similar (Fig. 6a). Both populations also consumed approximately the same relative numbers (N_i) of demersal crustaceans and demersal and pelagic fishes, while historic individuals consumed a much greater number of pelagic crustaceans than did modern individuals (34%N vs. 4%N) (Fig. 6b). Murie reported the identity of the demersal crustacean prey to be the squat lobster, *Munida quadrispina*, and shrimp. The demersal crustacean prey I observed were primarily shrimp, and I

did not observe any squat lobsters. Teleosts, especially pelagic fishes, accounted for the majority of diet mass in Murie's study, but were a small component in mine (66%M vs. 17%M), while the percent mass of demersal crustaceans in Murie's study was less than half that in mine (37%M vs. 77%M) (Fig. 6c).

Size-specific diet comparisons. — Three studies (Patten 1973, Prince & Gotshall 1976, Murie 1995) reported copper rockfish diet information from specific size classes that overlap the size range from my study (Table 1).

Patten (1973) only reported frequency of occurrence data, and very few specific diet categories overlap between his and the current studies, making detailed comparisons difficult. Patten reported O_i for two very broad prey categories: teleosts and crustaceans. For rockfish between 200-299 mm Patten reported roughly equal occurrence of teleost and crustacean prey (56%O and 63%O), while I saw low occurrence of teleosts and very high occurrence of crustaceans (16%O and 95%O) (Fig. 7a). For rockfish ≥ 300 mm Patten reported an increased occurrence of teleost prey and a slight drop in crustacean prey occurrence (81%O and 56%O). I saw a similar pattern with the larger size class of rockfish, with teleost occurrence rising and crustacean occurrence dropping (40%O and 80%O), although my results still showed a much greater dominance of crustacean over teleost prey (Fig. 7b). Despite the difference in crustacean contribution to copper rockfish diets between Patten's and my studies, the identities of the crustaceans Patten recorded were very similar to my findings, composed primarily of *Pandalus danae*, other shrimp species, and small crabs.

Prince and Gotshall (1976) reported numerical abundance (N_i) for 10 prey taxa for their largest size class, which I combined into 7 taxa for comparison to my data (Fig. 7c). The rockfish in Prince and Gotshall's study consumed far fewer shrimp (14%N in Prince and Gotshall vs.

62%N in my study), but consumed many more crabs (30%N vs. 15%N) and gammarid amphipods (17%N vs. 3%N). The crabs in Prince and Gotshall's study were primarily juvenile Dungeness crabs (*Metacarcinus magister*), while the crabs I observed included sharp-nosed, porcelain, black-clawed, and pygmy rock crabs (*S. acutifrons*, *Petrolisthes* sp., *L. bellus*, and *G. oregonensis*). Teleost prey was almost three times as abundant in Prince and Gotshall's study as in mine (13%N vs. 4%N). Prince and Gotshall reported percent by volume (V_i) of copper rockfish prey items, rather than percent by mass, but we can make rough comparisons between these metrics if we assume that the different prey types have roughly similar densities. Despite this measurement difference, the comparison between V_i and my M_i mirrored the comparison of N_i : I observed much greater contribution of shrimp to rockfish diet, and lower contribution of crabs and teleosts (Fig. 7d).

Murie (1995) reported frequency of occurrence, numerical abundance, and percent mass for broad diet categories of large copper rockfish. Occurrence, abundance, and mass of demersal crustacean prey were lower in Murie's study than in mine (53%O vs. 84%O; 27%N vs. 62%N; 21%M vs. 77%M), while all three metrics were higher in Murie's study for pelagic fish prey (50%O vs. 20%O; 20%N vs. 6%N; 76%M vs. 12%M) (Fig. 7e-g). Occurrence, abundance and mass of demersal fishes were low and comparable between the two studies. Although occurrence and mass of pelagic crustaceans were low and comparable between the two studies, abundance was considerably higher in Murie's study than in mine (60%N vs. 4%N).

DISCUSSION

Diet

The copper rockfish I sampled are generalist predators, consuming prey from 19 different categories. Shrimps and other crustaceans were the most numerically dominant prey items, occurred in almost all samples, and constituted most of the biomass consumed.

The similarity in individual-level prey richness and diversity between the two size classes of fish in this study is likely due to the low number of prey individuals found in each rockfish stomach. The larger population-level diet richness in smaller fish coupled with comparable individual-level richness, diversity, and prey items per individual indicates that both size classes tend to have the same low number of prey items in their stomachs, but smaller fish recognize more taxa as prey. The non-lethal nature of gastric lavage allows for tagging and recapture of individuals so that future studies of copper rockfish diet could determine if the broader population-level prey richness of smaller fish is due to individual-level preferences that converge as the fish grow, or if all small fish consume a wide range of prey but narrow their diet as they grow.

Although none of the prey species I observed in this study are novel, there is marked difference between these and previous findings in the relative contribution of prey items. Demersal crustaceans (particularly shrimp) were over-represented, and fishes (particularly pelagic fishes) were under-represented in this study compared to previous studies. Based on these results, I am unable to determine the underlying cause of the diet differences I observed, but I posit that this difference more likely reflects differences in prey availability than changing rockfish preferences. Many of the dominant prey items in previous studies that I did not observe here were locally abundant at the time of sampling (squat lobster and herring in Saanich Inlet

(Murie 1995), juvenile Dungeness crab in Humboldt Bay (Prince & Gotshall 1976)). Although I have not observed squat lobsters, herring, or juvenile Dungeness crabs in the fall in San Juan Channel, I regularly observe numerous shrimp (see Ch. 2). This implies that copper rockfish opportunistically prey on locally or seasonally abundant species, while relying on different prey items in other locations or at other times of year. Interestingly, the two studies of copper rockfish diet in the 1970s, also from the San Juan Archipelago, showed that the fish preyed on crustaceans in approximately equal numbers to those in the current study, but these crustaceans were primarily amphipods and other small crustaceans, with far fewer shrimp (Moulton 1977, Miller et al. 1977), perhaps suggesting that shrimp were less available (or small crustaceans were more available) in the past. Despite the low contribution of teleost prey to overall copper rockfish diet, both pelagic (e.g. juvenile gadids, sand lance) and demersal fishes (e.g. sculpins, gobies) are common in San Juan Channel (Ch. 2), and this low contribution of teleost prey could be due to low encounter rates or capture success. It is important to note both the spatial and temporal limitations of my study, and hence my results may not be indicative of the species as a whole.

Several species of demersal rockfishes besides coppers exist in the Salish Sea, and also feed on demersal crustaceans, including shrimp (Washington et al. 1978, Hueckel & Stayton 1982, Murie 1995, Eschmeyer & Herald 1999, Love et al. 2002, Yamanaka et al. 2006). Quillback rockfish diet overlaps copper rockfish to the greatest degree (Murie 1995); this species is the most commonly observed sympatric rockfish in San Juan Channel (Appendix A), and thus presents the most likely competitor. However, because rockfish populations are at historically low levels, interspecific competition is likely also low. In addition, although the diets of different rockfish species appear to overlap, niche overlap is likely much lower, reducing direct

competition between these species. Quillback and other rockfishes are typically found at greater depths than coppers (Richards 1986, Eschmeyer & Herald 1999, Love et al. 2002). Quillbacks also separate from coppers temporally, feeding primarily at midday, while coppers tend to feed at dawn and dusk (Murie 1995).

Lavage

The standard method of diet sampling, stomach excision, ensures a full accounting of the stomach contents (Bowen 1996), but the use of lethal methods should be minimized with Salish Sea rockfishes, given the depleted state of their populations. Instead, gastric lavage appears to be a viable alternative that allows for sampling of stomach contents while allowing the fish to be returned alive to the area of capture. Because of its non-lethal nature, lavage could allow researchers to track the feeding behavior of both populations and individuals through time, providing information on how individual preference drives rockfish predation habits. However, if handling and lavage affects feeding behavior, a fish recaptured too soon may not give an accurate picture of diet, and care should be taken when using lavage or other non-lethal methods for diet estimation when the possibility of recapture exists.

Although holding the esophagus open with a plastic tube allowed us to visually assess the anterior portion of rockfish stomachs for any prey remaining after lavage, I was not able to confirm full evacuation by stomach excision. The absolute efficacy of this method remains uncertain for rockfish, but has proven to be complete with many species (reviewed in Kamler & Pope 2001), including lingcod, a species with substantial diet overlap (Beaudreau & Essington 2007). Large or spiny prey are the likeliest candidates for food items that would not be recovered

through lavage (Foster 1977, Hartleb & Moring 1995), but I did recover numerous shrimp and crabs with legs and rostral spines still intact.

Gastric lavage does have disadvantages that must be considered in the development of a diet-monitoring plan. The long handling time in the field restricts the number of individuals that can be sampled, as evidenced by the small sample size I was able to use for this study, unlike large-scale capture methods like trawling and euthanasia (e.g. Brodeur & Percy 1984). The restriction of capture depth to less than 18 m may affect diet results, as many rockfish species are known to increase in size with increasing depth (Richards 1986), and diet is known to change with size (Patten 1973). In addition, the most at-risk rockfish species in the Salish Sea (bocaccio, canary, and yelloweye rockfish) are most abundant at much greater depths (~50m and deeper) (Moser 1996, Love et al. 2002, Johnson et al. 2003), so shallow hook-and-line capture, gastric lavage, and live release may not be possible for these species. Finally, the physical force of lavage may damage stomach contents more than stomach excision would, leading to bias against delicate or more rapidly digested prey (Foster 1977).

Conclusion

The differences in diet between my results and those from previous studies are likely due in part to a difference in prey availability. Juvenile Dungeness crabs, Pacific herring, and squat lobsters were not present in great numbers in San Juan Channel in the fall of 2010 when my sampling occurred. Other possible reasons for the differences in diet may be different food preferences at the individual or population level, or a shift in the food preferences of copper rockfish since the previous studies were conducted. Accurate diet information is needed to fully

identify the role of copper rockfish in benthic food webs. My results indicate a difference in rockfish diet from previous studies, and suggest the need for routine monitoring to track future changes, along with measures of prey availability. Given that rockfish populations are at risk in the Salish Sea, non-lethal methods, such as gastric lavage, are important for future studies.

Table 1. Studies included in diet comparisons, with sampling location, seasons and years sampled, and total length (TL) size ranges included in comparisons.

Study	Location	Seasons sampling occurred	Size ranges included in comparisons (mm TL)
(Patten 1973)	Puget Sound, WA	Autumn-Spring, 1963-1968	200-299, ≥ 300
(Prince & Gotshall 1976)	S. Humboldt Bay, CA	Year-round, 1971-1972	220-300
(Moulton 1977)	San Juan Islands, WA	Spring-Summer, 1976	Not reported
(Miller et al. 1977)	San Juan Islands, WA	Summer (?), 1974-1976	Not reported
(Rosenthal et al. 1988)	Gulf of Alaska, AK	Summer, 1980-1982	Not reported
(Murie 1995)	Saanich Inlet, BC	Year-round, 1986-1990	≥ 250
Present study	San Juan Channel, WA	Autumn, 2010	230-350

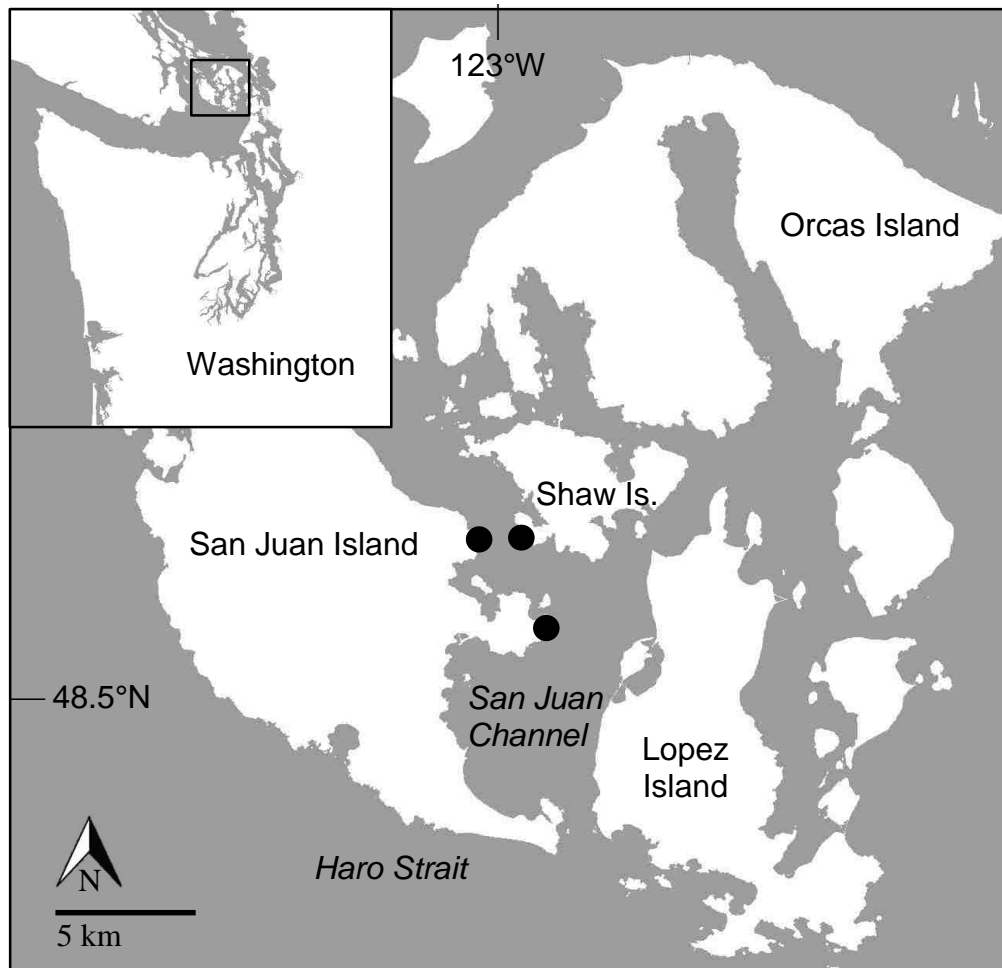


Figure 1. Map of the sampling region for copper rockfish in San Juan Channel. A total of 40 individuals (3 for preliminary methods testing, 37 for diet analysis) were captured from the three areas denoted by black circles. Map inset in upper-left corner shows the location of the San Juan Archipelago in Washington.

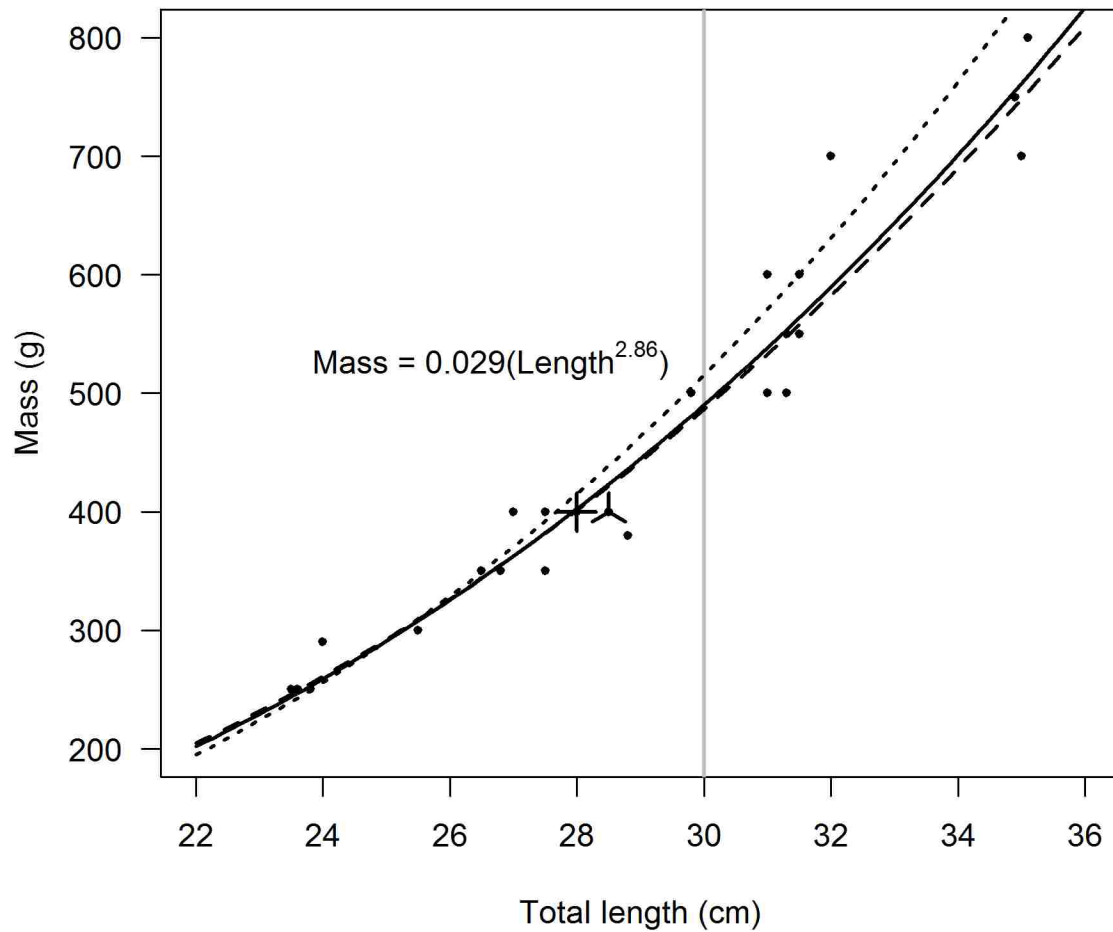


Figure 2. Length-mass relationship of copper rockfish with non-empty stomachs. Rockfish were divided into small (<299 mm total length) and large (≥ 300 mm) size categories (vertical grey line) (Patten 1973, Prince & Gotshall 1976). Each whisker around a point indicates a duplicate value. The length-mass relationship of the fish sampled in this study (solid curve and equation) is very similar to that observed in previous studies (dashed line: Wildermuth 1983, dotted line: Lea et al. 1999).

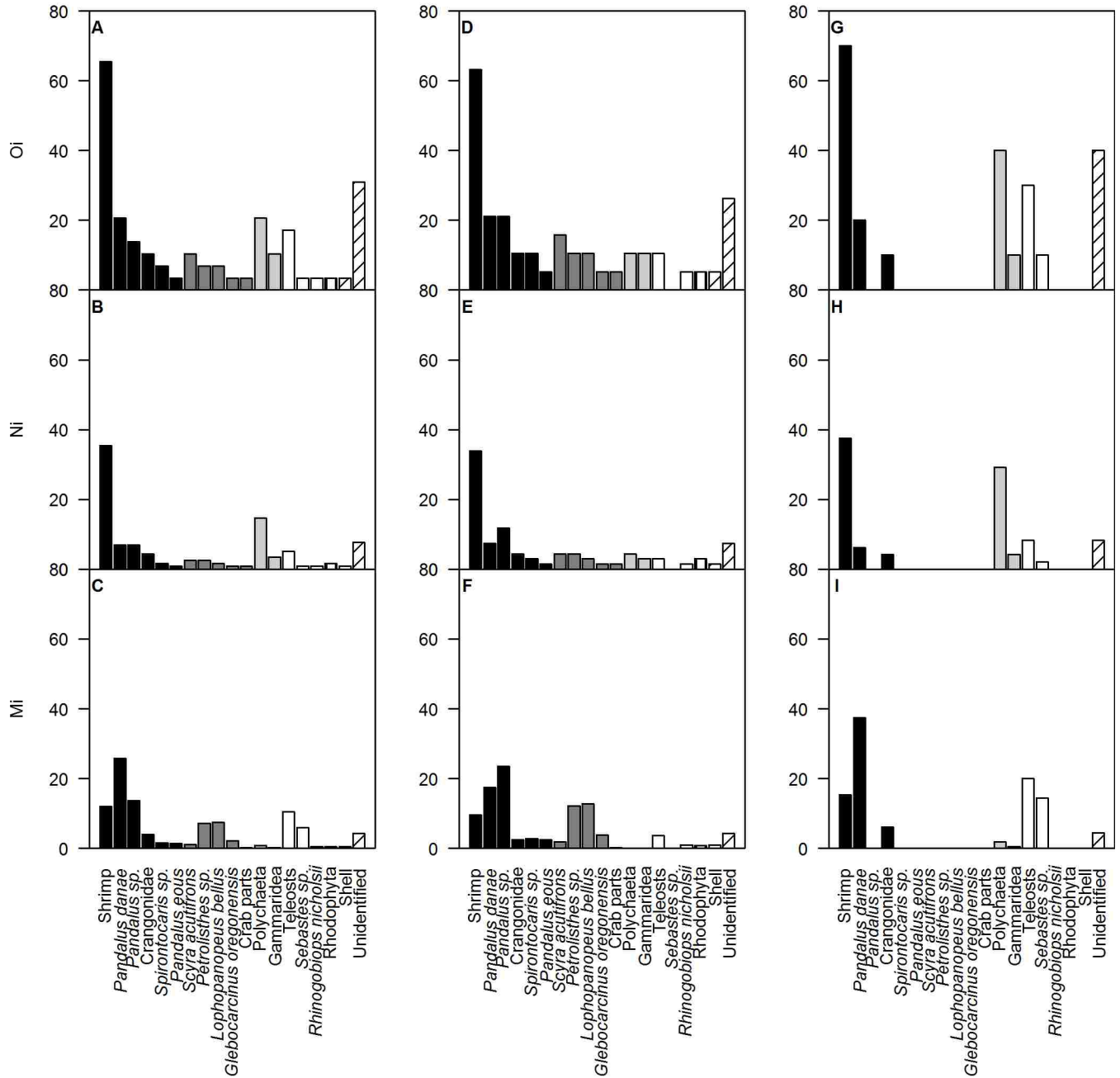


Figure 3. Frequency of occurrence (O_i), numerical abundance (N_i), and percent mass (M_i) of copper rockfish prey items from all individuals (A-C), individuals <299 mm total length ($n = 19$) (D-F) and individuals ≥ 300 mm ($n = 10$) (G-I). Shrimps were the most important source of prey for fish in both size ranges. Teleost prey was more important in the diet of larger fish than in that of smaller fish. Collectively, smaller fish consumed a greater diversity of prey types. Prey categories are shrimps (black bars), crabs (dark grey bars), other invertebrates (light grey bars), teleosts (empty bars), algae (vertically striped bars), and other items (hatched bars).

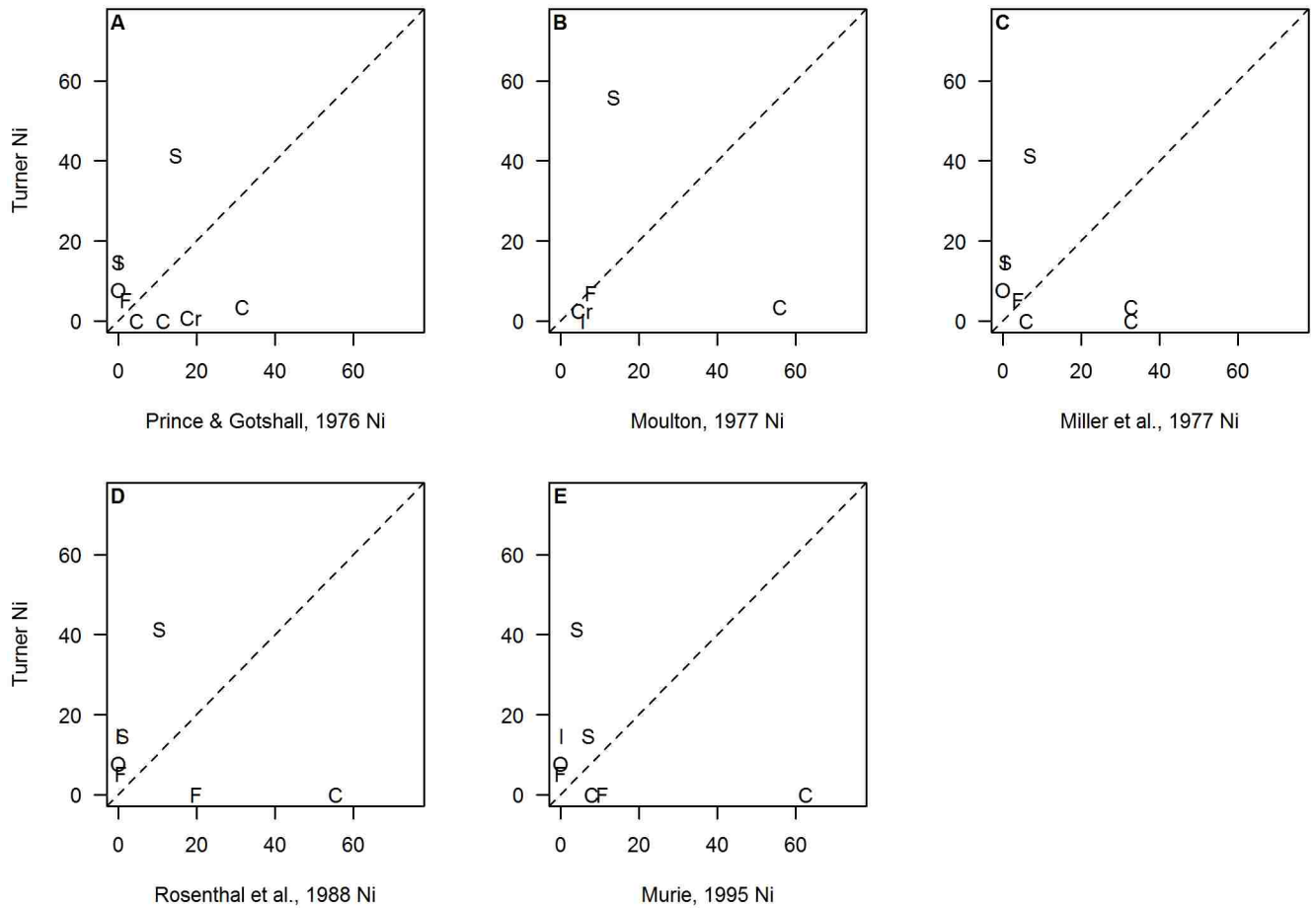


Figure 4. Comparison of numerical abundance (N_i) of prey items between five studies of copper rockfish diet and the current study (A: Prince & Gotshall 1976, B: Moulton 1977, C: Miller et al. 1977, D: Rosenthal et al. 1988, E: Murie 1995). Shrimps were much more abundant, and pelagic crustaceans, small demersal crustaceans, and fishes were less abundant, in my study than in previous studies. Dashed 1:1 line represents equal dietary importance in both studies. Only prey items accounting for >4.5%N in either my or the comparison study were included in this figure. Multiple symbols of the same type in one graph indicate different species from the same broader category. C: other crustaceans, Cr: crabs, F: fishes, I: other invertebrates, O: other, S: shrimps.

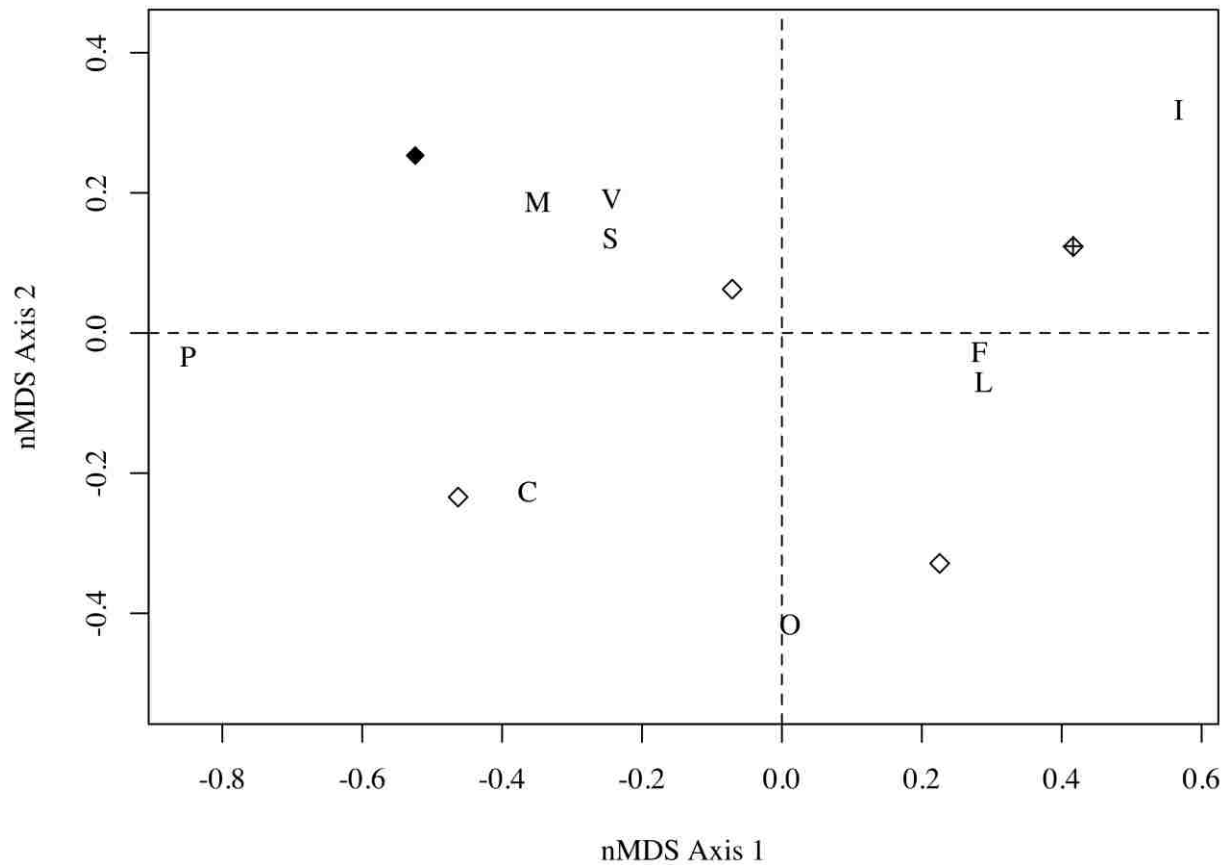


Figure 5. Non-metric multidimensional scaling plot of prey proportion by number from six copper rockfish diet studies. Open diamonds indicate three past studies (Prince & Gotshall 1976, Moulton 1977, Murie 1995), the crossed diamond indicates two separate past studies that mapped to the same ordination location (Miller et al. 1977, Rosenthal et al. 1988), and the filled diamond indicates the present study. Letters correspond to prey categories, and their position indicates an increase in the abundance of that prey category in the direction of the letter from the origin (dashed lines). Prey categories are based on those in Moulton (1977). C: Cancrid and Grapsid crabs, F: Fishes; I: Inorganic prey (rocks and shells); L: Larval and other small crustaceans (zoea, megalopae, amphipods, cumaceans, isopods, pelagic, parasitic, and unidentified crustaceans); M: Majid crabs; O: Other demersal crustaceans (Pinnotherid, Porcellanid, and unidentified crabs, and squat lobsters); P: Plants (eel grass and algae); S: Shrimp; V: Other invertebrates (annelids, barnacles, cnidarians, echinoderms, molluscs, nematodes, and tunicates).

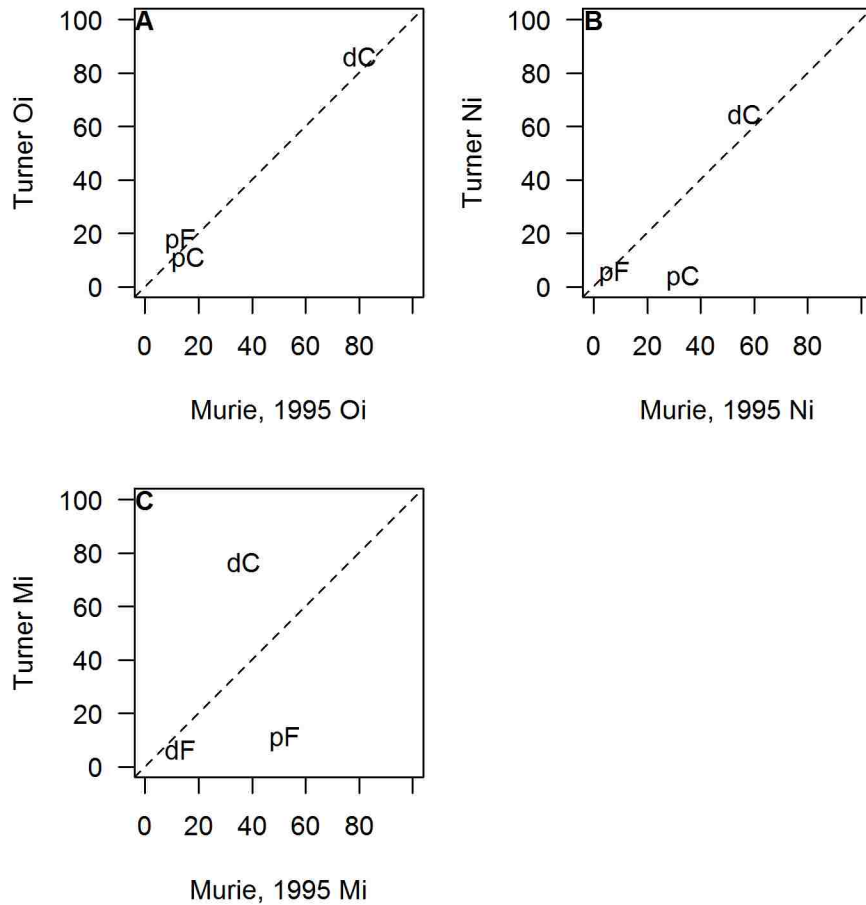


Figure 6. Comparison of frequency of occurrence (O_i) (A), numerical abundance (N_i) (B), and percent mass (M_i) (C) of copper rockfish prey items between Murie's (1995) fall season sampling and the current study. Dashed 1:1 line represents equal dietary importance in both studies. The occurrence of demersal and pelagic crustaceans and fishes are similar between the studies. The abundance of pelagic crustaceans was much higher in the 1995 study than in ours. The mass contribution of demersal crustaceans was much higher, and that of pelagic fishes was much lower, in my study than in Murie's. Only prey items accounting for >7%N in either my or the comparison study were included in this figure. dC: demersal crustaceans, dF: demersal fishes, pC: pelagic crustaceans, pF: pelagic fishes.

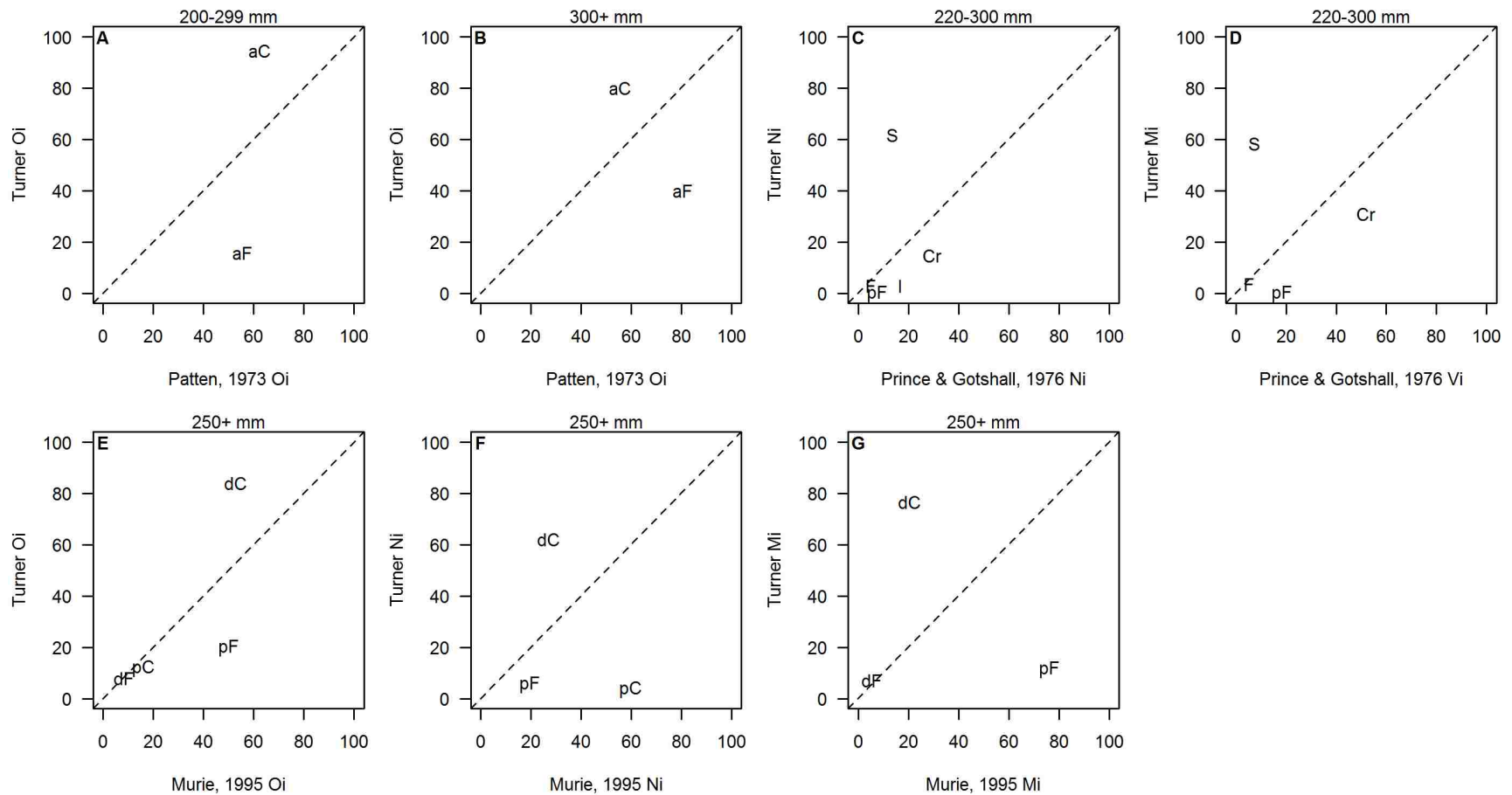


Figure 7. Comparison of size-specific copper rockfish diet between three historical studies and the current study. Patten (1973) measured frequency of occurrence (O_i) for fish between 200-299 mm (A) and 300 mm and larger (B). Prince and Gotshall (1976) measured numerical abundance (N_i) (C) and percent volume (V_i) (D) for fish from 230-300 mm. Murie (1995) measured O_i (E), N_i (F), and percent mass (M_i) (G) for fish 250 mm and larger. Dashed 1:1 line represents equal dietary importance in both studies. Crustaceans, especially shrimps and other demersal crustaceans, contributed more to the diet of rockfish in the current study than to that from previous studies. Only prey items accounting for >5% importance in either my or the comparison study were included in this figure. aC: all crustaceans, aF: all fishes, Cr: crabs, dC: demersal crustaceans, dF: demersal fishes, F: other fishes, I: other invertebrates, pC: pelagic crustaceans, pF: pelagic fishes, S: shrimps.

Table S1. Abundance of prey items in the diets of 29 copper rockfish.

Prey category	Prey species/group	Rockfish ID Code														
		A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
Shrimp	Crangonidae						2	1								
	<i>Pandalus danae</i>		2								2					
	<i>Pandalus eous</i>															
	<i>Pandalus</i> sp.	1					5								1	1
	Shrimp <i>Spirontocaris</i> sp.			3		1			3		2	1	3	2	1	
Crabs	Crab parts				1											
	<i>Glebocarcinus oregon.</i>						1									
	<i>Lophopanopeus bellus</i>					1										
	<i>Petrolisthes</i> sp.	1						2								
	<i>Scyra acutifrons</i>	1											1			
Other inverts	Gammaridea	1							1							
	Polychaeta															1
Teleosts	<i>Rhinogobiops nicholsii</i>										1					
	Sebastes sp.															
	Teleosts								1							
Algae	Rhodophyta						2									
Other	Shell							1								
	Unidentified	1		1						1						1

Table S1, continued.

Prey category	Prey species/group	Rockfish ID Code														
		P	Q	R	S	T	U	V	W	X	Y	Z	AA	BB	CC	
Shrimp	Crangonidae										2					
	<i>Pandalus danae</i>	1		1					1	1						
	<i>Pandalus eous</i>	1														
	<i>Pandalus</i> sp.															
	Shrimp <i>Spirontocaris</i> sp.	1	1	1			1	1	1	4	1	2	4	8		
Crabs	Crab parts															
	<i>Glebocarcinus oregon.</i>															
	<i>Lophopanopeus bellus</i>		1													
	<i>Petrolisthes</i> sp. <i>Scyra acutifrons</i>					1										
Other inverts	Gammaridea													2		
	Polychaeta	2							3		3			2	6	
Teleosts	<i>Rhinogobiops nicholsii</i>															
	Sebastes sp.														1	
	Teleosts	1			2			1	1							
Algae	Rhodophyta															
Other	Shell															
	Unidentified	1						1	1		1			1		

Table S2. Mass of prey items (g) in the diets of 29 copper rockfish.

Prey category	Prey species/group	Copper Rockfish ID Code														
		A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
Shrimp	Crangonidae						0.312	0.484								
	<i>Pandalus danae</i>		5.99								1.2					
	<i>Pandalus eous</i>															
	<i>Pandalus</i> sp.	0.91					3.825								0.8	2.0
	Shrimp <i>Spirontocaris</i> sp.			0.2		0.075		0.403 0.295			0.1	0.1	0.2	0.2	0.1	
Crabs	Crab parts				0.08											
	<i>Glebocarcinus oregon.</i>						1.22									
	<i>Lophopanopeus bellus</i>					3.42										
	<i>Petrolisthes</i> sp.	1.68						2.242								
	<i>Scyra acutifrons</i>	0.1											0.2			
Other inverts	Gammaridea	0.01							0.011							
	Polychaeta															0.01
Teleosts	<i>Rhinogobiops nicholsii</i>										0.3					
	Sebastes sp.															
	Teleosts								1.075							
Algae	Rhodophyta						0.247									
Other	Shell							0.306								
	Unidentified	0.01		1.23						0.1						0.01

Table S2, continued.

Prey category	Prey species/group	Copper Rockfish ID Code													
		P	Q	R	S	T	U	V	W	X	Y	Z	AA	BB	CC
Shrimp	Crangonidae										1.4				
	<i>Pandalus danae</i>	1.0		0.3					2.6	3.12					
	<i>Pandalus eous</i>	0.8													
	<i>Pandalus</i> sp.														
	Shrimp <i>Spirontocaris</i> sp.	0.1	0.2	0.2			0.01	0.01	0.6	1.222	0.8	0.7	1	0.4	
Crabs	Crab parts														
	<i>Glebocarcinus oregon.</i>														
	<i>Lophopanopeus bellus</i>		0.7												
	<i>Petrolisthes</i> sp. <i>Scyra acutifrons</i>					0.3									
Other inverts	Gammaridea													0.1	
	Polychaeta	0.01							0.1		0.1			0.01	0.2
Teleosts	<i>Rhinogobiops nicholsii</i>														
	Sebastes sp.														3.3
	Teleosts	0.1			2.0			2.4	0.2						
Algae	Rhodophyta														
Other	Shell														
	Unidentified	0.02						0.5	0.2		0.1			0.2	

CHAPTER 2

Top-down control of prey by predatory fishes in the San Juan Archipelago

ABSTRACT — Top-down community control is common in temperate marine food webs. The historic overharvest of predatory bottomfishes in the San Juan Archipelago, WA, and their more recent partial recovery due to spatial fishery closures and reduced bag limits, allowed us to test the effects of predator abundance and biomass on prey populations. The common predatory bottomfishes in this system are lingcod, rockfishes, greenling, and several species of large cottids. The prey of these fishes include shrimp, crabs, sculpins, gobies and other small fishes. Between 2010 and 2012 I surveyed predator and prey populations annually, and conducted two rounds of experimental exclusions of predators in the rocky subtidal habitats of San Juan Channel. Shrimp abundance was negatively correlated with predator biomass in channel-wide surveys. Both shrimp and prey fishes were more abundant inside cages than in areas open to predators. These results support the hypothesis of top-down population control in the rocky subtidal of San Juan Channel. Despite the strong trophic link between bottomfish and shrimp, I did not observe evidence of further predator effects at lower trophic levels, likely due to the broad diet of shrimp. Concurrent with the decline in rockfish populations over the last four decades has been an apparent increase in prey (sculpin) and competitor (greenling) abundance.

INTRODUCTION

Predation is a major controller of marine community composition and diversity (Sih et al. 1985, Shurin et al. 2002). Predators control zooplankton populations in the pelagic environment at local or seasonal scales (Micheli 1999, Daewel et al. 2013), limit the vertical distribution of prey species in the intertidal (Connell 1961, Paine 1966), prevent the monopolization of space by competitive dominants (Menge 1976, Menge & Sutherland 1976, Elahi & Sebens 2012), and can trigger major community shifts in the subtidal zone (Estes et al. 1998).

Human predation can also exert very effective top-down control, altering marine communities. Because high trophic-level fishes are often the species first targeted by fisheries (Pauly et al. 1998, Essington et al. 2006), impacts on prey species can be expected in areas where extraction is high. Natural experiments (*sensu* Diamond 1983) comparing communities before and after fishing effort began or ended, or in areas open and closed to fishing, have shown strong impacts from changes in predator abundance. Fishing decreased the abundance of lobsters and predatory fishes in California, the Mediterranean, and New Zealand, resulting in increases in urchin populations (Shears & Babcock 2002, Behrens & Lafferty 2004, Guidetti 2006). Heavy fishing on cod and other demersal fishes in New England released benthic crustacean populations to increase in abundance (Frank et al. 2005).

The predatory fishes in rocky subtidal habitats of the San Juan Archipelago, WA, are primarily lingcod (*Ophiodon elongatus*), several species of rockfish (*Sebastes* spp.) and kelp greenling (*Hexagrammos decagrammus*). Although killer whales (*Orcinus*

orca), Steller sea lions (*Eumetopias jubatus*), harbor seals (*Phoca vitulina*), and river otters (*Lontra canadensis*) sometimes consume these species, these fishes form only small portions of the mammals' diets (Ford & Ellis 2006, Lance et al. 2011, 2012, Buzzell et al. 2014) and thus their populations are unlikely to be controlled by such mammals. Sea otters (*Enhydra lutris*) were absent from the San Juan Archipelago for the duration of this research.

The demersal predatory fishes in this system have wide diet breadths, but all include shrimp and other benthic crustaceans in their diets. Lingcod are primarily piscivores, but Pandalid shrimp also compose a sizeable fraction of their diets (Beaudreau & Essington 2007). Rockfish also feed on fishes, but consume a much higher proportion of benthic crustaceans, especially Pandalid shrimp (Murie 1995, Ch. 1). Greenling feed primarily on benthic invertebrates, especially crustaceans (Moulton 1977, Miller et al. 1977, Simenstad et al. 1979).

Recreational fishing for lingcod and rockfish in the Salish Sea has been high over the last several decades (Palsson et al. 2009). As a result, populations of these demersal predators are now greatly reduced from pre-fishing levels, and three rockfish species are listed as Threatened or Endangered in the Salish Sea (NMFS 2010). Recent actions to recover rockfish populations have included sequential reductions in catch limits, spatial closures, and ultimately the complete closure of rockfishing in Washington's inland waters (Palsson et al. 2009, WAC 2010).

The reduction of demersal predatory fishes, and their subsequent partial recovery in closed fishing areas (Eisenhardt 2001) gave us the opportunity to explore the effects of these predators on their prey populations. Previous work in nearby Howe Sound and

eastern Georgia Strait has provided evidence to suggest that rockfish may control certain shrimp populations (Frid & Marliave 2010). I used surveys of predator and prey species at sites throughout San Juan Channel to see if prey abundance was negatively correlated with predatory fishes at a regional scale. I also used predator exclusion cages to experimentally test if predators can drive shrimp and other prey species abundance at a small spatial scale.

METHODS

Community surveys

I conducted a series of predatory fish and prey surveys throughout San Juan Channel, WA, to observe the influence of predators on prey species at a regional scale. Six locations within the channel were selected to include areas both open and closed to bottom fishing (Marine Research Preserves; WAC 1998) to encompass a wide range of bottomfish abundance. Locations were situated at least 1.5 km from each other, and covered a total distance of 10 km through northern San Juan Channel. At each location I selected two sites that contain contiguous bottomfish habitat (solid bedrock and large boulders; Palsson et al. 2009) between the surface and 30 m below mean lower low water (MLLW) (Table 1, Fig. 1). All survey dives occurred at or near slack tidal current.

Predator surveys – At each site I conducted two predatory fish surveys per year in summer to early fall from 2010-2012 (Table 2). The starting point for a survey was

chosen haphazardly by approaching the site by boat and descending on SCUBA to 27 m deep. The direction of the transect was chosen based on the direction of tidal current flow: with minimal flow I travelled in the direction of the current, and with stronger flow I swam against the current. My surveys were modeled after previous studies of bottomfish abundance in the San Juan Islands (Moulton 1977, Eisenhardt 2001, Palsson et al. 2009), with modifications to increase safety for survey divers.

From the survey starting point two divers used a measuring tape to swim a 30 m long transect, while maintaining a constant rate of ascent from 27 m to 21 m depth. Each diver recorded fishes within 2 m of the transect and less than 2 m from the bottom, for a total transect cross-section of 8 m² (4 m by 2 m) and substrate area of 120 m² (30 m by 4 m). I used T-shaped polyvinyl chloride pipes, 1 m long with a 40 cm head and marked in 1 cm increments, to measure total length for all rockfish (*Sebastes* spp.), lingcod (*O. elongatus*), greenling (*Hexagrammos* spp.), and large cottids (*Enophrys bison*, *Hemilepidotus* spp., *Myoxocephalus polyacanthocephalus*, and *Scorpaenichthys marmoratus*). Fishes were measured to the nearest 5 cm, or nearest 1 cm where possible. At the end of the transect I noted general habitat characteristics, including substrate type and algal species and cover. I started a new 30 m long transect at the end of the first transect, ascending from 21 m to 15 m depth, followed by a third 30 m long transect from 15 m to 9 m, a fourth 30 m long transect from 9 m to 3 m depth, and ending with a 15 m long transect from 3 m depth to the surface (60 m² substrate area). The total area covered on each survey was 540 m² per site. Fish lengths were converted to biomass using published relationships (Table 3), and summed across sites within each location and year.

Prey surveys – Demersal crustaceans and small fishes such as shrimp, crabs, sculpins and gobies are all likely prey of rockfish, lingcod and greenling (Moulton 1977, Murie 1995, Beaudreau & Essington 2007, Ch. 1). In 2009 I established permanent transects at each of the 12 sites to monitor these prey species. Transects were 10 m long, laid out horizontally at 9, 12, 15, 18 and 21 m below MLLW. These depths were chosen so as to cross the transition from kelp-dominated shallow waters to invertebrate-dominated deeper zones (Britton-Simmons et al. 2009). I surveyed these transects annually between October and January, to coincide with a long-term monitoring project established by K. P. Sebens in San Juan Channel (Table 2).

Shrimp were identified as *Pandalus platyceros*, *P. danae* and ‘other shrimp’. These three categories were chosen for the feasibility of *in situ* identification. I identified all crabs and small fishes to species. I tallied all shrimp and fishes within 0.5 m shoreward of the transect tape, for a total area of 5 m² per transect. Because they were far less abundant than shrimp and fishes, I tallied crabs within 1 m of both sides of the transect tape, for a total area of 20 m² per transect. Many of the crab and fish species are cryptic, and carapace width and total length limits of ≥ 3 cm were imposed to ensure count accuracy for these species. Fishes and crabs smaller than this limit were rarely observed, indicating that it is a reasonable limit for count accuracy. The abundance of each prey species was summed across depths and sites within each location and year.

Statistical analysis – I tested the effect of predator abundance and biomass on log-transformed prey abundance with linear mixed effect models, with predator biomass as the main effect and year as a random effect. I used AIC model selection to compare full

models with those lacking the predator term. Statistical analyses were conducted using the package ‘lme4’ (Bates et al. 2014) in R 3.1.2 (R Core Team 2014).

Predator exclusion experiment

I established replicated predator exclusion cages to experimentally test the patterns I observed in the community surveys, at two locations in San Juan Channel: Shady Cove Center on San Juan Island and Point George Center on Shaw Island (Table 1, Fig. 1). These two sites were chosen because they are within Marine Research Preserves closed to bottomfishing since 1990 (WAC 1998), and surveys of predatory fish abundance (see below; Eisenhardt 2001) showed that these sites had relatively high fish abundance compared to other sites in San Juan Channel. Both sites consist primarily of continuous bedrock at a 15-45° slope.

At each site I established five treatment blocks approximately 18 m below MLLW. This depth was selected to be deeper than understory kelp beds to prevent the cages from being entangled and smothered by kelp, while remaining shallow enough to allow access by SCUBA divers. Lingcod, rockfish and other predatory fishes are common at this depth (Appendix A). Each block consisted of a 2 m by 2 m caging area divided into two 2 m by 1 m sections, with the long axes parallel to isobaths (Fig. 2A). The cages consisted of three polyvinyl chloride pipe ribs, each a 2 m long straight bar with a 2.4 m long arc rising to 0.6 m above the ground. One section in each block was fully enclosed in thin filament black polypropylene mesh, with openings of 1.9 cm by 1.9 cm (Industrial Netting #OB1670). The other section was partially enclosed, with one

vertical mesh panel absent and two 40 cm by 40 cm windows cut into the arcing mesh panel to serve as a control for cage artifacts while allowing access to predatory fishes. The mesh extended into a skirt 0.5 m beyond the bottom edges of the ribs (Fig. 2B). I attached the cages to the benthos by cable tying the corners of the ribs to prepared steel bolts, and I sealed the cages to the uneven benthos by piling rocks on top of this skirt. The mesh size was large enough to allow likely prey of the large predatory fishes (i.e. small fishes, shrimp, and crabs: Moulton 1977, Murie 1995, Ch. 1) to move freely between treatments, while excluding the large predatory fishes. Very large prey, such as the shrimp *P. platyceros*, would be excluded by the mesh, but I rarely observe this species at these sites (Turner unpublished data).

The orientation of the cage (i.e. which treatment was closer to shore) was randomized for each block. Each treatment block also included a 2 m by 1 m uncaged area to which predatory fishes had access. This uncaged area was located either directly towards or away from shore relative to the cage, with the direction chosen at random. The uncaged area was greater than 1 m but less than 2 m from the cage. Although I lack quantitative estimates of predator abundance in the three treatments, I frequently observed lingcod, copper rockfish and kelp greenling inside the cage-control treatment, demonstrating that these fishes were not excluded from this treatment.

The cages were installed at the beginning of November 2010. I surveyed the treatment blocks for prey species of large fishes: shrimp (*P. danae*, *Eualus* sp., *Heptacarpus* sp., *Lebbeus* sp.), crabs (*Scyra acutifrons*, *Oregonia gracilis*, *Glebocarcinus oregonensis*, *Hyas lyratus*, juvenile *Lopholithodes mandtii*) and small fishes (*Jordania zonope*, *Artedius harringtoni*, *Rhinogobiops nicholsii*, *S. emphaeus*) (Moulton 1977,

Beaudreau & Essington 2007, Ch. 1). I counted shrimp of all sizes and counted and measured other mobile invertebrates and fishes ≥ 2 cm. Many of these species are cryptic, and this size limit was imposed to ensure count accuracy. I surveyed the blocks one month before and immediately prior to the installation of the cages, and 1, 4.5 and 9 mos after cage installation.

The cages were removed from the sites in April 2012. Preliminary analyses of data from this first round of experimental caging suggested the presence of significant cage effects, so I elected to conduct a second round of the experiment to confirm these effects. After several months of site recovery, I resurveyed the blocks and then reinstalled the cages at the beginning of July 2012. The orientations of the fully enclosed and partially enclosed treatments were re-randomized, but the position of the uncaged treatment was not re-randomized. I conducted additional surveys at 1, 2.5 and 4.5 mos after cage reinstallation. The end of my field season prevented a survey at 9 mos.

In the second round of the caging experiment, I also took photographs of four 25 cm by 35 cm benthic quadrats within each treatment area prior to cage reinstallation and 4.5 months later at the end of the experiment (Fig. 2C). These photos were analyzed for percent cover of sessile epibenthic organisms using 200 random points in CoralNet software (Beijbom et al. 2012). Because the four quadrats in each treatment were not independent of each other, data from the four photoquadrats were averaged to generate a single description of epibenthos cover for each treatment unit.

Statistical analysis – I tested the effect of predator exclusion on prey abundance with a generalized linear mixed effects model, with treatment and sampling period as main effects, and treatment block as a random effect, with a Poisson error distribution.

Separate analyses were used for the two experimental rounds (2010-2011 and 2012). I conducted post-hoc analyses of the statistical power of these models, using 1000 Monte Carlo simulations. I used nonmetric multidimensional scaling with Bray-Curtis dissimilarity to visualize epibenthos assemblage relationships, and multivariate linear models with arcsine-transformed and Wisconsin-standardized percent cover data to test the effects of time, treatment, and their interaction on assemblage composition. I used 1000 sample permutations for model comparisons and hypothesis testing, restricted within time periods to account for the repeated measures sampling design. Statistical analyses were conducted using the packages ‘lme4’ (Bates et al. 2014), ‘mvabund’ (Wang et al. 2014), ‘permute’ (Simpson et al. 2015), ‘simr’ (Green & MacLeod 2015), and ‘vegan’ (Oksanen et al. 2015) in R 3.1.2 (R Core Team 2014).

RESULTS

Community surveys

Copper rockfish (*S. caurinus*) were the most abundant predatory fish observed at all locations, except at Pear Point in 2010, where male kelp greenling were more abundant (Fig. 3A-C). Kelp greenling (*Hex. decagrammus*) were the next most abundant species, with males accounting for 73% of the total. Lingcod (*O. elongatus*) were present at all locations, but were not numerically dominant. Quillback rockfish (*S. maliger*) were present at low levels at most locations, but were very abundant only at Yellow Island in

2010 and 2011. The biomass of these four common predator species tracked abundance (i.e., the size of predators was approximately constant across locations), with the exception of lingcod (Fig. 3D-F). Lingcod at Pear Point, Shady Cove, and in 2011 at Point George were particularly large, leading to their dominance of the biomass at these locations. Other predatory fishes included vermillion, tiger, and brown rockfish (*S. miniatus*, *S. nigrocinctus* and *S. auriculatus*), cabezon (*Sco. marmoratus*), red Irish lord (*H. hemilepidotus*), buffalo (*E. bison*) and great (*M. polyacanthocephalus*) sculpins, and whitespotted greenling (*Hex. stelleri*). These species were rarely observed, and did not contribute substantially to predator biomass, except at Shady Cove in 2010, where I encountered two large cabezon.

Although bottomfish populations in the Salish Sea have not been systematically monitored since before expanded extraction started in the 1970s, two local studies from the 1970s surveyed bottomfishes at Point George, San Juan Channel (Fig. 1) and at nearby Barnes and Allan Islands in Rosario Strait (Moulton 1977, Miller et al. 1977). Copper rockfish density in the 1970s was typically less than 100 fish/ha, and often less than 50 fish/ha, quillback rockfish density was typically about half that of copper rockfish, and lingcod density was typically less than 30 fish/ha. In 2010-2012 (this study) copper rockfish density ranged from 10 to >400 fish/ha (mean = 161 fish/ha), quillback rockfish density ranged from 0 to >200 fish/ha (mean = 39 fish/ha), and lingcod ranged from 0 to >80 fish/ha (mean = 30 fish/ha). The range of bottomfish density in this study includes levels similar to those from the 1970s, as well as depleted levels and levels an order of magnitude higher.

Shrimp were an order of magnitude more abundant than other prey species at all locations (Fig. 4A-C). Approximately 60% of the shrimp were *P. danae*, with the remainder primarily belonging to the genera *Heptacarpus*, *Eualus*, and *Lebbeus*. *Pandalus platyceros* were only observed in a few isolated instances. Longfin sculpin (*J. zonope*), followed by scalyhead sculpin (*A. harringtoni*), were the most abundant small fish species at most locations, except at Mineral Point, where sediment among abundant boulders provided habitat for burrowing blackeye gobies (*R. nicholsii*) (Fig. 4D-F). Other small fish species included gunnels (Family Pholidae), mosshead warbonnets (*Chirolophis nugator*) and grunt sculpins (*Rhamphocottus richardsonii*). Crabs were the least abundant group of prey species (Fig. 4G-I). Among the crabs, the sharpnose crab (*Scy. acutifrons*) was the most abundant. Other common crabs included hermit crabs (Family Paguridae), graceful kelp crabs (*Pugettia gracilis*), and decorator crabs (*O. gracilis*). Rare crab species included Lithodid crabs (*Cryptolithodes* spp., *Rhinolithodes wosnessenskii*, *Phyllolithodes papillosus*, and *Lopholithodes mandtii*), Cancrid crabs (*G. oregonensis* and sub-adult *Cancer productus*), and helmet crabs (*Telmessus cheiragonus*).

Predator abundance was not a significant predictor of shrimp, small fish or crab densities in my community surveys ($\chi^2 = 0.25, 0.011, \text{ and } 0.003, p = 0.62, 0.92, \text{ and } 0.96$, respectively) (Fig. 5A-C). Even though the relative rank of predatory fish biomass at the six locations changed from year to year, predator biomass over the preceding six months was a significant negative predictor of shrimp abundance in autumn ($\chi^2 = 12.53, df = 1, p = 4.0 \times 10^{-4}$) (Fig. 5D). Predator biomass was not a significant predictor of small fish or

crab abundance over the three-year period ($\chi^2 = 1.16$ and 2.45 , $p = 0.28$ and 0.12 , respectively) (Fig. 5E, F).

Predator exclusion experiment

Round 1 – I summed the abundance of all shrimp species for analysis. In the first round of the caging experiment (September 2010 – July 2011), shrimp, small fish, and crab abundance both one month and immediately prior to caging did not significantly vary between treatments, with the exception of crabs immediately before caging (Table 4). Immediately prior to caging, crab abundance in areas destined to be in the control treatment was higher than in areas destined to be in the open treatment (blocked ANOVA, $F = 3.73$, $p = 0.044$; Tukey HSD, mean difference = 1.3 crabs/area, $p = 0.037$).

After cages were installed, shrimp abundance in the open treatment was somewhat, but not significantly, lower than in the caged treatment (GLMM, $z = -1.77$, $p = 0.077$) (Table 5, Fig. 6A). Shrimp abundance in the control treatment was not significantly different than abundance in either the caged treatment ($z = -0.53$, $p = 0.60$) or the open treatment (95% CI of the ratio of mean shrimp count in the Open:Control treatments = 0.23-1.39). The statistical power of the treatment effect test for shrimp was 40%. Shrimp abundance at month 1 and month 4.5 were both higher than at month 0 ($z = 3.53$ and 2.83 , $p = 4.1 \times 10^{-4}$ and 4.6×10^{-3} , respectively), while abundance at month 9 was lower than at month 0 ($z = -2.82$, $p = 4.9 \times 10^{-3}$). Shrimp abundance was also higher at month -1 than at month 0 ($z = 4.36$, $p = 1.3 \times 10^{-5}$).

Small fish abundance in the open treatment was 75% of that in the caged treatment in Round 1 ($z = -2.34$, $p = 0.019$) (Table 6, Fig. 6B). The statistical power of the treatment effect test for small fishes was 54%. Fish abundance was marginally lower 4.5 months and significantly lower 9 months after caging than immediately before caging in Round 1 ($z = -1.74$ and -3.29 , $p = 0.081$ and 0.001 , respectively). I did not observe an effect of caging on the abundance of crabs, analyzed either as individual species or as a functional group (Table 7, Fig. 6C). The statistical power of the treatment effect test for crabs was 41%. Crabs in Round 1 were more abundant in month 1 than immediately prior to caging ($z = 1.97$, $p = 0.049$), but declined again by the next sampling period, and remained indistinguishable from abundance at month 0 through the end of sampling.

Round 2 – In the second round of the caging experiment (July – December 2012), shrimp, small fish, and crab abundances immediately prior to caging did not significantly vary between treatments (Table 4). At the last sampling period, a lingcod became tangled in one of the cages and died, attracting very high numbers of scavenging shrimp to the caged and control treatments at this caging block. I removed these two data points prior to analysis.

After caging, shrimp abundance in the open treatment was 43% of that in the caged treatment (GLMM, $z = -2.98$, $p = 0.003$) (Table 5, Fig. 6D). Shrimp abundance in the control treatment was not significantly different from that in the caged treatment ($z = -1.23$, $p = 0.22$). Shrimp abundance in the open treatment was not significantly different from that in the control treatment (95% CI of the ratio of mean shrimp count in the Open:Control treatments = 0.34-1.06). The statistical power of the treatment effect test for shrimp was 76%. Shrimp abundance was consistently higher at sampling times after

the installation of the cages ($z = 4.67, 4.73$ and 6.92 , respectively for the comparisons of months 1, 2.5 and 4.5 to month 0, $p \ll 0.01$ for all).

Small fish abundance in the open treatment was 75% of that in the caged treatment, although this difference was not significant ($z = -1.70$, $p = 0.090$) (Table 6, Fig. 6E). The control treatment was not statistically distinguishable from either the caged or open treatments. The statistical power of the treatment effect test for small fishes was 39%. Small fish abundance was 40% higher one month after caging than immediately prior to caging ($z = 2.06$, $p = 0.039$), but abundance declined back to pre-caging levels by 2.5 months after caging, and remained there for the remainder of the experiment. Crab abundance was not affected by treatment, and did not significantly change between sampling periods (Table 7, Fig. 6F). The statistical power of the treatment effect test for crabs was 20%.

Benthic assemblages from photoquadrats did not significantly differ between treatments, and the interaction between treatment and time period was also non-significant ($p = 0.10$ and 0.99 , respectively). However, there was a significant change in assemblage composition between time periods ($p = 0.001$) (Table 8, Fig. 7). Because the treatment and interaction terms were non-significant, these terms were removed from the model. Model comparisons revealed that the reduced model was not significantly different than the full model ($p = 0.63$). Univariate comparisons using a step-down resampling method to control for family-wise error identified three epibenthos categories as significantly different between the two time periods: percent cover of serpulid worms and bleached crustose coralline algae both increased through time (accounting for 16% and 11% of the difference between time periods, $p = 0.009$ and 0.034 , respectively), and

“hydrozoan-bryozoan complex” decreased through time (accounting for 17% of the difference between time periods, $p = 0.003$) (Fig. 8). This “complex” category is of indeterminate taxonomic status, and appears as sediment bound in a three-dimensional matrix often including erect hydroids and/or bryozoans or parts thereof. This sediment may also be accreted to grazed hydroid, bryozoan or algal stalks, or in the mucous exuded from benthic organisms.

DISCUSSION

In this study I demonstrate that predatory fishes in the San Juan Archipelago strongly influence benthic shrimp populations. The experimental exclusion of large fishes led to a higher abundance of shrimp than in areas with fish access, and surveys across three years showed a similar pattern, with shrimp less abundant at sites where fish biomass was highest in the preceding six months. Predation pressure from large fishes in San Juan Channel is sufficiently high at present to control shrimp abundance in shallow rocky habitats.

Shrimp are common prey of rockfish, and previous studies in the Salish Sea have suggested that fish predation can alter shrimp populations (Frid & Marliave 2010). Although I did not track all shrimp species individually, my surveys corroborate the hypothesis that shrimp populations in these habitats can be altered by fish predation. To my knowledge, this caging experiment represents the first experimental manipulation of

benthic fish predation in the Salish Sea, and confirms that the absence or severe reduction of predators can rapidly change shrimp abundance at a local scale.

The spatial scale of the surveys is similar in magnitude to rockfish home ranges. Copper and quillback rockfish, the two most common species, both typically have home ranges less than 2500 m² in low-relief habitat (Tolimieri et al. 2009). This range shrinks to <100 m² and as little as 10 m² in high-relief habitat (Matthews 1990a, b), although this narrow range may occasionally be interspersed with farther excursions (Hannah & Rankin 2011). The sites used in this study were selected because of the presence of high relief bedrock and boulder habitat, which should bias the rockfish at these sites towards smaller home ranges. Lingcod tend to have considerably larger home ranges: ~3000 to 20,000 m² or more in summer, but narrowing to <2000 m² in winter (Tolimieri et al. 2009, Beaudreau & Essington 2011). Caging treatments larger than the 2 m² I used would better match bottomfish home range sizes and could allow for predator inclusions as well as exclusions, but are logistically untenable in the strong tidal currents of the San Juan Archipelago.

The higher abundance of shrimp inside cages than outside could be due to any or all of three potential mechanisms: fish predation exposed shrimp to higher mortality in open areas than in the cages, shrimp moved from open areas into the cages, or shrimp populations inside the cages endogenously increased in abundance. Pandalid shrimp sub-adults and adults begin recruiting to the population in summer to early fall (Berkeley 1931), (e.g., at the beginning of experimental Round 2, and perhaps explaining the overall increase in shrimp abundance over the duration of this round). Adult shrimp home range size is considerably larger than the 2 m² area of the cage treatments (Bergström

2000), so it is unlikely that the higher abundance of shrimp in the cages is due to differential adult recruitment and retention between the treatments, although they might use the cages as refugia at times.

With the results of this experiment, I am unable to differentiate categorically between shrimp movement behavior and fish predation (or both) as the direct cause of higher shrimp abundance inside the cages. In addition, the shrimp movement hypothesis may be broken into two sub-hypotheses: movement was caused by the perception of the cages as a refuge, and movement was caused by attraction to the three-dimensional structure of the cages for a reason other than predator avoidance. The refuge hypothesis is supported by the lack of a significant difference in shrimp abundance between the open and control treatments in both experimental rounds. The attraction hypothesis is supported by the lack of a significant difference in shrimp abundance between the cage and cage control treatments in both experimental rounds. Since shrimp were more abundant in both cage and cage control treatments, both structures probably acted as refugia from predation to some extent, allowing shrimp to avoid predation by a similar amount in the two treatments. The much lower abundance of shrimp in open areas indicates that fish predation controls shrimp abundance, compared to either treatment that offered some refuge.

Top-down control is common in marine food webs, and can be manifested in trophic cascades affecting multiple trophic levels (Pinnegar et al. 2000). However, cascading predator effects depend on strong trophic links (Paine 1980). In systems with generalist consumers, cascades are less likely to be observed, since predation pressure from one trophic level gets attenuated over many prey species (Polis & Strong 1996). If

fish predation reduced the abundance of other herbivorous or predatory invertebrates, in addition to shrimp, I might have seen a large change in abundance of algae or certain epibenthic invertebrates in caged treatments, but this was not the case. In the San Juan Archipelago, there is a strong link between predatory bottom fishes and shrimp, but this effect does not appear to cascade down to lower trophic levels. Results from benthic photoquadrats in the caging experiment indicate that there is no difference in assemblage composition between caged (abundant shrimp) and open (fewer shrimp) treatments. Further experimentation directly manipulating shrimp abundance may be conducted, but because shrimp tend to be generalist consumers and scavengers (Harvey et al. 2010), and so lack strong trophic connections to individual prey species, it is unlikely that they are involved in a trophic cascade in the San Juan Archipelago. This lack of a fish-mediated change in the epibenthos is mirrored by two studies in nearby habitats (Marliave et al. 2011, Elahi et al. 2013) where the minimal changes in benthic assemblage composition over 40 years cannot be attributed to changes in the fish assemblage over that period.

Although the positive effect of excluded predators on small fish abundance is not as pronounced as it is on shrimp, it is observable even on the relatively short time scales of these exclusion experiments. The sculpins and gobies observed in this study are demersal predators, feeding primarily on mesofauna <5 mm (Wiley 1973, Demetropoulos et al. 1990, Norton 1991a). Although the diets of these fishes are fairly broad, they specialize more than shrimp do, with crustaceans such as amphipods and crabs (for *J. zonope*, *A. harringtoni*, and *R. nicholsii*), and sedentary polychaetes (for *J. zonope*) comprising large portions of the diets. This specialization may be sufficient to form strong trophic links between the small fishes and their prey. I did not find a significant

change in polychaete percent cover over the course of the caging experiment, but *J. zonope* tends to nip polychaete tentacles, rather than consume entire animals, which may be inadequate damage to alter polychaete population size. I used an airlift suction device to sample mobile mesofauna from four 10 cm² areas within each caging treatment (Wahle & Steneck 1991). Although these samples were not sufficient for statistical analysis, I did not observe a noticeable difference in amphipod or other mesocrustacean abundance between caged and open treatments. Direct manipulations of small fish populations would help determine if these species are involved in a trophic cascade mediated by large fish predation pressure.

Despite the significant positive effect of predator exclusion on small fish abundance in the caging experiment, I did not observe higher abundance of small fishes at survey sites with low predator biomass. The cages completely excluded predator access, while even the survey areas with lowest predator biomass still had some predators present. This lack of a predator effect on small fishes in the surveys may be a result of few predators able to reduce the prey population below a detection threshold, such that additional predators do not further reduce prey abundance. Only in the absence of predation, as in the cages, are small fishes able to increase in density.

I did not observe an effect of predators on small crabs, either in the surveys or in the caging experiment. Crabs are consumed by predatory fishes in the San Juan Archipelago, but to a much lower degree than shrimp (Murie 1995, Beaudreau & Essington 2007, Ch. 1). Crab population density in this habitat is also much lower than shrimp, which may preclude my ability to detect an effect of predation.

The statistical power of the treatment effect for shrimp in Round 2 was relatively high (76%, nearly the generally accepted 80% threshold for power), providing supporting evidence that the cage control may not have been an adequate control, either by preventing sufficient access to predatory fishes, or by provided excessive refuge to shrimp. In all other cases these models had low statistical power. Additionally, in many cases the 95% confidence interval around the ratio estimate of prey abundance in different treatments encompasses meaningful effect sizes (e.g. in Round 1 shrimp abundance in the cage control treatment is estimated to be between one third and nearly double the abundance of shrimp in the cage treatment; Tables 5-7). Low power and large confidence intervals suggest that the sample size of these experiments may have been insufficient to detect all potential differences between the caging treatments (Hoenig & Heisey 2001). This set of experiments was limited to 10 caging blocks for logistical concerns. However, because the effects of caging appeared relatively quickly after cages were installed, the temporal duration of a future round of this experiment could be shortened in exchange for more caging blocks. Additionally, a future round of this experiment would benefit from a modified cage control in minimize refuge to prey and maximize access to predators.

Although it appears that the density of bottomfishes has increased locally within San Juan Channel over the last several decades, perhaps due to the >20-year history of Marine Research Preserves protecting bottomfish in San Juan Channel, the Washington Department of Fish and Wildlife's assessment finds that rockfish populations at the larger scale of the Salish Sea are currently depleted relative to historic levels (Palsson et al. 2009). Over the last several decades, abundance of copper rockfish in North Puget Sound

(including the San Juan Archipelago) has declined by more than 50%, total biomass has trended downwards, and spawning potential has declined by almost 70%. Consequently, prey populations could be benefiting from predator release, and prey abundance may be higher now than several decades ago prior to intense bottomfish harvest. Demersal fish surveys in the San Juan Archipelago from the 1970s, shortly after the active promotion of recreational bottomfishing commenced, found very low sculpin density (~ 0.005 individuals/m²; Moulton 1977, Miller et al. 1977). Surveys in 1985 and 1987, after rockfish populations were known to be in decline, found sculpin density to be many times higher (~ 2 individuals/m²; Demetropoulos et al. 1990, Norton 1991b). The surveys described in the current study show similarly high sculpin density (~ 0.5 individuals/m²).

Unfortunately, historical surveys of shrimp abundance do not exist to compare to the current study, but as for sculpins, I expect that current shrimp abundance is higher than historical levels. Alternatively, the reduction in rockfish abundance may have allowed competitors for shrimp prey, such as kelp greenling, to increase in abundance. In two scuba-based surveys in the San Juan Islands from the 1970s kelp greenling densities averaged about 10 to 45 individuals/ha (Moulton 1977, Miller et al. 1977). Kelp greenling density in the current study averaged about 100 individuals/ha, although their density was approximately 45 individuals/ha in a recent ROV survey in the San Juan Islands (Pacunski et al. 2013). The expected recovery of bottomfish over the coming decades due to the closure of rockfishing in Puget Sound (WAC 2010) will provide an opportunity to monitor the responses of prey and competitor populations to returning bottomfishes.

Table 1. Summary of site locations.

Site number	Location	Site name	Latitude (N)	Longitude (W)
1	Shady Cove	Shady Center	48° 33.023'	123° 00.319'
2	Shady Cove	Shady South	48° 32.835'	123° 00.316'
3	Mineral Point	Mineral Center	48° 35.532'	123° 04.463'
4	Mineral Point	Mineral North	48° 35.594'	123° 04.705'
5	Yellow Island	Yellow Island	48° 35.472'	123° 01.664'
6	Yellow Island	Low Island	48° 35.366'	123° 01.587'
7	Neck Point	Neck North	48° 34.797'	123° 00.975'
8	Neck Point	Neck South	48° 34.754'	123° 00.766'
9	Point George	George Center	48° 33.348'	122° 59.093'
10	Point George	George South	48° 33.182'	122° 58.792'
11	Pear Point	One Mile Reef	48° 32.245'	122° 59.221'
12	Pear Point	Minnesota Reef	48° 31.689'	122° 58.048'

Table 2. Summary of survey and experimental periods.

	Year	Month
Predator Surveys	2010	3-20 May 14-18 Aug
	2011	15 June - 8 July 8-12 Oct
	2012	24 June - 11 July 6-9 Aug
Prey Surveys	2010	Oct-Jan
	2011	Oct-Jan
	2012	Oct-Jan
Exclusion Experiment	2010-2011	Mo -1: 22-24 Sep Mo 0: 25-29 Oct Mo 1: 1-8 Dec Mo 3/4.5: 29-31 Jan, 16-18 Mar Mo 9: 18-26 July
	2012	Mo 0: 9-15 July Mo 1: 18-24 Aug Mo 2.5: 4-13 Oct Mo 4.5: 28 Nov - 13 Dec

Table 3. Length-mass and fork length-total length relationships for predatory bottomfish observed in the community surveys. M = biomass (g), F = Fork Length (cm), T = Total Length (cm).

Species	Length-mass relationship	Length-length relationship	Ref.
<i>Sebastes caurinus</i>	$M = 0.03811 F^{2.79}$	$F = 0.0005 + 0.988 T$	1, 2
<i>S. maliger</i>	$M = 0.02237 F^{2.95}$	$F = 0.9075 + 0.965 T$	1, 2
<i>S. nigrocinctus</i>	$M = 0.0090 T^{3.205}$	---	3
<i>S. miniatus</i>	$M = 0.02157 T^{2.92339}$	---	4
<i>S. auriculatus</i>	$M = 0.02631 F^{2.89}$	$F = 0.0634 + 0.993 T$	1, 2
<i>Ophiodon elongatus</i>	$M = 6.7289 \times 10^{-4} F^{3.6558}$	$F = -0.0521 + 0.981 T$	5, 6
<i>Hexagrammos decagrammus</i>	$M = 0.02535 F^{2.83}$	$F = 0.985 T$	1, 7
<i>Hex. stelleri</i>	$M = 2.875 \times 10^{-3} F^{3.45}$	$F = 0.991 T$	1, 7
<i>Scorpaenichthys marmoratus</i>	$M = 0.02260 F^{2.91}$	$F = 1.000 T$	1, 7

¹(Wildermuth 1983), ²(Echeverria & Lenarz 1984), ³(Lea et al. 1999), ⁴(Love et al. 1990),
⁵(Hart 1967), ⁶(Laidig et al. 1997), ⁷(Froese & Pauly 2015)

Table 4. Blocked ANOVA results of pre-caging abundance of shrimp, crabs and small fishes. In most cases, there was not a significant difference in prey species abundance among the three caging treatments prior to the installation of cages. In the one case where there was a significant difference in prey abundance, the difference was between the open and control treatments, not between the open and caged treatments.

Year	Species	Months prior to caging	F	p-value	Pairwise comparisons	Tukey HSD p-value
Round 1 (2010-2011)	Shrimp	1	0.0853	0.9186	n/a	
		0	0.5126	0.6074	n/a	
	Crabs	1	n/a*	n/a*	n/a	
		0	3.7331	0.0440	Open:Caged	0.24
					Open:Control	0.037
	Control:Caged	0.56				
Fishes	1	1.0772	0.3615	n/a		
	0	1.2674	0.3055	n/a		
Round 2 (2012)	Shrimp	0	1.8108	0.1921	n/a	
	Crabs	0	1.2632	0.3067	n/a	
	Fishes	0	0.1785	0.8380	n/a	

*I did not observe crabs in the sampling period one month prior to caging in Round 1. Bold values indicate significant differences ($p < 0.05$).

Table 5. Generalized linear mixed model summary for shrimp abundance in the predator exclusion experiment. Note that the comparisons are expressed as ratios, so that a 95% CI that overlaps 1 indicates no difference at $\alpha = 0.05$. In the first experimental round shrimp abundance was somewhat, but not significantly, higher in the caged treatment than in the open treatment, and this difference was significant in the second experimental round.

Year	Ratio of mean shrimp count	Variable	Estimate	95% CI	z-value	p-value
Round 1 (2010-2011)	Control:Cage	e^{β_1}	0.79	(0.32, 1.91)	-0.530	0.596
	Open:Cage	e^{β_2}	0.44	(0.18, 1.09)	-1.769	0.077
	Open:Control	$e^{\beta_2-\beta_1}$	0.56	(0.23, 1.39)		> 0.05*
	Month -1:Month 0	e^{β_3}	1.77	(1.37, 2.28)	4.359	1.3×10^{-5}
	Month 1:Month 0	e^{β_4}	1.60	(1.23, 2.08)	3.534	4.09×10^{-4}
	Month 4.5:Month 0	e^{β_5}	1.47	(1.13, 1.91)	2.831	4.64×10^{-3}
	Month 9:Month 0	e^{β_6}	0.62	(0.44, 0.87)	-2.817	4.85×10^{-3}
	Random block-to-block variation	e^{σ}	0.04			
Round 2 (2012)	Control:Cage	e^{β_1}	0.72	(0.42, 1.22)	-1.226	0.220
	Open:Cage	e^{β_2}	0.43	(0.25, 0.75)	-2.982	0.003
	Open:Control	$e^{\beta_2-\beta_1}$	0.60	(0.34, 1.06)		> 0.05*
	Month 1:Month 0	e^{β_3}	2.65	(1.76, 3.98)	4.668	3.04×10^{-6}
	Month 2.5:Month 0	e^{β_4}	2.68	(1.78, 4.03)	4.734	2.20×10^{-6}
	Month 4.5:Month 0	e^{β_5}	4.00	(2.70, 5.92)	6.916	4.66×10^{-12}
		Random block-to-block variation	e^{σ}	1.73		

Bold values indicate significant differences ($p < 0.05$).

*The GLMM does not explicitly test the null hypothesis that the ratio of mean shrimp count between Open and Control treatments equals 1, but a ratio estimate and 95% CI can be calculated from model output.

Table 6. Generalized linear mixed model summary for small fish abundance in the predator exclusion experiment. See interpretation notes in Table 5. In the first experimental round small fish abundance was significantly higher in the caged treatment than in the open treatment, but this pattern was not significant in the second experimental round.

Year	Ratio of mean shrimp count	Variable	Estimate	95% CI	z-value	p-value
Round 1 (2010- 2011)	Control:Cage	e^{β_1}	0.85	(0.67, 1.07)	-1.364	0.172
	Open:Cage	e^{β_2}	0.75	(0.59, 0.96)	-2.337	0.019
	Open:Control	$e^{\beta_2-\beta_1}$	0.88	(0.69, 1.13)		> 0.05
	Month -1:Month 0	e^{β_3}	0.87	(0.67, 1.13)	-1.050	0.294
	Month 1:Month 0	e^{β_4}	1.04	(0.81, 1.33)	0.315	0.753
	Month 4.5:Month 0	e^{β_5}	0.79	(0.61, 1.03)	-1.742	0.081
	Month 9:Month 0	e^{β_6}	0.62	(0.47, 0.83)	-3.287	0.001
	Random block-to-block variation	e^{σ}	0.02			
Round 2 (2012)	Control:Cage	e^{β_1}	0.97	(0.71, 1.34)	-0.167	0.8675
	Open:Cage	e^{β_2}	0.75	(0.54, 1.05)	-1.696	0.0898
	Open:Control	$e^{\beta_2-\beta_1}$	0.77	(0.55, 1.08)		> 0.05
	Month 1:Month 0	e^{β_3}	1.40	(1.17, 1.93)	2.061	0.0393
	Month 2.5:Month 0	e^{β_4}	1.17	(0.84, 1.63)	0.921	0.3572
	Month 4.5:Month 0	e^{β_5}	1.31	(0.95, 1.81)	1.620	0.1053
		Random block-to-block variation	e^{σ}	0.04		

Table 7. Generalized linear mixed model summary for crab abundance in the predator exclusion experiment. See interpretation notes in Table 5. Crab abundance was not affected by the exclusion of predatory fishes.

Year	Ratio of mean shrimp count	Variable	Estimate	95% CI	z-value	p-value
Round 1 (2010- 2011)	Control:Cage	e^{β_1}	1.20	(0.67, 2.15)	0.606	0.544
	Open:Cage	e^{β_2}	0.65	(0.35, 1.23)	-1.317	0.188
	Open:Control	$e^{\beta_2-\beta_1}$	0.54	(0.29, 1.02)		> 0.05
	Month -1:Month 0	e^{β_3}	1.26×10^{-8}	(0, ∞)	-0.010	0.991
	Month 1:Month 0	e^{β_4}	1.63	(1.00, 2.65)	1.970	0.049
	Month 4.5:Month 0	e^{β_5}	1.19	(0.71, 1.99)	0.641	0.521
	Month 9:Month 0	e^{β_6}	1.11	(0.66, 1.88)	0.392	0.695
	Random block-to-block variation	e^{σ}	0.23			
Round 2 (2012)	Control:Cage	e^{β_1}	1.62	(0.73, 3.63)	1.183	0.2370
	Open:Cage	e^{β_2}	1.33	(0.58, 3.02)	0.673	0.5010
	Open:Control	$e^{\beta_2-\beta_1}$	0.82	(0.38, 1.76)		> 0.05
	Month 1:Month 0	e^{β_3}	1.23	(0.58, 2.60)	0.543	0.5871
	Month 2.5:Month 0	e^{β_4}	1.85	(0.92, 3.69)	1.739	0.0821
	Month 4.5:Month 0	e^{β_5}	1.77	(0.88, 3.55)	1.606	0.1084
		Random block-to-block variation	e^{σ}	0.36		

Table 8. Model summaries and model selection for epibenthos assemblage multivariate linear models from the predator exclusion experiment. DF: degrees of freedom. Res. DF: residual degrees of freedom. LR: Likelihood ratio.

Factor		DF	Res. DF	F-value	p-value
Full Model (M1)	Treatment	2	51	37.18	0.101
	Time	1	50	90.02	0.001
	Tx * Time	2	48	14.03	0.998
Reduced Model (M2)	Treatment	2	51	37.18	0.097
	Time	1	50	90.02	0.001
Optimal Model (M3)	Time	1	52	89.00	0.001

Model Comparison	DF	Res. DF	LR	p-value
M1 vs. M2	2	48	30.77	0.752
M2 vs. M3	2	50	78.13	0.581
M1 vs. M3	4	48	108.9	0.625

Bold values indicate significant effects ($p < 0.05$).

Table 9. Species codes used for epibenthos assemblage analysis in the predator exclusion experiment.

Code	Species
ALGA	Erect algae
AMPH	Amphipod tubes
BAEL	<i>Balanophyllia elegans</i>
BARE	Bare Rock
BARN	Barnacles
BRAC	Brachiopods
BRYO	Encrusting bryozoans
	Bleached crustose coralline
CCAB	algae
CCAL	Crustose coralline algae
CRIS	<i>Crisia</i> sp.
DEAD	Dead fauna
DICL	<i>Diaperoecia californica</i>
DIOC	<i>Distaplia occidentalis</i>
DOCO	<i>Dodecaceria concharum</i>
ENNA	<i>Entodesma navicula</i>
ENRA	Encrusting fleshy red algae
HBCO	Hydro-bryo complex
HEPA	<i>Heteropora pacifica</i>
HYDR	Hydroids
IDSA	<i>Idanthyrsus saxicavus</i>
META	<i>Metandrocarpa taylori</i>
POMA	<i>Pododesmus macrochisma</i>
PSOL	<i>Psolus/Psolidium</i>
SERP	Serpulids
SPON	Sponges
STYL	<i>Stylanteca</i> sp.
TUNI	Solitary tunicates

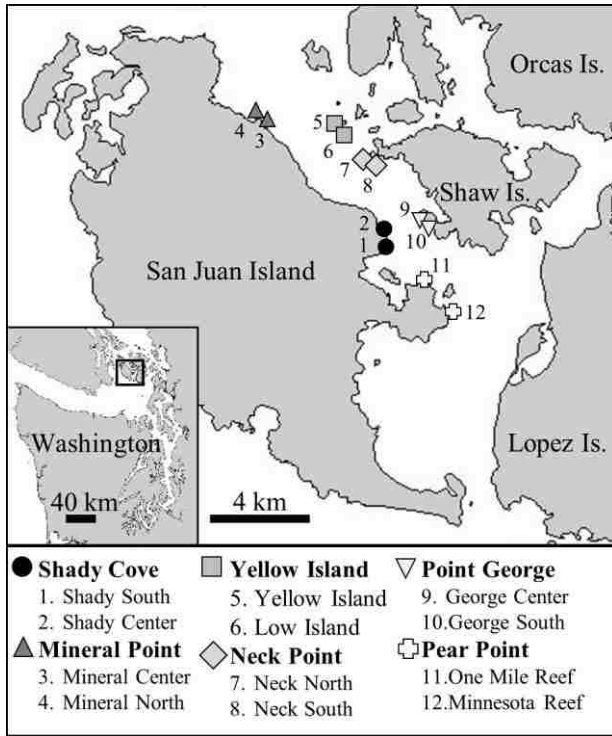


Figure 1. Research sites in the San Juan Archipelago, Washington. Community surveys were conducted at 12 sites in San Juan Channel, each nested in one of six locations (different symbol types). The predator exclusion experiments were conducted at Shady Center (2) and George Center (9).

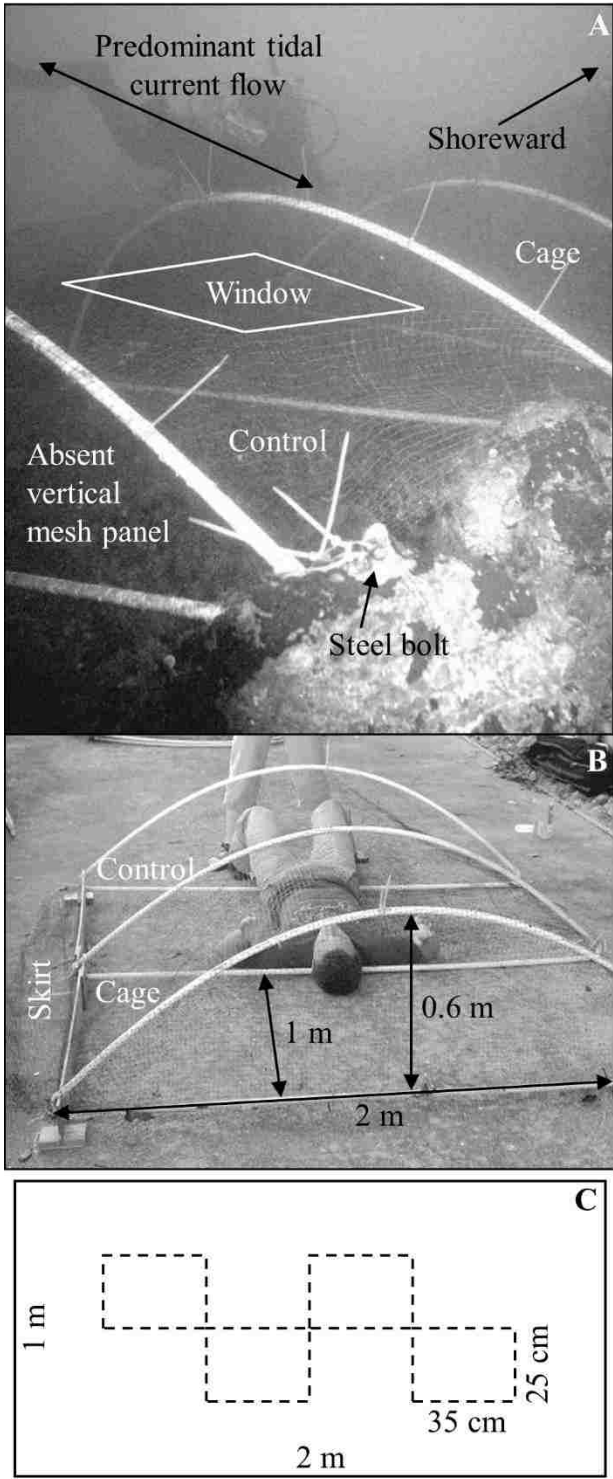


Figure 2. Cages used in the predator exclusion experiment. Each cage consisted of two 2 m by 1 m sections, one of which was fully enclosed with polypropylene mesh, and the other of which was partially enclosed with mesh. The cages were oriented with the PVC ribs parallel to isobaths and the predominant tidal current flow direction (A). The control treatment had two windows cut in the mesh (one of these is highlighted), and lacked mesh on the vertical end of the treatment, visible on the left. Mesh extended into a skirt around the base of the cage, which was sealed to the uneven benthos with piles of rocks (B). Note that in (B) the author's head penetrates from the control into the caged treatment, but in a fully assembled cage a vertical mesh panel completely sealed off the cage treatment from the control treatment. I took four 35 cm by 25 cm photographs of the epibenthos inside each treatment, indicated by dashed lines in (C). Photos by Megan Cook (A) and Alexander Lowe (B).

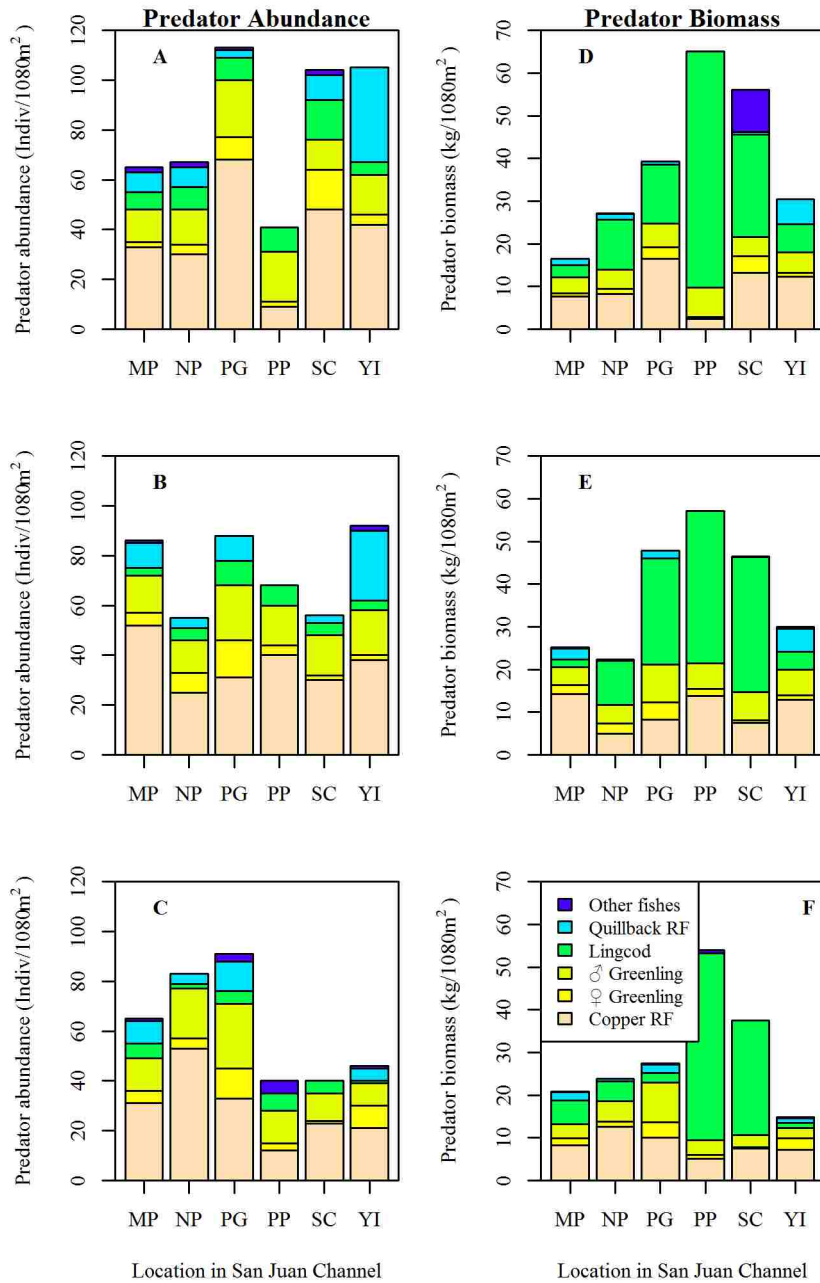


Figure 3. Predatory fish abundance in 2010 (A), 2011 (B), and 2012 (C), and predatory fish biomass in 2010 (D), 2011 (E), and 2012 (F), from predator surveys. MP: Mineral Point, NP: Neck Point, PG: Point George, PP: Pear Point, SC: Shady Cove, YI: Yellow Island.

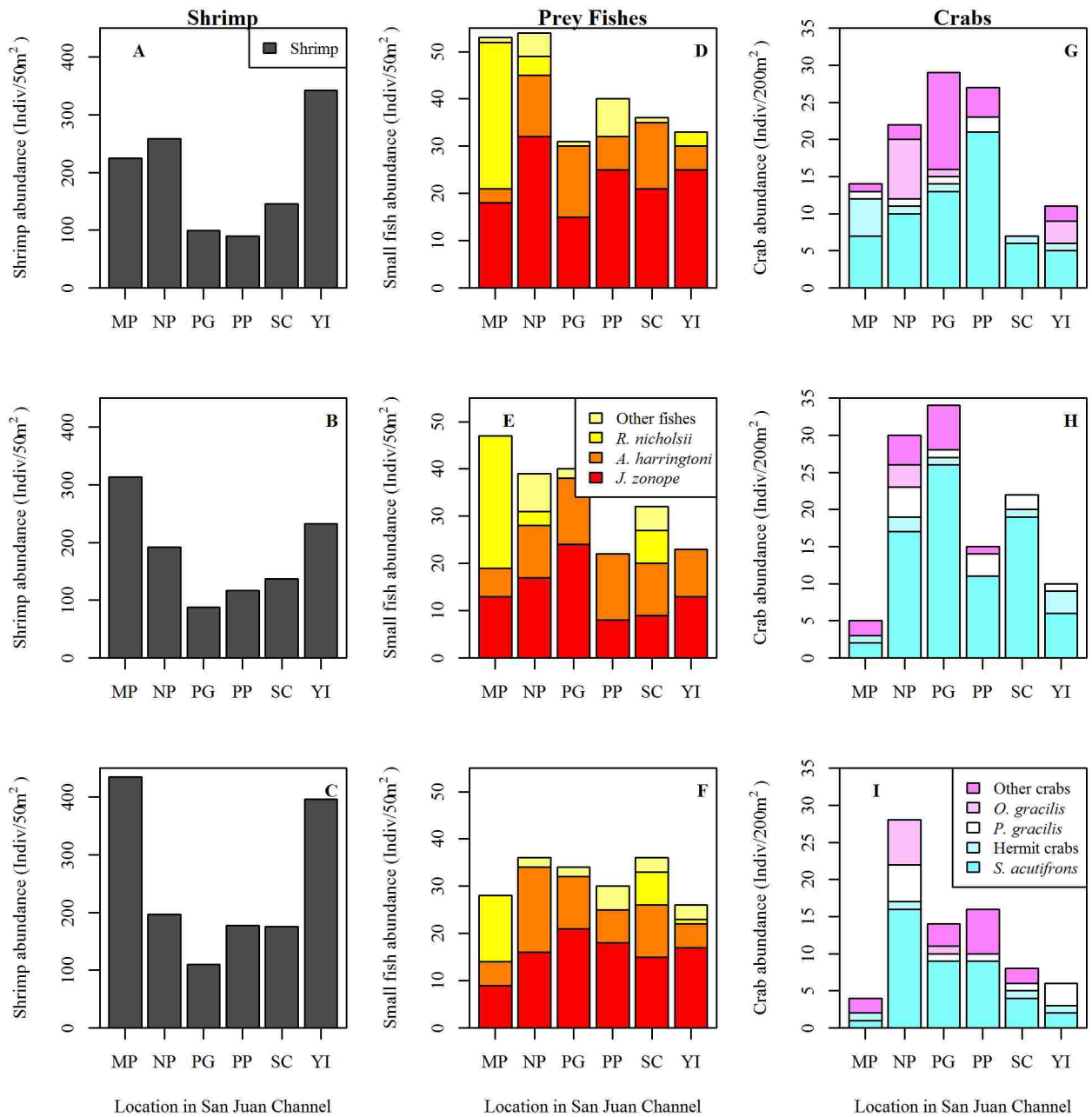


Figure 4. Shrimp abundance in 2010 (A), 2011 (B) and 2012 (C), small fish abundance in 2010 (D), 2011 (E), and 2012 (F), and small crab abundance in 2010 (G), 2011 (H), and 2012 (I). Note the different y-axis scales for the three functional groups. Location abbreviations as in Fig. 3.

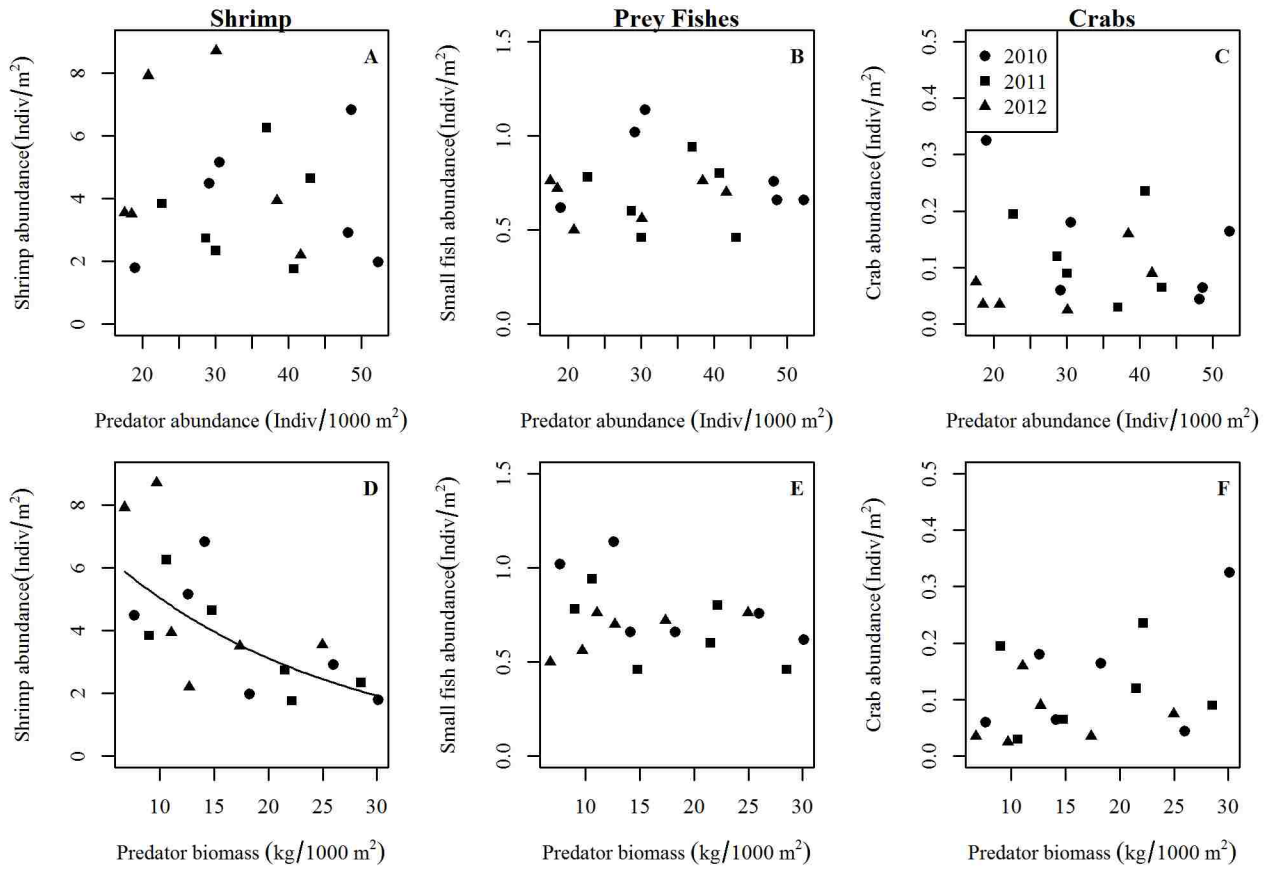


Figure 5. Predatory fish abundance and biomass compared to prey abundance over three years of surveys. Predator abundance over the preceding six months was not a significant predictor of shrimp (A), small fish (B), or crab (C) abundance. Predator biomass over the preceding six months was a strong predictor of shrimp abundance in the autumn (D), but was not a predictor of small fish (E) or crab (F) abundance. The black line in (D) shows the significant negative relationship between predator biomass and shrimp abundance. Circles denote data from 2010, squares from 2011, and triangles from 2012.

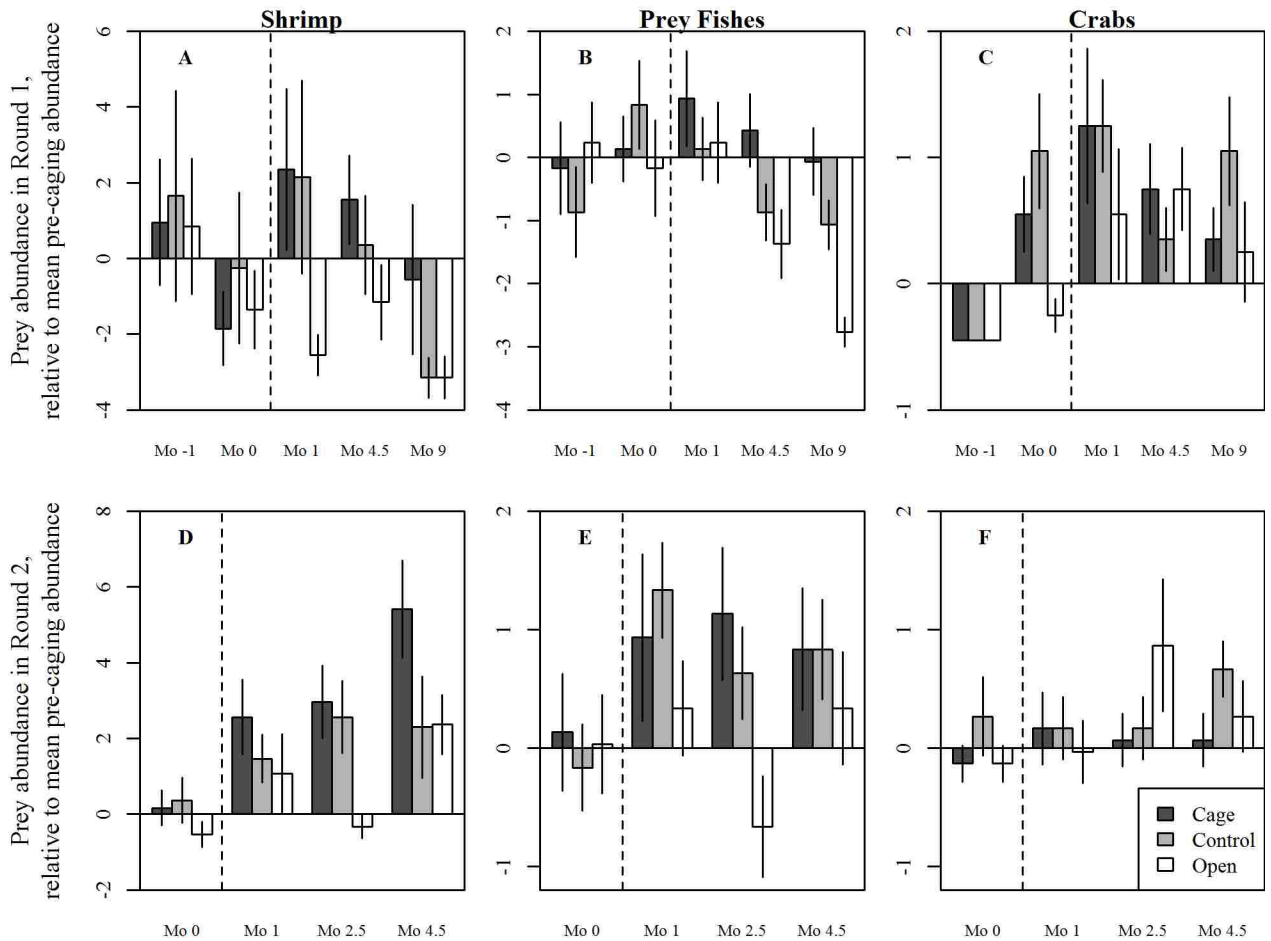


Figure 6. Relative abundance of shrimp, small fishes, and crabs per 2m² in Rounds 1 and 2 of the predator exclusion experiment. The average abundance of each prey category in all three treatments prior to the installation of the cages (Months -1 and 0) was set as zero. Positive values indicate higher abundance than this pre-caging baseline, and negative values indicate lower abundance than baseline. The dashed line indicates the installation of the cages. In Round 1, shrimp abundance was higher in the caged treatment than in the open treatment, but this difference was not significant at $\alpha=0.05$ (A). Small fish abundance was significantly greater in the caged treatment than in the open treatment (B). Caging treatment did not have a significant effect on crab abundance (C). In Round 2, shrimp abundance was significantly greater in the caged treatment than in the open treatment (D). Although small fish abundance was higher in the caged treatment than in the open treatment, this difference was not significant at $\alpha=0.05$ (E). Caging treatment did not have a significant effect on crab abundance (F). One shrimp abundance data point was removed from each of the Cage and Control treatments at Month 4.5 (see text for details). Error bars are standard error.

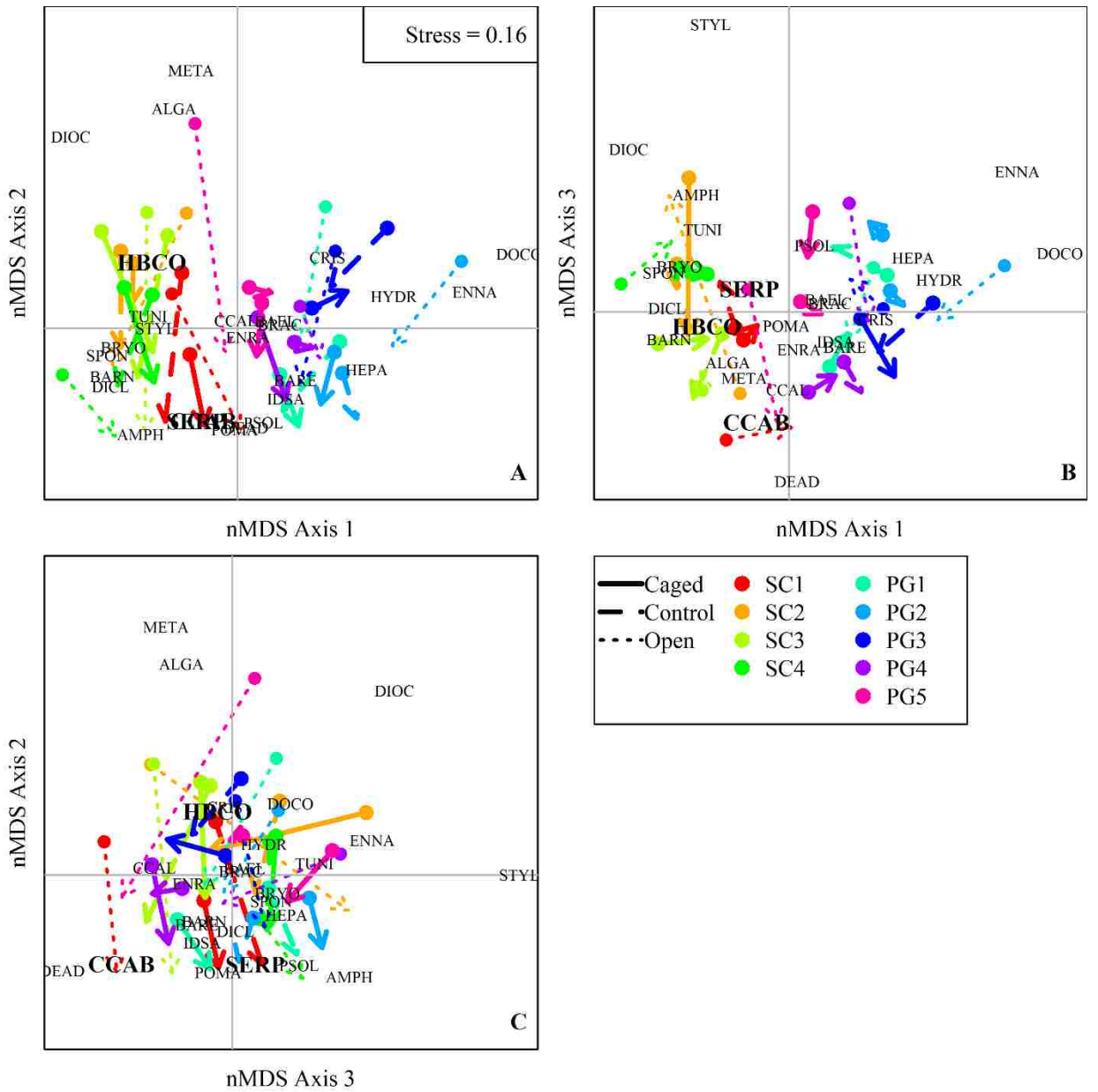


Figure 7. Non-metric multidimensional scaling plot of epibenthos assemblages in the predator exclusion experiment. A three-dimensional ordination was used to bring stress below 0.2. Different colors represent different experimental blocks. Solid lines are caged treatments, dashed lines are control treatments, and dotted lines are open treatments. Arrow bases are the assemblage at the beginning of the experiment (July 2012), and arrow heads are the assemblage at the end of the experiment (December 2012). There is a strongly significant effect of time on assemblage composition. Species identified as contributing significantly to the time effect are identified in bold (see Fig. 8, species names in Table 9). SC: Shady Cove; PG: Point George. The fifth Shady Cove block was removed from this analysis due to possibly spurious data at 4.5 months (see text for details).

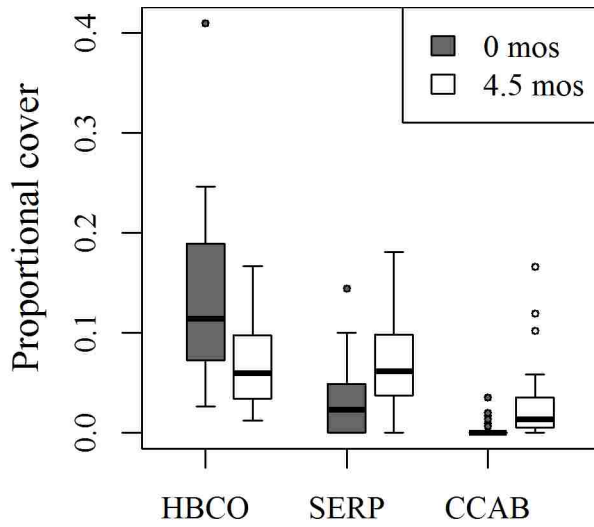


Figure 8. Boxplot of the three epibenthos species in the predator exclusion experiment whose proportional cover changed significantly from the beginning (0 mos, July 2012) to the end of the experiment (4.5 mos, December 2012). Hydrozoan-bryozoan complex (HBCO) decreased in cover, and serpulid worms (SERP) and bleached crustose coralline algae (CCAB) increased in cover.

CHAPTER 3

Correspondence between bottomfishes and benthic assemblages in the rocky subtidal zone of the San Juan Archipelago

ABSTRACT — Trophic cascades are a common pattern in temperate marine systems, often observed after the reduction or recovery of a top predator. Demersal predatory fishes, including lingcod, rockfish and greenling, were historically depleted in the San Juan Archipelago, but have since partially recovered in some areas. These fishes are known to affect their prey abundance, and my objective here was to determine if the impact of predatory fishes extends to other members of the benthic community as well. Between 2010 and 2012 I surveyed predatory fish, sessile epibenthos, and mobile invertebrate assemblages annually at shallow and deep transects in the rocky subtidal habitats of San Juan Channel. I found some evidence of predatory fishes co-varying with both the sessile epibenthos and mobile invertebrates at shallow, but not deep, transects, but the species involved in these co-variations do not suggest obvious trophic links between predatory fishes and the other assemblages. More likely, these co-variations are coincidental, represent an association of the predatory fishes with biotic habitat provided by the benthic species, or are explained by mutual association with other metrics such as current flow. I also directly compared the sessile epibenthos and mobile invertebrate assemblages, and found very strong correspondence between the two at both shallow and deep transects. At shallow depths, the dominant species involved in this correspondence included urchins, chitons, kelp, and social ascidians. Urchin abundance was negatively correlated with kelp cover, supporting the classic view of urchins as important herbivores on attached kelp. Urchins and chitons interacted to significantly reduce *Metandrocarpa taylori* cover, extending our understanding of this relationship from invertebrate-dominated rock walls to algae-dominated sloping surfaces. At deep transects, the correspondence between mobile invertebrates and sessile epibenthos was likely a result

of their shared correlation with current flow. My results show that the rocky subtidal community in the San Juan Archipelago is not structured by a trophic cascade initiated by demersal fishes. Instead, the correspondence seen between the three assemblages suggests a combination of consumptive interactions between lower trophic level organisms at shallow depths, and some dependence on current flow, particularly at deeper depths.

INTRODUCTION

Top predators may control the population of intermediate consumers, which may in turn control low-level consumers or producers. This pattern is known as a trophic cascade, where a change in the abundance of a top-level species may induce changes in the abundance of species at multiple lower trophic levels. The concept of the trophic cascade was first proposed by Hairston et al. (1960) to explain the “greenness” of the world. They argued that, while producers and predators are resource-limited, herbivores are predator-limited. In extreme examples, the presence or absence of a top predator may shift a community from a plant-dominated to an animal-dominated one. Available nutrients dictate how much potential primary production a system may support (“bottom-up” control), but predation dictates how much of that production is realized (Carpenter et al. 1985).

Some of the first examples of observed trophic cascades occurred in freshwater systems where the presence of planktivorous fishes altered the composition of the zooplankton, leading to large changes in the standing stock of phytoplankton. In lakes without fish, zooplankton populations boomed, leading to low phytoplankton abundance (Brooks & Dodson 1965). Trophic cascades have also been observed in streams (e.g. Power et al. 1985) and terrestrial settings (e.g. Terborgh et al. 2001, reviewed in Pace et al. 1999). However, of all habitat types, the effect size of a change in predator abundance is strongest in benthic marine systems (Shurin 2002), and consumer-driven control may be the driving factor of community structure in nearshore benthic ecosystems (Heck & Valentine 2007).

Strong cascades have been observed in both coastal (e.g. Estes et al. 1998) and open ocean systems (Baum & Worm 2009). Fishing typically targets high trophic-level species (Pauly et al. 1998), and many of the clearest examples of marine cascades have involved the harvest of top predators. One of the first studies to explicitly include humans as a top predator found that the exclusion of humans (through spatial harvest closures) increased the abundance of *Concholepas concholepas*, an intertidal predatory gastropod that feeds on spatially dominant mussels. In the absence of harvest, mussel populations are kept low, leaving space available for a more diverse intertidal community (Castilla & Duran 1985).

Subtidal examples of trophic cascades triggered by fishing come from tropical and temperate locations around the world. Extraction of predatory fishes can lead to significant changes in the abundance of tropical reef-building corals and temperate kelps, both important habitat-forming species, by releasing sea stars and sea urchins (respectively) from predation (Shears & Babcock 2002, Behrens & Lafferty 2004, Dulvy et al. 2004, Micheli et al. 2005, Guidetti 2006). Other wide-reaching impacts from fishing include situations where the removal of top predators can alter the fish assemblage from a large predator and small planktivore assemblage to one composed primarily of small piscivores (Lamb & Johnson 2010). A change in predator numbers can also alter the abundance of planktivorous fishes, changing the planktonic community from a large zooplankton-dominated condition to one dominated by small zooplankton and phytoplankton (Frank et al. 2005, Daskalov et al. 2007).

The occurrence and strength of trophic cascades may depend on certain species or community characteristics (Polis 1999). A meta-analysis (Borer et al. 2005) shows that

the most important predictors of trophic cascade strength are predator taxonomy, predator thermal regulation and herbivore metabolic rate (vertebrate endothermic predators and invertebrate herbivores led to stronger cascades). Across all ecosystem types, neither predator nor herbivore species richness reliably predicts cascade strength. In a review of trophic cascades observed in areas open and closed to fishing, Pinnegar et al. (2000) found that cascades most commonly involve urchins, possibly because they are consumed by fewer specialist predators than fishes are. Strong impacts on the community may only result from the removal of strong interactors, or of species that prey on strong interactors (sensu Paine 1980).

A diverse predator assemblage can alter the strength of top-down control, depending on the individual characteristics of the species involved (Schmitz 2007, Otto et al. 2008, Bruno & Cardinale 2008). Multiple predators may act synergistically, each imposing its own unique control over prey abundance or behavior and thereby enhancing the strength of a trophic cascade over that involving only one of the predators (Byrnes et al. 2006, Snyder et al. 2006). Conversely, interference between the multiple predators may reduce the strength of a cascade (Bruno & O'Connor 2005, Griffen & Byers 2006, O'Gorman et al. 2008). Finally, if the predators are functionally similar enough to act as substitutes for each other, a diverse predator assemblage will not trigger any different cascade than a single predator species would (Finke & Denno 2005).

The shallow subtidal zone of the San Juan Islands, in northwestern Washington State, is dominated by kelp beds (primarily *Agarum fimbriatum*) and harbors numerous urchins (*Mesocentrotus franciscanus* and *Strongylocentrotus droebachiensis*). Unlike in other temperate systems where urchin abundance is negatively correlated with standing

kelp biomass (Sala et al. 1998, Estes et al. 1998, Shears & Babcock 2002, Behrens & Lafferty 2004), large aggregations of urchins exist in the San Juans side-by-side with thick beds of kelp. Live *A. fimbriatum* is unpalatable due to its high concentration of phenolics (Vadas 1977, Steinberg 1985), and urchins in this system typically do not forage for live kelp (Britton-Simmons et al. 2009). Instead, they rely on strong tidal currents to bring drift algae to them, which may also provide more palatable food due to degradation of phenolics in aged kelp (Dethier et al. 2014). Experimental removals of urchins do not alter kelp biomass (Carter et al. 2007). In addition, predators of urchins are at very low abundance (*Anarrhichthys ocellatus* wolf eels: T. Parra, *personal communication*), were extirpated decades ago (*Enhydra lutris* sea otters: Lance et al. 2004) or are unable to consume large urchins (*Pycnopodia helianthoides* sea stars: Moitza & Phillips 1979, Duggins 1983). Therefore it is unlikely that the San Juan benthic community is strongly influenced by a predator-urchin-algae trophic cascade.

In this study I examine the co-occurrence of species in the rocky subtidal benthic community in the San Juan Archipelago. The top predators in this community are large fishes, including lingcod (*Ophiodon elongatus*), several species of rockfish (*Sebastes* spp.), kelp greenlings (*Hexagrammos decagrammus*), and several species of large cottids. These fishes feed on smaller demersal fishes, including sculpins and gobies, and on demersal invertebrates such as shrimp and crabs (O'Connell 1953, Moulton 1977, Nemeth 1997, Beaudreau & Essington 2007, Napazakov 2009, Ch. 1). In some cases there is also some intraguild predation, particularly large lingcod feeding on smaller rockfishes (Beaudreau & Essington 2007). The intermediate consumer fishes in the system tend to be generalist invertivores, targeting small mobile and sessile invertebrates

(Demetropoulos et al. 1990, Norton 1991a, Harvey et al. 2010). The epibenthos is composed of several species of kelp and other erect algae (primarily *A. fimbriatum*), encrusting algae, and filter-feeding invertebrates including bryozoans, sponges, tube worms, and tunicates. Finally, mobile invertebrates, including snails, chitons, urchins, sea cucumbers, and asteroids, make up another consumer assemblage. These non-prey mobile invertebrates tend to be grazers and predators on the epibenthic organisms.

In previous studies I have established that there is a strong trophic link between demersal predatory fishes and their prey in the San Juan Archipelago. The objective of this study is to determine if these predators influence lower trophic levels as well. Additionally, I seek to determine if there are co-occurrence relationships between the mobile invertebrates and the sessile epibenthos.

METHODS

Community Surveys

I conducted a series of benthic community surveys throughout San Juan Channel, WA, to observe the patterns of species distribution at a regional scale. Six locations within the channel were selected to include areas both open and closed to bottom fishing (Marine Research Preserves; WAC 1998) to encompass a wide range of bottomfish abundance. Locations were situated at least 1.5 km from each other, and covered a total distance of 10 km through northern San Juan Channel. At each location I selected two sites that contain contiguous bottomfish habitat (solid bedrock and large boulders;

Palsson et al. 2009) between the surface and 30 m below MLLW, for a total of 12 sites (Table 1, Fig. 1). At these survey sites I quantified three different groups of organisms (predatory fishes, mobile benthic invertebrates, and sessile epibenthic organisms) with three different survey methods, described below. All survey dives occurred at or near slack tidal current.

Predatory fish surveys – At each site I conducted two predatory fish surveys per year between 2010-2012 (Table 2). The start point for a survey was chosen haphazardly by approaching the site by boat and descending on SCUBA to 27 m deep. The direction of the transect was chosen based on the direction of tidal current flow: with minimal flow I travelled in the direction of the current, and with stronger flow I swam against the current. My surveys were modeled after previous studies of bottomfish abundance in the San Juan Islands (Moulton 1977, Eisenhardt 2001, Palsson et al. 2009), with modifications to increase safety for survey divers.

From the survey starting point two divers swam a 30 m long transect, while maintaining a constant rate of ascent from 27 m to 21 m depth. Each diver recorded fishes within 2 m of the transect and less than 2 m from the bottom, for a total transect cross-section of 4 m by 2 m. I counted and measured, to the nearest 5 cm, or nearest 1 cm where possible, total length for all rockfish (*Sebastes* spp.), lingcod (*O. elongatus*), greenling (*Hexagrammos* spp.), and large cottids (*Enophrys bison*, *Hemilepidotus* spp., *Myoxocephalus polyacanthocephalus*, and *Scorpaenichthys marmoratus*). I started a new 30 m long transect at the end of the first transect, ascending from 21 m to 15 m depth, followed by a third 30 m long transect from 15 m to 9 m, and a fourth 30 m long transect from 9 m to 3 m depth. I pooled the data from the 27 to 21 m and 21 to 15 m transects

into a “deep” community, and the data from the 15 to 9 m and 9 to 3 m transects into a “shallow” community. The total area covered in each of these two depth categories was 240 m². Fish lengths were converted to biomass using published relationships (see Ch. 2 and references therein).

Mobile invertebrate and epibenthos surveys – At each of the 12 sites I also conducted an annual survey of benthic organisms. In 2009 I established permanent transects at each site, extending 10 m horizontally at 9, 12, 18 and 21 m below MLLW. These depths were chosen so as to cross the transition from kelp-dominated shallow waters to invertebrate-dominated deeper zones (Britton-Simmons et al. 2009). Data from the 9 and 12 m transects were pooled into a “shallow” community, and data from the 18 and 21 m transects were pooled into a “deep” community.

I quantified mobile invertebrates (e.g. echinoderms, gastropods, etc.) by counting all individuals within 1 m of the transect, for a sample area of 20 m². Due to the cryptic appearance of many of these species, a lower size limit of 3 cm was chosen for inclusion in the surveys to ensure count accuracy. I did not consider crabs or shrimp in these surveys, as these are known prey items of the predatory fishes, and I was primarily interested in relationships beyond a single trophic link (see Ch. 2 for details of the effect of predatory fishes on shrimp, crabs, and prey fishes).

Sessile epibenthic organisms were quantified with a point-intercept transect, where the organism directly under the transect tape was recorded every 10 cm, for a total of 100 points per transect. In the event of overlapping epibenthic organisms (e.g. a kelp blade overlying a bryozoan crust) I recorded the uppermost organism only. Although this provides an incomplete view of the whole sessile community, I judged this to give a good

representation of the “fish’s eye view” of the epibenthos. I surveyed these transects annually between October and January, to coincide with a long-term monitoring project established by K. P. Sebens in San Juan Channel (Table 2). All species were identified to the lowest taxonomic level possible. Rare species were subsequently pooled together for analyses to avoid the strong distortions they can impose on the results of community analyses.

Shrimp and crabs were not included as part of the “mobile invertebrate” assemblage in this study, but their abundance was quantified separately for comparison to the sessile epibenthic assemblage. I counted crabs ≥ 3 cm within 1 m of the permanent transects, for a sample area of 20 m². I counted all shrimp within 0.5 m of one side of the transects, for a sample area of 5 m². Additionally, I counted all small fishes (another likely prey group of the predatory fishes, which includes sculpins, gobies and gunnels) within 0.5 m of one side of the transects (see Ch. 2 for details of the shrimp, crab, and fish surveys).

Current flow

In November 2011 I deployed alabaster clod cards at each of the mobile invertebrate and sessile epibenthos transects to quantify relative water motion between transects, depths, and sites (Eckman et al. 1989, Leichter & Witman 1997, but see Porter et al. 2000). The clod cards were square blocks of solid alabaster, measuring approximately 55 mm on a side and approximately 12 mm high. These blocks were affixed to acrylic plates with silicone caulking, and these plates were in turn attached to bricks with cable ties. I measured the surface area of each block, its initial mass, and its

final mass after being left in the field for between 9 and 13 days, to calculate mass lost, standardized per day and exposed surface area ($\text{g day}^{-1} \text{cm}^{-2}$). I ran a total of three consecutive rounds of clod card deployments, covering 34 days, or just over one full lunar tide cycle (Table 2). Relative water motion was expressed as the number of standard deviations from the global mean of standardized mass loss across all three deployments at all transects. A higher value indicates greater water flow at the transect, relative to transects with smaller values.

Urchins, algae, chitons, and ascidians

Results from the comparison between sessile epibenthos and mobile invertebrates led us to more fully explore the relationships between urchins, algae, chitons, and social ascidians. Urchins are well known mediators of algal abundance (Pinnegar et al. 2000), and are also known to interact with chitons to maintain open space on rocky surfaces, especially by clearing the spatially dominant social ascidian, *Metandrocarpa taylori* (Elahi & Sebens 2012, 2013).

Urchins were primarily red sea urchins, *M. franciscanus*, although a small number were green sea urchins, *S. droebachiensis*. Because both red and green urchins are important herbivores, and there were so few green urchins in my surveys, I pooled the two species for analyses. Chitons were treated as a group, and consisted of *Mopalia* and *Tonicella* species. Although the gumboot chiton, *Cryptochiton stelleri*, was part of my mobile invertebrate surveys, I did not include them in the direct comparisons to algae and ascidians because their large size makes them functionally distinct from the smaller chiton species (*C. stelleri* averaged 13.2 ± 0.3 cm [mean \pm s.e.], while *Mopalia* and

Tonicella were all ≤ 6 cm). Kelp species were treated as a group, and were predominantly *A. fimbriatum*, although also included *Saccharina* spp., *Costaria costata*, *Nereocystis luetkeana*, and *Laminaria complanata*. Erect red algae were treated as a group, and included species such as *Opuntella californica*, *Plocamium* spp., *Callophyllis* spp., and many other species. Crustose algae were treated as a group, and included both coralline and non-coralline encrusting species.

Metandrocarpa taylori ascidians were occasionally observed in my point-intercept surveys of the sessile epibenthos, but because of their small size they were frequently overlain by kelp and other canopy species, and so were not counted in the surveys. To more accurately assess *M. taylori* cover, I used a set of photographs taken at the same transects as the sessile epibenthos and mobile invertebrate surveys. Along each 10 m transect, I photographed ten randomly placed 25 cm by 35 cm quadrats. The objective of these photos was to record the primary space occupiers (i.e. not canopy or epibiotic organisms), so algal blades and other canopy organisms were moved out of the frame as much as possible without removal. I visually assessed *M. taylori* percent cover from these photos.

Statistical analysis

I compared the three different groups of organisms to each other using three different methods: principal coordinates analysis (PCoA), the BIO-BIO procedure, and multivariate linear models. These methods provide information about how two different assemblages relate to each other, but provide that information in slightly different ways. To help normalize data prior to analysis, I square-root transformed the predatory fish and

mobile invertebrate abundance matrices, and arcsine transformed the sessile epibenthos matrix. All matrices were then standardized using the Wisconsin double standardization.

PCoA is an unconstrained ordination, and provides a graphical representation of multivariate dissimilarity by identifying the axes of greatest variation in one dataset. PCoA is identical to principal components analysis, except that it allows the use of similarity metrics other than Euclidean distance. In this case, I used Bray-Curtis similarity because of the high frequency of zeros in the dataset. PCoA does not directly compare one community to another, but indirect comparisons of two communities can be made by correlating the primary PCoA axes of two separate communities. High correlations between these axes would indicate high correspondence between those communities.

The BIO-BIO procedure is a modification of Clarke and Ainsworth's (1993) BIO-ENV procedure, which seeks to explain the variation of one abundance matrix (e.g. the predatory fish assemblage) with the optimum subset of variables from a second abundance matrix (e.g. the sessile epibenthos assemblage). The procedure begins by calculating a Spearman rank correlation between the Bray-Curtis similarity matrices of a predictor and a response abundance matrix, and then repeating the process for every possible subset of the predictor matrix to find the subset that maximizes the correlation between the two similarity matrices. I used Mantel tests with 999 permutations to test the significance of correlations. With very large matrices, this procedure is extremely computationally intensive, and as a result I was forced to limit the maximum number of species the deep sessile epibenthos assemblage could identify as the best predictors of the other two assemblages to no more than five species (i.e. all 284,273 possible

combinations of up to five of the 33 deep sessile epibenthos species were assessed through BIO-BIO subset testing).

In addition to considering the predatory fishes as a multivariate assemblage, as in the previous two methods, I used multivariate linear models to compare the multivariate sessile epibenthos and mobile invertebrate assemblages to univariate measures of pooled predatory fish abundance and biomass (with 9999 resampling permutations to determine significance). Because of the high degree of diet overlap in the predatory fish assemblage (especially of demersal crustaceans and small fishes; Miller et al. 1977, Murie 1995, Beaudreau & Essington 2007, Ch. 1), pooling the predatory fishes is a reasonable action to test their additive effects rather than their effects as an assemblage. To normalize the pooled predatory fish data, I square-root transformed fish abundance and log transformed fish biomass. Sessile epibenthos and mobile invertebrate matrices were normalized and standardized as described above. When significant predatory fish effects were found I used univariate tests, adjusted for multiple testing using a step-down resampling procedure, to determine which species in the response matrices significantly vary with predatory fishes.

I explored the effects of current flow on the three assemblages with two methods. First, I tested correlations of current flow to the first and second principal coordinate axes of each assemblage. Second, I used multivariate linear models, with flow predicting each assemblage type, following the same methods described above to determine which species responded significantly to flow. Because current is known to affect the richness of sessile benthic assemblages (Palardy & Witman 2011, Elahi et al. 2014), I also tested

correlations between current flow and sessile epibenthic richness. Finally, I also compared shrimp, crab, and small fish abundance to current flow using correlation tests.

I tested possible associations of shrimp, crabs, and small fishes with the sessile epibenthos assemblage using correlations between the PCoA axes of the sessile epibenthos and abundance of the three species groups. To normalize the abundance values I square-root transformed shrimp, crab, and small fish abundance prior to analysis.

I used multivariate linear models to compare urchin abundance to algal cover, and standard linear models to compare urchin abundance to chiton abundance and to compare urchin and chiton abundance to *M. taylori* cover. I square root transformed urchin and chiton abundance and arcsine transformed algal and *M. taylori* cover prior to analysis to normalize the data, and pooled the *M. taylori* data across quadrats within each transect.

All statistical analyses were conducted in R 3.1.2 (R Core Team 2014), using the packages ‘mvabund’ (Wang et al. 2014), ‘sinkr’ (Taylor 2015), and ‘vegan’ (Oksanen et al. 2015).

RESULTS

Eight predatory fish, 36 sessile epibenthic, and 16 mobile invertebrate species and functional groups were identified for inclusion in this study (Tables 3-5).

Sessile epibenthos and predatory fishes

PCoA – There was a weak, but non-significant, correlation between the first principal coordinate axes of the sessile epibenthos and predatory fishes at shallow

transects. The correlation between the sessile epibenthos and predatory fishes first axes was also not significant at deep transects. Correlations between the sessile epibenthos first axis and predatory fishes second axis, and vice versa, at both depths were all non-significant. The correlation between the epibenthos and predatory fishes second axes was highly significant for shallow transects, and weak but non-significant for deep transects. See Figs. 2-4 for details about individual principal coordinates analyses for each organism group, and Table 6 for correlation coefficients between groups.

BIO-BIO – There is a weak, but significant, correlation between the predatory fishes and the sessile epibenthos at shallow depths (Spearman $\rho = 0.14$, $p = 0.034$). (Table 6). BIO-BIO subset analysis of the shallow assemblages, with predatory fishes as the variable predictor matrix, shows that copper rockfish and cottids provide the best predictors of epibenthic assemblage ($\rho = 0.22$) (Fig. 5). Turning the analysis around, with the sessile epibenthos as the predictor matrix, shows that non-coralline encrusting algae, erect red algae, the social ascidian *M. taylori*, and erect coralline algae are the best predictors of the predatory fish assemblage ($\rho = 0.26$) (Fig. 6). There is not a significant correlation between predatory fishes and sessile epibenthos at the deeper transects ($\rho = -0.03$, $p = 0.65$).

Univariate analysis – There is a significant relationship between pooled predatory fish abundance and the sessile epibenthos at shallow transects ($p = 0.044$). Of the sessile epibenthos, erect red algae was the only group that was significantly related to predatory fish abundance ($p = 0.025$). There was a weak, but non-significant, relationship between predatory fish abundance and sessile epibenthos at deep transects ($p = 0.079$). There is not a significant relationship between pooled predatory fish biomass and the sessile

epibenthos at either the shallow or deep transects ($p = 0.179$ and 0.185 , respectively) (Figs. 7, S1-S4).

Mobile invertebrates and predatory fishes

PCoA – At shallow transects, the correlation between the first principal coordinate axis of the mobile invertebrates and predatory fishes is not significant, nor is the correlation between the second principal coordinate axes, or between the first predatory fish axis and the second mobile invertebrate axis. The first mobile invertebrate axis is significantly correlated with the second predatory fish axis.

At deep transects, the first axes of the predatory fish and mobile invertebrate ordinations are significantly correlated, but correlations between the second axes are not significant. Correlations between the mobile invertebrate first axis and predatory fish second axis, and vice versa, were not significant.

BIO-BIO – There is not a significant correlation between predatory fish and mobile invertebrate assemblages at either the shallow ($\rho = 0.09$, $p = 0.13$) or deep transects ($\rho = 0.004$, $p = 0.46$).

Univariate analysis – Pooled predatory fish abundance was a weak, but not significant, predictor of mobile invertebrate assemblage at shallow transects ($p = 0.066$), and was not related to the mobile invertebrate assemblage at deep transects ($p = 0.24$). Pooled predatory fish biomass was a strong predictor of the shallow mobile invertebrate assemblage ($p = 0.004$), and was not related to the mobile invertebrate assemblage at deep transects ($p = 0.65$). Of the shallow mobile invertebrates, the holothurian

Parastichopus californicus was the only individual species that significantly varied with shallow predatory fish biomass ($p = 0.021$) (Figs. 8, S5-S8).

Sessile epibenthos and mobile invertebrates

PCoA – At shallow transects the first principal coordinate axes of the sessile epibenthos and mobile invertebrate assemblages are significantly correlated. The first mobile invertebrate axis is significantly correlated with the second sessile epibenthos axis, as are the second mobile invertebrate and first sessile epibenthos axes. The second principal coordinate axes of sessile epibenthos and mobile invertebrate assemblages are not significantly correlated.

At deep transects the first principal coordinate axes of the sessile epibenthos and mobile invertebrate assemblages are significantly correlated, but the second axes are not correlated with either the first axes or with each other.

BIO-BIO – There is a highly significant correlation between sessile epibenthos and mobile invertebrates at both shallow and deep transects ($\rho = 0.26$ and 0.29 , $p = 0.001$ and 0.001 , respectively) (Table 6). *BIO-BIO* subset analysis of the shallow transects, with mobile invertebrates as the variable predictor matrix, shows that *Dirona* spp., *Mopalia* spp., *Nucella* spp., and Strongylocentrotid urchins provide the best predictors of the epibenthic assemblage ($\rho = 0.50$) (Fig. 9). Turning the analysis around, with the sessile epibenthos as the variable predictor matrix, shows that *A. fimbriatum*, *M. taylori*, non-coraline encrusting algae, sponges, and solitary tube worms are the best predictors of the mobile invertebrate assemblage ($\rho = 0.40$) (Fig. 10).

At the deep transects, with mobile invertebrates as the variable predictor matrix, *Henricia* spp., *Nucella* spp., *P. californicus*, Strongylocentrotids, *Triopha catalinae*, and dorid nudibranchs are the best predictors of the sessile epibenthic assemblage ($\rho = 0.42$) (Fig. 11). With sessile epibenthos as the variable predictor matrix, *A. fimbriatum*, barnacles, *Diaperoecia californica*, solitary tunicates, and colonial tubeworms are the best predictors of the mobile invertebrate assemblage ($\rho = 0.26$) (Fig. 12).

Current flow

There was considerable variation in relative current flow between the survey sites at both depth strata (Tables S1-S2). At shallow transects, relative current flow was significantly correlated only with the first principal coordinates axis of the mobile invertebrate assemblage, and the second axes of the sessile epibenthos and predatory fish assemblages. At deep transects, current flow was significantly correlated only with the first axes of the sessile epibenthos and mobile invertebrate assemblages, although it was weakly but non-significantly correlated with the second axis of the predatory fish assemblage (Figs. 2-4, S9-S12, Table 6).

Multivariate linear modeling showed similar patterns of current flow correlating with the three assemblages. At shallow transect sites, flow significantly predicted sessile epibenthos and mobile invertebrate assemblages ($p < 0.001$). Flow was positively correlated with erect fleshy and coralline algae, *Cryptochiton stelleri*, and dorid nudibranchs (all $p < 0.05$), and was negatively, but not significantly, correlated with large asteroids ($p = 0.065$). At deep transects flow significantly predicted all three assemblage types ($p < 0.05$). Flow was positively correlated with *Abietinaria* spp., *Terebratalia*

transversa, colonial tube worms, *Chlamys hastata*, *Henricia* spp., dorid nudibranchs, and kelp greenling, and was negatively correlated with encrusting non-coralline algae, hydrozoan-bryozoan complex, solitary tube worms, and Strongylocentrotid urchins (all $p < 0.01$), and was negatively, but not significantly, correlated with *P. californica*, ($p = 0.087$).

Current flow was not significantly linearly correlated with sessile epibenthic richness at either shallow or deep transects ($p = 0.44$ and 0.25 , respectively). However, at deep transects this lack of statistical significance appeared to be driven by depressed richness at the two highest flow sites (One Mile Reef and Point George Center, Fig. 1). Quadratic regression at deep transects showed a highly significant effect of current on sessile epibenthic richness, with richness initially increasing with increasing current flow, and then declining again at very high flow ($p < 0.001$) (Fig. 13).

Shrimp, crabs, and small fishes

At shallow transects there was a significant correlation between small fish abundance and the first PCoA axis of the sessile epibenthos ($p = 0.02$). There were not significant correlations between shrimp or crabs and the first PCoA axis ($p = 0.24$ and 0.68 , respectively), nor were there significant correlations between any of the three species groups and the second PCoA axis ($p = 0.10$, 0.84 , and 0.93 , respectively for shrimp, crabs, and small fishes) (Figs. 14A-B, 15A-B, 16A-B).

At deep transects there was a significant correlation between the first PCoA axis of the sessile epibenthos and both shrimp abundance ($p < 0.001$) and crab abundance ($p = 0.01$). There was not a significant correlation between shrimp and the second PCoA axis

($p = 0.35$), and a non-significant trend between crabs and the second PCoA axis ($p = 0.07$). Small fish abundance was not significantly correlated to either the first or second PCoA axis ($p = 0.72$ and 0.36 , respectively) (Figs. 14C-D, 15C-D, 16C-D).

Shrimp abundance was strongly negatively correlated with current flow at both shallow ($p < 0.001$) and deep ($p = 0.005$) transects (Fig. 17A, D). Crab abundance was weakly but not significantly correlated with current flow at shallow transects ($p = 0.08$), but was strongly positively correlated with current flow at deep transects ($p < 0.001$) (Fig. 17B, E). Small fish abundance was weakly but not significantly correlated with current flow at shallow transects ($p = 0.10$), and was not correlated with current flow at deep transects ($p = 0.22$) (Fig. 17C, F).

Urchins, algae, chitons, and ascidians

At shallow transects, urchin abundance is a significant predictor of the algal assemblage ($p \ll 0.001$). With increasing urchin abundance, kelp cover and erect red algal cover both decrease ($p = 0.020$ and 0.020 , respectively), and crustose algal cover increases ($p \ll 0.001$) (Fig. 18A). Urchin abundance was also positively correlated with chiton abundance at shallow transects ($p = 0.002$) (Fig. 19A).

At deep transects, the correlation between urchin abundance and the algal assemblage is statistically significant ($p = 0.049$), but the biological effect size is small. With corrections for multiple testing, none of the individual algal groups appear significantly related to urchin abundance ($p = 0.12$, 0.17 , and 0.37 , for kelp, erect red algae, and crustose algae, respectively). Without corrections for multiple testing, kelp appears to significantly, but weakly, relate to urchins ($p = 0.04$), but erect red algae and

crustose algae still do not ($p = 0.09$ and 0.37 , respectively) (Fig. 18B). Urchin abundance was not correlated with chiton abundance at deep transects ($p = 0.88$) (Fig. 19B).

Because urchin and chiton abundance were not related at deep transects, I tested their relationship to *M. taylori* abundance only at shallow transects. At shallow transects, neither urchins nor chitons were significant predictors of *M. taylori* ($p = 0.19$ and 0.25 , respectively), but the interaction between urchins and chitons was highly significant ($p = 0.008$) (Fig. 20).

DISCUSSION

The predatory fish assemblage in San Juan Channel, WA, does not appear to exert a strong signal of top-down control on sessile or mobile members of the rocky subtidal community which are not likely to be prey. Previous work (Ch. 2) has shown an influence of predatory fishes on the abundance of their primary prey species (shrimp and small fishes). These mid-level consumers prey on a wide diversity of benthic organisms, including amphipods, worms, and scavenged prey. Despite the strong effect previously demonstrated of top predators on these intermediate-level species, there appear not to be further cascading effects in the benthic communities surveyed. This is likely due in part to the wide diet breadths of both the top and intermediate predators, and in part to the survey methods used. Lingcod and rockfish both feed on a variety of pelagic prey in addition to demersal crustaceans and fishes, attenuating the focus of this first trophic link by distributing it over a wider prey base. At the second trophic step, the broad diets of

demersal crustaceans and fishes serve to further attenuate any remaining potential top-down signal.

Additionally, the sessile epibenthos surveys primarily sampled canopy organisms, which were dominated by algae, particularly at the shallow transects. Algae compose a small or non-existent part of the diet of the intermediate species, so it may be reasonable to not observe an effect of top predators on the sessile epibenthos assemblage by way of these intermediate species. Despite this methodological limitation, studies of the understory sessile epibenthos in the context of a predator exclusion experiment also failed to show an effect of predatory fishes (Ch. 2). Benthic predatory fishes in the San Juan Archipelago do not appear to trigger a multi-level trophic cascade. This result supports the previously reported finding of minimal change in the sessile benthic assemblage on vertical rock walls in the San Juan Archipelago across 40 years, despite the large decline in predatory fish populations in that time (Elahi et al. 2013).

Even if predatory fishes are not having a strong influence on epibenthic assemblage composition, they could still be associating with particular types of epibenthos, for example where their prey are more abundant. In this study, the predatory fish assemblage is weakly associated with both the sessile epibenthos and mobile invertebrate assemblages at shallow transects, but there is no apparent correspondence between the assemblage types at deep transects. Despite the lack of reasonable trophic connections between predatory fishes and either the mobile invertebrate or sessile epibenthos assemblage, there was still moderate evidence of correspondence between predatory fishes and the other two assemblages at shallow transects: the second PCoA axis of the predatory fishes was significantly negatively correlated with the first mobile

invertebrate PCoA axis and second sessile epibenthos PCoA axis. These three axes also all have significant correlations with current flow (positive for mobile invertebrates and sessile epibenthos, negative for predatory fishes), suggesting that they could be related to each other by way of this physical parameter, rather than directly related. Additionally, three of the species identified as significantly related to current flow, erect coralline algae, erect red algae, and large asteroids, were also identified as significantly related to the predatory fish assemblage.

Predatory fishes also showed some evidence of relation to the other two shallow assemblages when considered by pooled abundance and biomass, rather than by assemblage composition. Pooled predatory fish abundance was significantly related to the shallow sessile epibenthos assemblage, and pooled predatory fish biomass was significantly related to the shallow mobile invertebrate assemblage. The individual species that change with predatory fish abundance and biomass (erect red algae and *P. californicus* sea cucumbers) are again not known to be prey items of the predatory fishes or their prey.

The observed relationship between predatory fishes and the sessile epibenthos may be a result of habitat association, rather than consumptive or abiotic effects. Habitat complexity, including biotic habitat, is positively associated with fish diversity and survival (Connell & Jones 1991, Ferreira et al. 2001, Lazzari & Tupper 2002). The predatory fishes in this study are associated with high complexity habitats, particularly those with high rocky relief, but also those with algal cover (Palsson et al. 2009). In addition, Pandalid shrimp, the preferred prey of copper rockfish, are positively associated with *Agarum* beds (Marliave & Roth 1995). Factors besides trophic links may again be

responsible for the apparent relationships between predatory fishes and the other two assemblages examined.

Comparisons of shrimp, crabs, and small fishes to the sessile epibenthos assemblages support the hypothesis that the correspondence between sessile epibenthos and predatory fishes may be a result of an association between fish prey and the epibenthos. All three groups of prey species showed significant correlation with the sessile epibenthos assemblage, although only the small fishes showed a correlation with the shallow sessile epibenthos, the assemblage with which the predatory fishes showed the greatest degree of correspondence.

For shrimp and crabs, the absence of a correlation with the shallow sessile epibenthos may be a result of the kelp dominance at this depth; from the perspective of these crustaceans there may be insufficient variation in the epibenthos to influence their distribution. In the absence of kelp along the deep transects, the shrimp may be responding to the identity of the sessile epibenthic assemblage. However, both shrimp and crab abundance also strongly correlate with current flow, and their correlation with the sessile epibenthic assemblage may instead result from mutual dependence on water motion. Interestingly, although my findings show a negative correlation between shrimp abundance and current flow, previous observations of *Pandalus danae*, the most abundant shrimp species, found them in areas of high tidal current flow (Butler 1964).

There is strong evidence that the sessile epibenthos and mobile invertebrate assemblages vary together in predictable ways at both shallow and deep transects. Using BIO-BIO, the two sessile epibenthic species that best predict the shallow mobile invertebrate assemblage are *A. fimbriatum* and non-coralline encrusting algae, and two of

the mobile invertebrate species that best predict the shallow sessile epibenthic assemblage are urchins and chitons (*Mopalia* spp.) (Figs. 9, 10).

Globally, urchins are known to be important ecosystem engineers in temperate marine systems. Urchin herbivory can initiate major shifts in algal cover, which can in turn trigger changes in other community members dependent on the food, habitat, or other services provided by algae (Pinnegar et al. 2000). However, red urchins in San Juan Channel do not tend to form foraging fronts and move long distances in pursuit of live algae (Dean et al. 1984, Carter & VanBlaricom 2002), and instead rely on drift algae brought by strong tidal current flow or on omnivory (Britton-Simmons et al. 2009, Elahi & Sebens 2012). Experimental removals of urchins from large (400 m²) shallow (6-10 m depth) areas in San Juan Channel did not result in an increase in algal abundance (Carter et al. 2007). However, urchin additions on deeper vertical rock walls (12-18 m depth) at a much smaller scale (5 m²) resulted in a reduction of the cover of macroalgae and certain invertebrates (Elahi & Sebens 2012). In addition, chitons have been suggested as associates of urchins, taking advantage of space made available by urchin grazing and helping to maintain available space, particularly by clearing colonial ascidians (Elahi & Sebens 2012, 2013).

My results from sloping and horizontal rock surfaces at intermediate scale (20 m²) and depth (9-12 m depth) support urchins as mediators of benthic algal abundance, showing evidence that the presence of urchins reduces macroalgal cover, while allowing an increase in encrusting algae. My surveys also show a positive relationship between urchins and chitons, and a significant effect of their interaction on the social ascidian, *M. taylori*. These results all support those observed on nearby rock walls (Elahi & Sebens

2012, 2013), although the relative abundance of the sessile species are different on sloping and horizontal rock surfaces. The more horizontal aspect of my survey sites gives the sites greater access to light, leading to higher overall algal cover, and also exposes the sites to greater sedimentation, which is detrimental to ascidian recruitment and growth, leading to lower overall *M. taylori* cover (Jackson 1977). The generally lower ascidian cover compared to vertical surfaces makes it particularly surprising that I could detect an effect of chitons and urchins.

One hypothesis to explain urchins feeding on invertebrates on rock walls is that this habitat lacks sufficient attached algae for them, and they turn to omnivory. Although there was abundant kelp at my sloping transects, the dominant species, *A. fimbriatum*, is heavily chemically defended (Steinberg 1985), which may also encourage urchins to seek alternate food sources such as benthic invertebrates and drift algae.

The discrepancy between my results and those from Carter et al. (2007) may be a factor of the scale at which the work was done. Although urchins in San Juan Channel do not form destructive foraging fronts, they likely consume algae in their immediate vicinity. With high urchin density, kelp and other erect algae are locally depleted, opening space for other epibenthic species such as encrusting algae and invertebrates. Although urchins in the San Juan Archipelago do not conform to the paradigm of system-wide ecosystem engineers, they do appear to exert control over the benthic community at a local scale (Elahi & Sebens 2013, Lowe et al. 2015).

Despite the strong correspondence between mobile invertebrate and sessile epibenthos assemblages at the deep transects, the species identified as important predictors of assemblages do not have direct associations with each other. In general, the

mobile invertebrate species (*Henricia*, *P. californicus*, urchins, *Nucella*, *T. catalinae*, and dorid nudibranchs) are not known predators of the identified epibenthic species (*A. fimbriatum*, *D. californica*, solitary tunicates, colonial tubeworms, and barnacles), with two exceptions: urchins prey on *A. fimbriatum*, and *Nucella* prey on barnacles. As described above, there is a weak positive relationship between urchin and kelp abundance at deep transects, suggesting that urchins at deep transects could be homing in on the rare kelp that is present. However, because overall kelp cover is very low along deep transects (typically <5% cover), urchin predation is unlikely to have a meaningful biological impact on kelp and kelp-associated species at this depth.

There is a significant ($p \ll 0.01$) positive relationship between transformed *Nucella* abundance and barnacle cover. The majority of transects lacked both *Nucella* and barnacles, and this relationship is driven by a single transect with relatively high abundance of both species (18 *Nucella* and 10% cover of barnacles). Additionally, *T. catalinae* are known to feed on arborescent bryozoans, and there is a positive but not significant correlation between transformed *D. californica* cover and *T. catalinae* abundance ($p = 0.14$). However, *T. catalinae* typically feeds on less calcified arborescent bryozoans such as *Dendrobeania* and *Crisia* (Nybakken & Eastman 1977, Harvell 1984), so the identification of *D. californica* and nudibranchs as indicators of sessile and mobile assemblages may be coincidental. Although many species of dorid nudibranchs are known to feed on bryozoans, the dorids included in this study (Table 5) are predators on sponges or non-calcified bryozoans (McDonald & Nybakken 1997).

One alternate explanation for the apparent strong correspondence between deep sessile epibenthos and mobile invertebrates is their mutual correspondence with another

variable. The first principal coordinates axes of both assemblages are highly correlated with relative current flow. Of the six mobile invertebrate species groups that significantly relate to the sessile epibenthos assemblage, four also co-vary with current flow (*Henricia* spp., dorid nudibranchs, *P. californicus*, and urchins). Sea cucumbers and urchins were both negatively correlated with flow, which is known to limit both of their distributions through dislodgement and behavioral changes (Da Silva et al. 1986, Siddon & Witman 2003). Dorids and *Henricia* are both predators on sponges and other encrusting invertebrates, many of which benefit from living in higher flow (LaBarbera 1984, Sebens 1984, Eckman & Duggins 1993). Consequently, dorids and *Henricia* may be more abundant at high flow sites in response to prey distributions. Sponges were not identified as strong drivers of the sessile epibenthos assemblage, but this may have been a result of the survey method, which preferentially identified canopy organisms (e.g. algae, erect bryozoans and hydroids) at the expense of primary space occupiers like sponges.

Apart from the possible response of *Henricia* and dorids, it seems more likely that the correspondence in assemblage types between deep sessile epibenthos and deep mobile invertebrates is a result of each assemblage independently responding to current flow, rather than there being a direct trophic link between these two groups of organisms. For example, sessile epibenthic species richness initially increased with increasing current flow, up until the highest flows measured, where richness declined. The decrease in richness at very high flows may be a result of some species being unable to settle as larvae or maintain their position after recruitment (Denny 1988, Abelson & Denny 1997, Hurd 2000).

Conclusions

Habitat type and quality are strong determinants of bottomfish residence. Rockfish prefer high-relief, high-complexity rocky habitats (Pacunski & Palsson 2001, Palsson et al. 2009). In addition to abiotic habitat, biotic habitat-forming kelp is also an important predictor of rockfish prevalence, particularly in lower-relief habitats (Richards 1987, Matthews 1990a, Palsson et al. 2009). Although I did not find evidence for top-down control by predatory bottomfishes on the sessile epibenthos or most mobile invertebrates, the correspondence I observed between predatory fishes and the other two assemblages suggests that predatory fishes may view the sessile epibenthos or some species of mobile invertebrates as components of their biotic habitat and cues to the likely abundance of their preferred prey. The type of benthic assemblage present could influence predatory fish abundance and species composition by providing additional physical structure.

There was a very strong correspondence between the mobile invertebrate and sessile epibenthos assemblages. In some cases this correspondence seems to be the result of consumptive interactions, while in others it seems to be a byproduct of the two assemblages responding in the same ways to water movement. San Juan Channel is characterized by strong tidal currents, often exceeding 1 m/sec, and it is reasonable that the subtidal community would be strongly influenced by water motion. The mechanisms I have discussed here focus on post-recruitment processes, but mechanisms such as larval supply, the identity of previous recruits, and post-settlement mortality may all influence the community that develops in a location (Rodriguez et al. 1993).

It is important to recall that this is an observational study, and hence the relationships described here between members of the rocky subtidal community should be seen as correlative, and not always causative. In the case of the ascidian, *M. taylori*, these results provide supporting evidence of patterns observed in previous experiments, extending those findings to new habitats. In the case of the urchin-algae relationship, these results rekindle the question of whether urchins in the San Juan Archipelago act as kelp-limiting herbivores, as in so many other temperate systems, or if they rely on drift to the extent that they do not affect kelp standing stock. The answer to this question may be scale dependent, where urchins do control algae at the transect scale, but not at the site scale. Although there are no significant predators in the San Juan Islands that consume adult red urchins, the distribution of the urchins is patchy, with sites of very high abundance and sites of near absence. Current flow likely plays a part in setting this distribution, but other factors such as food availability (both attached and drifting) may also contribute. However urchin variation develops, that variation does appear to play some role in controlling kelp cover in the San Juan Islands, a role not previously thought to be important in this system (Carter et al. 2007).

Predatory fishes in the rocky subtidal of the San Juan Archipelago do not appear to exert a strong influence on either the mobile invertebrates or sessile epibenthos (except for shrimp). This result is perhaps not surprising, given that these fishes do not prey directly on the mobile invertebrate and sessile epibenthos species quantified here, and the prey species the predatory fishes do control have diets too broad to have strong trophic links. As demersal predatory fishes recover from their historic lows in the San Juan

Archipelago, we should not expect marked changes in the rocky subtidal mobile invertebrate or sessile epibenthos assemblages.

Table 1. Summary of site locations.

Site number	Location	Site name	Latitude (N)	Longitude (W)
1	Shady Cove	Shady South	48° 33.023'	123° 00.319'
2	Shady Cove	Shady Center	48° 32.835'	123° 00.316'
3	Mineral Point	Mineral Center	48° 35.532'	123° 04.463'
4	Mineral Point	Mineral North	48° 35.594'	123° 04.705'
5	Yellow Island	Yellow Island	48° 35.472'	123° 01.664'
6	Yellow Island	Low Island	48° 35.366'	123° 01.587'
7	Neck Point	Neck North	48° 34.797'	123° 00.975'
8	Neck Point	Neck South	48° 34.754'	123° 00.766'
9	Point George	George Center	48° 33.348'	122° 59.093'
10	Point George	George South	48° 33.182'	122° 58.792'
11	Pear Point	One Mile Reef	48° 32.245'	122° 59.221'
12	Pear Point	Minnesota Reef	48° 31.689'	122° 58.048'

Table 2. Summary of survey periods.

	Year	Month
Predator Surveys	2010	3-20 May
		14-18 August
	2011	15 June - 8 July
		8-12 October
	2012	24 June - 11 July
		6-9 August
Epibenthos and Invertebrate Surveys	2010	Oct-Jan
	2011	Oct-Jan
	2012	Oct-Jan
Clod card deployments	2011	5-7 Nov to 17-19 Nov
		17-19 Nov to 28-30 Nov
		28-30 Nov to 7-9 Dec

Table 3. Predatory fish species.

Common name	Species
Copper rockfish	<i>Sebastes caurinus</i>
Quillback rockfish	<i>S. maliger</i>
Brown rockfish	<i>S. auriculatus</i>
Tiger rockfish	<i>S. nigrocinctus</i>
Lingcod	<i>Ophiodon elongatus</i>
Kelp Greenling	<i>Hexagrammos decagrammus</i>
Whitespotted Greenling	<i>H. stelleri</i>
Cottids	<i>Enophrys bison</i> , <i>Hemilepidotus hemilepidotus</i> , <i>Myoxocephalus polyacanthocephalus</i> , <i>Scorpaenichthys marmoratus</i>

Table 4. Sessile epibenthos species codes.

Code	Species
ABTI	<i>Abietinaria</i> spp.
AGFI	<i>Agarum fimbriatum</i>
BAEL	<i>Balanophyllia elegans</i>
BANU	<i>Balanus nubilus</i>
BARE	Bare rock
BARN	Other barnacles – <i>Balanus crenatus</i> , <i>Semibalanus cariosus</i>
BRBR	Erect bryozoans – <i>Bugula californica</i> , <i>Dendrobeatia murrayana</i>
CCAP	Crustose coralline algae
CRGI	<i>Crassodoma gigantean</i>
CRIS	<i>Crisia</i> spp.
DICA	<i>Didemnum carnulentum</i>
DICL	<i>Diaperoecia californica</i>
DOCO	<i>Dodecaceria concharum</i>
EALM	Non-coralline encrusting algae
ENBR	Other encrusting bryozoans
ERCR	Erect coralline algae
EUBI	<i>Eurystomella bilabiata</i>
HBCO	Hydrozoan-bryozoan complex – indeterminate taxonomic status, appearing as sediment bound in a three-dimensional matrix often including erect hydroids and/or bryozoans or parts thereof
HEPA	<i>Heteropora pacifica</i>
HYSP	Other hydroids – <i>Aglaophenia</i> spp., <i>Hydrallmania distans</i> , <i>Lafoea dumosa</i> , <i>Obelia</i> spp.
KELP	Other kelps – <i>Saccharina</i> spp., <i>Costaria costata</i> , <i>Nereocystis luetkeana</i> , <i>Laminaria complanata</i>
META	<i>Metandrocarpa taylori</i>
MOMD	<i>Modiolus modiolus</i>
PDMC	<i>Pododesmus macrochisma</i>
PSCH	<i>Psolus chitonoides</i>
RFSP	Erect red algae – <i>Opuntiella californica</i> , <i>Plocamium</i> spp., <i>Callophyllis</i> spp., others
SCUN	<i>Schizoporella</i> spp.
SPUN	Sponges – <i>Halichondria</i> spp., <i>Ophlitaspongia pennata</i> , others
STYL	<i>Stylantheca</i> spp.
TETR	<i>Terebratalia transversa</i>
TUBC	Amphipod colony
TUSO	Solitary tunicates – <i>Cnemidocarpa finmarkiensis</i> , <i>Halocynthia igaboja</i> , <i>Pyura haustor</i> , <i>Styela</i> spp., <i>Boltenia villosa</i> , <i>Chelyosoma</i> spp.
TWCO	Colonial tube worms – <i>Phyllochaetopterus</i> spp., <i>Dodecaceria fewkesi</i>
TWSO	Solitary tube worms – <i>Serpula columbiana</i> , <i>Idanthyrus saxicavus</i> , others
ULVA	<i>Ulva</i> spp.
XEED	<i>Xestospongia edapha</i>

Table 5. Mobile invertebrate species codes.

Code	Species
CFO	<i>Ceratostoma foliatum</i>
CHA	<i>Chlamys hastata</i>
CST	<i>Cryptochiton stelleri</i>
DOR	Dorid nudibranchs – <i>Acanthodoris hudsoni</i> , <i>A. nanaimoensis</i> , <i>Cadlina luteomarginata</i> , <i>C. modesta</i> , <i>Diaulula sandiegensis</i> , <i>Doris montereyensis</i> , <i>D. odhneri</i> , <i>Geitodoris heathi</i> , <i>Peltodoris nobilis</i>
DEN	<i>Dendronotus</i> spp.
DIR	<i>Dirona</i> spp.
FOR	<i>Fusitriton oregonensis</i>
HEN	<i>Henricia</i> spp.
LST	Large asteroids – <i>Dermasterias imbricata</i> , <i>Evasterias troschelli</i> , <i>Mediaster aequalis</i> , <i>Orthasterias koehleri</i> , <i>Pisaster ochraceus</i> , <i>Pteraster tesselatus</i> , <i>Solaster dawsoni</i> , <i>S. stimpsoni</i> , <i>S. endeca</i>
MKE	<i>Mopalia</i> spp.
NUC	<i>Nucella</i> spp.
PCA	<i>Parastichopus californicus</i>
PHE	<i>Pycnopodia helianthoides</i>
STR	Strongylocentrotid urchins – <i>Mesocentrotus franciscanus</i> , <i>Strongylocentrotus droebachiensis</i>
TCA	<i>Triopha catalinae</i>
TLI	<i>Tonicella</i> spp.

Table 6. Correlation coefficients for associations between the three organism groups and current flow at shallow and deep transects. Correlations are between the first and second principal coordinates axes of each organism group, between the principal coordinate axes and relative current flow, and BIO-BIO Spearman correlations (ρ). Text in bold indicates significant ($p < 0.05$) correlation coefficients.

Shallow		Current	Predators		Invertebrates	
			Axis 1	Axis 2	Axis 1	Axis 2
Sessile Epibenthos	Axis 1	0.10	-0.30	-0.05	-0.34	0.41
	Axis 2	0.41	0.22	-0.43	0.37	-0.05
	ρ		0.14		0.26	
Mobile Invertebrates	Axis 1	0.71	0.12	-0.38		
	Axis 2	0.10	-0.16	-0.22		
	ρ		0.09			
Predatory fishes	Axis 1	0.24				
	Axis 2	-0.44				

Deep		Current	Predators		Invertebrates	
			Axis 1	Axis 2	Axis 1	Axis 2
Sessile Epibenthos	Axis 1	0.83	-0.22	-0.43	0.81	0.11
	Axis 2	0.21	-0.23	-0.28	0.32	-0.29
	ρ		-0.03		0.29	
Mobile Invertebrates	Axis 1	0.78	-0.38	-0.19		
	Axis 2	0.04	-0.18	-0.09		
	ρ		0.004			
Predatory fishes	Axis 1	-0.18				
	Axis 2	-0.31				

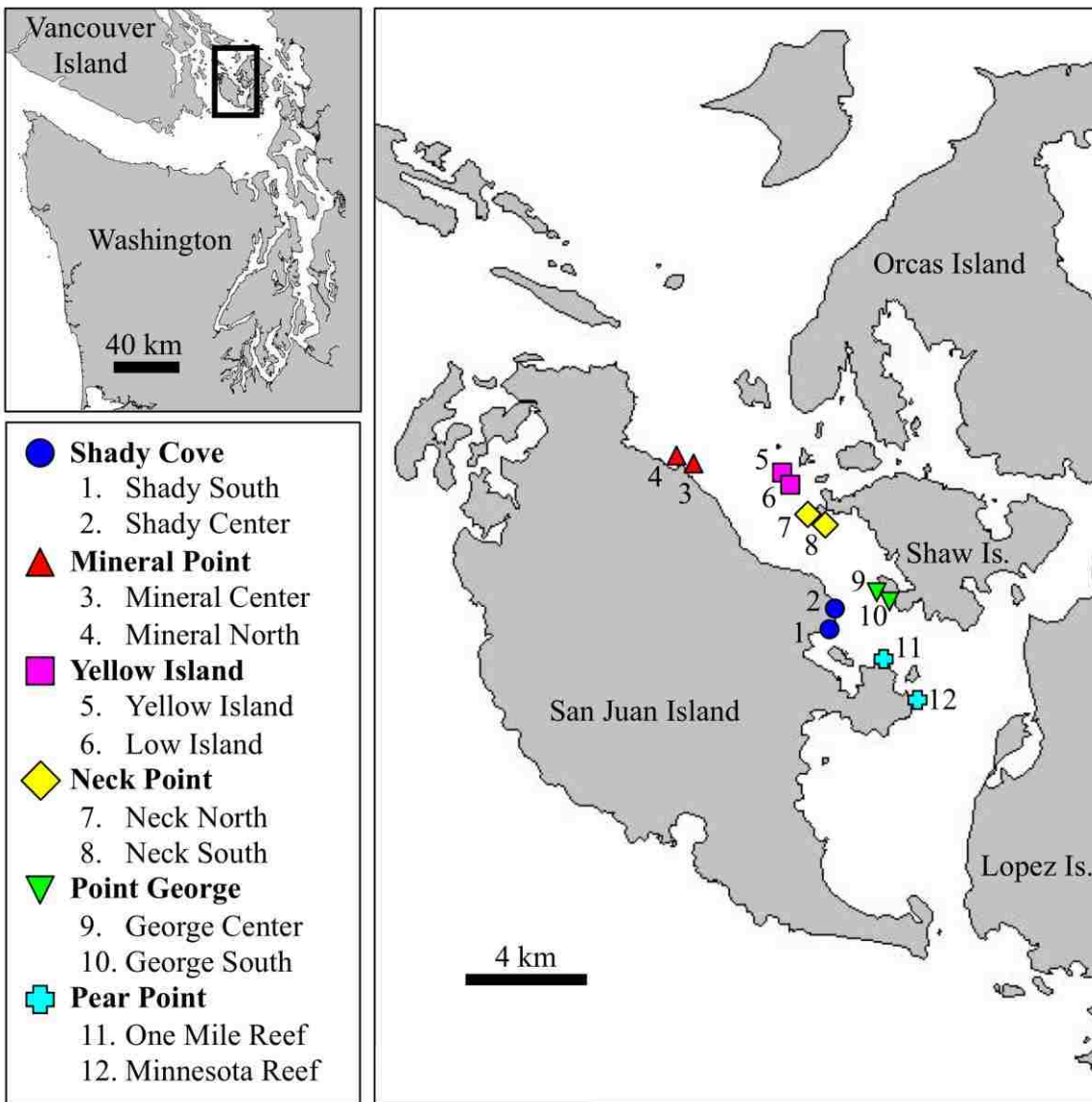


Figure 1. The San Juan Archipelago, Washington. Community surveys were conducted at 12 sites in San Juan Channel, each nested in one of six locations (different symbol types).

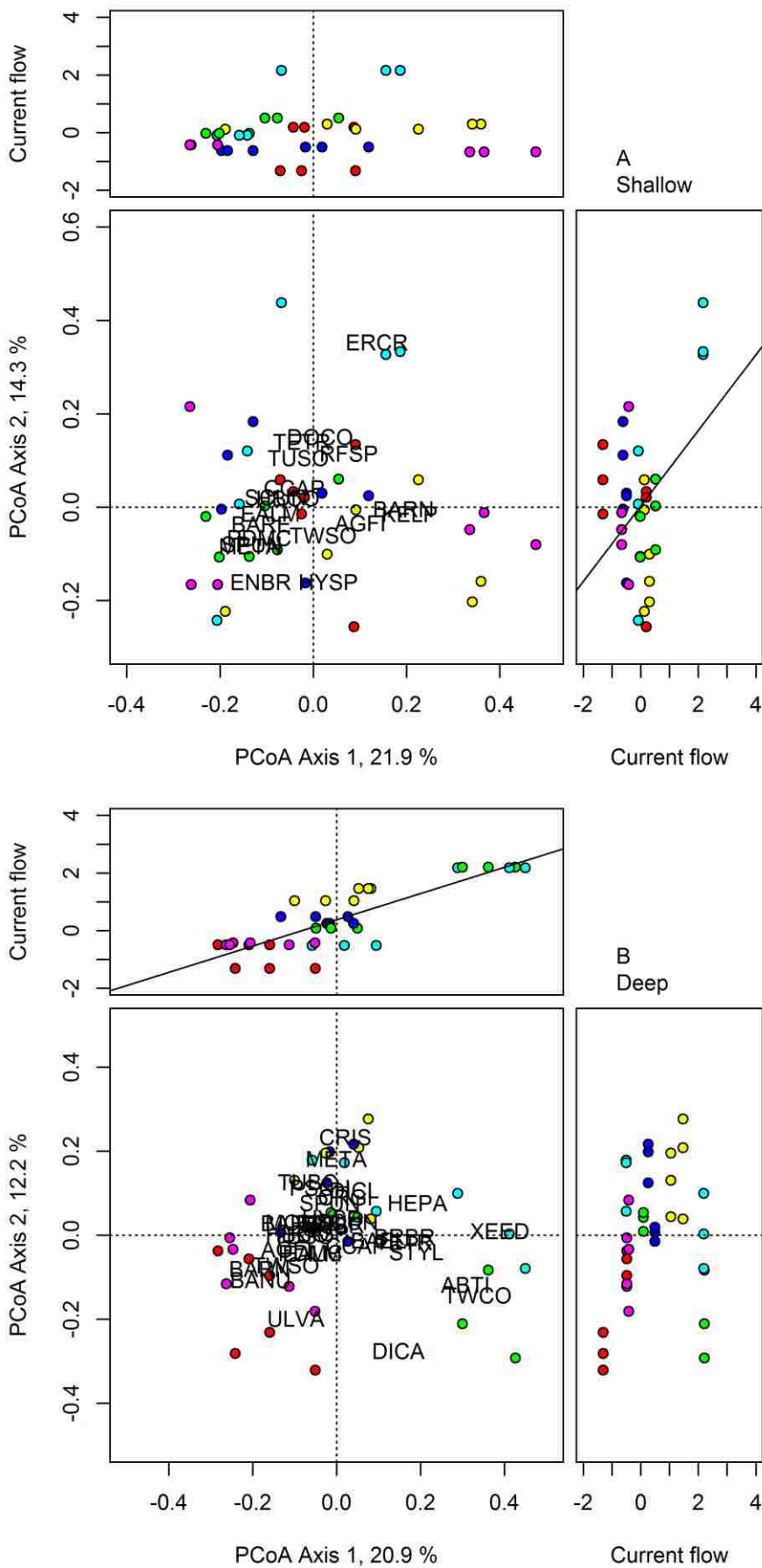


Figure 2. PCoA of shallow (A) and deep (B) sessile epibenthos, with marginal correlations between PCoA axes and relative current flow. Values in the axis labels indicate the percent of total assemblage variability explained by each axis. Different colors indicate different locations, as in Fig. 1. Four-letter codes correspond to sessile epibenthos species in Table 4. Species cover increases at sites in the direction of that species' code from the origin (dashed lines), proportional to the distance of the code from the origin. Solid lines indicate significant correlations between current flow and PCoA axes.

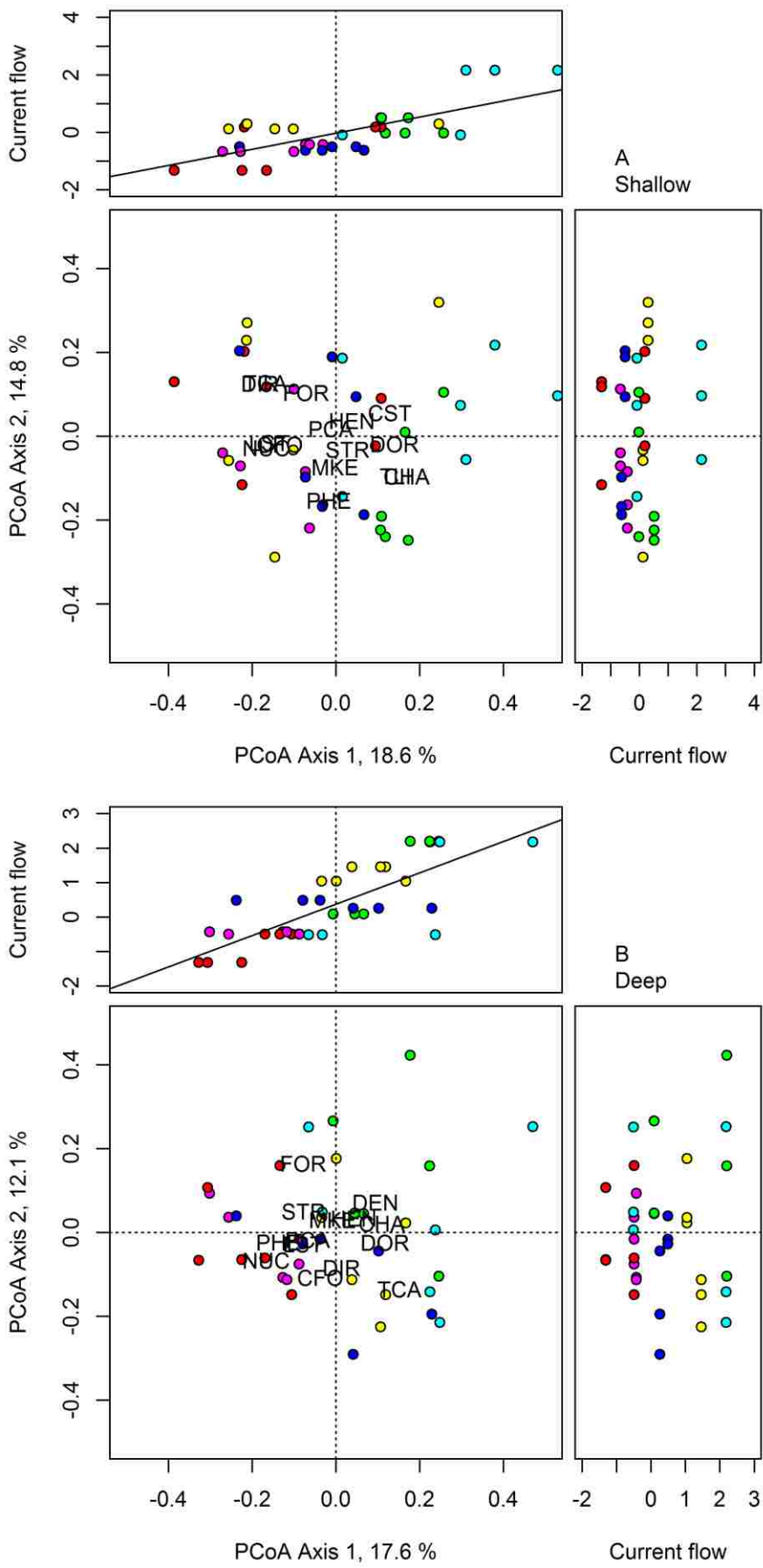


Figure 3. PCoA of shallow (A) and deep (B) mobile invertebrates, with marginal correlations between PCoA axes and relative current flow. Three-letter codes correspond to mobile invertebrate species in Table 5. Key as in Fig. 2.

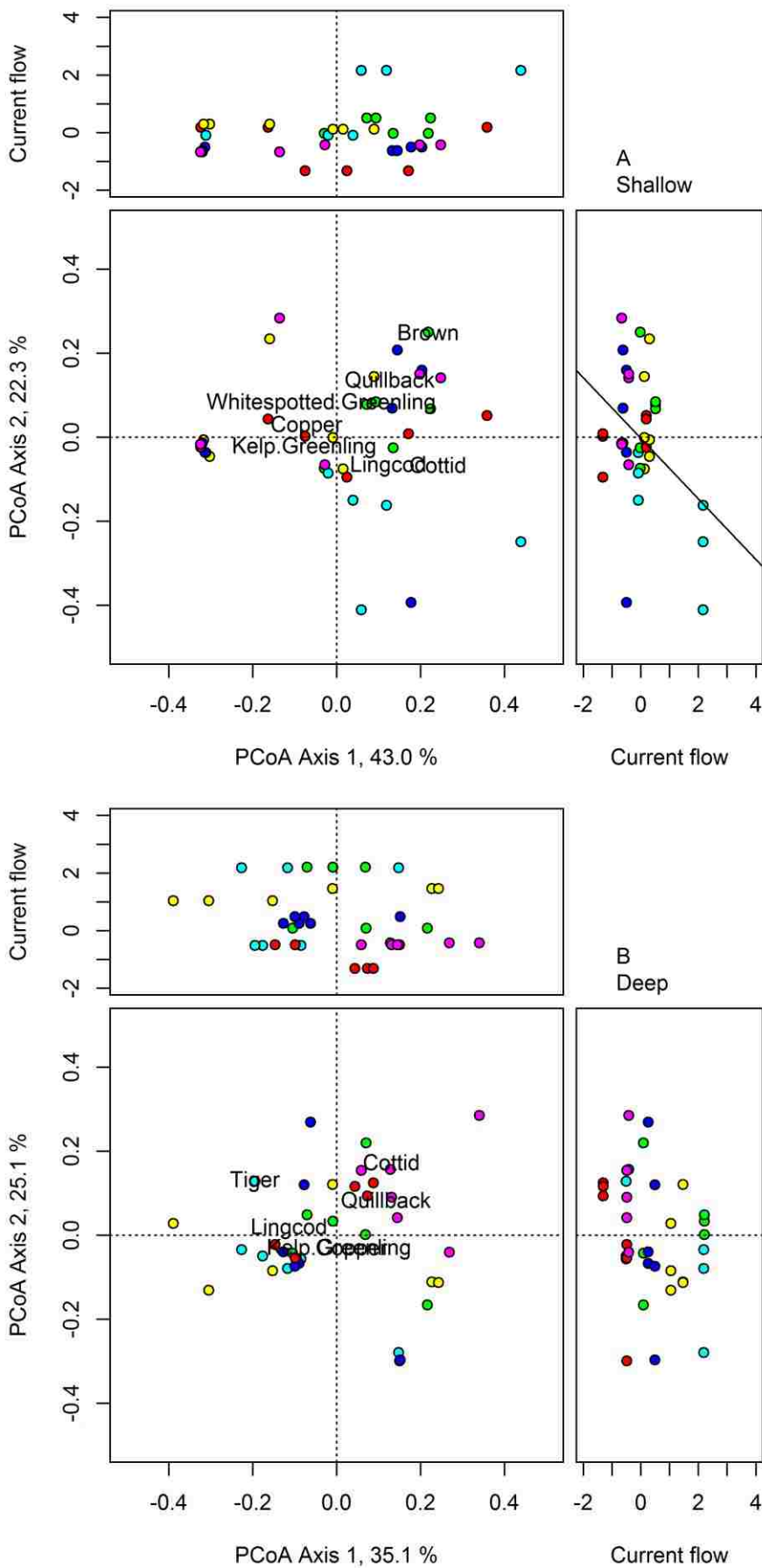


Figure 4. PCoA of shallow (A) and deep (B) predatory fishes, with marginal correlations between PCoA axes and relative current flow. Key as in Fig. 2.

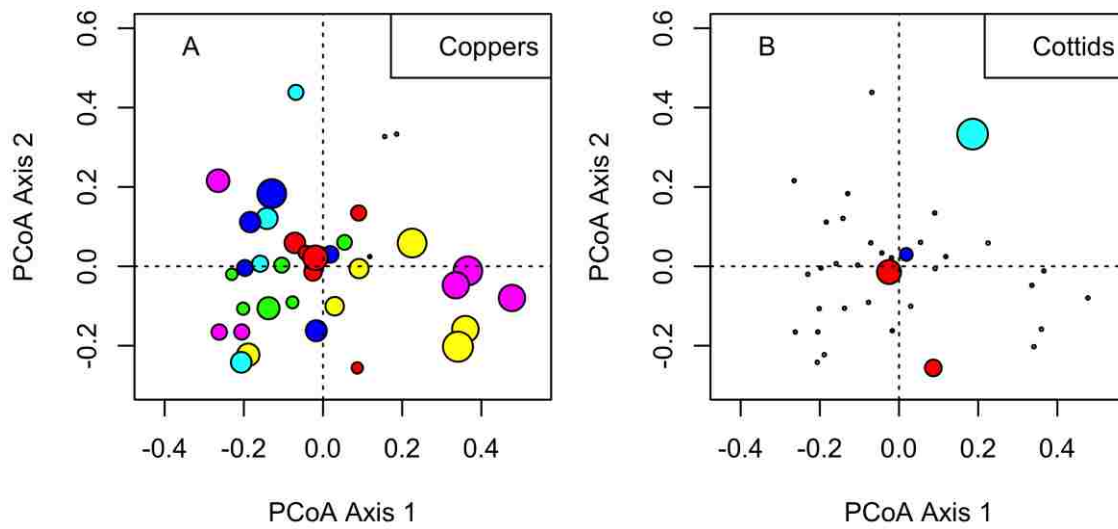


Figure 5. PCoA of the shallow sessile epibenthos assemblage, with overlays of predatory fish abundance. BIO-BIO analysis shows that copper rockfish and cottids are the species that together best predict the sessile epibenthos assemblage (A, B). Point diameter is proportional to fish species abundance. Point colors as in Fig. 2.

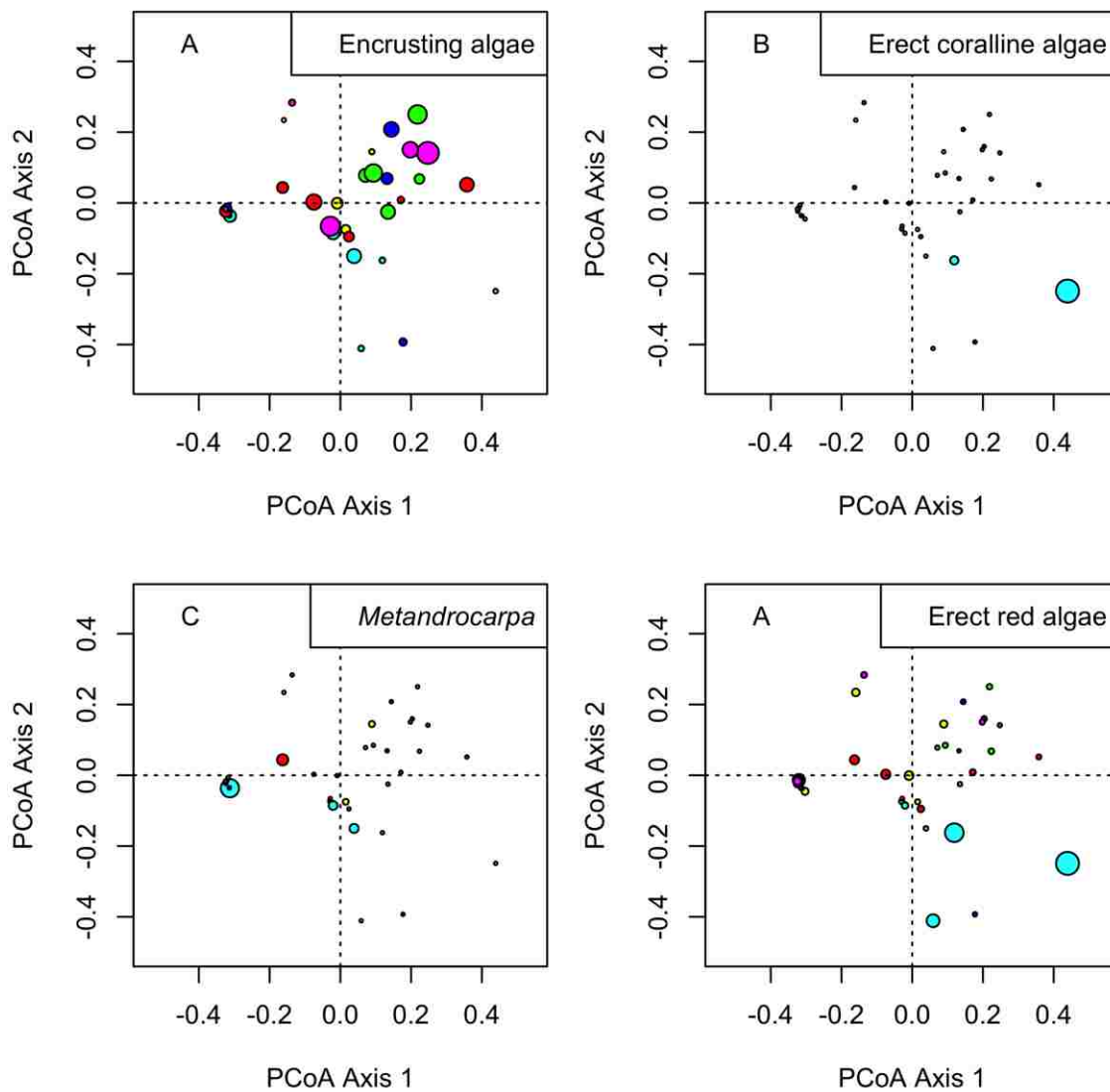


Figure 6. PCoA of the shallow predatory fish assemblage, with overlays of sessile epibenthos cover. BIO-BIO analysis shows that non-coralline encrusting algae (A), erect coralline algae (B), *Metandrocarpa taylori* (C), and erect red algae (D) together are the species that best predict the shallow predatory fish assemblage. Point diameter is proportional to epibenthic species cover. Point colors as in Fig. 2.

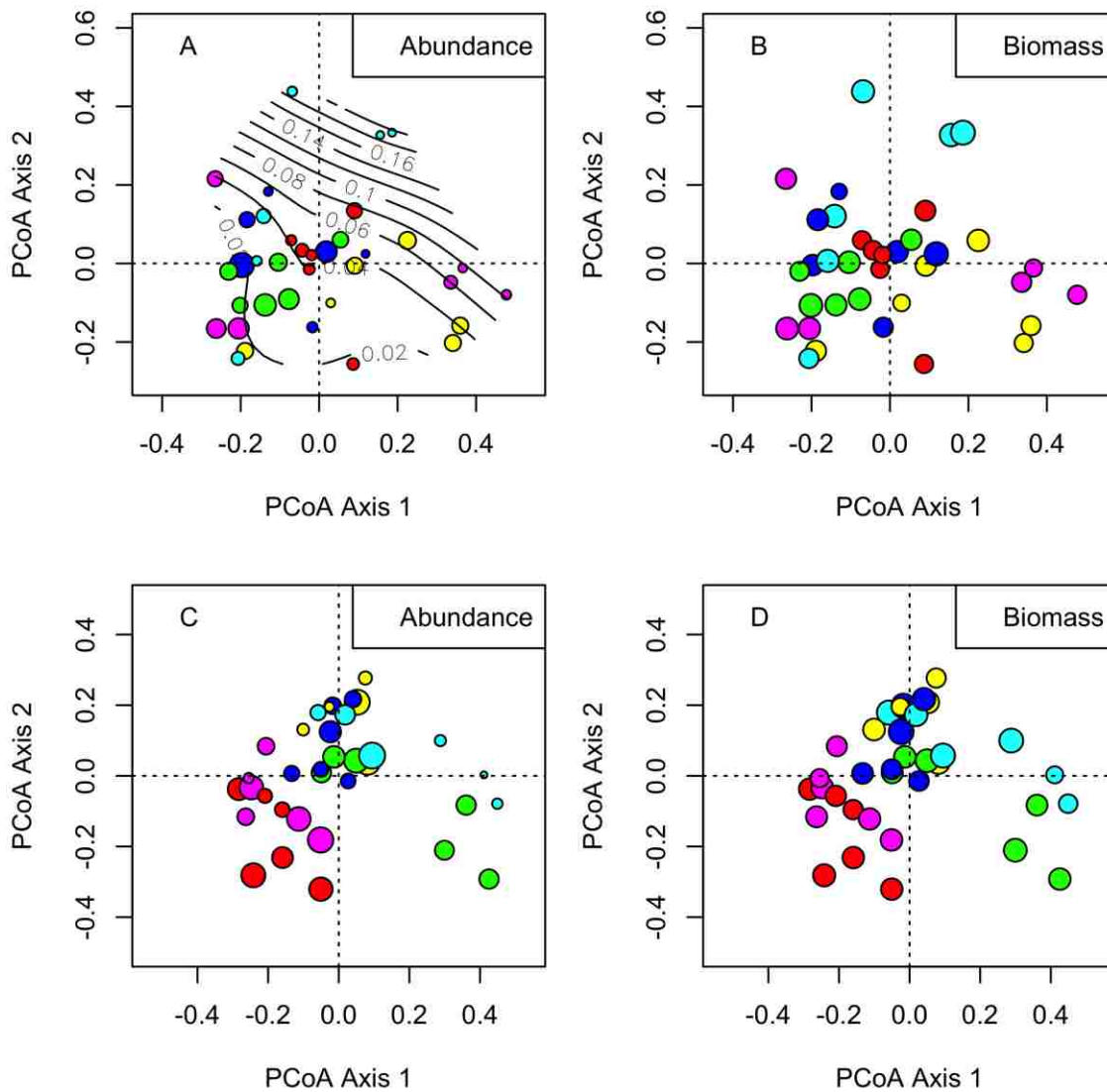


Figure 7. PCoA of shallow (A, B) and deep (C, D) sessile epibenthos assemblages, with overlays of pooled predatory fish abundance (A, C) and biomass (B, D). Predatory fish abundance is a significant predictor of the sessile epibenthos assemblage at shallow, but not deep, transects. Of the shallow sessile epibenthos, erect red algae is the only group that is significantly predicted by predatory fish abundance. Predatory fish biomass is not a significant predictor of the sessile epibenthos assemblage at either shallow or deep transects. The surface lines in A indicate transformed cover of erect red algae on shallow transects. Point diameter is proportional to relative fish abundance or biomass. Point colors as in Fig. 2.

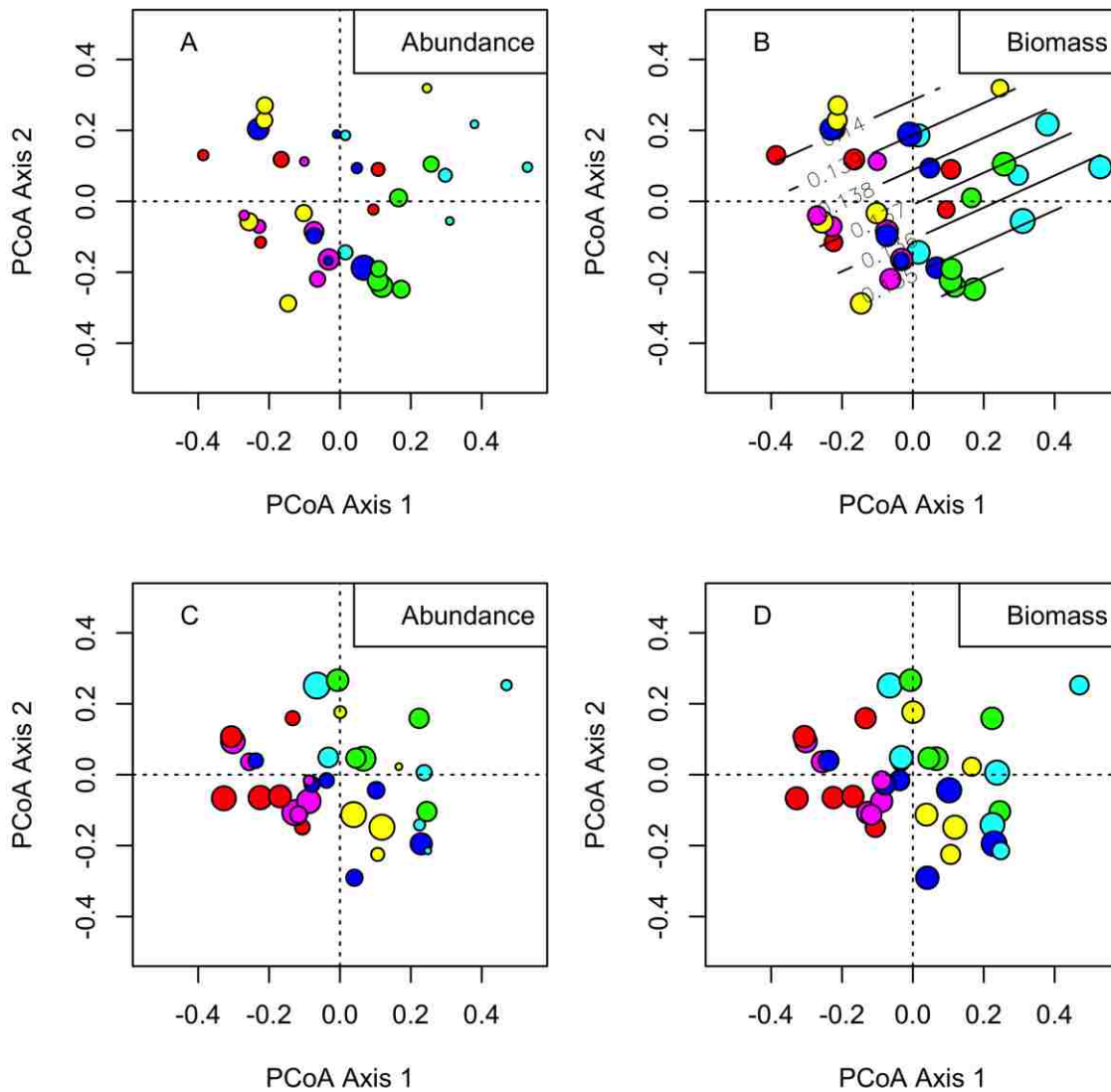


Figure 8. PCoA of shallow (A, B) and deep (C, D) mobile invertebrate assemblages, with overlays of pooled predatory fish abundance (A, C) and biomass (B, D). Predator abundance is not a significant predictor of the mobile invertebrate assemblage at either shallow or deep transects. Predatory fish biomass is a significant predictor of the mobile invertebrate assemblage at shallow, but not deep, transects. Of the mobile invertebrates, *Parastichopus californicus* is the only species that is significantly predicted by predatory fish biomass. The surface lines in B indicate transformed abundance of *Parastichopus* on shallow transects. Point diameter is proportional to relative fish abundance or biomass. Point colors as in Fig. 2.

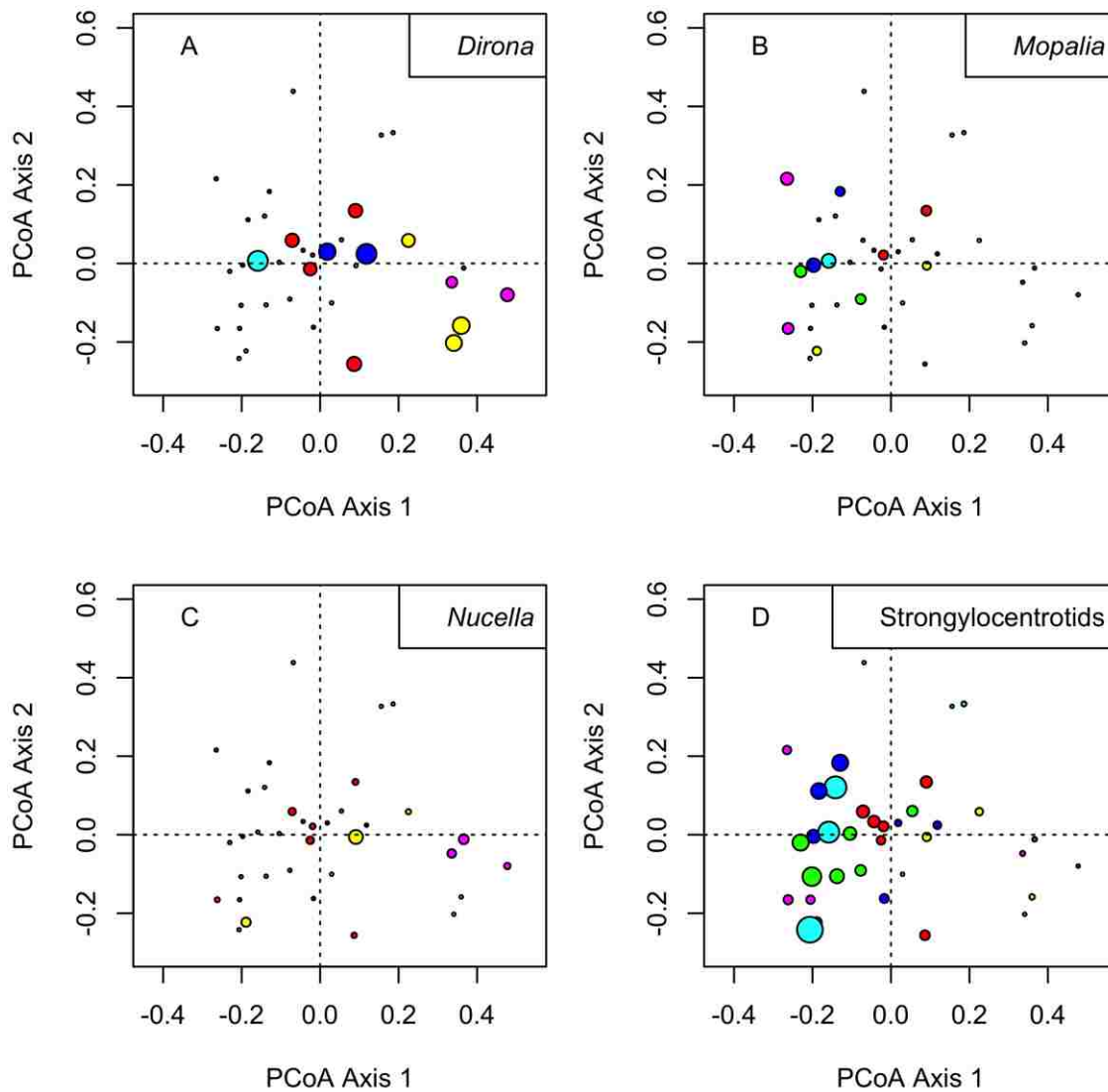


Figure 9. PCoA of the shallow sessile epibenthos assemblage, with overlays of mobile invertebrate abundance. BIO-BIO analysis shows that *Dirona* spp. (A), *Mopalia* spp. (B), *Nucella* spp. (C), and Strongylocentrotid urchins (D) are the species that best predict the sessile epibenthos assemblage. Point diameter is proportional to mobile invertebrate species abundance. Point colors as in Fig. 2.

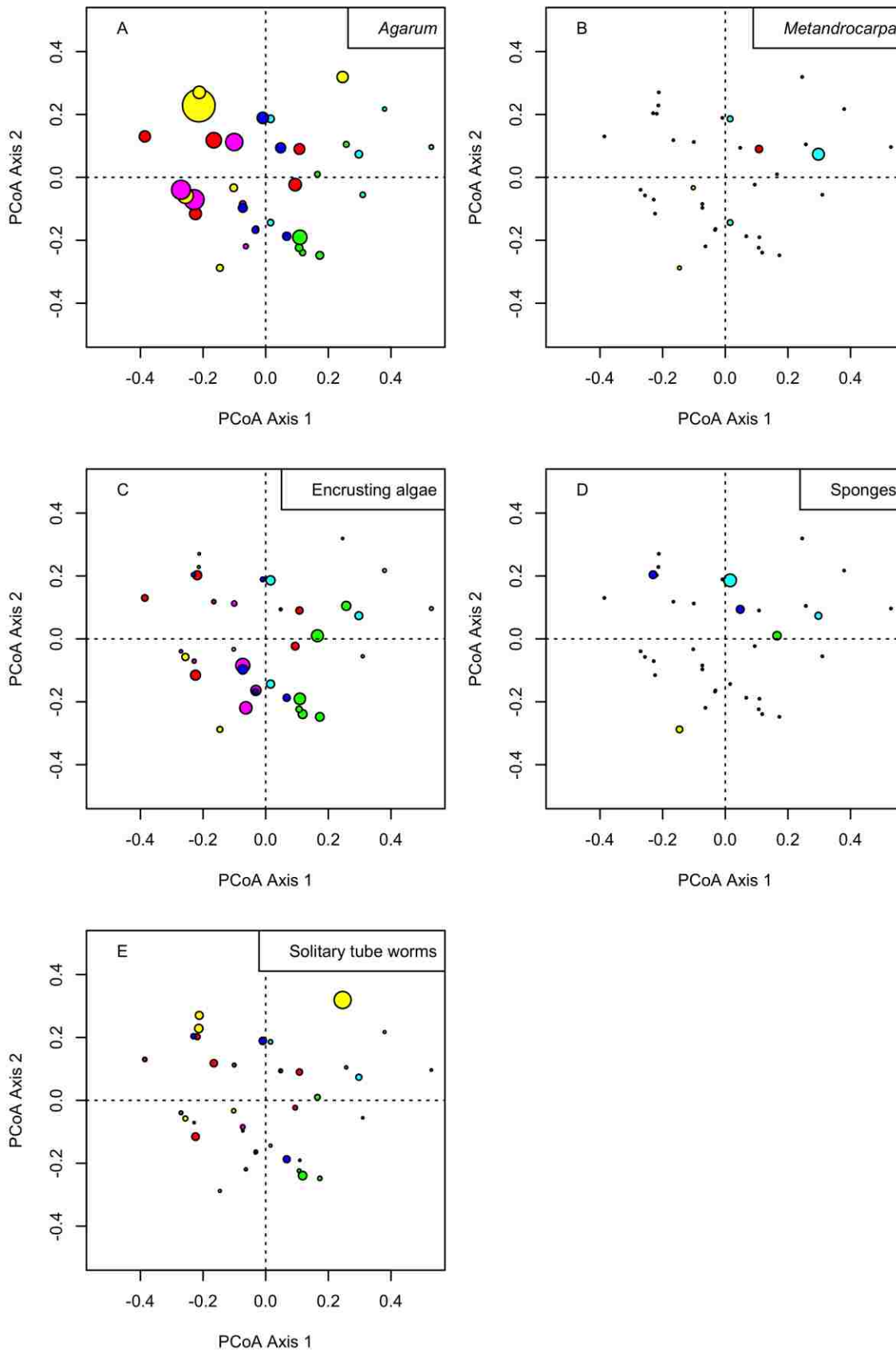


Figure 10. PCoA of the shallow mobile invertebrate assemblage, with overlays of sessile epibenthos cover. BIO-BIO analysis indicates that *Agarum fimbriatum* (A), *Metandrocarpa taylori* (B), non-coralline encrusting algae (C), sponges (D), and solitary tube worms (E), of the sessile epibenthos, together best predict the shallow mobile invertebrate assemblage. Point diameter is proportional to sessile epibenthic species cover. Point colors as in Fig. 2.

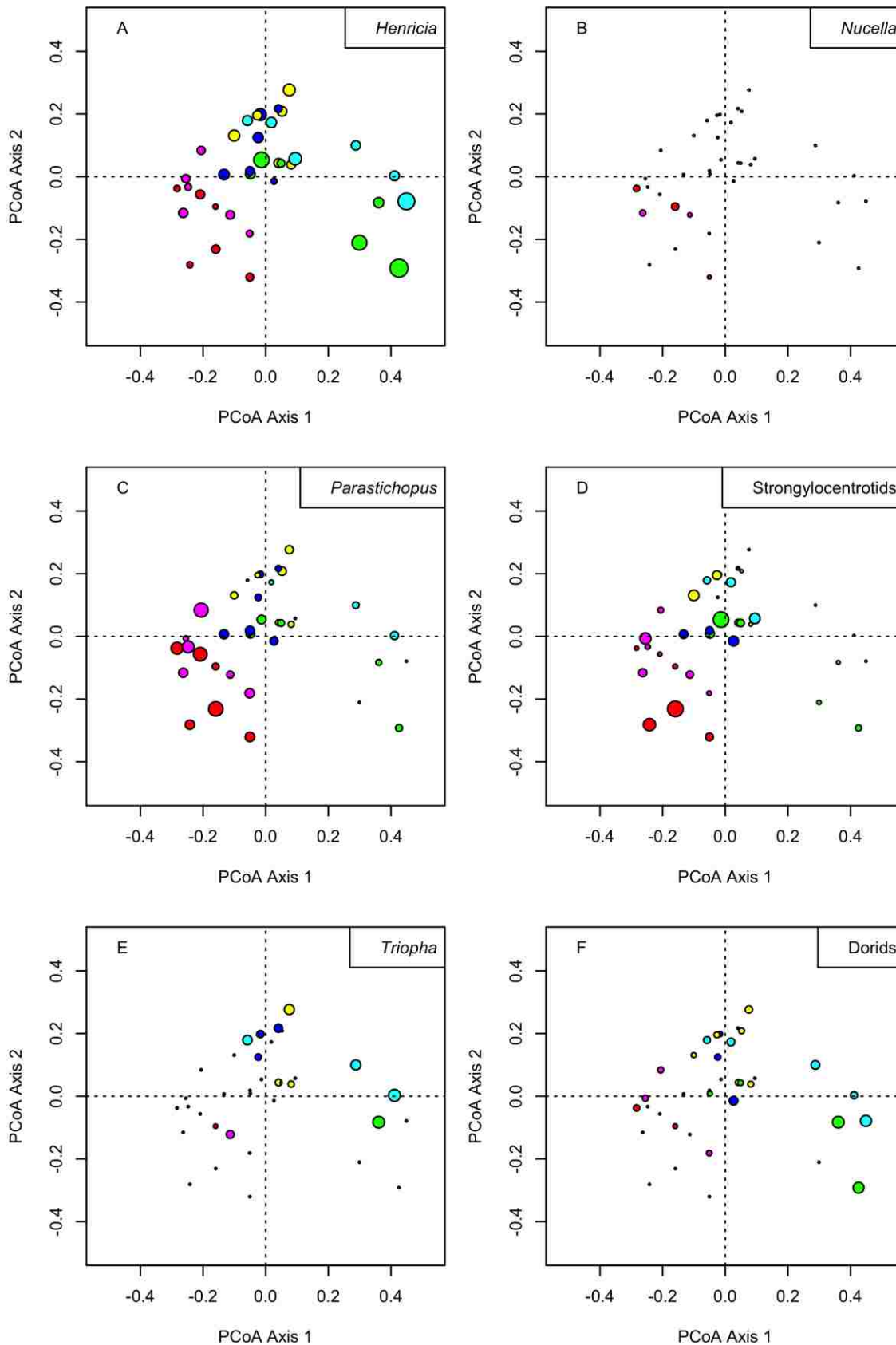


Figure 11. PCoA of the deep sessile epibenthos assemblage, with overlays of mobile invertebrate abundance. BIO-BIO analysis shows that *Henricia* spp. (A), *Nucella* spp. (B), *Parastichopus californicus* (C), Strongylocentrotid urchins (D), *Triopha catalinae* (E), and Dorid nudibranchs (F) together are the species that best predict the sessile epibenthos assemblage. Point diameter is proportional to mobile invertebrate species abundance. Point colors as in Fig. 2.

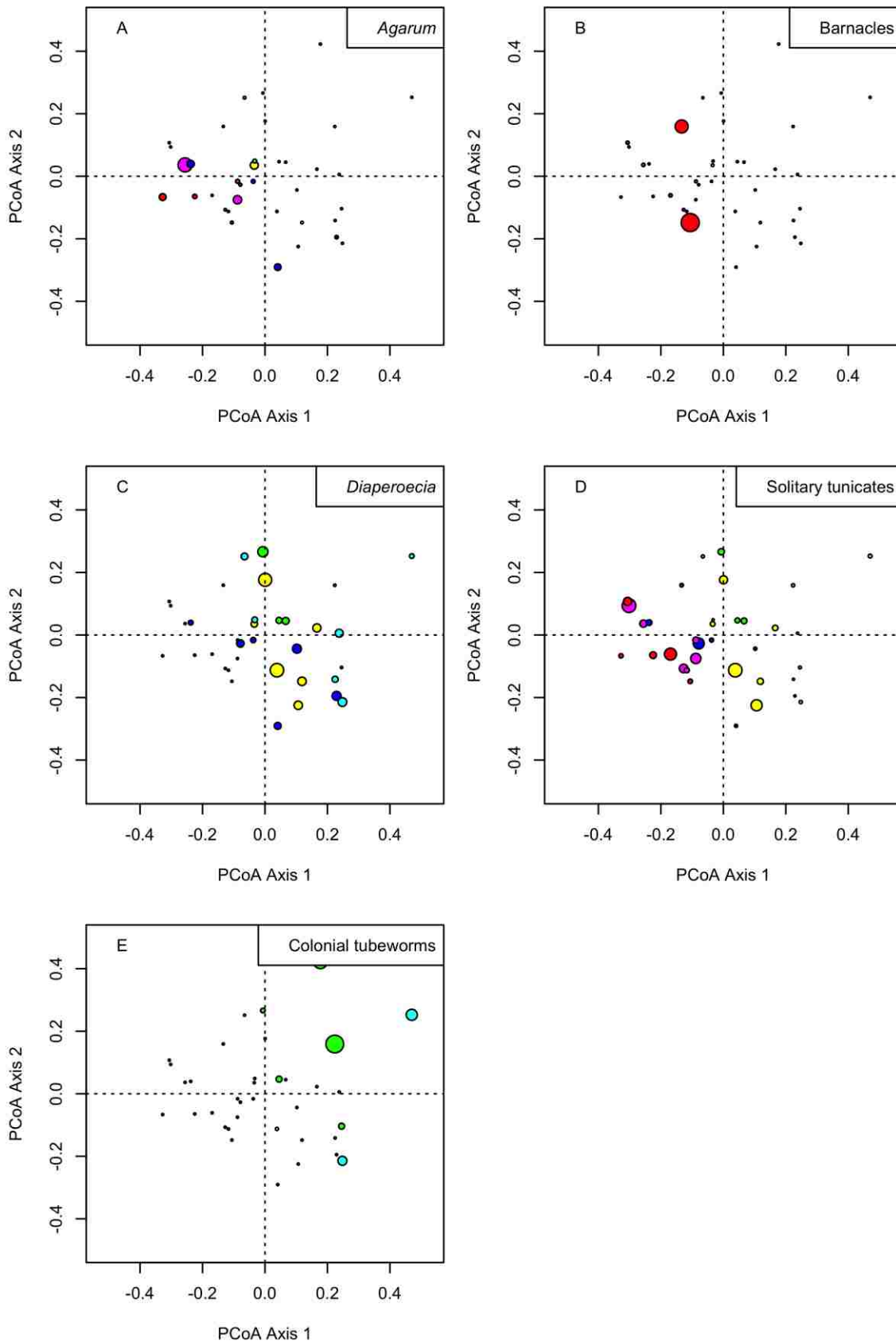


Figure 12. PCoA of the deep mobile invertebrate assemblage, with overlays of sessile epibenthos cover. BIO-BIO analysis indicates that *Agarum fimbriatum* (A), barnacles (B), *Diaperoecia californica* (C), solitary tunicates (D), and colonial tubeworms (E) together are the species that best predict the mobile invertebrate assemblage. Point diameter is proportional to sessile epibenthic species cover. Point colors as in Fig. 2.

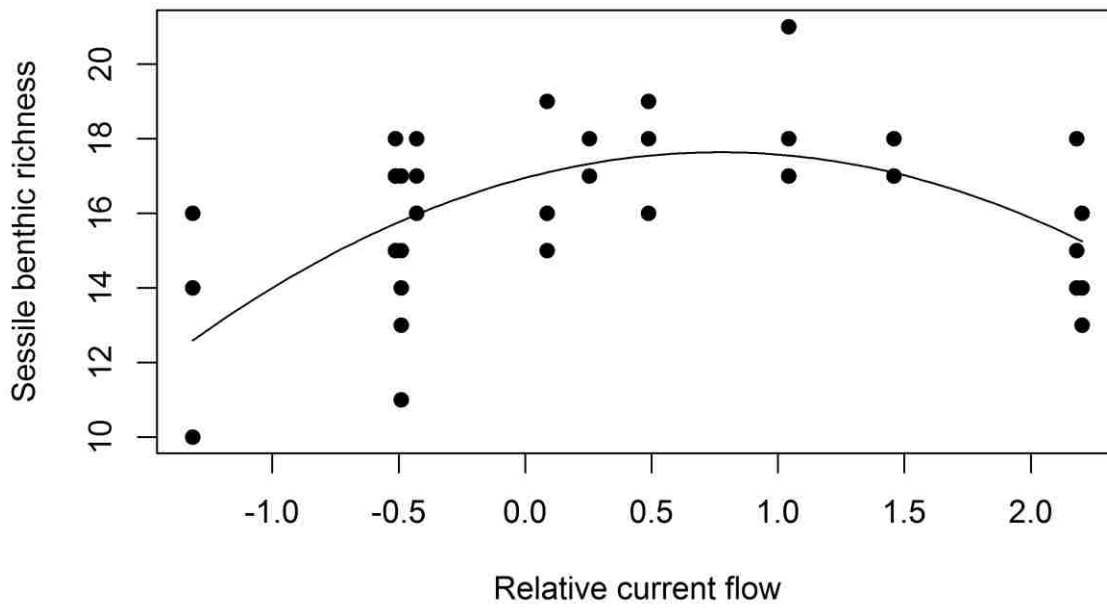


Figure 13. At deep transects there is a significant parabolic correlation between relative current flow and sessile epibenthic richness, with richness initially increasing with flow, and declining at very high flow ($p < 0.001$).

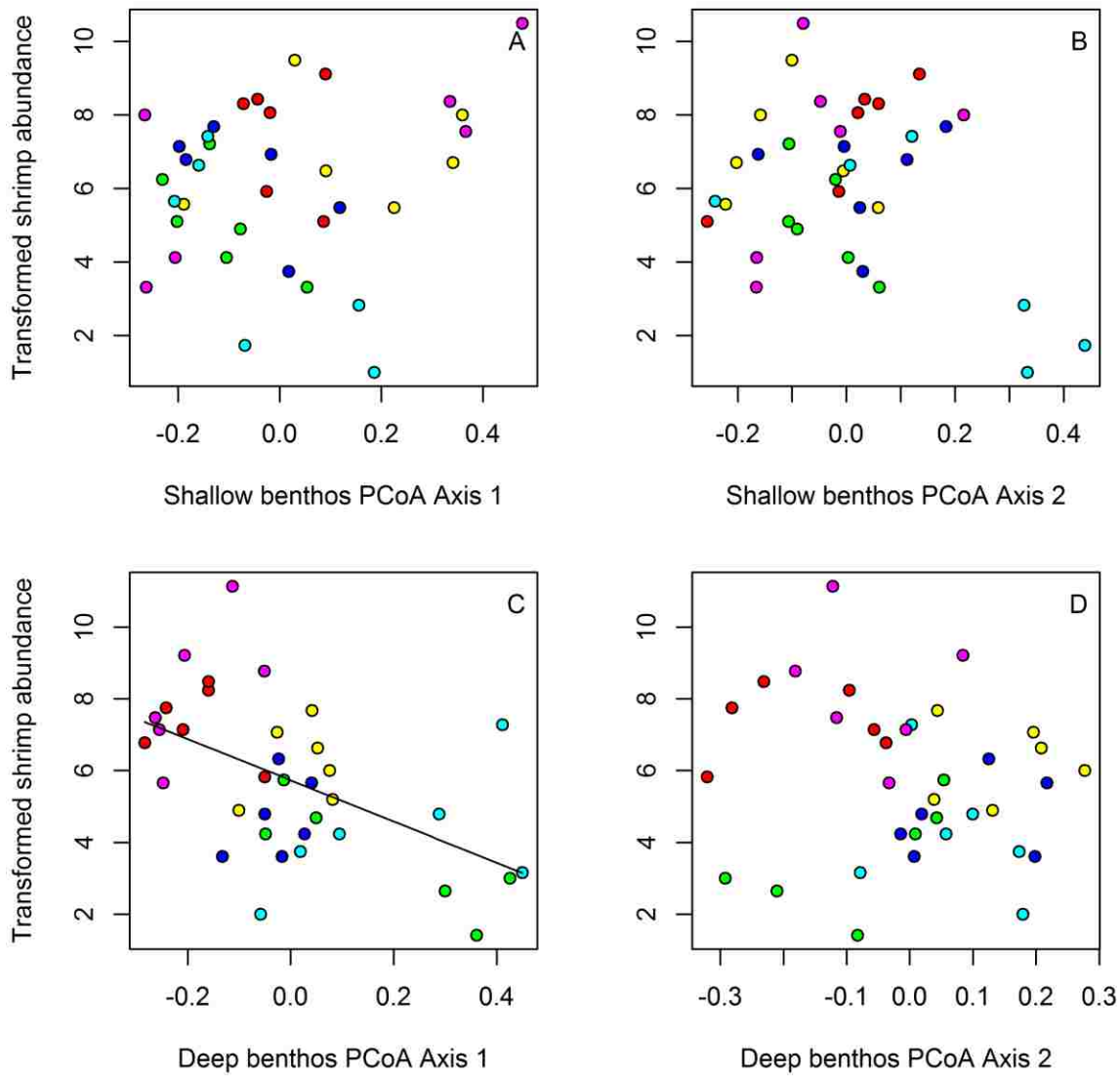


Figure 14. At shallow transects there is not a significant correlation between square-root transformed shrimp abundance and either the first (A) or second (B) principal coordinate axis of the sessile epibenthos assemblage. At deep transects there is a significant correlation (solid line) between shrimp abundance and the first PCoA axis (C), but not with the second PCoA axis (D). Point colors as in Fig. 2.

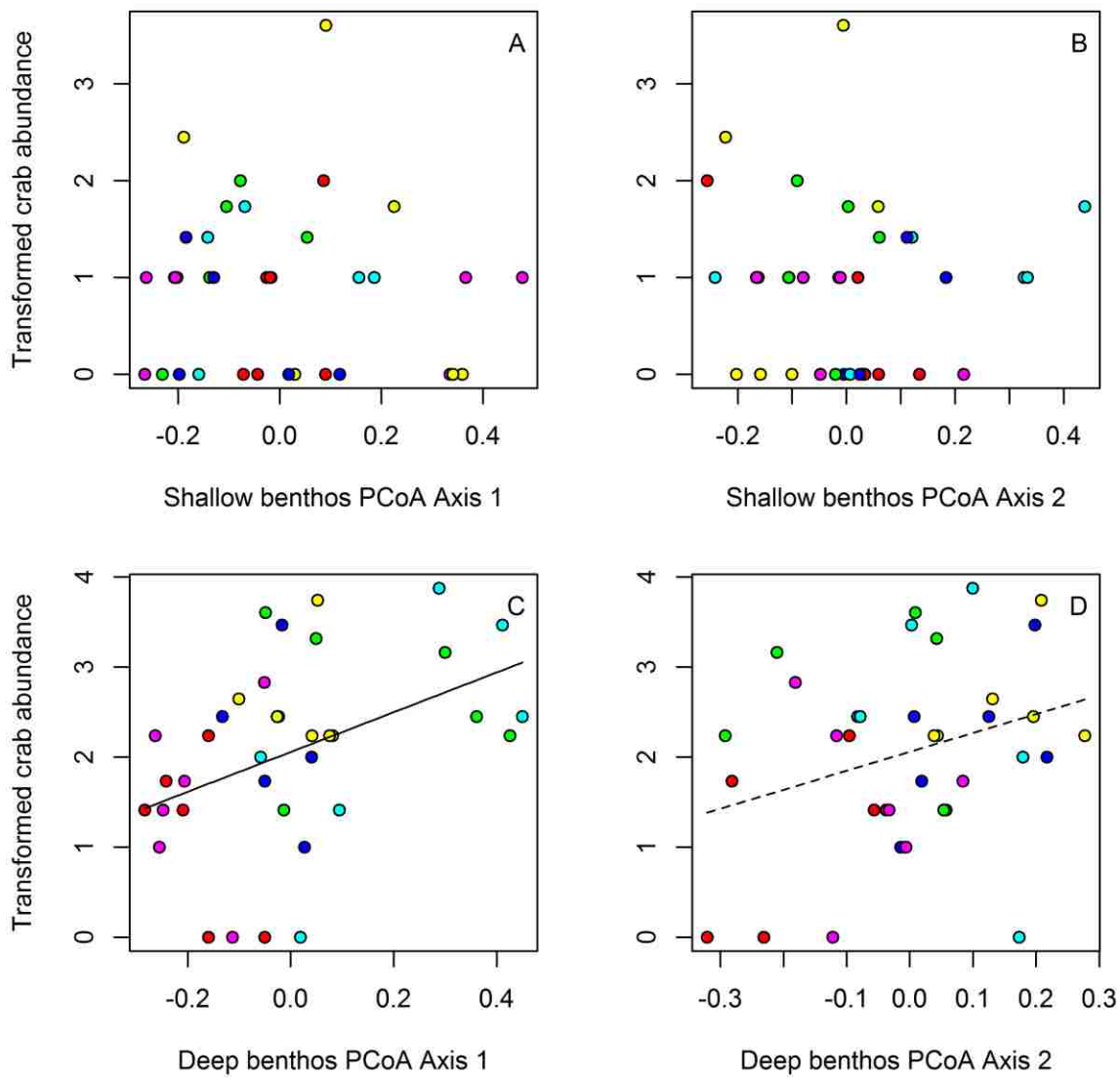


Figure 15. At shallow transects there is not a significant correlation between square-root transformed crab abundance and either the first (A) or second (B) principal coordinate axis of the sessile epibenthos assemblage. At deep transects there is a significant correlation (solid line) between crab abundance and the first PCoA axis (C), and a non-significant trend (dashed line) with the second PCoA axis (D). Point colors as in Fig. 2.

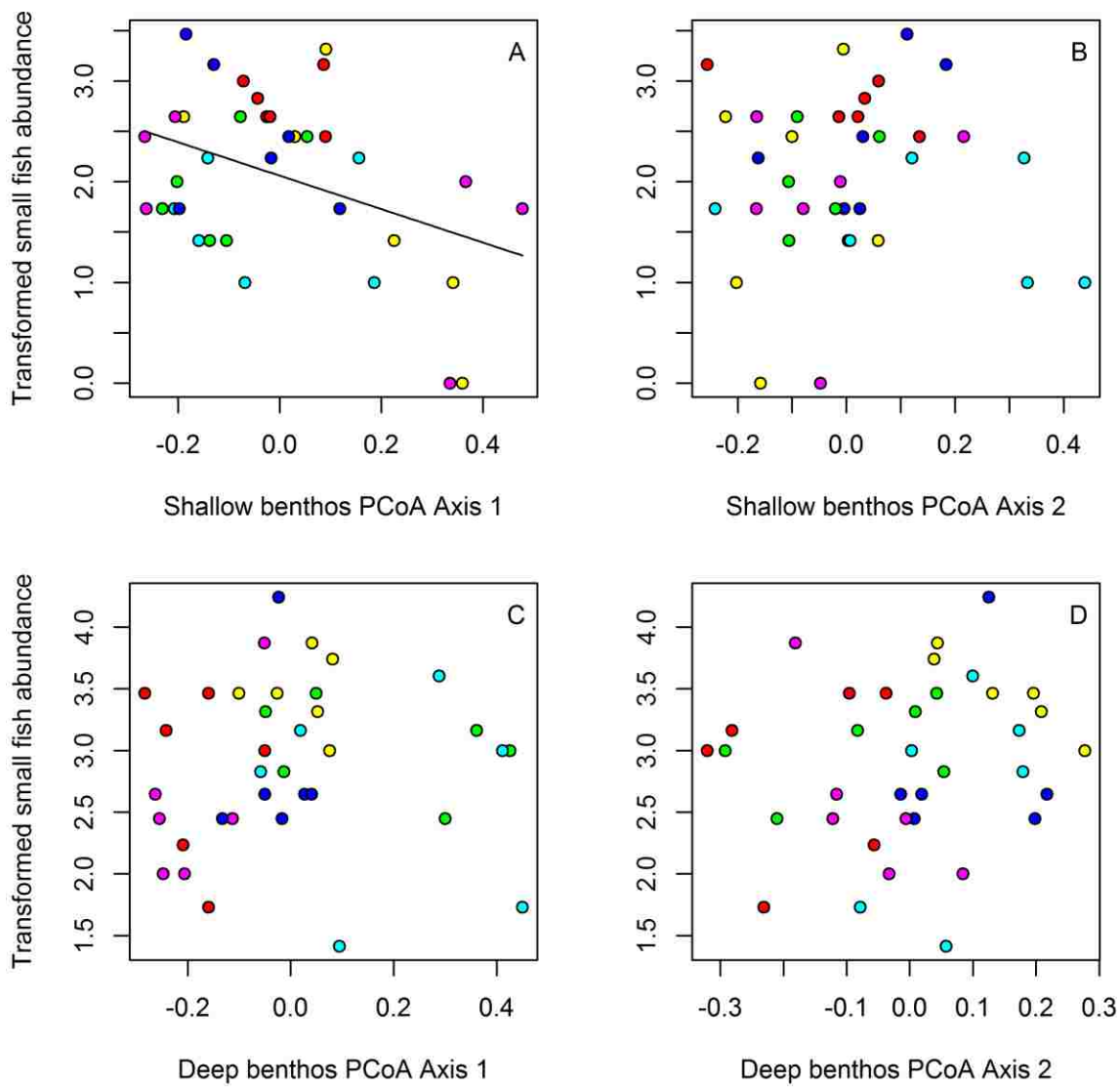


Figure 16. At shallow transects there is a significant correlation (solid line) between square-root transformed small fish abundance and the first principal coordinate axis of the sessile epibenthos assemblage (A), but not with the second PCoA axis (B). At deep transects there is not a significant correlation between shrimp abundance and either the first (C) or second (D) PCoA axis. Point colors as in Fig. 2.

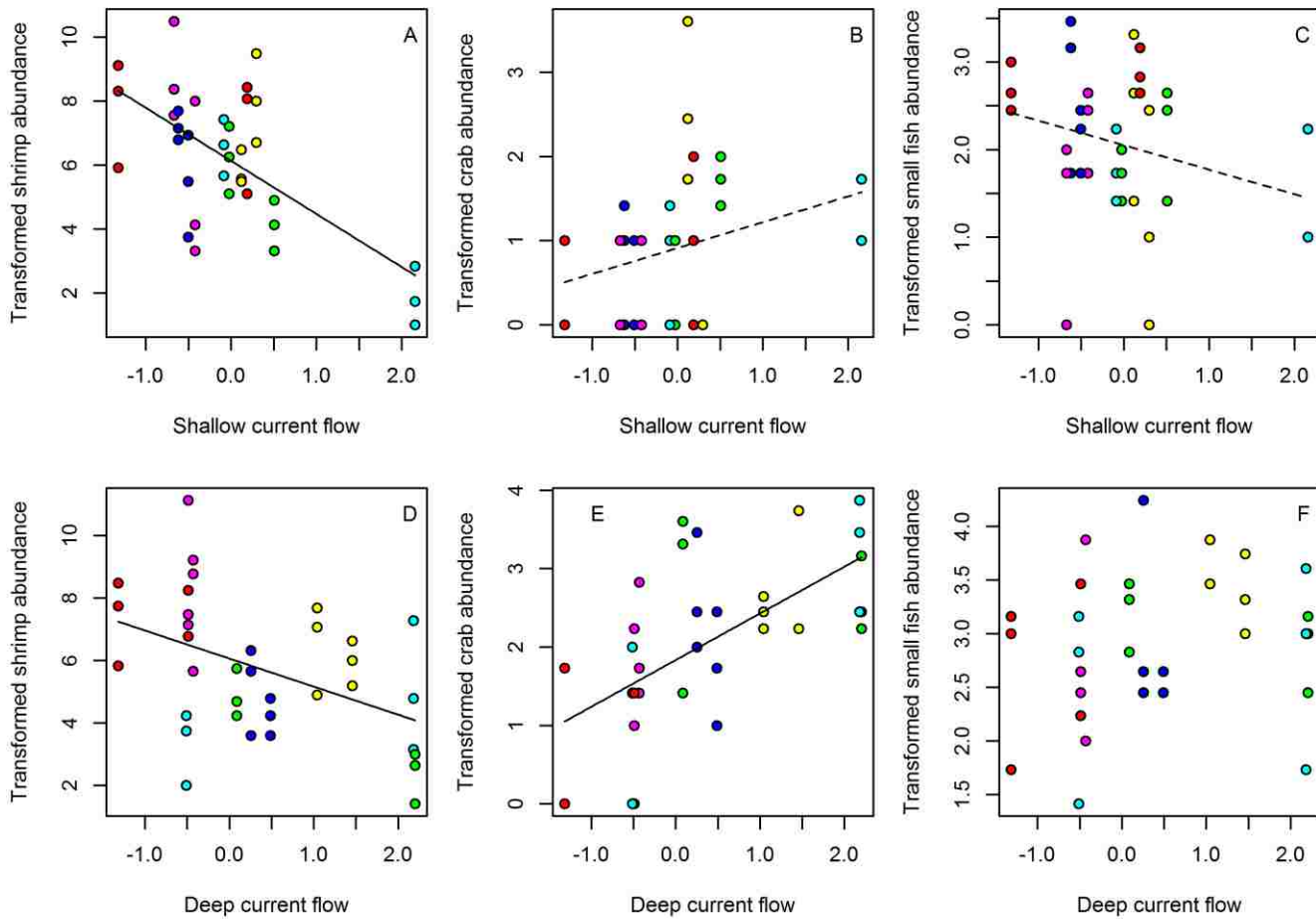


Figure 17. Current flow is strongly negatively correlated with shrimp abundance at both shallow and deep transects, and positively correlated with crab abundance at deep transects only (solid lines) (A, D-E). Crab and small fish abundance were both weakly, but not significantly, correlated with current flow at shallow transects (dashed lines) (B-C). Small fish abundance was not correlated with current flow at deep transects (F).

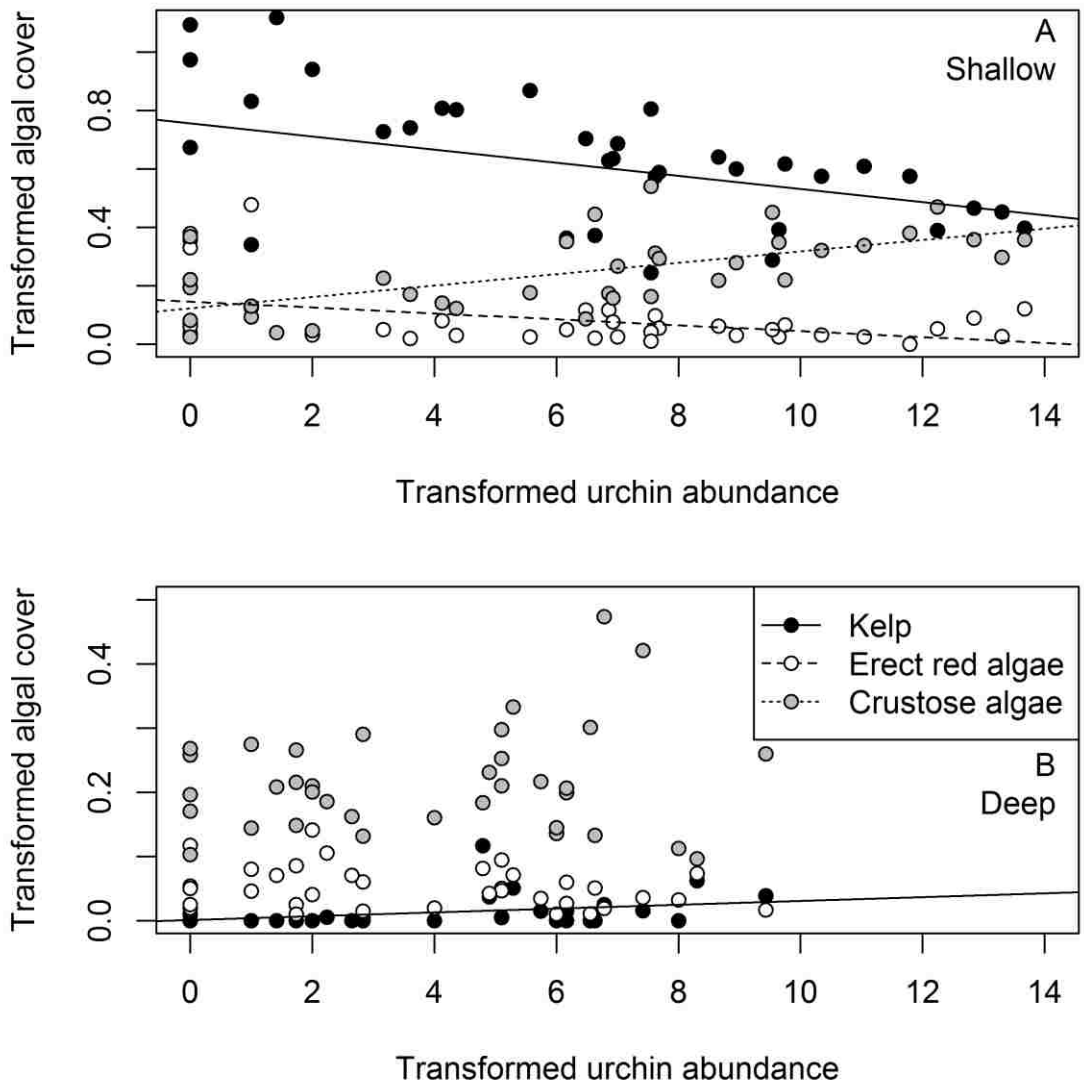


Figure 18. At shallow transects (A) there is a significant negative correlation between urchins and both kelp (black points) and erect red algae (white points), and a significant positive correlation between urchins and crustose algae (gray points). At deep transects (B) the relationship between urchins and kelp is only statistically significant without corrections for multiple testing. There is not a relationship between urchins and either erect red algae or crustose algae. Lines indicate significant relationships between urchins and algal functional groups (note that the “significant” line in (B) assumes no correction for multiple testing).

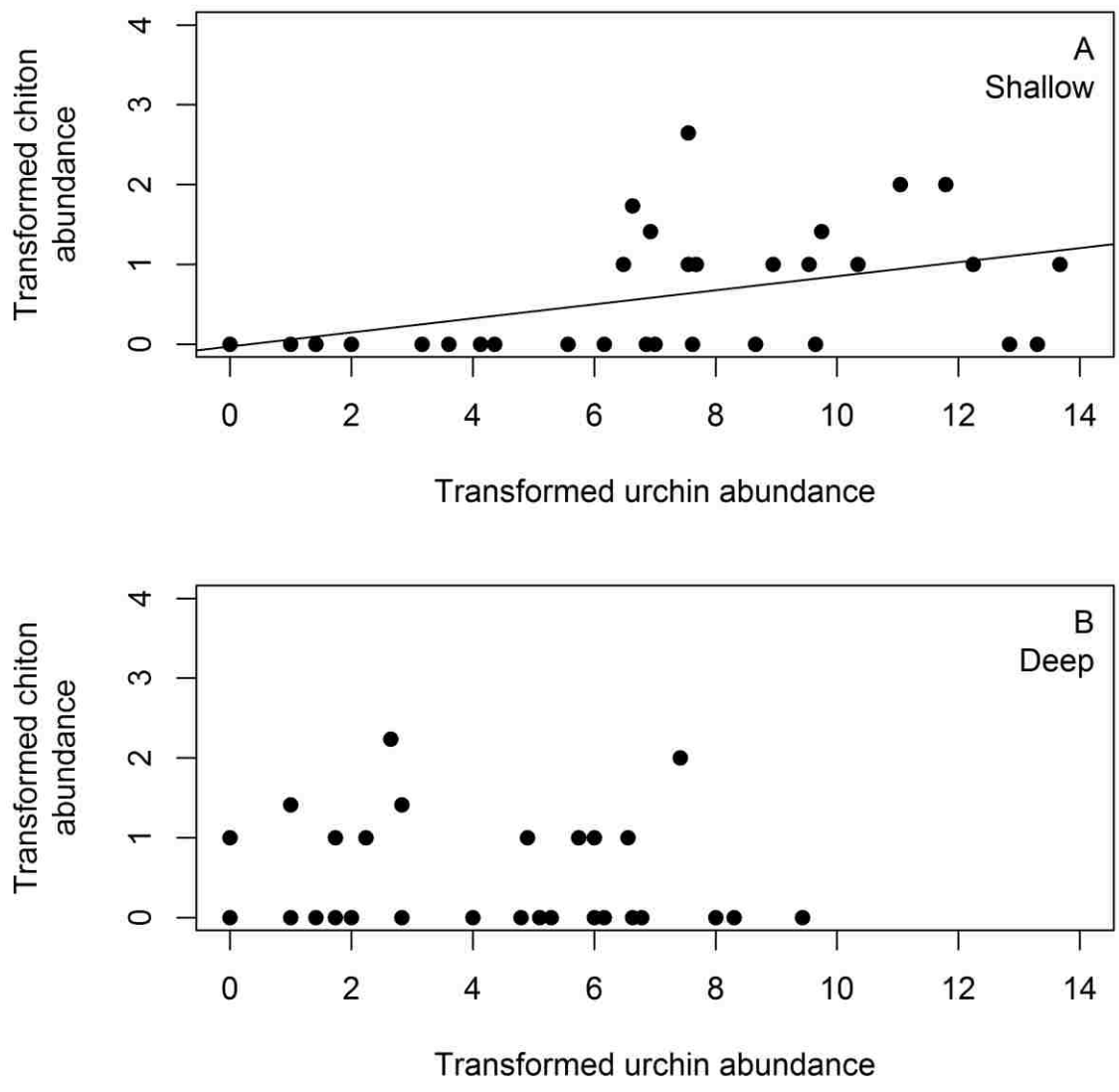


Figure 19. At shallow transects (A) there is a significant positive correlation between urchin and chiton abundance. At deep transects (B) there is not a significant correlation between urchins and chitons.

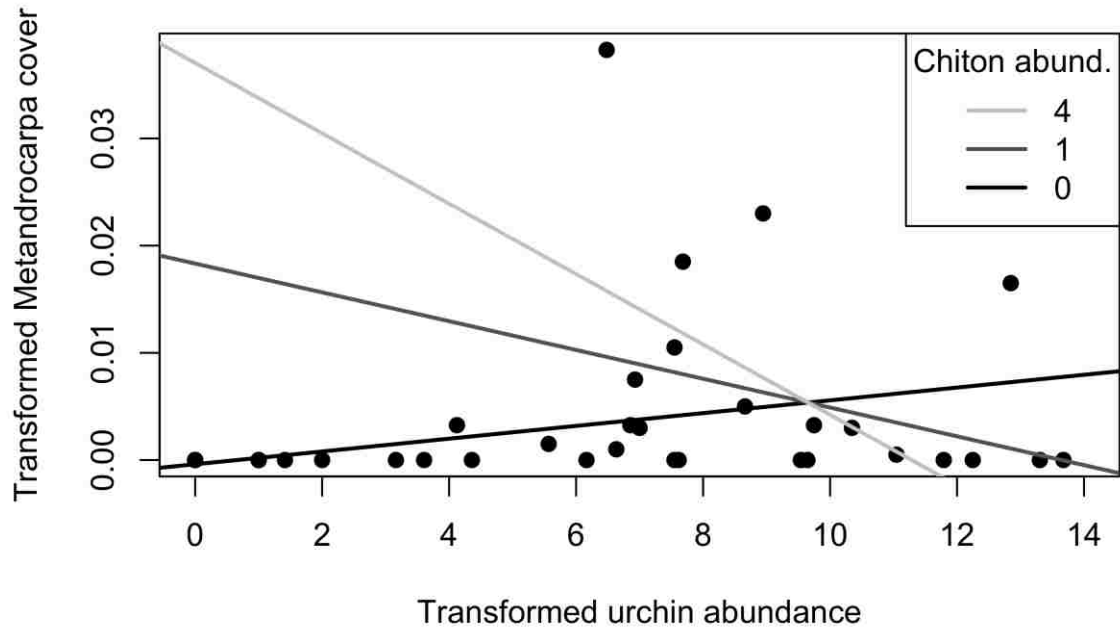


Figure 20. There is a strong effect of the interaction between urchin and chiton abundance on *Metandrocarpa taylori* cover at shallow transects. When chitons are absent there is a positive relationship between urchin abundance and *M. taylori* cover (black line), but this relationship becomes negative as chiton abundance increases (gray lines).

Table S1. Clod card mass loss and summary information from shallow transects. Round mean and standard deviation (SD) mass loss were calculated across all depths (9, 12, 15, 18, and 21 m depth) within each of three deployment rounds (R1, R2, and R3), and used to calculate the number of SD from the round mean for each clod card. Finally, the number of SD from each round mean for each depth was averaged to calculate the mean number of SD for each site. This value was used as the estimate of relative current flow for each site.

Location	Site	Depth	Mass Loss (g / cm ² / day)			Num. of SD from the Round Mean			Mean num. of SD
			R1	R2	R3	R1	R2	R3	
Shady Cove	Shady South	9 m	0.07	0.09	0.06	-0.83	-0.62	-0.49	-0.62
		12 m	0.06	0.07	0.06	-0.49	-0.62	-0.69	
	Shady Center	9 m	0.08	0.09	0.07	-0.79	-0.59	-0.69	-0.51
		12 m	0.09	0.10	0.08	-0.60	0.02	-0.39	
Mineral Point	Mineral Center	9 m	0.06	0.06	0.05	-1.26	-1.84	-1.45	-1.32
		12 m	0.06	0.07	0.06	-1.03	-1.30	-1.06	
	Mineral North	9 m	0.09	0.08	0.09	-0.14	-0.88	0.11	0.19
		12 m	0.10	0.13	0.09	0.23	1.44	0.38	
Yellow Island	Yellow Island	9 m	0.07	0.08	0.06	-0.97	-0.73	-0.97	-0.67
		12 m	0.07	0.09	0.07	-0.77	-0.19	-0.41	
	Low Island	9 m	0.07	0.09	0.07	-0.61	-0.20	-0.40	-0.42
		12 m	0.08	0.09	0.07	-0.51	-0.36	-0.45	
Neck Point	Neck North	9 m	0.09	0.11	0.09	-0.20	0.53	0.04	0.30
		12 m	0.10	0.11	0.10	0.31	0.64	0.45	
	Neck South	9 m	0.07	0.09	0.07	-0.71	-0.32	-0.40	0.12
		12 m	0.10	0.12	0.11	0.41	0.88	0.86	
Point George	George Center	9 m	0.10	0.10	0.09	0.34	0.09	0.22	0.51
		12 m	0.12	0.11	0.11	1.08	0.47	0.85	
	George South	9 m	0.08	0.09	0.08	-0.31	-0.35	-0.10	-0.03
		12 m	0.10	0.10	0.09	0.21	0.03	0.36	
Pear Point	One Mile Reef	9 m	n.d.	n.d.	0.15	n.d.	n.d.	2.53	2.16
		12 m	0.14	0.14	0.14	1.74	2.07	2.28	
	Minnesota Reef	9 m	0.11	0.12	0.09	0.73	0.94	0.27	-0.09
		12 m	0.08	0.07	0.06	-0.58	-1.06	-0.83	

Round Overall Mean	0.09	0.10	0.08
Round Overall SD	0.03	0.02	0.02

Table S2. Clod card mass loss and summary information from deep transects. Calculations and interpretation as in Table S1.

Location	Site	Depth	Mass Loss (g / cm ² / day)			Num. of SD from the Round Mean			Mean num. of SD
			R1	R2	R3	R1	R2	R3	
Shady Cove	Shady South	18 m	0.09	0.11	0.08	-0.08	0.49	-0.09	0.49
		21 m	0.10	0.13	0.10	0.38	1.73	0.49	
	Shady Center	18 m	0.15	0.10	0.09	2.34	0.30	0.40	0.25
		21 m	0.08	0.09	0.07	-0.53	-0.33	-0.66	
Mineral Point	Mineral Center	18 m	n.d.	0.08	0.07	n.d.	-0.77	-0.71	-1.32
		21 m	0.06	0.04	0.05	-1.19	-2.65	-1.26	
	Mineral North	18 m	0.09	0.09	0.09	-0.18	-0.39	0.25	-0.49
		21 m	0.06	n.d.	0.06	-1.15	n.d.	-0.98	
Yellow Island	Yellow Island	18 m	0.15	0.07	0.05	2.20	-1.07	-1.26	-0.49
		21 m	0.06	0.08	0.06	-1.18	-0.66	-0.96	
	Low Island	18 m	0.09	0.09	0.07	-0.19	-0.32	-0.41	-0.43
		21 m	0.08	0.08	0.07	-0.56	-0.62	-0.47	
Neck Point	Neck North	18 m	0.10	0.12	0.11	0.51	1.21	0.90	1.04
		21 m	0.11	0.13	0.11	0.87	1.62	1.15	
	Neck South	18 m	0.13	0.13	0.12	1.42	1.78	1.66	1.46
		21 m	0.13	0.13	0.11	1.32	1.43	1.14	
Point George	George Center	18 m	0.16	n.d.	0.15	2.63	n.d.	2.82	2.20
		21 m	0.14	0.14	0.12	1.78	2.16	1.63	
	George South	18 m	0.11	0.10	0.10	0.72	0.35	0.75	0.09
		21 m	0.08	0.08	0.07	-0.28	-0.60	-0.42	
Pear Point	One Mile Reef	18 m	0.15	n.d.	0.14	2.18	n.d.	2.33	2.18
		21 m	n.d.	0.14	0.13	n.d.	2.22	2.00	
	Minnesota Reef	18 m	0.08	0.08	0.06	-0.60	-0.95	-0.95	-0.51
		21 m	0.09	0.10	0.07	-0.19	0.19	-0.58	

Round Overall Mean	0.09	0.10	0.08
Round Overall SD	0.03	0.02	0.02

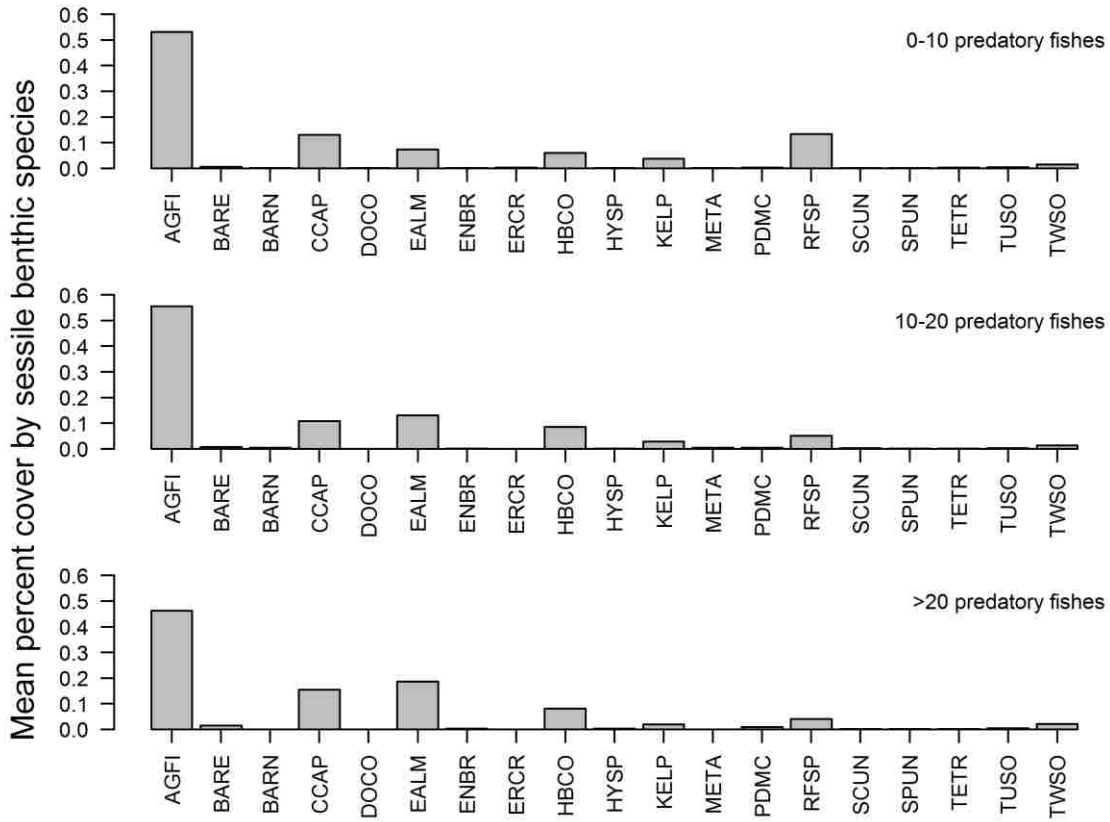


Figure S1. Mean percent cover of sessile epibenthic species at shallow transects, across three levels of predatory fish abundance: 0-10 fishes (n = 14), 10-20 fishes (n = 16), and >20 fishes (n = 6). Species codes as in Table 4.

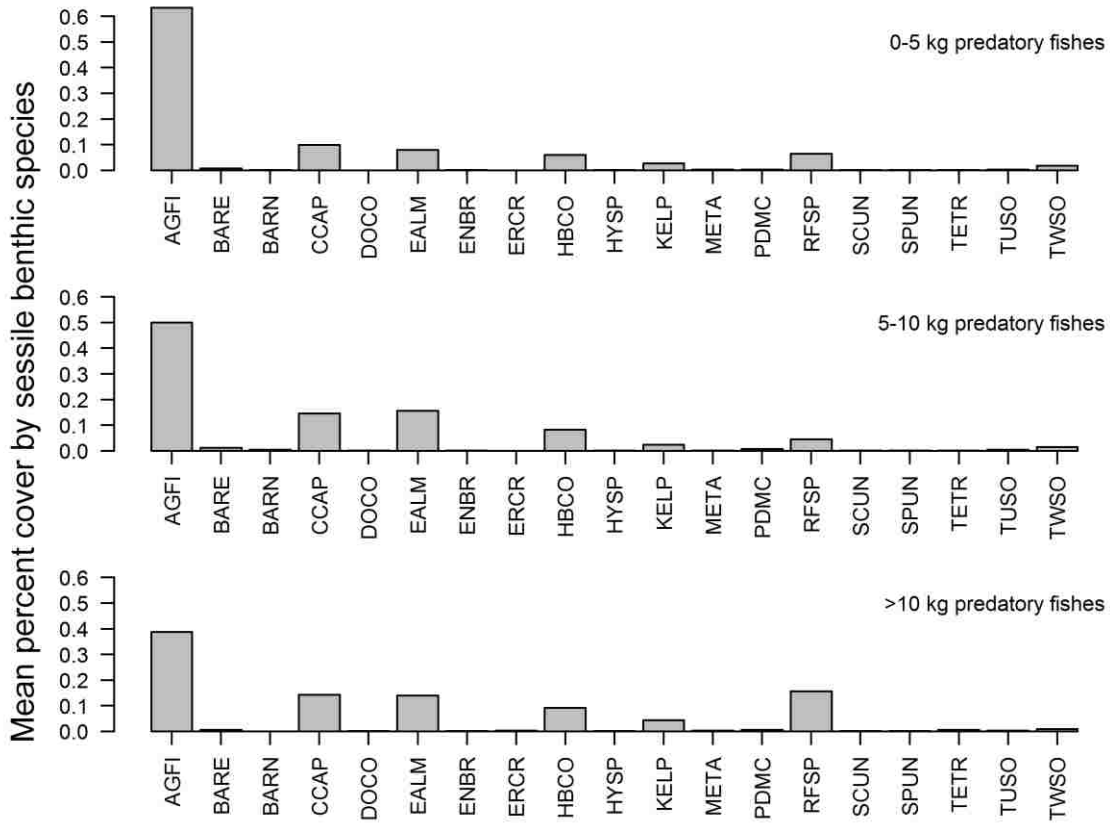


Figure S2. Mean percent cover of sessile epibenthic species at shallow transects, across three levels of predatory fish biomass: 0-5 kg of fishes (n = 16), 5-10 kg of fishes (n = 11), and >10 kg of fishes (n = 9). Species codes as in Table 4.

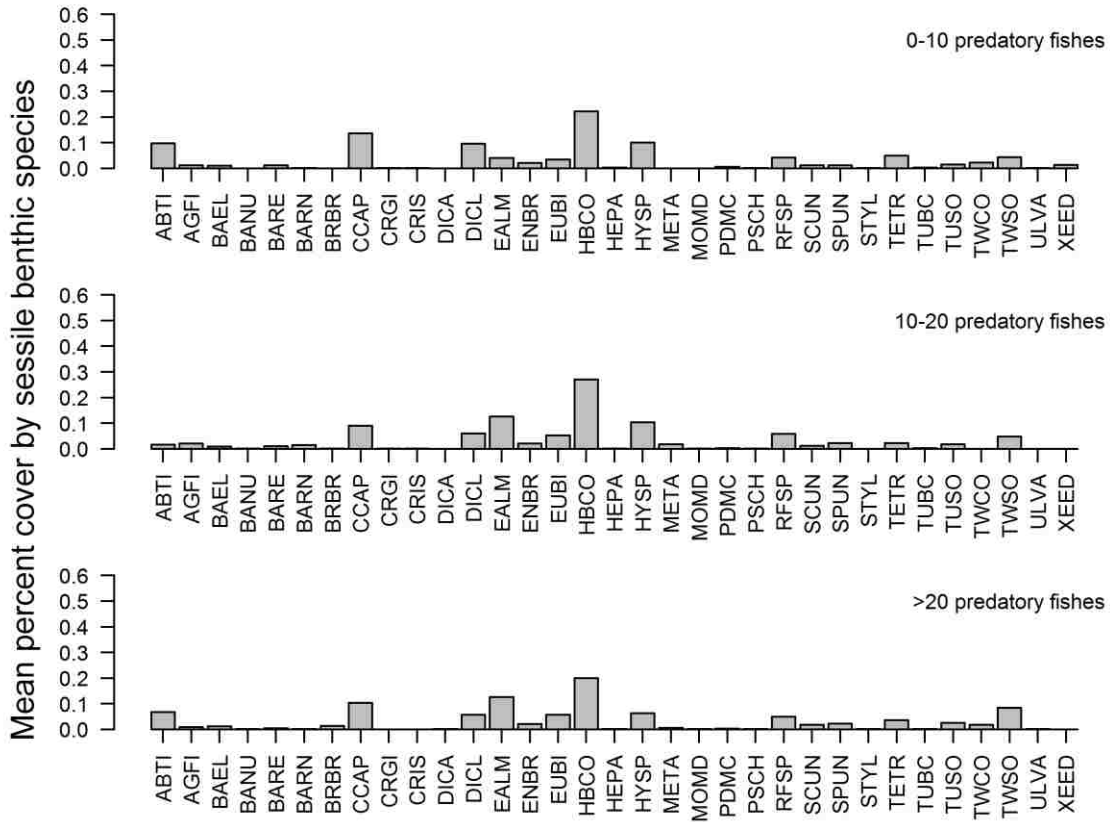


Figure S3. Mean percent cover of sessile epibenthic species at deep transects, across three levels of predatory fish abundance: 0-10 fishes (n = 7), 10-20 fishes (n = 11), and >20 fishes (n = 18). Species codes as in Table 4.

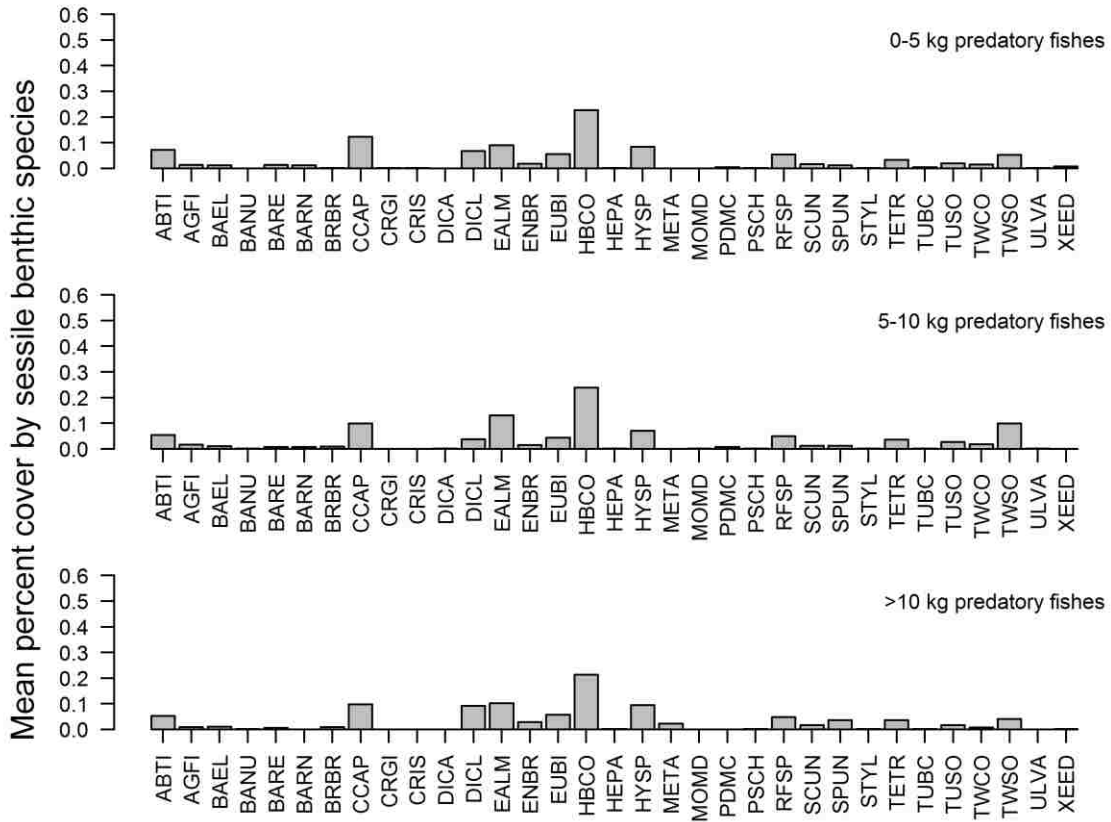


Figure S4. Mean percent cover of sessile epibenthic species at deep transects, across three levels of predatory fish biomass: 0-5 kg of fishes (n = 10), 5-10 kg of fishes (n = 13), and >10 kg of fishes (n = 13). Species codes as in Table 4.

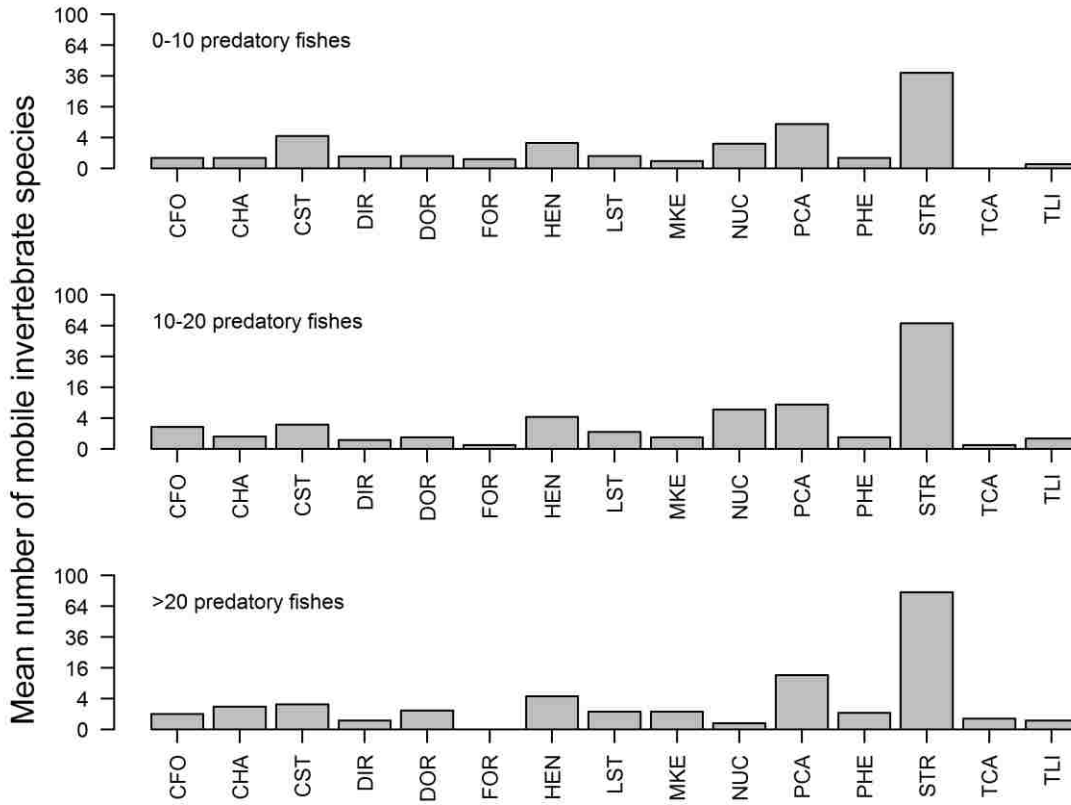


Figure S5. Mean percent cover of mobile invertebrate species at shallow transects, across three levels of predatory fish abundance. Categories and sample sizes as in Fig. S1, species codes as in Table 5.

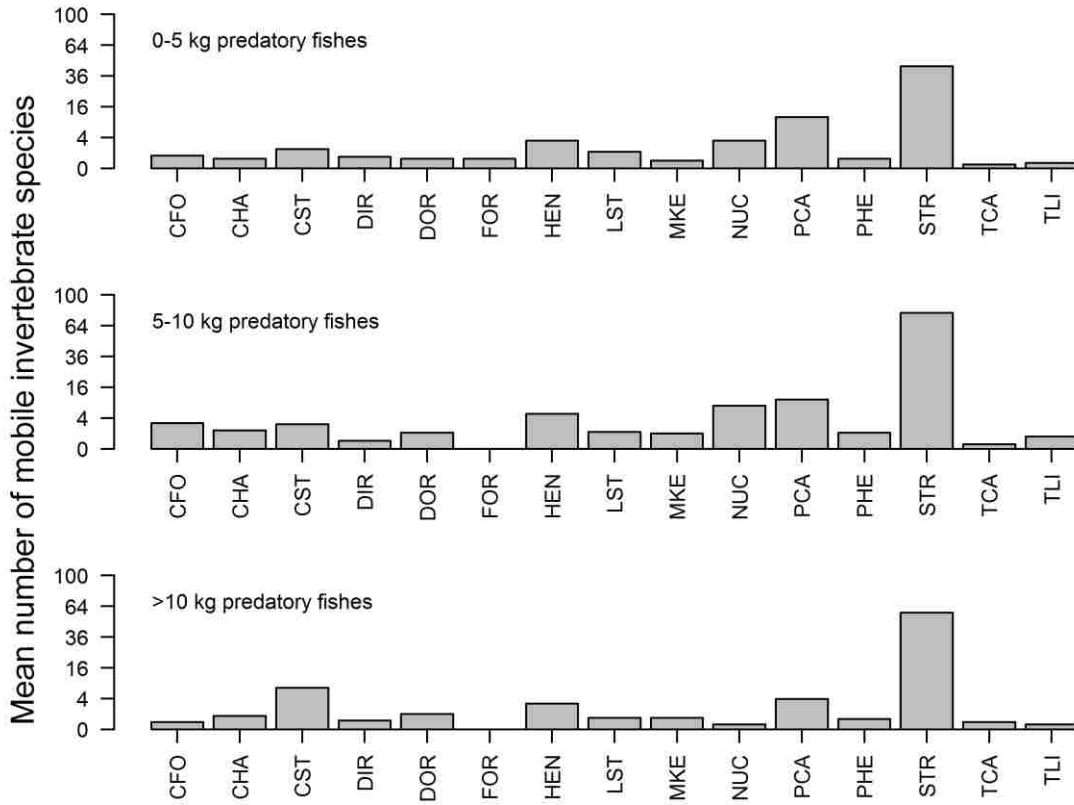


Figure S6. Mean percent cover of mobile invertebrate species at shallow transects, across three levels of predatory fish biomass. Categories and sample sizes as in Fig. S2, species codes as in Table 5.

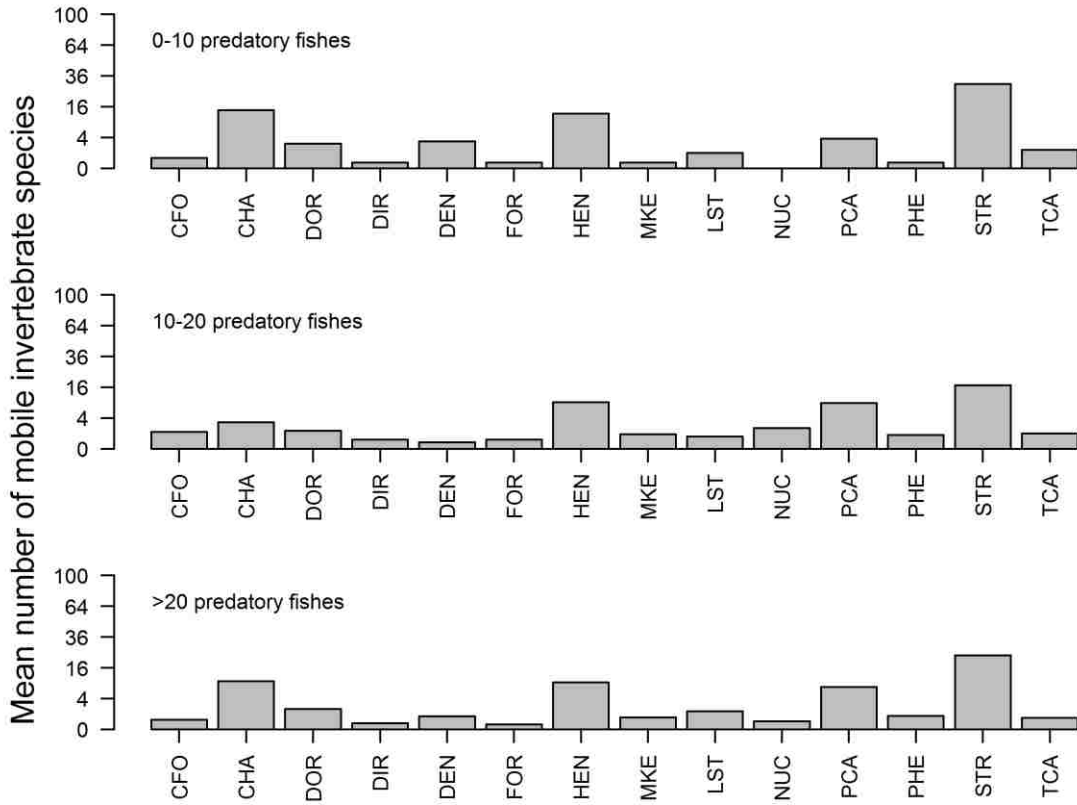


Figure S7. Mean percent cover of mobile invertebrate species at deep transects, across three levels of predatory fish abundance. Categories and sample sizes as in Fig. S3, species codes as in Table 5.

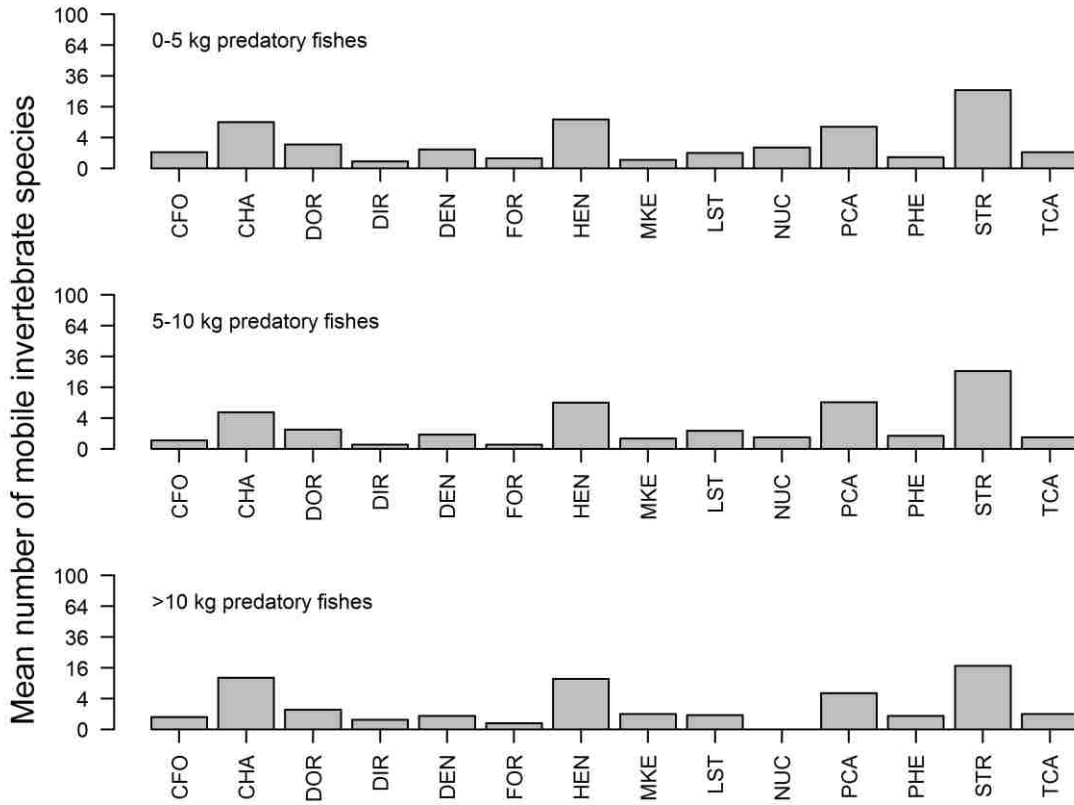


Figure S8. Mean percent cover of mobile invertebrate species at deep transects, across three levels of predatory fish biomass. Categories and sample sizes as in Fig. S4, species codes as in Table 5.

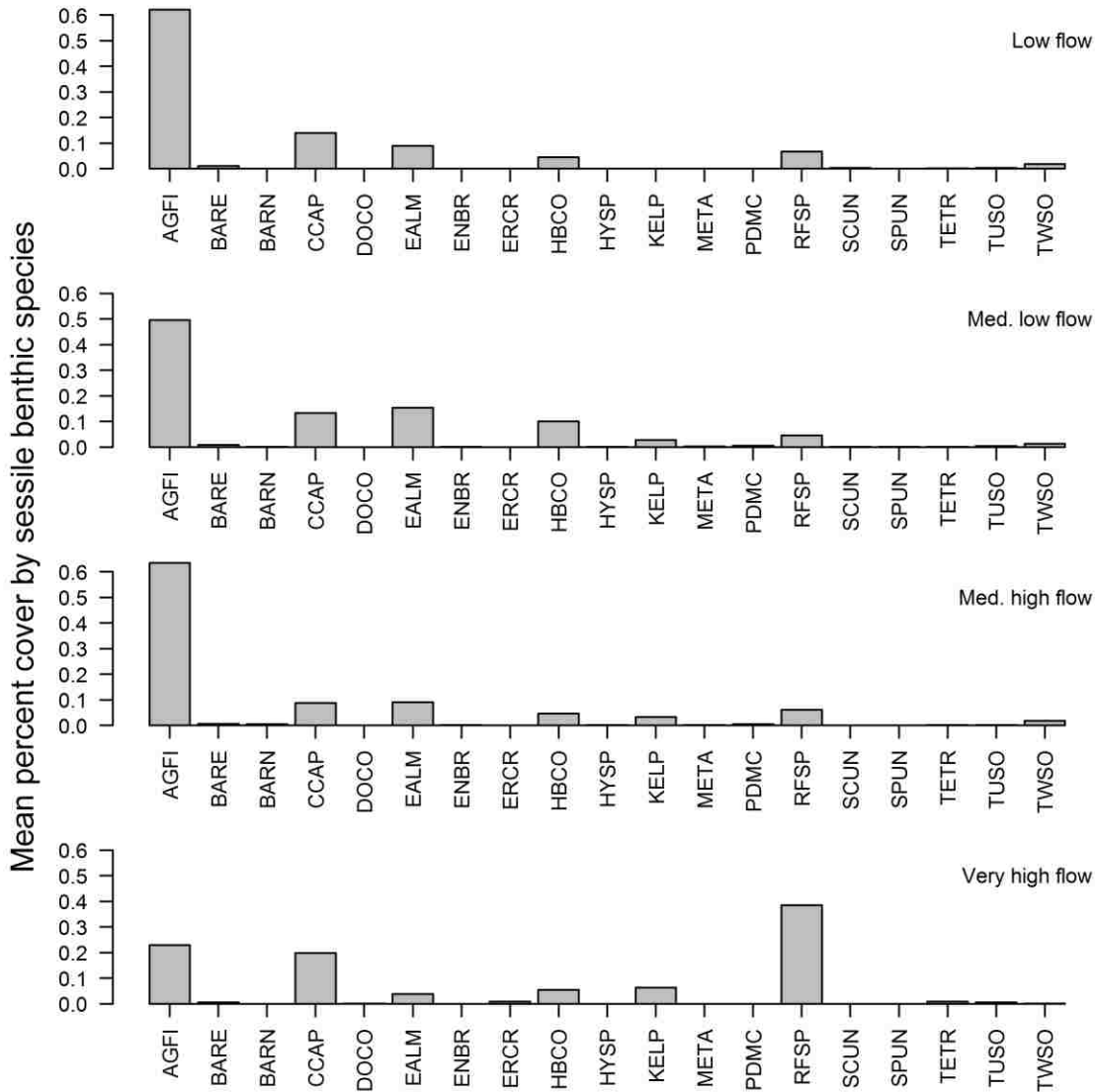


Table S9. Mean percent cover of sessile epibenthic species at shallow transects, across four levels of relative current flow. Low: >1 standard deviation (SD) below mean alabaster dissolution rate (see text and Table 7 for details) (n = 3); Med. low: 0 to 1 SD below the mean (n = 18); Med. high: 0 to 1 SD above the mean (n = 12); Very high: >2 SD above the mean (n = 3). Species codes as in Table 4.

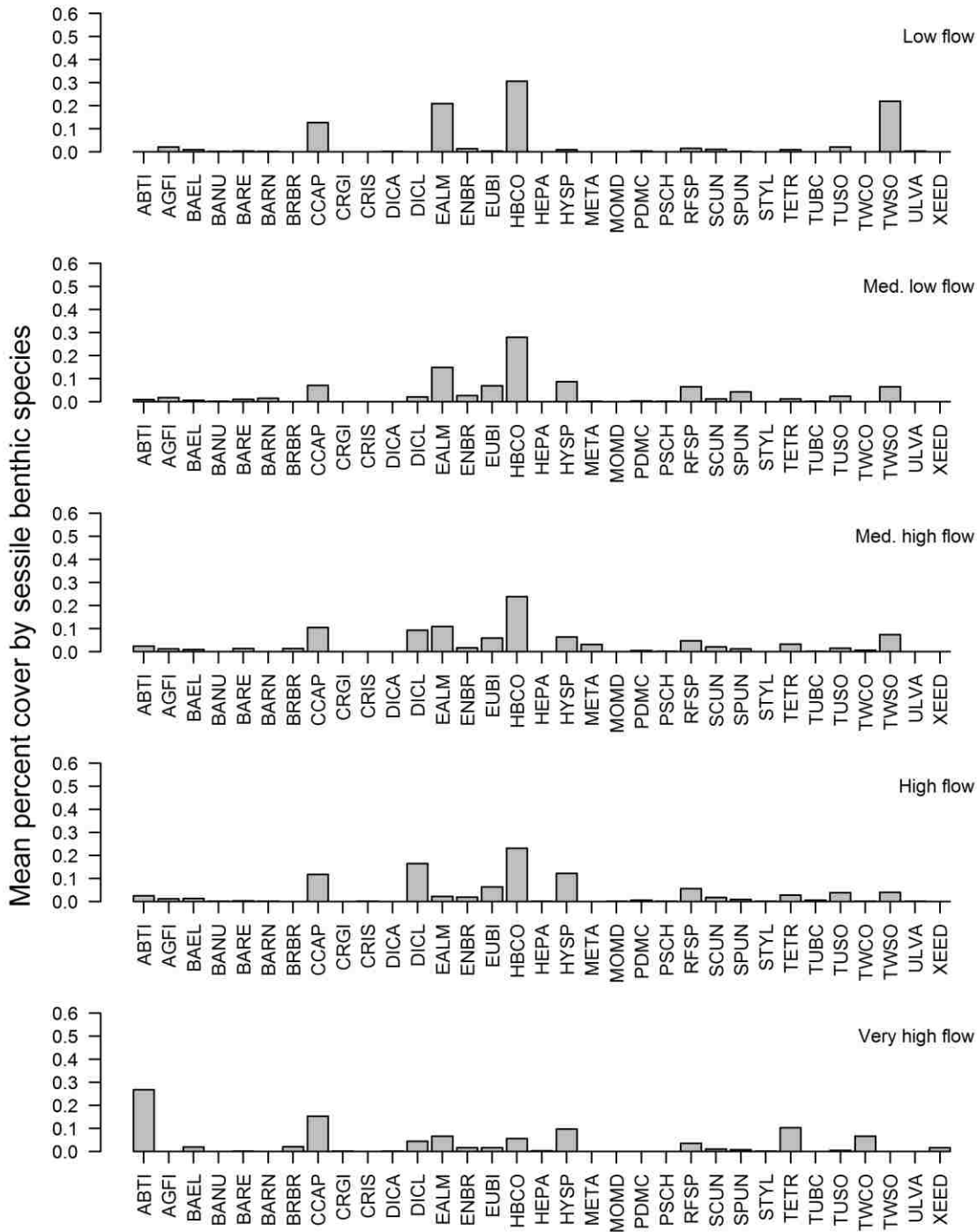


Figure S10. Mean percent cover of sessile epibenthic species at deep transects, across five levels of relative current flow. Low: >1 standard deviation (SD) below mean alabaster dissolution rate (see text and Table 7 for details) ($n = 3$); Med. low: 0 to 1 SD below the mean ($n = 12$); Med. high: 0 to 1 SD above the mean ($n = 9$); High: 1 to 2 SD above the mean ($n = 6$); Very high: >2 SD above the mean ($n = 6$). Species codes as in Table 4.

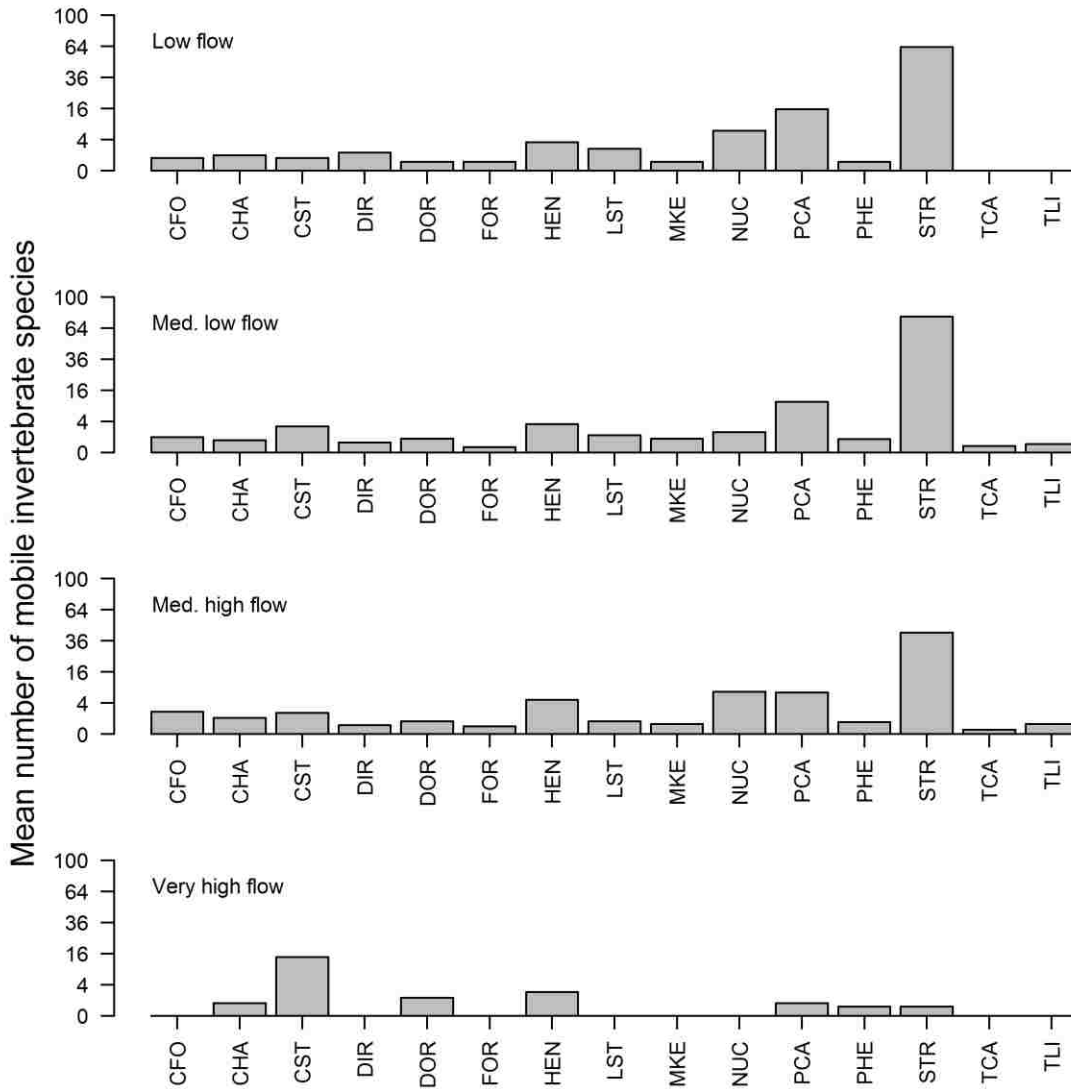


Figure S11. Mean percent cover of mobile invertebrate species at shallow transects, across four levels of relative current flow. Categories and sample sizes as in Fig. S9, species codes as in Table 5.

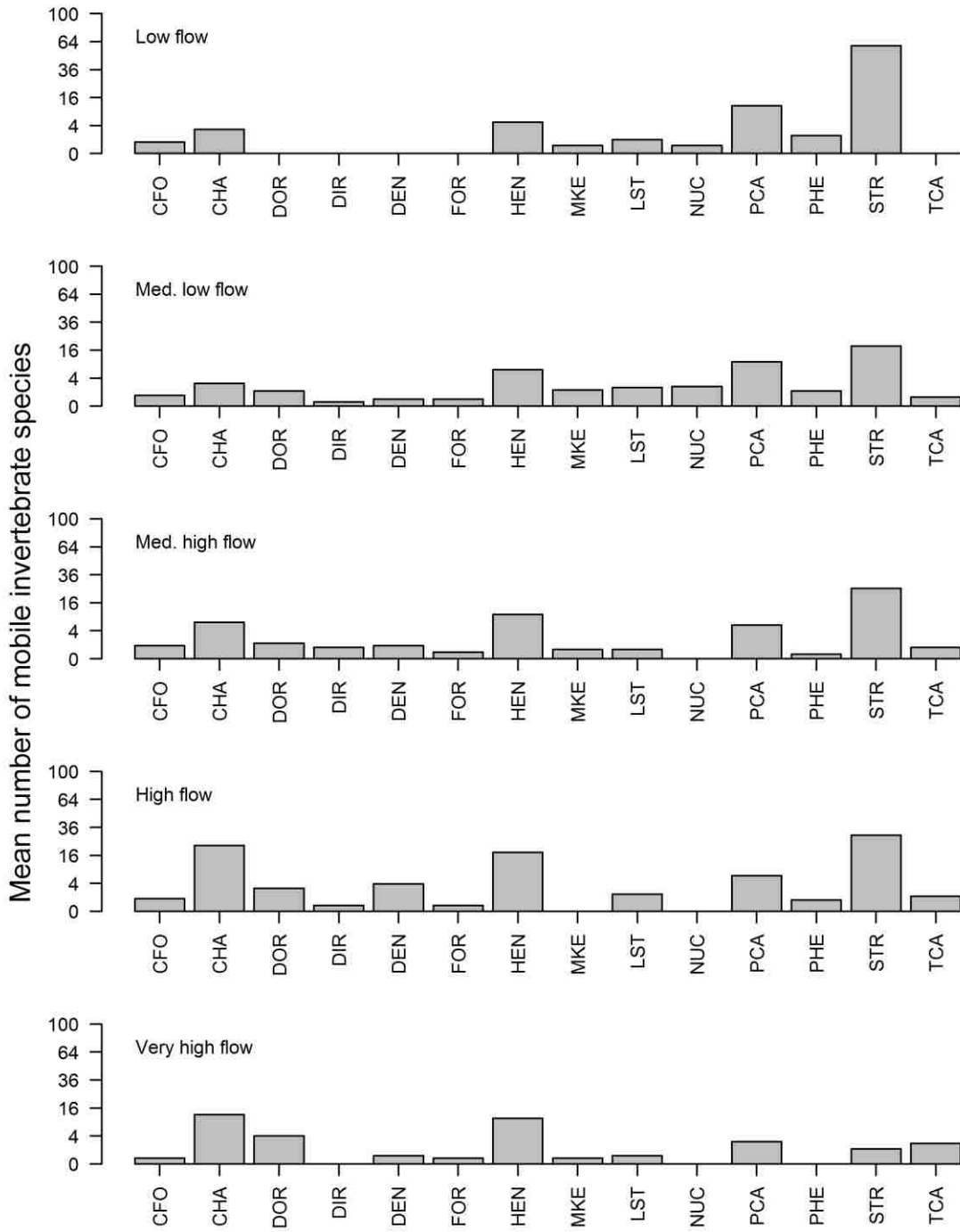


Figure S12. Mean percent cover of mobile invertebrate species at deep transects, across five levels of relative current flow. Categories and sample sizes as in Fig. S10, species codes as in Table 5.

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Appendix A. Predatory fish survey data. See Chapter 2, Table 1 and Figure 1 for location details.

Year	Date	Location	Depth	Species	Length (cm)
2010	4-May-10	NP-South	27-21 m	Copper	15
2010	4-May-10	NP-South	27-21 m	Copper	25
2010	4-May-10	NP-South	27-21 m	Male kelp greenling	25
2010	4-May-10	NP-South	27-21 m	Quillback	17
2010	4-May-10	NP-South	27-21 m	Quillback	30
2010	4-May-10	NP-South	21-15 m	Copper	20
2010	4-May-10	NP-South	21-15 m	Copper	23
2010	4-May-10	NP-South	21-15 m	Copper	30
2010	4-May-10	NP-South	21-15 m	Male kelp greenling	25
2010	4-May-10	NP-South	21-15 m	Male kelp greenling	25
2010	4-May-10	NP-South	21-15 m	Male kelp greenling	45
2010	4-May-10	NP-South	15-9 m	Copper	15
2010	4-May-10	NP-South	15-9 m	Female kelp greenling	25
2010	4-May-10	NP-South	15-9 m	Lingcod	60
2010	4-May-10	NP-South	15-9 m	Male kelp greenling	25
2010	4-May-10	SC-South	27-21 m	Lingcod	35
2010	4-May-10	SC-South	27-21 m	Lingcod	40
2010	4-May-10	SC-South	27-21 m	Lingcod	40
2010	4-May-10	SC-South	21-15 m	Copper	15
2010	4-May-10	SC-South	21-15 m	Copper	25
2010	4-May-10	SC-South	21-15 m	Male kelp greenling	20
2010	4-May-10	SC-South	21-15 m	Quillback	6
2010	4-May-10	SC-South	21-15 m	Quillback	10
2010	4-May-10	SC-South	15-9 m	Copper	15
2010	4-May-10	SC-South	15-9 m	Copper	18
2010	4-May-10	SC-South	15-9 m	Copper	18
2010	4-May-10	SC-South	15-9 m	Female kelp greenling	18
2010	4-May-10	SC-South	15-9 m	Lingcod	30
2010	4-May-10	SC-South	15-9 m	Lingcod	40
2010	4-May-10	SC-South	15-9 m	Lingcod	45
2010	4-May-10	SC-South	15-9 m	Male kelp greenling	23
2010	4-May-10	SC-South	15-9 m	Quillback	10
2010	4-May-10	SC-South	9-3 m	Female kelp greenling	30
2010	4-May-10	SC-South	9-3 m	Male kelp greenling	15
2010	6-May-10	MP-North	27-21 m	Copper	18
2010	6-May-10	MP-North	27-21 m	Copper	20
2010	6-May-10	MP-North	27-21 m	Copper	20
2010	6-May-10	MP-North	27-21 m	Copper	25
2010	6-May-10	MP-North	27-21 m	Male kelp greenling	28
2010	6-May-10	MP-North	27-21 m	Male kelp greenling	38

2010	6-May-10	MP-North	21-15 m	Lingcod	30
2010	6-May-10	MP-North	21-15 m	Male kelp greenling	20
2010	6-May-10	MP-North	15-9 m	Buffalo sculpin	18
2010	6-May-10	MP-North	15-9 m	Lingcod	37
2010	6-May-10	MP-North	9-3 m	Copper	12
2010	6-May-10	PG-South	27-21 m	Copper	15
2010	6-May-10	PG-South	27-21 m	Copper	15
2010	6-May-10	PG-South	27-21 m	Copper	15
2010	6-May-10	PG-South	27-21 m	Copper	20
2010	6-May-10	PG-South	27-21 m	Copper	20
2010	6-May-10	PG-South	27-21 m	Copper	20
2010	6-May-10	PG-South	27-21 m	Lingcod	25
2010	6-May-10	PG-South	27-21 m	Male kelp greenling	23
2010	6-May-10	PG-South	15-9 m	Copper	20
2010	6-May-10	PG-South	15-9 m	Copper	22
2010	6-May-10	PG-South	15-9 m	Male kelp greenling	20
2010	6-May-10	PG-South	9-3 m	Female kelp greenling	25
2010	6-May-10	PG-South	9-3 m	Lingcod	27
2010	6-May-10	PG-South	3-0 m	Whitespotted greenling	15
2010	6-May-10	YI-Low	27-21 m	Copper	20
2010	6-May-10	YI-Low	27-21 m	Copper	20
2010	6-May-10	YI-Low	27-21 m	Copper	25
2010	6-May-10	YI-Low	27-21 m	Copper	30
2010	6-May-10	YI-Low	27-21 m	Copper	37
2010	6-May-10	YI-Low	27-21 m	Male kelp greenling	20
2010	6-May-10	YI-Low	27-21 m	Male kelp greenling	20
2010	6-May-10	YI-Low	27-21 m	Male kelp greenling	40
2010	6-May-10	YI-Low	27-21 m	Quillback	10
2010	6-May-10	YI-Low	27-21 m	Quillback	12
2010	6-May-10	YI-Low	27-21 m	Quillback	15
2010	6-May-10	YI-Low	27-21 m	Quillback	15
2010	6-May-10	YI-Low	27-21 m	Quillback	15
2010	6-May-10	YI-Low	27-21 m	Quillback	15
2010	6-May-10	YI-Low	15-9 m	Copper	25
2010	6-May-10	YI-Low	15-9 m	Copper	25
2010	6-May-10	YI-Low	15-9 m	Copper	26
2010	6-May-10	YI-Low	15-9 m	Copper	28
2010	6-May-10	YI-Low	15-9 m	Female kelp greenling	25
2010	6-May-10	YI-Low	15-9 m	Quillback	20
2010	6-May-10	YI-Low	15-9 m	Quillback	25
2010	6-May-10	YI-Low	9-3 m	Copper	18
2010	6-May-10	YI-Low	9-3 m	Copper	22
2010	6-May-10	YI-Low	9-3 m	Lingcod	65

2010	9-May-10	MP-Center	27-21 m	Copper	20
2010	9-May-10	MP-Center	21-15 m	Copper	20
2010	9-May-10	MP-Center	21-15 m	Copper	23
2010	9-May-10	MP-Center	21-15 m	Copper	28
2010	9-May-10	MP-Center	21-15 m	Male kelp greenling	25
2010	9-May-10	MP-Center	21-15 m	Male kelp greenling	32
2010	9-May-10	MP-Center	15-9 m	Male kelp greenling	25
2010	9-May-10	MP-Center	9-3 m	Buffalo sculpin	14
2010	9-May-10	NP-North	27-21 m	Lingcod	20
2010	9-May-10	NP-North	27-21 m	Lingcod	60
2010	9-May-10	NP-North	15-9 m	Copper	20
2010	9-May-10	NP-North	15-9 m	Female kelp greenling	28
2010	9-May-10	NP-North	15-9 m	Male kelp greenling	20
2010	9-May-10	PG-Center	27-21 m	Copper	20
2010	9-May-10	PG-Center	27-21 m	Copper	20
2010	9-May-10	PG-Center	27-21 m	Copper	20
2010	9-May-10	PG-Center	27-21 m	Copper	20
2010	9-May-10	PG-Center	27-21 m	Copper	20
2010	9-May-10	PG-Center	27-21 m	Copper	23
2010	9-May-10	PG-Center	27-21 m	Copper	25
2010	9-May-10	PG-Center	27-21 m	Copper	25
2010	9-May-10	PG-Center	27-21 m	Copper	25
2010	9-May-10	PG-Center	27-21 m	Copper	27
2010	9-May-10	PG-Center	27-21 m	Copper	28
2010	9-May-10	PG-Center	27-21 m	Lingcod	25
2010	9-May-10	PG-Center	27-21 m	Lingcod	40
2010	9-May-10	PG-Center	21-15 m	Copper	20
2010	9-May-10	PG-Center	21-15 m	Copper	23
2010	9-May-10	PG-Center	21-15 m	Copper	25
2010	9-May-10	PG-Center	21-15 m	Copper	35
2010	9-May-10	PG-Center	21-15 m	Male kelp greenling	25
2010	9-May-10	PG-Center	21-15 m	Male kelp greenling	25
2010	9-May-10	PG-Center	21-15 m	Male kelp greenling	25
2010	9-May-10	PG-Center	15-9 m	Copper	20
2010	9-May-10	PG-Center	15-9 m	Female kelp greenling	15
2010	9-May-10	PG-Center	15-9 m	Female kelp greenling	20
2010	9-May-10	PG-Center	15-9 m	Female kelp greenling	25
2010	9-May-10	PG-Center	15-9 m	Lingcod	80
2010	9-May-10	PG-Center	15-9 m	Male kelp greenling	20
2010	9-May-10	PG-Center	15-9 m	Male kelp greenling	25
2010	9-May-10	PG-Center	15-9 m	Male kelp greenling	30
2010	9-May-10	PG-Center	9-3 m	Copper	12
2010	9-May-10	PG-Center	9-3 m	Copper	20

2010	9-May-10	PG-Center	9-3 m	Copper	25
2010	9-May-10	PG-Center	9-3 m	Female kelp greenling	27
2010	20-May-10	PP-One Mile	27-21 m	Male kelp greenling	35
2010	20-May-10	PP-One Mile	21-15 m	Lingcod	115
2010	20-May-10	PP-One Mile	21-15 m	Male kelp greenling	30
2010	20-May-10	PP-One Mile	15-9 m	Lingcod	80
2010	20-May-10	PP-One Mile	15-9 m	Lingcod	80
2010	20-May-10	PP-One Mile	15-9 m	Male kelp greenling	20
2010	3-Jun-10	PP-Minnesota	27-21 m	Copper	30
2010	3-Jun-10	PP-Minnesota	27-21 m	Lingcod	40
2010	3-Jun-10	PP-Minnesota	21-15 m	Copper	20
2010	3-Jun-10	PP-Minnesota	21-15 m	Male kelp greenling	20
2010	3-Jun-10	PP-Minnesota	21-15 m	Male kelp greenling	20
2010	3-Jun-10	PP-Minnesota	21-15 m	Male kelp greenling	35
2010	3-Jun-10	PP-Minnesota	15-9 m	Copper	20
2010	3-Jun-10	PP-Minnesota	15-9 m	Copper	25
2010	3-Jun-10	PP-Minnesota	15-9 m	Copper	30
2010	3-Jun-10	PP-Minnesota	15-9 m	Male kelp greenling	15
2010	3-Jun-10	PP-Minnesota	3-0 m	Lingcod	37
2010	3-Jun-10	YI-Yellow	27-21 m	Lingcod	43
2010	3-Jun-10	YI-Yellow	21-15 m	Copper	20
2010	3-Jun-10	YI-Yellow	21-15 m	Male kelp greenling	30
2010	3-Jun-10	YI-Yellow	21-15 m	Quillback	30
2010	3-Jun-10	YI-Yellow	15-9 m	Copper	30
2010	3-Jun-10	YI-Yellow	15-9 m	Copper	30
2010	3-Jun-10	YI-Yellow	15-9 m	Female kelp greenling	30
2010	3-Jun-10	YI-Yellow	15-9 m	Male kelp greenling	18
2010	5-Jun-10	SC-Center	27-21 m	Copper	25
2010	5-Jun-10	SC-Center	27-21 m	Copper	25
2010	5-Jun-10	SC-Center	27-21 m	Copper	30
2010	5-Jun-10	SC-Center	27-21 m	Lingcod	60
2010	5-Jun-10	SC-Center	27-21 m	Male kelp greenling	55
2010	5-Jun-10	SC-Center	21-15 m	Copper	20
2010	5-Jun-10	SC-Center	21-15 m	Copper	30
2010	5-Jun-10	SC-Center	21-15 m	Copper	33
2010	5-Jun-10	SC-Center	21-15 m	Female kelp greenling	20
2010	5-Jun-10	SC-Center	21-15 m	Lingcod	100
2010	5-Jun-10	SC-Center	21-15 m	Quillback	10
2010	5-Jun-10	SC-Center	15-9 m	Copper	19
2010	5-Jun-10	SC-Center	15-9 m	Copper	30
2010	5-Jun-10	SC-Center	15-9 m	Copper	35
2010	5-Jun-10	SC-Center	15-9 m	Female kelp greenling	18
2010	5-Jun-10	SC-Center	15-9 m	Female kelp greenling	20

2010	5-Jun-10	SC-Center	15-9 m	Male kelp greenling	20
2010	5-Jun-10	SC-Center	15-9 m	Quillback	12
2010	5-Jun-10	SC-Center	15-9 m	Quillback	12
2010	5-Jun-10	SC-Center	15-9 m	Quillback	15
2010	5-Jun-10	SC-Center	9-3 m	Copper	8
2010	5-Jun-10	SC-Center	9-3 m	Copper	10
2010	5-Jun-10	SC-Center	9-3 m	Copper	10
2010	5-Jun-10	SC-Center	9-3 m	Copper	15
2010	5-Jun-10	SC-Center	9-3 m	Copper	15
2010	5-Jun-10	SC-Center	9-3 m	Copper	15
2010	5-Jun-10	SC-Center	9-3 m	Copper	15
2010	5-Jun-10	SC-Center	9-3 m	Copper	20
2010	5-Jun-10	SC-Center	9-3 m	Copper	22
2010	5-Jun-10	SC-Center	9-3 m	Copper	25
2010	5-Jun-10	SC-Center	9-3 m	Copper	30
2010	5-Jun-10	SC-Center	9-3 m	Lingcod	50
2010	5-Jun-10	SC-Center	3-0 m	Copper	20
2010	5-Jun-10	SC-Center	3-0 m	Lingcod	55
2010	14-Aug-10	MP-North	27-21 m	Copper	20
2010	14-Aug-10	MP-North	27-21 m	Copper	30
2010	14-Aug-10	MP-North	27-21 m	Lingcod	35
2010	14-Aug-10	MP-North	21-15 m	Copper	20
2010	14-Aug-10	MP-North	21-15 m	Female kelp greenling	30
2010	14-Aug-10	MP-North	21-15 m	Lingcod	35
2010	14-Aug-10	MP-North	15-9 m	Female kelp greenling	30
2010	14-Aug-10	MP-North	15-9 m	Lingcod	45
2010	14-Aug-10	MP-North	9-3 m	Copper	20
2010	14-Aug-10	MP-North	9-3 m	Male kelp greenling	20
2010	14-Aug-10	MP-North	9-3 m	Quillback	30
2010	14-Aug-10	SC-Center	27-21 m	Cabezón	75
2010	14-Aug-10	SC-Center	27-21 m	Copper	20
2010	14-Aug-10	SC-Center	27-21 m	Copper	25
2010	14-Aug-10	SC-Center	27-21 m	Copper	30
2010	14-Aug-10	SC-Center	27-21 m	Copper	30
2010	14-Aug-10	SC-Center	27-21 m	Copper	35
2010	14-Aug-10	SC-Center	27-21 m	Copper	35
2010	14-Aug-10	SC-Center	27-21 m	Copper	35
2010	14-Aug-10	SC-Center	27-21 m	Female kelp greenling	25
2010	14-Aug-10	SC-Center	27-21 m	Lingcod	30
2010	14-Aug-10	SC-Center	27-21 m	Lingcod	50
2010	14-Aug-10	SC-Center	27-21 m	Male kelp greenling	25
2010	14-Aug-10	SC-Center	21-15 m	Copper	23
2010	14-Aug-10	SC-Center	21-15 m	Copper	25

2010	14-Aug-10	SC-Center	21-15 m	Copper	30
2010	14-Aug-10	SC-Center	21-15 m	Female kelp greenling	40
2010	14-Aug-10	SC-Center	21-15 m	Lingcod	40
2010	14-Aug-10	SC-Center	21-15 m	Lingcod	50
2010	14-Aug-10	SC-Center	15-9 m	Cabezon	60
2010	14-Aug-10	SC-Center	15-9 m	Female kelp greenling	20
2010	14-Aug-10	SC-Center	15-9 m	Female kelp greenling	35
2010	14-Aug-10	SC-Center	15-9 m	Lingcod	50
2010	14-Aug-10	SC-Center	9-3 m	Copper	15
2010	14-Aug-10	SC-Center	9-3 m	Copper	15
2010	14-Aug-10	SC-Center	9-3 m	Copper	15
2010	15-Aug-10	MP-Center	27-21 m	Copper	15
2010	15-Aug-10	MP-Center	27-21 m	Copper	20
2010	15-Aug-10	MP-Center	27-21 m	Copper	20
2010	15-Aug-10	MP-Center	27-21 m	Copper	20
2010	15-Aug-10	MP-Center	27-21 m	Copper	20
2010	15-Aug-10	MP-Center	27-21 m	Copper	25
2010	15-Aug-10	MP-Center	27-21 m	Copper	25
2010	15-Aug-10	MP-Center	27-21 m	Copper	25
2010	15-Aug-10	MP-Center	27-21 m	Copper	25
2010	15-Aug-10	MP-Center	27-21 m	Copper	25
2010	15-Aug-10	MP-Center	27-21 m	Copper	25
2010	15-Aug-10	MP-Center	27-21 m	Lingcod	45
2010	15-Aug-10	MP-Center	27-21 m	Male kelp greenling	20
2010	15-Aug-10	MP-Center	27-21 m	Male kelp greenling	25
2010	15-Aug-10	MP-Center	27-21 m	Quillback	15
2010	15-Aug-10	MP-Center	27-21 m	Quillback	15
2010	15-Aug-10	MP-Center	27-21 m	Quillback	20
2010	15-Aug-10	MP-Center	27-21 m	Quillback	20
2010	15-Aug-10	MP-Center	27-21 m	Quillback	20
2010	15-Aug-10	MP-Center	27-21 m	Quillback	20
2010	15-Aug-10	MP-Center	27-21 m	Quillback	20
2010	15-Aug-10	MP-Center	21-15 m	Copper	20
2010	15-Aug-10	MP-Center	21-15 m	Copper	20
2010	15-Aug-10	MP-Center	21-15 m	Copper	25
2010	15-Aug-10	MP-Center	21-15 m	Copper	25
2010	15-Aug-10	MP-Center	21-15 m	Copper	25
2010	15-Aug-10	MP-Center	21-15 m	Copper	25
2010	15-Aug-10	MP-Center	21-15 m	Copper	30
2010	15-Aug-10	MP-Center	21-15 m	Lingcod	40
2010	15-Aug-10	MP-Center	21-15 m	Male kelp greenling	30
2010	15-Aug-10	MP-Center	21-15 m	Male kelp greenling	30
2010	15-Aug-10	MP-Center	15-9 m	Copper	25
2010	15-Aug-10	MP-Center	15-9 m	Copper	30
2010	15-Aug-10	MP-Center	15-9 m	Male kelp greenling	30

2010	15-Aug-10	MP-Center	9-3 m	Copper	20
2010	15-Aug-10	MP-Center	9-3 m	Copper	20
2010	15-Aug-10	MP-Center	9-3 m	Male kelp greenling	25
2010	15-Aug-10	NP-North	21-15 m	Male kelp greenling	25
2010	15-Aug-10	NP-North	15-9 m	Male kelp greenling	25
2010	15-Aug-10	NP-North	9-3 m	Male kelp greenling	30
2010	15-Aug-10	NP-North	3-0 m	Buffalo sculpin	10
2010	15-Aug-10	NP-North	3-0 m	Whitespotted greenling	25
2010	15-Aug-10	PP-Minnesota	27-21 m	Lingcod	80
2010	15-Aug-10	PP-Minnesota	27-21 m	Lingcod	90
2010	15-Aug-10	PP-Minnesota	27-21 m	Male kelp greenling	30
2010	15-Aug-10	PP-Minnesota	27-21 m	Male kelp greenling	35
2010	15-Aug-10	PP-Minnesota	27-21 m	Male kelp greenling	35
2010	15-Aug-10	PP-Minnesota	21-15 m	Copper	20
2010	15-Aug-10	PP-Minnesota	21-15 m	Lingcod	85
2010	15-Aug-10	PP-Minnesota	21-15 m	Male kelp greenling	30
2010	15-Aug-10	PP-Minnesota	21-15 m	Male kelp greenling	30
2010	15-Aug-10	PP-Minnesota	15-9 m	Male kelp greenling	20
2010	15-Aug-10	PP-Minnesota	15-9 m	Male kelp greenling	30
2010	15-Aug-10	PP-Minnesota	15-9 m	Male kelp greenling	30
2010	15-Aug-10	PP-Minnesota	15-9 m	Male kelp greenling	30
2010	15-Aug-10	PP-Minnesota	15-9 m	Male kelp greenling	35
2010	15-Aug-10	PP-Minnesota	15-9 m	Male kelp greenling	35
2010	15-Aug-10	PP-Minnesota	9-3 m	Male kelp greenling	20
2010	15-Aug-10	PP-Minnesota	9-3 m	Male kelp greenling	30
2010	16-Aug-10	NP-South	27-21 m	Copper	25
2010	16-Aug-10	NP-South	27-21 m	Copper	25
2010	16-Aug-10	NP-South	27-21 m	Copper	25
2010	16-Aug-10	NP-South	27-21 m	Copper	35
2010	16-Aug-10	NP-South	27-21 m	Lingcod	35
2010	16-Aug-10	NP-South	27-21 m	Lingcod	40
2010	16-Aug-10	NP-South	27-21 m	Male kelp greenling	25
2010	16-Aug-10	NP-South	27-21 m	Quillback	20
2010	16-Aug-10	NP-South	21-15 m	Copper	15
2010	16-Aug-10	NP-South	21-15 m	Copper	20
2010	16-Aug-10	NP-South	21-15 m	Copper	20
2010	16-Aug-10	NP-South	21-15 m	Copper	23
2010	16-Aug-10	NP-South	21-15 m	Copper	26
2010	16-Aug-10	NP-South	21-15 m	Copper	28
2010	16-Aug-10	NP-South	21-15 m	Copper	30
2010	16-Aug-10	NP-South	21-15 m	Copper	32
2010	16-Aug-10	NP-South	21-15 m	Copper	33
2010	16-Aug-10	NP-South	21-15 m	Female kelp greenling	27
2010	16-Aug-10	NP-South	21-15 m	Lingcod	40

2010	16-Aug-10	NP-South	21-15 m	Lingcod	65
2010	16-Aug-10	NP-South	21-15 m	Lingcod	70
2010	16-Aug-10	NP-South	21-15 m	Male kelp greenling	25
2010	16-Aug-10	NP-South	21-15 m	Male kelp greenling	30
2010	16-Aug-10	NP-South	21-15 m	Male kelp greenling	32
2010	16-Aug-10	NP-South	21-15 m	Quillback	7
2010	16-Aug-10	NP-South	21-15 m	Quillback	12
2010	16-Aug-10	NP-South	21-15 m	Quillback	12
2010	16-Aug-10	NP-South	21-15 m	Quillback	15
2010	16-Aug-10	NP-South	21-15 m	Quillback	30
2010	16-Aug-10	NP-South	15-9 m	Copper	10
2010	16-Aug-10	NP-South	15-9 m	Copper	15
2010	16-Aug-10	NP-South	15-9 m	Copper	15
2010	16-Aug-10	NP-South	15-9 m	Copper	17
2010	16-Aug-10	NP-South	15-9 m	Copper	20
2010	16-Aug-10	NP-South	15-9 m	Copper	20
2010	16-Aug-10	NP-South	15-9 m	Copper	20
2010	16-Aug-10	NP-South	15-9 m	Copper	20
2010	16-Aug-10	NP-South	15-9 m	Copper	30
2010	16-Aug-10	NP-South	15-9 m	Copper	35
2010	16-Aug-10	NP-South	15-9 m	Female kelp greenling	30
2010	16-Aug-10	NP-South	15-9 m	Lingcod	35
2010	16-Aug-10	NP-South	15-9 m	Male kelp greenling	30
2010	16-Aug-10	PG-South	27-21 m	Copper	25
2010	16-Aug-10	PG-South	27-21 m	Copper	27
2010	16-Aug-10	PG-South	27-21 m	Copper	30
2010	16-Aug-10	PG-South	27-21 m	Copper	38
2010	16-Aug-10	PG-South	27-21 m	Lingcod	50
2010	16-Aug-10	PG-South	27-21 m	Lingcod	60
2010	16-Aug-10	PG-South	27-21 m	Male kelp greenling	30
2010	16-Aug-10	PG-South	27-21 m	Male kelp greenling	30
2010	16-Aug-10	PG-South	21-15 m	Copper	15
2010	16-Aug-10	PG-South	21-15 m	Copper	17
2010	16-Aug-10	PG-South	21-15 m	Copper	17
2010	16-Aug-10	PG-South	21-15 m	Copper	18
2010	16-Aug-10	PG-South	21-15 m	Copper	20
2010	16-Aug-10	PG-South	21-15 m	Copper	20
2010	16-Aug-10	PG-South	21-15 m	Copper	20
2010	16-Aug-10	PG-South	21-15 m	Copper	20
2010	16-Aug-10	PG-South	21-15 m	Copper	20
2010	16-Aug-10	PG-South	21-15 m	Copper	22
2010	16-Aug-10	PG-South	21-15 m	Copper	22
2010	16-Aug-10	PG-South	21-15 m	Copper	23

2010	16-Aug-10	PG-South	21-15 m	Copper	25
2010	16-Aug-10	PG-South	21-15 m	Copper	25
2010	16-Aug-10	PG-South	21-15 m	Copper	25
2010	16-Aug-10	PG-South	21-15 m	Copper	27
2010	16-Aug-10	PG-South	21-15 m	Copper	27
2010	16-Aug-10	PG-South	21-15 m	Copper	28
2010	16-Aug-10	PG-South	21-15 m	Lingcod	70
2010	16-Aug-10	PG-South	21-15 m	Male kelp greenling	25
2010	16-Aug-10	PG-South	21-15 m	Male kelp greenling	30
2010	16-Aug-10	PG-South	15-9 m	Copper	12
2010	16-Aug-10	PG-South	15-9 m	Copper	15
2010	16-Aug-10	PG-South	15-9 m	Copper	15
2010	16-Aug-10	PG-South	15-9 m	Copper	18
2010	16-Aug-10	PG-South	15-9 m	Copper	20
2010	16-Aug-10	PG-South	15-9 m	Copper	20
2010	16-Aug-10	PG-South	15-9 m	Copper	20
2010	16-Aug-10	PG-South	15-9 m	Copper	22
2010	16-Aug-10	PG-South	15-9 m	Copper	24
2010	16-Aug-10	PG-South	15-9 m	Copper	25
2010	16-Aug-10	PG-South	15-9 m	Copper	27
2010	16-Aug-10	PG-South	15-9 m	Copper	28
2010	16-Aug-10	PG-South	15-9 m	Copper	30
2010	16-Aug-10	PG-South	15-9 m	Copper	32
2010	16-Aug-10	PG-South	15-9 m	Female kelp greenling	29
2010	16-Aug-10	PG-South	15-9 m	Lingcod	50
2010	16-Aug-10	PG-South	15-9 m	Male kelp greenling	15
2010	16-Aug-10	PG-South	15-9 m	Male kelp greenling	25
2010	16-Aug-10	PG-South	15-9 m	Male kelp greenling	27
2010	16-Aug-10	PG-South	15-9 m	Male kelp greenling	30
2010	16-Aug-10	PG-South	15-9 m	Male kelp greenling	30
2010	16-Aug-10	PG-South	15-9 m	Male kelp greenling	30
2010	16-Aug-10	PG-South	9-3 m	Copper	19
2010	16-Aug-10	PG-South	9-3 m	Female kelp greenling	30
2010	16-Aug-10	PG-South	9-3 m	Male kelp greenling	20
2010	16-Aug-10	PG-South	3-0 m	Male kelp greenling	10
2010	16-Aug-10	SC-South	27-21 m	Copper	25
2010	16-Aug-10	SC-South	27-21 m	Copper	25
2010	16-Aug-10	SC-South	27-21 m	Copper	35
2010	16-Aug-10	SC-South	27-21 m	Male kelp greenling	30
2010	16-Aug-10	SC-South	21-15 m	Female kelp greenling	23
2010	16-Aug-10	SC-South	21-15 m	Male kelp greenling	35
2010	16-Aug-10	SC-South	15-9 m	Copper	20
2010	16-Aug-10	SC-South	15-9 m	Copper	20

2010	16-Aug-10	SC-South	15-9 m	Copper	23
2010	16-Aug-10	SC-South	15-9 m	Copper	24
2010	16-Aug-10	SC-South	15-9 m	Female kelp greenling	17
2010	16-Aug-10	SC-South	15-9 m	Female kelp greenling	20
2010	16-Aug-10	SC-South	15-9 m	Female kelp greenling	20
2010	16-Aug-10	SC-South	15-9 m	Female kelp greenling	23
2010	16-Aug-10	SC-South	15-9 m	Female kelp greenling	35
2010	16-Aug-10	SC-South	15-9 m	Lingcod	43
2010	16-Aug-10	SC-South	15-9 m	Male kelp greenling	23
2010	16-Aug-10	SC-South	15-9 m	Male kelp greenling	25
2010	16-Aug-10	SC-South	15-9 m	Male kelp greenling	25
2010	16-Aug-10	SC-South	15-9 m	Male kelp greenling	25
2010	16-Aug-10	SC-South	15-9 m	Quillback	18
2010	16-Aug-10	SC-South	15-9 m	Quillback	20
2010	16-Aug-10	SC-South	15-9 m	Quillback	20
2010	16-Aug-10	SC-South	9-3 m	Copper	12
2010	16-Aug-10	SC-South	9-3 m	Copper	20
2010	16-Aug-10	SC-South	9-3 m	Female kelp greenling	20
2010	16-Aug-10	YI-Yellow	27-21 m	Copper	11
2010	16-Aug-10	YI-Yellow	27-21 m	Copper	17
2010	16-Aug-10	YI-Yellow	27-21 m	Copper	20
2010	16-Aug-10	YI-Yellow	27-21 m	Copper	20
2010	16-Aug-10	YI-Yellow	27-21 m	Copper	25
2010	16-Aug-10	YI-Yellow	27-21 m	Copper	25
2010	16-Aug-10	YI-Yellow	27-21 m	Copper	25
2010	16-Aug-10	YI-Yellow	27-21 m	Copper	25
2010	16-Aug-10	YI-Yellow	27-21 m	Copper	30
2010	16-Aug-10	YI-Yellow	27-21 m	Male kelp greenling	30
2010	16-Aug-10	YI-Yellow	27-21 m	Male kelp greenling	30
2010	16-Aug-10	YI-Yellow	27-21 m	Quillback	12
2010	16-Aug-10	YI-Yellow	27-21 m	Quillback	15
2010	16-Aug-10	YI-Yellow	27-21 m	Quillback	15
2010	16-Aug-10	YI-Yellow	27-21 m	Quillback	20
2010	16-Aug-10	YI-Yellow	27-21 m	Quillback	20
2010	16-Aug-10	YI-Yellow	27-21 m	Quillback	20
2010	16-Aug-10	YI-Yellow	27-21 m	Quillback	20
2010	16-Aug-10	YI-Yellow	21-15 m	Copper	15
2010	16-Aug-10	YI-Yellow	21-15 m	Copper	18
2010	16-Aug-10	YI-Yellow	21-15 m	Copper	20
2010	16-Aug-10	YI-Yellow	21-15 m	Copper	20
2010	16-Aug-10	YI-Yellow	21-15 m	Copper	20
2010	16-Aug-10	YI-Yellow	21-15 m	Copper	25
2010	16-Aug-10	YI-Yellow	21-15 m	Copper	27

2010	16-Aug-10	YI-Yellow	21-15 m	Copper	27
2010	16-Aug-10	YI-Yellow	21-15 m	Female kelp greenling	23
2010	16-Aug-10	YI-Yellow	21-15 m	Male kelp greenling	20
2010	16-Aug-10	YI-Yellow	21-15 m	Male kelp greenling	20
2010	16-Aug-10	YI-Yellow	21-15 m	Male kelp greenling	38
2010	16-Aug-10	YI-Yellow	21-15 m	Quillback	20
2010	16-Aug-10	YI-Yellow	21-15 m	Quillback	24
2010	16-Aug-10	YI-Yellow	15-9 m	Copper	15
2010	17-Aug-10	PP-One Mile	27-21 m	Lingcod	25
2010	17-Aug-10	PP-One Mile	27-21 m	Male kelp greenling	25
2010	17-Aug-10	PP-One Mile	21-15 m	Copper	25
2010	17-Aug-10	PP-One Mile	21-15 m	Female kelp greenling	25
2010	17-Aug-10	PP-One Mile	21-15 m	Lingcod	31
2010	17-Aug-10	PP-One Mile	15-9 m	Copper	20
2010	17-Aug-10	PP-One Mile	15-9 m	Copper	25
2010	17-Aug-10	PP-One Mile	15-9 m	Female kelp greenling	25
2010	17-Aug-10	YI-Low	27-21 m	Copper	20
2010	17-Aug-10	YI-Low	27-21 m	Copper	25
2010	17-Aug-10	YI-Low	27-21 m	Copper	25
2010	17-Aug-10	YI-Low	27-21 m	Copper	32
2010	17-Aug-10	YI-Low	27-21 m	Male kelp greenling	35
2010	17-Aug-10	YI-Low	27-21 m	Quillback	7
2010	17-Aug-10	YI-Low	27-21 m	Quillback	15
2010	17-Aug-10	YI-Low	27-21 m	Quillback	15
2010	17-Aug-10	YI-Low	27-21 m	Quillback	15
2010	17-Aug-10	YI-Low	27-21 m	Quillback	18
2010	17-Aug-10	YI-Low	27-21 m	Quillback	18
2010	17-Aug-10	YI-Low	27-21 m	Quillback	18
2010	17-Aug-10	YI-Low	27-21 m	Quillback	20
2010	17-Aug-10	YI-Low	27-21 m	Quillback	20
2010	17-Aug-10	YI-Low	27-21 m	Quillback	20
2010	17-Aug-10	YI-Low	27-21 m	Quillback	34
2010	17-Aug-10	YI-Low	21-15 m	Copper	25
2010	17-Aug-10	YI-Low	21-15 m	Copper	27
2010	17-Aug-10	YI-Low	21-15 m	Lingcod	37
2010	17-Aug-10	YI-Low	21-15 m	Male kelp greenling	20
2010	17-Aug-10	YI-Low	21-15 m	Male kelp greenling	20
2010	17-Aug-10	YI-Low	21-15 m	Male kelp greenling	25
2010	17-Aug-10	YI-Low	21-15 m	Male kelp greenling	30
2010	17-Aug-10	YI-Low	21-15 m	Quillback	18
2010	17-Aug-10	YI-Low	21-15 m	Quillback	18
2010	17-Aug-10	YI-Low	21-15 m	Quillback	20
2010	17-Aug-10	YI-Low	21-15 m	Quillback	20

2010	17-Aug-10	YI-Low	15-9 m	Copper	28
2010	17-Aug-10	YI-Low	15-9 m	Copper	37
2010	17-Aug-10	YI-Low	15-9 m	Female kelp greenling	25
2010	17-Aug-10	YI-Low	15-9 m	Lingcod	40
2010	17-Aug-10	YI-Low	15-9 m	Lingcod	65
2010	17-Aug-10	YI-Low	15-9 m	Quillback	13
2010	17-Aug-10	YI-Low	15-9 m	Quillback	14
2010	17-Aug-10	YI-Low	15-9 m	Quillback	22
2010	17-Aug-10	YI-Low	15-9 m	Quillback	27
2010	17-Aug-10	YI-Low	9-3 m	Copper	18
2010	17-Aug-10	YI-Low	9-3 m	Copper	26
2010	17-Aug-10	YI-Low	9-3 m	Male kelp greenling	20
2010	17-Aug-10	YI-Low	9-3 m	Quillback	25
2010	18-Aug-10	PG-Center	21-15 m	Copper	22
2010	18-Aug-10	PG-Center	21-15 m	Copper	32
2010	18-Aug-10	PG-Center	21-15 m	Male kelp greenling	30
2010	18-Aug-10	PG-Center	21-15 m	Quillback	15
2010	18-Aug-10	PG-Center	15-9 m	Copper	20
2010	18-Aug-10	PG-Center	15-9 m	Copper	28
2010	18-Aug-10	PG-Center	15-9 m	Female kelp greenling	35
2010	18-Aug-10	PG-Center	15-9 m	Male kelp greenling	18
2010	18-Aug-10	PG-Center	15-9 m	Male kelp greenling	30
2010	18-Aug-10	PG-Center	15-9 m	Quillback	25
2010	18-Aug-10	PG-Center	15-9 m	Quillback	27
2010	18-Aug-10	PG-Center	3-0 m	Female kelp greenling	32
2011	15-Jun-11	SC-Center	27-21 m	Copper	25
2011	15-Jun-11	SC-Center	27-21 m	Copper	25
2011	15-Jun-11	SC-Center	27-21 m	Copper	30
2011	15-Jun-11	SC-Center	21-15 m	Copper	30
2011	15-Jun-11	SC-Center	15-9 m	Copper	30
2011	15-Jun-11	SC-Center	15-9 m	Male kelp greenling	25
2011	15-Jun-11	SC-Center	15-9 m	Male kelp greenling	25
2011	15-Jun-11	SC-Center	15-9 m	Male kelp greenling	40
2011	15-Jun-11	SC-Center	15-9 m	Male kelp greenling	45
2011	15-Jun-11	SC-Center	9-3 m	Copper	22
2011	15-Jun-11	YI-Yellow	27-21 m	Lingcod	60
2011	15-Jun-11	YI-Yellow	27-21 m	Male kelp greenling	40
2011	15-Jun-11	YI-Yellow	27-21 m	Quillback	15
2011	15-Jun-11	YI-Yellow	27-21 m	Quillback	15
2011	15-Jun-11	YI-Yellow	21-15 m	Copper	23
2011	15-Jun-11	YI-Yellow	21-15 m	Copper	25
2011	15-Jun-11	YI-Yellow	21-15 m	Copper	40
2011	15-Jun-11	YI-Yellow	21-15 m	Male kelp greenling	30

2011	15-Jun-11	YI-Yellow	21-15 m	Quillback	30
2011	15-Jun-11	YI-Yellow	15-9 m	Copper	23
2011	15-Jun-11	YI-Yellow	15-9 m	Copper	25
2011	15-Jun-11	YI-Yellow	15-9 m	Quillback	15
2011	15-Jun-11	YI-Yellow	9-3 m	Copper	22
2011	15-Jun-11	YI-Yellow	9-3 m	Copper	28
2011	15-Jun-11	YI-Yellow	9-3 m	Female kelp greenling	35
2011	16-Jun-11	NP-North	27-21 m	Lingcod	70
2011	16-Jun-11	NP-North	27-21 m	Male kelp greenling	30
2011	16-Jun-11	NP-North	21-15 m	Female kelp greenling	25
2011	16-Jun-11	NP-North	21-15 m	Female kelp greenling	30
2011	16-Jun-11	NP-North	21-15 m	Lingcod	65
2011	16-Jun-11	NP-North	21-15 m	Male kelp greenling	30
2011	16-Jun-11	NP-North	15-9 m	Copper	10
2011	16-Jun-11	NP-North	15-9 m	Copper	10
2011	16-Jun-11	NP-North	15-9 m	Copper	20
2011	16-Jun-11	NP-North	15-9 m	Copper	22
2011	16-Jun-11	NP-North	15-9 m	Copper	25
2011	16-Jun-11	NP-North	15-9 m	Female kelp greenling	30
2011	16-Jun-11	NP-North	9-3 m	Copper	10
2011	16-Jun-11	NP-North	9-3 m	Copper	15
2011	16-Jun-11	NP-North	9-3 m	Copper	15
2011	16-Jun-11	NP-North	9-3 m	Copper	20
2011	16-Jun-11	NP-North	9-3 m	Female kelp greenling	30
2011	22-Jun-11	PG-Center	27-21 m	Male kelp greenling	35
2011	22-Jun-11	PG-Center	21-15 m	Copper	20
2011	22-Jun-11	PG-Center	21-15 m	Lingcod	40
2011	22-Jun-11	PG-Center	21-15 m	Lingcod	50
2011	22-Jun-11	PG-Center	21-15 m	Lingcod	75
2011	22-Jun-11	PG-Center	21-15 m	Male kelp greenling	25
2011	22-Jun-11	PG-Center	21-15 m	Male kelp greenling	35
2011	22-Jun-11	PG-Center	15-9 m	Copper	21
2011	22-Jun-11	PG-Center	15-9 m	Copper	23
2011	22-Jun-11	PG-Center	15-9 m	Copper	25
2011	22-Jun-11	PG-Center	15-9 m	Copper	25
2011	22-Jun-11	PG-Center	15-9 m	Copper	30
2011	22-Jun-11	PG-Center	15-9 m	Female kelp greenling	25
2011	22-Jun-11	PG-Center	15-9 m	Lingcod	40
2011	22-Jun-11	PG-Center	15-9 m	Lingcod	60
2011	22-Jun-11	PG-Center	15-9 m	Male kelp greenling	30
2011	22-Jun-11	PG-Center	15-9 m	Male kelp greenling	30
2011	22-Jun-11	PG-Center	15-9 m	Quillback	15
2011	22-Jun-11	PG-Center	15-9 m	Quillback	18

2011	22-Jun-11	PG-Center	15-9 m	Quillback	20
2011	22-Jun-11	PG-Center	15-9 m	Quillback	25
2011	22-Jun-11	PG-Center	15-9 m	Quillback	30
2011	22-Jun-11	PG-Center	9-3 m	Lingcod	50
2011	23-Jun-11	MP-Center	27-21 m	Copper	18
2011	23-Jun-11	MP-Center	27-21 m	Copper	25
2011	23-Jun-11	MP-Center	27-21 m	Copper	30
2011	23-Jun-11	MP-Center	27-21 m	Male kelp greenling	33
2011	23-Jun-11	MP-Center	27-21 m	Quillback	8
2011	23-Jun-11	MP-Center	27-21 m	Quillback	15
2011	23-Jun-11	MP-Center	27-21 m	Quillback	20
2011	23-Jun-11	MP-Center	27-21 m	Quillback	25
2011	23-Jun-11	MP-Center	27-21 m	Quillback	25
2011	23-Jun-11	MP-Center	27-21 m	Quillback	30
2011	23-Jun-11	MP-Center	27-21 m	Quillback	30
2011	23-Jun-11	MP-Center	21-15 m	Copper	23
2011	23-Jun-11	MP-Center	21-15 m	Copper	30
2011	23-Jun-11	MP-Center	21-15 m	Lingcod	40
2011	23-Jun-11	MP-Center	21-15 m	Lingcod	45
2011	23-Jun-11	MP-Center	21-15 m	Male kelp greenling	30
2011	23-Jun-11	MP-Center	21-15 m	Male kelp greenling	30
2011	23-Jun-11	MP-Center	15-9 m	Copper	20
2011	23-Jun-11	MP-Center	15-9 m	Copper	23
2011	23-Jun-11	MP-Center	15-9 m	Male kelp greenling	30
2011	23-Jun-11	MP-Center	9-3 m	Copper	20
2011	24-Jun-11	PP-Minnesota	27-21 m	Copper	25
2011	24-Jun-11	PP-Minnesota	27-21 m	Lingcod	80
2011	24-Jun-11	PP-Minnesota	27-21 m	Male kelp greenling	35
2011	24-Jun-11	PP-Minnesota	27-21 m	Male kelp greenling	35
2011	24-Jun-11	PP-Minnesota	21-15 m	Copper	25
2011	24-Jun-11	PP-Minnesota	21-15 m	Copper	25
2011	24-Jun-11	PP-Minnesota	21-15 m	Copper	30
2011	24-Jun-11	PP-Minnesota	21-15 m	Lingcod	40
2011	24-Jun-11	PP-Minnesota	21-15 m	Male kelp greenling	35
2011	24-Jun-11	PP-Minnesota	15-9 m	Copper	20
2011	24-Jun-11	PP-Minnesota	15-9 m	Copper	25
2011	24-Jun-11	PP-Minnesota	15-9 m	Copper	25
2011	24-Jun-11	PP-Minnesota	15-9 m	Copper	25
2011	24-Jun-11	PP-Minnesota	15-9 m	Copper	28
2011	24-Jun-11	PP-Minnesota	15-9 m	Copper	30
2011	24-Jun-11	PP-Minnesota	15-9 m	Copper	30
2011	24-Jun-11	PP-Minnesota	15-9 m	Male kelp greenling	20
2011	24-Jun-11	PP-Minnesota	15-9 m	Male kelp greenling	25

2011	7-Jul-11	MP-North	27-21 m	Copper	22
2011	7-Jul-11	MP-North	27-21 m	Copper	23
2011	7-Jul-11	MP-North	27-21 m	Copper	27
2011	7-Jul-11	MP-North	27-21 m	Copper	32
2011	7-Jul-11	MP-North	21-15 m	Copper	23
2011	7-Jul-11	MP-North	21-15 m	Copper	25
2011	7-Jul-11	MP-North	21-15 m	Copper	27
2011	7-Jul-11	MP-North	15-9 m	Copper	20
2011	7-Jul-11	MP-North	15-9 m	Male kelp greenling	22
2011	7-Jul-11	MP-North	15-9 m	Male kelp greenling	23
2011	7-Jul-11	MP-North	15-9 m	Whitespotted greenling	25
2011	7-Jul-11	MP-North	9-3 m	Copper	20
2011	7-Jul-11	SC-South	27-21 m	Male kelp greenling	25
2011	7-Jul-11	SC-South	27-21 m	Male kelp greenling	35
2011	7-Jul-11	SC-South	27-21 m	Male kelp greenling	40
2011	7-Jul-11	SC-South	21-15 m	Lingcod	30
2011	7-Jul-11	SC-South	15-9 m	Copper	8
2011	7-Jul-11	SC-South	15-9 m	Copper	10
2011	7-Jul-11	SC-South	15-9 m	Copper	10
2011	7-Jul-11	SC-South	15-9 m	Copper	10
2011	7-Jul-11	SC-South	15-9 m	Copper	10
2011	7-Jul-11	SC-South	15-9 m	Copper	10
2011	7-Jul-11	SC-South	15-9 m	Copper	18
2011	7-Jul-11	SC-South	15-9 m	Lingcod	82
2011	7-Jul-11	SC-South	15-9 m	Male kelp greenling	23
2011	7-Jul-11	SC-South	15-9 m	Quillback	10
2011	7-Jul-11	SC-South	15-9 m	Quillback	11
2011	7-Jul-11	SC-South	9-3 m	Copper	12
2011	7-Jul-11	SC-South	9-3 m	Copper	15
2011	7-Jul-11	YI-Low	27-21 m	Copper	20
2011	7-Jul-11	YI-Low	27-21 m	Copper	25
2011	7-Jul-11	YI-Low	27-21 m	Copper	30
2011	7-Jul-11	YI-Low	27-21 m	Copper	30
2011	7-Jul-11	YI-Low	27-21 m	Copper	34
2011	7-Jul-11	YI-Low	27-21 m	Male kelp greenling	25
2011	7-Jul-11	YI-Low	27-21 m	Male kelp greenling	30
2011	7-Jul-11	YI-Low	27-21 m	Male kelp greenling	30
2011	7-Jul-11	YI-Low	27-21 m	Male kelp greenling	33
2011	7-Jul-11	YI-Low	27-21 m	Quillback	18
2011	7-Jul-11	YI-Low	27-21 m	Quillback	18
2011	7-Jul-11	YI-Low	27-21 m	Quillback	20
2011	7-Jul-11	YI-Low	27-21 m	Quillback	20
2011	7-Jul-11	YI-Low	27-21 m	Quillback	23

2011	7-Jul-11	YI-Low	27-21 m	Quillback	25
2011	7-Jul-11	YI-Low	27-21 m	Quillback	28
2011	7-Jul-11	YI-Low	21-15 m	Copper	25
2011	7-Jul-11	YI-Low	21-15 m	Copper	27
2011	7-Jul-11	YI-Low	21-15 m	Great sculpin	26
2011	7-Jul-11	YI-Low	21-15 m	Male kelp greenling	25
2011	7-Jul-11	YI-Low	21-15 m	Male kelp greenling	25
2011	7-Jul-11	YI-Low	21-15 m	Quillback	22
2011	7-Jul-11	YI-Low	15-9 m	Lingcod	36
2011	7-Jul-11	YI-Low	9-3 m	Copper	17
2011	7-Jul-11	YI-Low	9-3 m	Copper	18
2011	7-Jul-11	YI-Low	9-3 m	Copper	18
2011	7-Jul-11	YI-Low	9-3 m	Copper	20
2011	7-Jul-11	YI-Low	9-3 m	Copper	20
2011	7-Jul-11	YI-Low	9-3 m	Copper	20
2011	7-Jul-11	YI-Low	9-3 m	Copper	20
2011	7-Jul-11	YI-Low	9-3 m	Copper	20
2011	7-Jul-11	YI-Low	9-3 m	Copper	25
2011	7-Jul-11	YI-Low	9-3 m	Copper	25
2011	7-Jul-11	YI-Low	9-3 m	Copper	25
2011	7-Jul-11	YI-Low	9-3 m	Copper	27
2011	7-Jul-11	YI-Low	9-3 m	Copper	27
2011	7-Jul-11	YI-Low	9-3 m	Copper	30
2011	7-Jul-11	YI-Low	9-3 m	Male kelp greenling	23
2011	7-Jul-11	YI-Low	9-3 m	Whitespotted greenling	26
2011	8-Jul-11	NP-South	27-21 m	Quillback	15
2011	8-Jul-11	NP-South	21-15 m	Copper	25
2011	8-Jul-11	NP-South	21-15 m	Male kelp greenling	25
2011	8-Jul-11	NP-South	21-15 m	Male kelp greenling	30
2011	8-Jul-11	NP-South	15-9 m	Copper	20
2011	8-Jul-11	NP-South	15-9 m	Copper	22
2011	8-Jul-11	NP-South	15-9 m	Copper	25
2011	8-Jul-11	NP-South	15-9 m	Lingcod	60
2011	8-Jul-11	NP-South	15-9 m	Male kelp greenling	30
2011	8-Jul-11	NP-South	15-9 m	Quillback	15
2011	8-Jul-11	NP-South	15-9 m	Quillback	16
2011	8-Jul-11	NP-South	3-0 m	Lingcod	47
2011	8-Jul-11	PG-South	27-21 m	Copper	25
2011	8-Jul-11	PG-South	27-21 m	Copper	27
2011	8-Jul-11	PG-South	27-21 m	Copper	30
2011	8-Jul-11	PG-South	27-21 m	Copper	30
2011	8-Jul-11	PG-South	27-21 m	Male kelp greenling	35
2011	8-Jul-11	PG-South	21-15 m	Copper	20
2011	8-Jul-11	PG-South	21-15 m	Copper	28

2011	8-Jul-11	PG-South	21-15 m	Female kelp greenling	27
2011	8-Jul-11	PG-South	21-15 m	Male kelp greenling	20
2011	8-Jul-11	PG-South	21-15 m	Male kelp greenling	25
2011	8-Jul-11	PG-South	21-15 m	Male kelp greenling	30
2011	8-Jul-11	PG-South	15-9 m	Female kelp greenling	27
2011	8-Jul-11	PG-South	15-9 m	Lingcod	98
2011	8-Jul-11	PG-South	15-9 m	Male kelp greenling	23
2011	8-Jul-11	PG-South	15-9 m	Quillback	17
2011	8-Jul-11	PG-South	9-3 m	Female kelp greenling	33
2011	8-Jul-11	PG-South	9-3 m	Lingcod	35
2011	8-Jul-11	PP-One Mile	27-21 m	Copper	31
2011	8-Jul-11	PP-One Mile	27-21 m	Male kelp greenling	30
2011	8-Jul-11	PP-One Mile	21-15 m	Copper	22
2011	8-Jul-11	PP-One Mile	21-15 m	Lingcod	39
2011	8-Jul-11	PP-One Mile	21-15 m	Male kelp greenling	25
2011	8-Jul-11	PP-One Mile	21-15 m	Male kelp greenling	32
2011	8-Jul-11	PP-One Mile	3-0 m	Lingcod	50
2011	8-Oct-11	YI-Yellow	27-21 m	Male kelp greenling	28
2011	8-Oct-11	YI-Yellow	27-21 m	Male kelp greenling	30
2011	8-Oct-11	YI-Yellow	27-21 m	Quillback	10
2011	8-Oct-11	YI-Yellow	27-21 m	Quillback	10
2011	8-Oct-11	YI-Yellow	27-21 m	Quillback	20
2011	8-Oct-11	YI-Yellow	21-15 m	Copper	30
2011	8-Oct-11	YI-Yellow	21-15 m	Male kelp greenling	24
2011	8-Oct-11	YI-Yellow	21-15 m	Quillback	12
2011	8-Oct-11	YI-Yellow	21-15 m	Quillback	22
2011	8-Oct-11	YI-Yellow	15-9 m	Copper	27
2011	8-Oct-11	YI-Yellow	15-9 m	Copper	28
2011	8-Oct-11	YI-Yellow	15-9 m	Male kelp greenling	30
2011	8-Oct-11	YI-Yellow	9-3 m	Copper	26
2011	8-Oct-11	YI-Yellow	9-3 m	Copper	30
2011	9-Oct-11	NP-North	27-21 m	Male kelp greenling	25
2011	9-Oct-11	NP-North	27-21 m	Male kelp greenling	30
2011	9-Oct-11	NP-North	21-15 m	Lingcod	55
2011	9-Oct-11	NP-North	15-9 m	Copper	22
2011	9-Oct-11	NP-North	15-9 m	Copper	25
2011	9-Oct-11	NP-North	15-9 m	Female kelp greenling	30
2011	9-Oct-11	NP-North	15-9 m	Quillback	15
2011	9-Oct-11	NP-North	9-3 m	Copper	25
2011	9-Oct-11	NP-North	9-3 m	Female kelp greenling	27
2011	9-Oct-11	PG-South	27-21 m	Copper	20
2011	9-Oct-11	PG-South	27-21 m	Copper	20
2011	9-Oct-11	PG-South	27-21 m	Copper	25

2011	9-Oct-11	PG-South	27-21 m	Copper	27
2011	9-Oct-11	PG-South	27-21 m	Copper	30
2011	9-Oct-11	PG-South	27-21 m	Male kelp greenling	30
2011	9-Oct-11	PG-South	27-21 m	Quillback	23
2011	9-Oct-11	PG-South	21-15 m	Copper	17
2011	9-Oct-11	PG-South	21-15 m	Copper	18
2011	9-Oct-11	PG-South	21-15 m	Copper	20
2011	9-Oct-11	PG-South	21-15 m	Copper	21
2011	9-Oct-11	PG-South	21-15 m	Copper	28
2011	9-Oct-11	PG-South	21-15 m	Male kelp greenling	30
2011	9-Oct-11	PG-South	15-9 m	Copper	20
2011	9-Oct-11	PG-South	15-9 m	Copper	22
2011	9-Oct-11	PG-South	15-9 m	Female kelp greenling	20
2011	9-Oct-11	PG-South	15-9 m	Female kelp greenling	30
2011	9-Oct-11	PG-South	9-3 m	Copper	20
2011	9-Oct-11	PG-South	9-3 m	Female kelp greenling	20
2011	9-Oct-11	PG-South	9-3 m	Female kelp greenling	25
2011	9-Oct-11	PG-South	9-3 m	Female kelp greenling	25
2011	9-Oct-11	PG-South	9-3 m	Female kelp greenling	30
2011	9-Oct-11	SC-South	27-21 m	Copper	20
2011	9-Oct-11	SC-South	27-21 m	Copper	20
2011	9-Oct-11	SC-South	27-21 m	Copper	23
2011	9-Oct-11	SC-South	27-21 m	Copper	25
2011	9-Oct-11	SC-South	27-21 m	Copper	30
2011	9-Oct-11	SC-South	27-21 m	Copper	30
2011	9-Oct-11	SC-South	27-21 m	Copper	30
2011	9-Oct-11	SC-South	21-15 m	Lingcod	55
2011	9-Oct-11	SC-South	21-15 m	Male kelp greenling	25
2011	9-Oct-11	SC-South	21-15 m	Male kelp greenling	25
2011	9-Oct-11	SC-South	21-15 m	Male kelp greenling	30
2011	9-Oct-11	SC-South	15-9 m	Copper	26
2011	9-Oct-11	SC-South	15-9 m	Quillback	15
2011	10-Oct-11	MP-Center	27-21 m	Copper	20
2011	10-Oct-11	MP-Center	27-21 m	Copper	25
2011	10-Oct-11	MP-Center	27-21 m	Copper	25
2011	10-Oct-11	MP-Center	27-21 m	Copper	25
2011	10-Oct-11	MP-Center	27-21 m	Copper	27
2011	10-Oct-11	MP-Center	27-21 m	Copper	31
2011	10-Oct-11	MP-Center	27-21 m	Copper	32
2011	10-Oct-11	MP-Center	27-21 m	Male kelp greenling	25
2011	10-Oct-11	MP-Center	27-21 m	Quillback	17
2011	10-Oct-11	MP-Center	27-21 m	Quillback	18
2011	10-Oct-11	MP-Center	27-21 m	Quillback	31

2011	10-Oct-11	MP-Center	21-15 m	Copper	15
2011	10-Oct-11	MP-Center	21-15 m	Copper	15
2011	10-Oct-11	MP-Center	21-15 m	Copper	20
2011	10-Oct-11	MP-Center	21-15 m	Copper	20
2011	10-Oct-11	MP-Center	21-15 m	Copper	22
2011	10-Oct-11	MP-Center	21-15 m	Copper	26
2011	10-Oct-11	MP-Center	21-15 m	Copper	30
2011	10-Oct-11	MP-Center	21-15 m	Copper	30
2011	10-Oct-11	MP-Center	21-15 m	Male kelp greenling	25
2011	10-Oct-11	MP-Center	15-9 m	Copper	21
2011	10-Oct-11	MP-Center	15-9 m	Female kelp greenling	35
2011	10-Oct-11	MP-Center	15-9 m	Lingcod	45
2011	10-Oct-11	PP-One Mile	21-15 m	Male kelp greenling	30
2011	10-Oct-11	PP-One Mile	15-9 m	Female kelp greenling	20
2011	10-Oct-11	PP-One Mile	15-9 m	Lingcod	100
2011	10-Oct-11	PP-One Mile	15-9 m	Male kelp greenling	23
2011	10-Oct-11	PP-One Mile	15-9 m	Male kelp greenling	30
2011	11-Oct-11	MP-North	27-21 m	Copper	20
2011	11-Oct-11	MP-North	27-21 m	Copper	20
2011	11-Oct-11	MP-North	27-21 m	Copper	22
2011	11-Oct-11	MP-North	27-21 m	Copper	25
2011	11-Oct-11	MP-North	27-21 m	Copper	25
2011	11-Oct-11	MP-North	27-21 m	Copper	27
2011	11-Oct-11	MP-North	27-21 m	Copper	28
2011	11-Oct-11	MP-North	27-21 m	Copper	30
2011	11-Oct-11	MP-North	27-21 m	Male kelp greenling	25
2011	11-Oct-11	MP-North	27-21 m	Male kelp greenling	30
2011	11-Oct-11	MP-North	21-15 m	Copper	20
2011	11-Oct-11	MP-North	21-15 m	Copper	20
2011	11-Oct-11	MP-North	21-15 m	Copper	20
2011	11-Oct-11	MP-North	21-15 m	Copper	21
2011	11-Oct-11	MP-North	21-15 m	Copper	22
2011	11-Oct-11	MP-North	21-15 m	Copper	23
2011	11-Oct-11	MP-North	21-15 m	Copper	24
2011	11-Oct-11	MP-North	21-15 m	Copper	26
2011	11-Oct-11	MP-North	21-15 m	Copper	28
2011	11-Oct-11	MP-North	21-15 m	Female kelp greenling	29
2011	11-Oct-11	MP-North	21-15 m	Female kelp greenling	30
2011	11-Oct-11	MP-North	21-15 m	Male kelp greenling	20
2011	11-Oct-11	MP-North	21-15 m	Male kelp greenling	20
2011	11-Oct-11	MP-North	21-15 m	Male kelp greenling	25
2011	11-Oct-11	MP-North	15-9 m	Copper	21
2011	11-Oct-11	MP-North	15-9 m	Copper	25

2011	11-Oct-11	MP-North	15-9 m	Female kelp greenling	30
2011	11-Oct-11	MP-North	15-9 m	Male kelp greenling	30
2011	11-Oct-11	MP-North	9-3 m	Female kelp greenling	32
2011	11-Oct-11	MP-North	9-3 m	Male kelp greenling	30
2011	11-Oct-11	NP-South	27-21 m	Female kelp greenling	20
2011	11-Oct-11	NP-South	27-21 m	Male kelp greenling	30
2011	11-Oct-11	NP-South	21-15 m	Copper	25
2011	11-Oct-11	NP-South	21-15 m	Copper	30
2011	11-Oct-11	NP-South	21-15 m	Male kelp greenling	25
2011	11-Oct-11	NP-South	21-15 m	Male kelp greenling	30
2011	11-Oct-11	NP-South	21-15 m	Male kelp greenling	33
2011	11-Oct-11	NP-South	15-9 m	Copper	15
2011	11-Oct-11	NP-South	15-9 m	Copper	20
2011	11-Oct-11	NP-South	15-9 m	Copper	20
2011	11-Oct-11	NP-South	15-9 m	Copper	20
2011	11-Oct-11	NP-South	15-9 m	Copper	23
2011	11-Oct-11	NP-South	15-9 m	Copper	25
2011	11-Oct-11	NP-South	15-9 m	Copper	26
2011	11-Oct-11	NP-South	15-9 m	Female kelp greenling	30
2011	11-Oct-11	NP-South	15-9 m	Male kelp greenling	25
2011	11-Oct-11	NP-South	15-9 m	Male kelp greenling	30
2011	11-Oct-11	PG-Center	27-21 m	Lingcod	65
2011	11-Oct-11	PG-Center	27-21 m	Male kelp greenling	27
2011	11-Oct-11	PG-Center	27-21 m	Male kelp greenling	30
2011	11-Oct-11	PG-Center	27-21 m	Male kelp greenling	30
2011	11-Oct-11	PG-Center	27-21 m	Male kelp greenling	35
2011	11-Oct-11	PG-Center	21-15 m	Copper	20
2011	11-Oct-11	PG-Center	21-15 m	Copper	20
2011	11-Oct-11	PG-Center	21-15 m	Copper	25
2011	11-Oct-11	PG-Center	21-15 m	Copper	25
2011	11-Oct-11	PG-Center	21-15 m	Copper	27
2011	11-Oct-11	PG-Center	21-15 m	Male kelp greenling	25
2011	11-Oct-11	PG-Center	21-15 m	Male kelp greenling	30
2011	11-Oct-11	PG-Center	21-15 m	Male kelp greenling	30
2011	11-Oct-11	PG-Center	21-15 m	Male kelp greenling	45
2011	11-Oct-11	PG-Center	21-15 m	Quillback	15
2011	11-Oct-11	PG-Center	21-15 m	Quillback	20
2011	11-Oct-11	PG-Center	15-9 m	Copper	22
2011	11-Oct-11	PG-Center	15-9 m	Female kelp greenling	25
2011	11-Oct-11	PG-Center	15-9 m	Female kelp greenling	30
2011	11-Oct-11	PG-Center	15-9 m	Female kelp greenling	30
2011	11-Oct-11	PG-Center	15-9 m	Lingcod	45
2011	11-Oct-11	PG-Center	15-9 m	Male kelp greenling	25

2011	11-Oct-11	PG-Center	15-9 m	Male kelp greenling	35
2011	11-Oct-11	PG-Center	15-9 m	Quillback	20
2011	11-Oct-11	PG-Center	9-3 m	Female kelp greenling	20
2011	11-Oct-11	PG-Center	9-3 m	Female kelp greenling	30
2011	11-Oct-11	SC-Center	27-21 m	Copper	25
2011	11-Oct-11	SC-Center	27-21 m	Copper	30
2011	11-Oct-11	SC-Center	27-21 m	Male kelp greenling	20
2011	11-Oct-11	SC-Center	21-15 m	Copper	20
2011	11-Oct-11	SC-Center	21-15 m	Copper	22
2011	11-Oct-11	SC-Center	21-15 m	Copper	23
2011	11-Oct-11	SC-Center	21-15 m	Copper	30
2011	11-Oct-11	SC-Center	21-15 m	Copper	30
2011	11-Oct-11	SC-Center	21-15 m	Female kelp greenling	30
2011	11-Oct-11	SC-Center	21-15 m	Lingcod	80
2011	11-Oct-11	SC-Center	21-15 m	Lingcod	110
2011	11-Oct-11	SC-Center	21-15 m	Male kelp greenling	20
2011	11-Oct-11	SC-Center	21-15 m	Male kelp greenling	20
2011	11-Oct-11	SC-Center	21-15 m	Male kelp greenling	35
2011	11-Oct-11	SC-Center	15-9 m	Female kelp greenling	25
2011	11-Oct-11	SC-Center	3-0 m	Male kelp greenling	35
2011	12-Oct-11	PP-Minnesota	27-21 m	Copper	20
2011	12-Oct-11	PP-Minnesota	27-21 m	Copper	22
2011	12-Oct-11	PP-Minnesota	27-21 m	Copper	22
2011	12-Oct-11	PP-Minnesota	27-21 m	Copper	23
2011	12-Oct-11	PP-Minnesota	27-21 m	Copper	25
2011	12-Oct-11	PP-Minnesota	27-21 m	Copper	25
2011	12-Oct-11	PP-Minnesota	27-21 m	Copper	25
2011	12-Oct-11	PP-Minnesota	27-21 m	Copper	25
2011	12-Oct-11	PP-Minnesota	27-21 m	Copper	25
2011	12-Oct-11	PP-Minnesota	27-21 m	Copper	25
2011	12-Oct-11	PP-Minnesota	27-21 m	Copper	25
2011	12-Oct-11	PP-Minnesota	27-21 m	Copper	25
2011	12-Oct-11	PP-Minnesota	27-21 m	Copper	25
2011	12-Oct-11	PP-Minnesota	27-21 m	Copper	25
2011	12-Oct-11	PP-Minnesota	27-21 m	Copper	27
2011	12-Oct-11	PP-Minnesota	27-21 m	Copper	28
2011	12-Oct-11	PP-Minnesota	27-21 m	Copper	30
2011	12-Oct-11	PP-Minnesota	27-21 m	Lingcod	60
2011	12-Oct-11	PP-Minnesota	27-21 m	Male kelp greenling	30
2011	12-Oct-11	PP-Minnesota	27-21 m	Male kelp greenling	30
2011	12-Oct-11	PP-Minnesota	21-15 m	Copper	20
2011	12-Oct-11	PP-Minnesota	21-15 m	Copper	22
2011	12-Oct-11	PP-Minnesota	21-15 m	Copper	25
2011	12-Oct-11	PP-Minnesota	21-15 m	Copper	25
2011	12-Oct-11	PP-Minnesota	21-15 m	Copper	25
2011	12-Oct-11	PP-Minnesota	21-15 m	Copper	25
2011	12-Oct-11	PP-Minnesota	21-15 m	Copper	25

2011	12-Oct-11	PP-Minnesota	21-15 m	Copper	25
2011	12-Oct-11	PP-Minnesota	21-15 m	Copper	25
2011	12-Oct-11	PP-Minnesota	21-15 m	Copper	30
2011	12-Oct-11	PP-Minnesota	21-15 m	Copper	31
2011	12-Oct-11	PP-Minnesota	21-15 m	Copper	32
2011	12-Oct-11	PP-Minnesota	21-15 m	Copper	35
2011	12-Oct-11	PP-Minnesota	21-15 m	Copper	35
2011	12-Oct-11	PP-Minnesota	21-15 m	Female kelp greenling	28
2011	12-Oct-11	PP-Minnesota	21-15 m	Female kelp greenling	31
2011	12-Oct-11	PP-Minnesota	21-15 m	Lingcod	65
2011	12-Oct-11	PP-Minnesota	21-15 m	Male kelp greenling	40
2011	12-Oct-11	PP-Minnesota	15-9 m	Female kelp greenling	38
2011	12-Oct-11	PP-Minnesota	15-9 m	Lingcod	95
2011	12-Oct-11	PP-Minnesota	15-9 m	Male kelp greenling	20
2011	12-Oct-11	PP-Minnesota	9-3 m	Male kelp greenling	30
2011	12-Oct-11	YI-Low	27-21 m	Copper	25
2011	12-Oct-11	YI-Low	27-21 m	Copper	30
2011	12-Oct-11	YI-Low	27-21 m	Male kelp greenling	25
2011	12-Oct-11	YI-Low	27-21 m	Male kelp greenling	28
2011	12-Oct-11	YI-Low	27-21 m	Quillback	15
2011	12-Oct-11	YI-Low	27-21 m	Quillback	16
2011	12-Oct-11	YI-Low	27-21 m	Quillback	21
2011	12-Oct-11	YI-Low	27-21 m	Quillback	21
2011	12-Oct-11	YI-Low	27-21 m	Quillback	24
2011	12-Oct-11	YI-Low	27-21 m	Quillback	25
2011	12-Oct-11	YI-Low	27-21 m	Quillback	26
2011	12-Oct-11	YI-Low	27-21 m	Quillback	27
2011	12-Oct-11	YI-Low	21-15 m	Copper	27
2011	12-Oct-11	YI-Low	21-15 m	Quillback	23
2011	12-Oct-11	YI-Low	15-9 m	Copper	27
2011	12-Oct-11	YI-Low	15-9 m	Copper	30
2011	12-Oct-11	YI-Low	15-9 m	Lingcod	45
2011	12-Oct-11	YI-Low	15-9 m	Lingcod	52
2011	12-Oct-11	YI-Low	15-9 m	Male kelp greenling	25
2011	12-Oct-11	YI-Low	15-9 m	Male kelp greenling	25
2011	12-Oct-11	YI-Low	15-9 m	Quillback	21
2011	12-Oct-11	YI-Low	15-9 m	Quillback	27
2011	12-Oct-11	YI-Low	9-3 m	Copper	25
2011	12-Oct-11	YI-Low	9-3 m	Female kelp greenling	33
2011	12-Oct-11	YI-Low	9-3 m	Male kelp greenling	35
2012	24-Jun-12	MP-Center	27-21 m	Copper	20
2012	24-Jun-12	MP-Center	27-21 m	Copper	24
2012	24-Jun-12	MP-Center	27-21 m	Copper	25

2012	24-Jun-12	MP-Center	27-21 m	Copper	25
2012	24-Jun-12	MP-Center	27-21 m	Copper	27
2012	24-Jun-12	MP-Center	27-21 m	Copper	35
2012	24-Jun-12	MP-Center	27-21 m	Lingcod	45
2012	24-Jun-12	MP-Center	27-21 m	Male kelp greenling	25
2012	24-Jun-12	MP-Center	27-21 m	Male kelp greenling	30
2012	24-Jun-12	MP-Center	27-21 m	Quillback	15
2012	24-Jun-12	MP-Center	27-21 m	Quillback	20
2012	24-Jun-12	MP-Center	27-21 m	Quillback	20
2012	24-Jun-12	MP-Center	27-21 m	Quillback	25
2012	24-Jun-12	MP-Center	27-21 m	Quillback	25
2012	24-Jun-12	MP-Center	21-15 m	Copper	22
2012	24-Jun-12	MP-Center	21-15 m	Male kelp greenling	25
2012	24-Jun-12	MP-Center	15-9 m	Lingcod	45
2012	24-Jun-12	MP-Center	15-9 m	Male kelp greenling	28
2012	24-Jun-12	MP-Center	9-3 m	Female kelp greenling	25
2012	24-Jun-12	MP-Center	9-3 m	Quillback	20
2012	24-Jun-12	MP-Center	3-0 m	Copper	10
2012	25-Jun-12	SC-Center	27-21 m	Copper	25
2012	25-Jun-12	SC-Center	27-21 m	Copper	25
2012	25-Jun-12	SC-Center	27-21 m	Copper	26
2012	25-Jun-12	SC-Center	27-21 m	Copper	28
2012	25-Jun-12	SC-Center	27-21 m	Copper	30
2012	25-Jun-12	SC-Center	27-21 m	Copper	30
2012	25-Jun-12	SC-Center	27-21 m	Copper	30
2012	25-Jun-12	SC-Center	27-21 m	Male kelp greenling	28
2012	25-Jun-12	SC-Center	27-21 m	Male kelp greenling	30
2012	25-Jun-12	SC-Center	21-15 m	Lingcod	50
2012	25-Jun-12	SC-Center	21-15 m	Lingcod	70
2012	25-Jun-12	SC-Center	15-9 m	Lingcod	45
2012	25-Jun-12	SC-Center	15-9 m	Lingcod	110
2012	25-Jun-12	SC-Center	15-9 m	Male kelp greenling	25
2012	26-Jun-12	NP-North	27-21 m	Male kelp greenling	25
2012	26-Jun-12	NP-North	21-15 m	Copper	30
2012	26-Jun-12	NP-North	21-15 m	Lingcod	27
2012	26-Jun-12	NP-North	21-15 m	Male kelp greenling	27
2012	26-Jun-12	NP-North	15-9 m	Copper	13
2012	26-Jun-12	NP-North	15-9 m	Copper	18
2012	26-Jun-12	NP-North	15-9 m	Copper	20
2012	26-Jun-12	NP-North	15-9 m	Female kelp greenling	25
2012	26-Jun-12	NP-North	15-9 m	Male kelp greenling	18
2012	26-Jun-12	NP-North	15-9 m	Male kelp greenling	25
2012	26-Jun-12	PG-Center	27-21 m	Copper	35

2012	26-Jun-12	PG-Center	27-21 m	Lingcod	47
2012	26-Jun-12	PG-Center	27-21 m	Male kelp greenling	35
2012	26-Jun-12	PG-Center	27-21 m	Quillback	22
2012	26-Jun-12	PG-Center	21-15 m	Copper	21
2012	26-Jun-12	PG-Center	21-15 m	Copper	23
2012	26-Jun-12	PG-Center	21-15 m	Copper	25
2012	26-Jun-12	PG-Center	21-15 m	Copper	26
2012	26-Jun-12	PG-Center	21-15 m	Copper	27
2012	26-Jun-12	PG-Center	21-15 m	Male kelp greenling	28
2012	26-Jun-12	PG-Center	21-15 m	Male kelp greenling	30
2012	26-Jun-12	PG-Center	21-15 m	Male kelp greenling	30
2012	26-Jun-12	PG-Center	21-15 m	Male kelp greenling	33
2012	26-Jun-12	PG-Center	21-15 m	Male kelp greenling	33
2012	26-Jun-12	PG-Center	21-15 m	Quillback	21
2012	26-Jun-12	PG-Center	21-15 m	Quillback	25
2012	26-Jun-12	PG-Center	15-9 m	Copper	23
2012	26-Jun-12	PG-Center	15-9 m	Copper	25
2012	26-Jun-12	PG-Center	15-9 m	Copper	28
2012	26-Jun-12	PG-Center	15-9 m	Copper	30
2012	26-Jun-12	PG-Center	15-9 m	Male kelp greenling	25
2012	26-Jun-12	PG-Center	15-9 m	Male kelp greenling	30
2012	26-Jun-12	PG-Center	15-9 m	Male kelp greenling	30
2012	26-Jun-12	PG-Center	15-9 m	Male kelp greenling	32
2012	26-Jun-12	PG-Center	15-9 m	Quillback	20
2012	26-Jun-12	PG-Center	15-9 m	Quillback	23
2012	26-Jun-12	SC-South	27-21 m	Copper	20
2012	26-Jun-12	SC-South	27-21 m	Copper	23
2012	26-Jun-12	SC-South	27-21 m	Copper	25
2012	26-Jun-12	SC-South	27-21 m	Copper	25
2012	26-Jun-12	SC-South	27-21 m	Copper	25
2012	26-Jun-12	SC-South	27-21 m	Copper	25
2012	26-Jun-12	SC-South	27-21 m	Copper	25
2012	26-Jun-12	SC-South	27-21 m	Copper	30
2012	26-Jun-12	SC-South	27-21 m	Copper	30
2012	26-Jun-12	SC-South	27-21 m	Copper	32
2012	26-Jun-12	SC-South	27-21 m	Male kelp greenling	25
2012	26-Jun-12	SC-South	27-21 m	Male kelp greenling	25
2012	26-Jun-12	SC-South	27-21 m	Male kelp greenling	25
2012	26-Jun-12	SC-South	9-3 m	Copper	6
2012	26-Jun-12	YI-Low	27-21 m	Copper	25
2012	26-Jun-12	YI-Low	27-21 m	Male kelp greenling	22
2012	26-Jun-12	YI-Low	21-15 m	Copper	26
2012	26-Jun-12	YI-Low	15-9 m	Copper	22

2012	26-Jun-12	YI-Low	15-9 m	Copper	25
2012	26-Jun-12	YI-Low	15-9 m	Copper	26
2012	26-Jun-12	YI-Low	15-9 m	Copper	27
2012	26-Jun-12	YI-Low	15-9 m	Copper	28
2012	26-Jun-12	YI-Low	15-9 m	Male kelp greenling	25
2012	26-Jun-12	YI-Low	9-3 m	Female kelp greenling	25
2012	26-Jun-12	YI-Low	9-3 m	Female kelp greenling	30
2012	27-Jun-12	MP-North	27-21 m	Copper	24
2012	27-Jun-12	MP-North	27-21 m	Copper	25
2012	27-Jun-12	MP-North	21-15 m	Copper	20
2012	27-Jun-12	MP-North	21-15 m	Copper	25
2012	27-Jun-12	MP-North	21-15 m	Copper	25
2012	27-Jun-12	MP-North	21-15 m	Copper	30
2012	27-Jun-12	MP-North	21-15 m	Male kelp greenling	27
2012	27-Jun-12	MP-North	15-9 m	Copper	27
2012	27-Jun-12	MP-North	15-9 m	Female kelp greenling	20
2012	27-Jun-12	MP-North	9-3 m	Copper	12
2012	27-Jun-12	MP-North	9-3 m	Female kelp greenling	25
2012	27-Jun-12	PG-South	27-21 m	Copper	12
2012	27-Jun-12	PG-South	27-21 m	Copper	24
2012	27-Jun-12	PG-South	27-21 m	Copper	25
2012	27-Jun-12	PG-South	27-21 m	Copper	25
2012	27-Jun-12	PG-South	27-21 m	Copper	27
2012	27-Jun-12	PG-South	27-21 m	Female kelp greenling	25
2012	27-Jun-12	PG-South	27-21 m	Female kelp greenling	25
2012	27-Jun-12	PG-South	27-21 m	Female kelp greenling	25
2012	27-Jun-12	PG-South	27-21 m	Male kelp greenling	30
2012	27-Jun-12	PG-South	21-15 m	Copper	20
2012	27-Jun-12	PG-South	21-15 m	Copper	24
2012	27-Jun-12	PG-South	21-15 m	Copper	26
2012	27-Jun-12	PG-South	21-15 m	Copper	27
2012	27-Jun-12	PG-South	21-15 m	Copper	35
2012	27-Jun-12	PG-South	21-15 m	Female kelp greenling	30
2012	27-Jun-12	PG-South	21-15 m	Male kelp greenling	25
2012	27-Jun-12	PG-South	15-9 m	Female kelp greenling	25
2012	27-Jun-12	PG-South	15-9 m	Female kelp greenling	25
2012	27-Jun-12	PG-South	15-9 m	Male kelp greenling	25
2012	27-Jun-12	PG-South	15-9 m	Quillback	15
2012	27-Jun-12	PG-South	9-3 m	Female kelp greenling	20
2012	27-Jun-12	PP-Minnesota	27-21 m	Copper	25
2012	27-Jun-12	PP-Minnesota	27-21 m	Copper	30
2012	27-Jun-12	PP-Minnesota	27-21 m	Copper	34
2012	27-Jun-12	PP-Minnesota	27-21 m	Lingcod	60

2012	27-Jun-12	PP-Minnesota	27-21 m	Male kelp greenling	25
2012	27-Jun-12	PP-Minnesota	27-21 m	Male kelp greenling	27
2012	27-Jun-12	PP-Minnesota	27-21 m	Tiger	23
2012	27-Jun-12	PP-Minnesota	27-21 m	Tiger	25
2012	27-Jun-12	PP-Minnesota	27-21 m	Tiger	25
2012	27-Jun-12	PP-Minnesota	21-15 m	Copper	23
2012	27-Jun-12	PP-Minnesota	21-15 m	Copper	27
2012	27-Jun-12	PP-Minnesota	21-15 m	Copper	29
2012	27-Jun-12	PP-Minnesota	21-15 m	Copper	30
2012	27-Jun-12	PP-Minnesota	21-15 m	Lingcod	35
2012	27-Jun-12	PP-Minnesota	21-15 m	Lingcod	40
2012	27-Jun-12	PP-Minnesota	21-15 m	Male kelp greenling	25
2012	27-Jun-12	PP-Minnesota	21-15 m	Male kelp greenling	25
2012	27-Jun-12	PP-Minnesota	21-15 m	Male kelp greenling	30
2012	27-Jun-12	PP-Minnesota	15-9 m	Copper	20
2012	27-Jun-12	PP-Minnesota	15-9 m	Copper	27
2012	27-Jun-12	PP-Minnesota	15-9 m	Male kelp greenling	25
2012	27-Jun-12	PP-Minnesota	3-0 m	Male kelp greenling	20
2012	28-Jun-12	NP-South	27-21 m	Male kelp greenling	24
2012	28-Jun-12	NP-South	27-21 m	Male kelp greenling	30
2012	28-Jun-12	NP-South	27-21 m	Male kelp greenling	30
2012	28-Jun-12	NP-South	27-21 m	Quillback	19
2012	28-Jun-12	NP-South	21-15 m	Copper	22
2012	28-Jun-12	NP-South	21-15 m	Copper	22
2012	28-Jun-12	NP-South	21-15 m	Copper	23
2012	28-Jun-12	NP-South	21-15 m	Copper	23
2012	28-Jun-12	NP-South	21-15 m	Copper	25
2012	28-Jun-12	NP-South	21-15 m	Copper	25
2012	28-Jun-12	NP-South	21-15 m	Copper	27
2012	28-Jun-12	NP-South	21-15 m	Copper	27
2012	28-Jun-12	NP-South	21-15 m	Copper	27
2012	28-Jun-12	NP-South	21-15 m	Male kelp greenling	25
2012	28-Jun-12	NP-South	21-15 m	Male kelp greenling	30
2012	28-Jun-12	NP-South	21-15 m	Quillback	22
2012	28-Jun-12	NP-South	15-9 m	Copper	17
2012	28-Jun-12	NP-South	15-9 m	Copper	25
2012	28-Jun-12	NP-South	15-9 m	Copper	32
2012	28-Jun-12	NP-South	15-9 m	Female kelp greenling	30
2012	28-Jun-12	NP-South	9-3 m	Copper	16
2012	28-Jun-12	NP-South	9-3 m	Copper	18
2012	29-Jun-12	YI-Yellow	27-21 m	Male kelp greenling	28
2012	29-Jun-12	YI-Yellow	21-15 m	Male kelp greenling	30
2012	29-Jun-12	YI-Yellow	15-9 m	Female kelp greenling	28

2012	11-Jul-12	PP-One Mile	27-21 m	Copper	35
2012	11-Jul-12	PP-One Mile	27-21 m	Male kelp greenling	25
2012	11-Jul-12	PP-One Mile	15-9 m	Lingcod	120
2012	11-Jul-12	PP-One Mile	15-9 m	Red Irish Lord	17
2012	11-Jul-12	PP-One Mile	15-9 m	Red Irish Lord	18
2012	6-Aug-12	MP-North	27-21 m	Copper	25
2012	6-Aug-12	MP-North	27-21 m	Lingcod	62
2012	6-Aug-12	MP-North	21-15 m	Copper	23
2012	6-Aug-12	MP-North	21-15 m	Copper	25
2012	6-Aug-12	MP-North	21-15 m	Copper	25
2012	6-Aug-12	MP-North	21-15 m	Copper	25
2012	6-Aug-12	MP-North	15-9 m	Male kelp greenling	20
2012	6-Aug-12	MP-North	15-9 m	Male kelp greenling	30
2012	6-Aug-12	MP-North	9-3 m	Copper	12
2012	6-Aug-12	MP-North	3-0 m	Whitespotted greenling	22
2012	6-Aug-12	NP-North	27-21 m	Male kelp greenling	25
2012	6-Aug-12	NP-North	21-15 m	Male kelp greenling	27
2012	6-Aug-12	NP-North	15-9 m	Copper	25
2012	6-Aug-12	NP-North	15-9 m	Male kelp greenling	18
2012	6-Aug-12	NP-North	15-9 m	Male kelp greenling	20
2012	6-Aug-12	NP-North	15-9 m	Male kelp greenling	25
2012	6-Aug-12	NP-North	9-3 m	Copper	10
2012	6-Aug-12	NP-North	9-3 m	Copper	11
2012	6-Aug-12	NP-North	9-3 m	Copper	12
2012	6-Aug-12	NP-North	9-3 m	Copper	12
2012	6-Aug-12	NP-North	9-3 m	Copper	21
2012	6-Aug-12	NP-North	9-3 m	Copper	22
2012	6-Aug-12	NP-North	9-3 m	Copper	23
2012	6-Aug-12	NP-North	3-0 m	Female kelp greenling	25
2012	6-Aug-12	PG-Center	27-21 m	Male kelp greenling	25
2012	6-Aug-12	PG-Center	27-21 m	Male kelp greenling	30
2012	6-Aug-12	PG-Center	27-21 m	Male kelp greenling	36
2012	6-Aug-12	PG-Center	21-15 m	Copper	23
2012	6-Aug-12	PG-Center	21-15 m	Copper	25
2012	6-Aug-12	PG-Center	21-15 m	Copper	29
2012	6-Aug-12	PG-Center	21-15 m	Male kelp greenling	27
2012	6-Aug-12	PG-Center	21-15 m	Male kelp greenling	30
2012	6-Aug-12	PG-Center	15-9 m	Copper	26
2012	6-Aug-12	PG-Center	15-9 m	Female kelp greenling	30
2012	6-Aug-12	PG-Center	15-9 m	Lingcod	48
2012	6-Aug-12	PG-Center	15-9 m	Male kelp greenling	27
2012	6-Aug-12	PG-Center	9-3 m	Female kelp greenling	30
2012	6-Aug-12	PG-Center	9-3 m	Female kelp greenling	30

2012	6-Aug-12	PG-Center	3-0 m	Female kelp greenling	33
2012	6-Aug-12	SC-Center	27-21 m	Copper	25
2012	6-Aug-12	SC-Center	27-21 m	Copper	28
2012	6-Aug-12	SC-Center	27-21 m	Male kelp greenling	30
2012	6-Aug-12	SC-Center	21-15 m	Lingcod	70
2012	6-Aug-12	SC-Center	21-15 m	Male kelp greenling	27
2012	6-Aug-12	SC-Center	21-15 m	Male kelp greenling	27
2012	6-Aug-12	SC-Center	15-9 m	Female kelp greenling	27
2012	7-Aug-12	PG-South	27-21 m	Copper	25
2012	7-Aug-12	PG-South	27-21 m	Copper	27
2012	7-Aug-12	PG-South	27-21 m	Copper	29
2012	7-Aug-12	PG-South	27-21 m	Lingcod	38
2012	7-Aug-12	PG-South	27-21 m	Male kelp greenling	25
2012	7-Aug-12	PG-South	27-21 m	Male kelp greenling	34
2012	7-Aug-12	PG-South	27-21 m	Male kelp greenling	41
2012	7-Aug-12	PG-South	27-21 m	Quillback	23
2012	7-Aug-12	PG-South	27-21 m	Red Irish Lord	21
2012	7-Aug-12	PG-South	21-15 m	Lingcod	25
2012	7-Aug-12	PG-South	21-15 m	Male kelp greenling	25
2012	7-Aug-12	PG-South	21-15 m	Male kelp greenling	25
2012	7-Aug-12	PG-South	21-15 m	Male kelp greenling	25
2012	7-Aug-12	PG-South	21-15 m	Quillback	24
2012	7-Aug-12	PG-South	15-9 m	Brown	22
2012	7-Aug-12	PG-South	15-9 m	Copper	13
2012	7-Aug-12	PG-South	15-9 m	Copper	17
2012	7-Aug-12	PG-South	15-9 m	Copper	20
2012	7-Aug-12	PG-South	15-9 m	Copper	22
2012	7-Aug-12	PG-South	15-9 m	Copper	26
2012	7-Aug-12	PG-South	15-9 m	Female kelp greenling	29
2012	7-Aug-12	PG-South	15-9 m	Lingcod	25
2012	7-Aug-12	PG-South	15-9 m	Male kelp greenling	23
2012	7-Aug-12	PG-South	15-9 m	Quillback	12
2012	7-Aug-12	PG-South	15-9 m	Quillback	13
2012	7-Aug-12	PG-South	15-9 m	Quillback	17
2012	7-Aug-12	PG-South	15-9 m	Quillback	17
2012	7-Aug-12	PG-South	9-3 m	Copper	22
2012	7-Aug-12	PG-South	3-0 m	Whitespotted greenling	19
2012	7-Aug-12	PP-Minnesota	27-21 m	Copper	30
2012	7-Aug-12	PP-Minnesota	27-21 m	Lingcod	50
2012	7-Aug-12	PP-Minnesota	27-21 m	Lingcod	75
2012	7-Aug-12	PP-Minnesota	27-21 m	Male kelp greenling	33
2012	7-Aug-12	PP-Minnesota	21-15 m	Copper	27
2012	7-Aug-12	PP-Minnesota	21-15 m	Male kelp greenling	25

2012	7-Aug-12	PP-Minnesota	21-15 m	Male kelp greenling	28
2012	7-Aug-12	PP-Minnesota	15-9 m	Female kelp greenling	26
2012	7-Aug-12	PP-Minnesota	15-9 m	Lingcod	95
2012	7-Aug-12	PP-Minnesota	9-3 m	Female kelp greenling	25
2012	7-Aug-12	YI-Low	27-21 m	Copper	20
2012	7-Aug-12	YI-Low	27-21 m	Copper	25
2012	7-Aug-12	YI-Low	27-21 m	Copper	25
2012	7-Aug-12	YI-Low	27-21 m	Copper	27
2012	7-Aug-12	YI-Low	27-21 m	Copper	27
2012	7-Aug-12	YI-Low	27-21 m	Female kelp greenling	30
2012	7-Aug-12	YI-Low	27-21 m	Female kelp greenling	33
2012	7-Aug-12	YI-Low	27-21 m	Male kelp greenling	25
2012	7-Aug-12	YI-Low	27-21 m	Quillback	19
2012	7-Aug-12	YI-Low	27-21 m	Quillback	22
2012	7-Aug-12	YI-Low	27-21 m	Quillback	22
2012	7-Aug-12	YI-Low	27-21 m	Quillback	23
2012	7-Aug-12	YI-Low	27-21 m	Quillback	25
2012	7-Aug-12	YI-Low	21-15 m	Copper	20
2012	7-Aug-12	YI-Low	21-15 m	Male kelp greenling	25
2012	7-Aug-12	YI-Low	15-9 m	Copper	24
2012	7-Aug-12	YI-Low	15-9 m	Copper	25
2012	7-Aug-12	YI-Low	15-9 m	Lingcod	52
2012	7-Aug-12	YI-Low	15-9 m	Male kelp greenling	25
2012	7-Aug-12	YI-Low	9-3 m	Copper	25
2012	7-Aug-12	YI-Low	9-3 m	Copper	30
2012	7-Aug-12	YI-Low	9-3 m	Female kelp greenling	27
2012	8-Aug-12	MP-Center	27-21 m	Female kelp greenling	35
2012	8-Aug-12	MP-Center	27-21 m	Male kelp greenling	25
2012	8-Aug-12	MP-Center	27-21 m	Quillback	22
2012	8-Aug-12	MP-Center	27-21 m	Quillback	22
2012	8-Aug-12	MP-Center	21-15 m	Copper	22
2012	8-Aug-12	MP-Center	21-15 m	Copper	28
2012	8-Aug-12	MP-Center	21-15 m	Copper	30
2012	8-Aug-12	MP-Center	21-15 m	Lingcod	38
2012	8-Aug-12	MP-Center	21-15 m	Male kelp greenling	25
2012	8-Aug-12	MP-Center	21-15 m	Male kelp greenling	25
2012	8-Aug-12	MP-Center	21-15 m	Male kelp greenling	32
2012	8-Aug-12	MP-Center	21-15 m	Quillback	30
2012	8-Aug-12	MP-Center	15-9 m	Copper	12
2012	8-Aug-12	MP-Center	15-9 m	Copper	24
2012	8-Aug-12	MP-Center	15-9 m	Copper	25
2012	8-Aug-12	MP-Center	15-9 m	Copper	28
2012	8-Aug-12	MP-Center	15-9 m	Female kelp greenling	32

2012	8-Aug-12	MP-Center	15-9 m	Lingcod	40
2012	8-Aug-12	MP-Center	15-9 m	Lingcod	50
2012	8-Aug-12	MP-Center	15-9 m	Male kelp greenling	27
2012	8-Aug-12	MP-Center	9-3 m	Copper	18
2012	8-Aug-12	MP-Center	9-3 m	Copper	20
2012	8-Aug-12	MP-Center	9-3 m	Male kelp greenling	20
2012	8-Aug-12	NP-South	27-21 m	Copper	20
2012	8-Aug-12	NP-South	27-21 m	Copper	20
2012	8-Aug-12	NP-South	27-21 m	Copper	23
2012	8-Aug-12	NP-South	27-21 m	Copper	25
2012	8-Aug-12	NP-South	27-21 m	Copper	30
2012	8-Aug-12	NP-South	27-21 m	Male kelp greenling	25
2012	8-Aug-12	NP-South	27-21 m	Male kelp greenling	27
2012	8-Aug-12	NP-South	27-21 m	Male kelp greenling	30
2012	8-Aug-12	NP-South	27-21 m	Quillback	20
2012	8-Aug-12	NP-South	27-21 m	Quillback	20
2012	8-Aug-12	NP-South	21-15 m	Copper	20
2012	8-Aug-12	NP-South	21-15 m	Copper	20
2012	8-Aug-12	NP-South	21-15 m	Copper	20
2012	8-Aug-12	NP-South	21-15 m	Copper	20
2012	8-Aug-12	NP-South	21-15 m	Copper	23
2012	8-Aug-12	NP-South	21-15 m	Copper	25
2012	8-Aug-12	NP-South	21-15 m	Copper	25
2012	8-Aug-12	NP-South	21-15 m	Copper	25
2012	8-Aug-12	NP-South	21-15 m	Copper	25
2012	8-Aug-12	NP-South	21-15 m	Copper	25
2012	8-Aug-12	NP-South	21-15 m	Copper	25
2012	8-Aug-12	NP-South	21-15 m	Copper	28
2012	8-Aug-12	NP-South	21-15 m	Male kelp greenling	25
2012	8-Aug-12	NP-South	21-15 m	Male kelp greenling	25
2012	8-Aug-12	NP-South	21-15 m	Male kelp greenling	30
2012	8-Aug-12	NP-South	15-9 m	Copper	16
2012	8-Aug-12	NP-South	15-9 m	Copper	20
2012	8-Aug-12	NP-South	15-9 m	Copper	22
2012	8-Aug-12	NP-South	15-9 m	Copper	25
2012	8-Aug-12	NP-South	15-9 m	Copper	25
2012	8-Aug-12	NP-South	15-9 m	Copper	26
2012	8-Aug-12	NP-South	15-9 m	Copper	28
2012	8-Aug-12	NP-South	15-9 m	Copper	30
2012	8-Aug-12	NP-South	15-9 m	Copper	30
2012	8-Aug-12	NP-South	15-9 m	Female kelp greenling	30
2012	8-Aug-12	NP-South	15-9 m	Lingcod	75
2012	8-Aug-12	NP-South	9-3 m	Copper	18
2012	8-Aug-12	NP-South	9-3 m	Copper	18

2012	8-Aug-12	PP-One Mile	21-15 m	Male kelp greenling	30
2012	8-Aug-12	PP-One Mile	9-3 m	Male kelp greenling	25
2012	8-Aug-12	PP-One Mile	3-0 m	Female kelp greenling	30
2012	8-Aug-12	SC-South	27-21 m	Copper	25
2012	8-Aug-12	SC-South	15-9 m	Copper	20
2012	8-Aug-12	SC-South	15-9 m	Copper	20
2012	8-Aug-12	SC-South	15-9 m	Male kelp greenling	12
2012	8-Aug-12	SC-South	15-9 m	Male kelp greenling	30
2012	9-Aug-12	YI-Yellow	27-21 m	Male kelp greenling	27
2012	9-Aug-12	YI-Yellow	27-21 m	Male kelp greenling	31
2012	9-Aug-12	YI-Yellow	21-15 m	Buffalo sculpin	25
2012	9-Aug-12	YI-Yellow	21-15 m	Copper	30
2012	9-Aug-12	YI-Yellow	21-15 m	Female kelp greenling	25
2012	9-Aug-12	YI-Yellow	15-9 m	Copper	24
2012	9-Aug-12	YI-Yellow	15-9 m	Copper	27
2012	9-Aug-12	YI-Yellow	15-9 m	Copper	37
2012	9-Aug-12	YI-Yellow	15-9 m	Female kelp greenling	25
2012	9-Aug-12	YI-Yellow	15-9 m	Female kelp greenling	30

Appendix B. Annual prey survey data. See Chapter 2, Table 1 and Figure 1 for location details.

Year	Site	Depth (m)	Shrimp	Small fishes	Crabs
2010	MP-Center	9	8	2	0
2010	MP-Center	12	27	5	1
2010	MP-Center	15	24	3	0
2010	MP-Center	18	28	7	0
2010	MP-Center	21	6	2	0
2010	MP-North	9	12	4	0
2010	MP-North	12	14	6	4
2010	MP-North	15	38	9	4
2010	MP-North	18	21	7	3
2010	MP-North	21	47	5	2
2010	NP-North	9	38	3	0
2010	NP-North	12	52	3	0
2010	NP-North	15	36	6	2
2010	NP-North	18	45	10	0
2010	NP-North	21	14	5	5
2010	NP-South	9	13	5	4
2010	NP-South	12	18	2	2
2010	NP-South	15	15	9	4
2010	NP-South	18	17	8	1
2010	NP-South	21	10	6	4
2010	PG-Center	9	6	1	1
2010	PG-Center	12	11	1	2
2010	PG-Center	15	3	4	4
2010	PG-Center	18	1	2	1
2010	PG-Center	21	1	8	5
2010	PG-South	9	41	2	0
2010	PG-South	12	11	0	1
2010	PG-South	15	3	4	4
2010	PG-South	18	11	4	5
2010	PG-South	21	11	8	6
2010	PP-One Mile	9	3	1	1
2010	PP-One Mile	12	0	0	2
2010	PP-One Mile	15	5	3	4
2010	PP-One Mile	18	6	7	8
2010	PP-One Mile	21	17	6	7
2010	PP-Minnesota	9	22	2	1
2010	PP-Minnesota	12	10	1	0
2010	PP-Minnesota	15	23	7	0

Year	Site	Depth (m)	Shrimp	Small fishes	Crabs
2010	PP-Minnesota	18	1	5	2
2010	PP-Minnesota	21	3	3	2
2010	SC-Center	9	4	0	0
2010	SC-Center	12	10	6	0
2010	SC-Center	15	14	1	0
2010	SC-Center	18	25	11	0
2010	SC-Center	21	15	7	6
2010	SC-South	9	27	1	0
2010	SC-South	12	24	2	0
2010	SC-South	15	9	2	0
2010	SC-South	18	5	4	0
2010	SC-South	21	13	3	1
2010	YI-Low	9	8	1	0
2010	YI-Low	12	3	2	1
2010	YI-Low	15	23	3	0
2010	YI-Low	18	44	10	4
2010	YI-Low	21	33	5	4
2010	YI-Yellow	9	22	1	0
2010	YI-Yellow	12	35	3	1
2010	YI-Yellow	15	50	2	1
2010	YI-Yellow	18	72	3	0
2010	YI-Yellow	21	52	3	0
2011	MP-Center	9	24	4	0
2011	MP-Center	12	45	5	0
2011	MP-Center	15	46	4	0
2011	MP-Center	18	36	5	2
2011	MP-Center	21	24	5	1
2011	MP-North	9	32	4	0
2011	MP-North	12	39	4	0
2011	MP-North	15	24	4	0
2011	MP-North	18	28	10	1
2011	MP-North	21	18	2	1
2011	NP-North	9	28	0	0
2011	NP-North	12	36	0	0
2011	NP-North	15	22	2	0
2011	NP-North	18	13	7	5
2011	NP-North	21	11	5	2
2011	NP-South	9	20	6	12
2011	NP-South	12	22	5	1
2011	NP-South	15	4	5	5
2011	NP-South	18	26	6	1

Year	Site	Depth (m)	Shrimp	Small fishes	Crabs
2011	NP-South	21	10	3	4
2011	PG-Center	9	16	2	1
2011	PG-Center	12	8	5	3
2011	PG-Center	15	0	8	4
2011	PG-Center	18	7	3	6
2011	PG-Center	21	0	3	4
2011	PG-South	9	12	3	0
2011	PG-South	12	14	1	1
2011	PG-South	15	13	4	2
2011	PG-South	18	1	4	3
2011	PG-South	21	17	7	10
2011	PP-One Mile	9	0	1	1
2011	PP-One Mile	12	8	4	0
2011	PP-One Mile	15	14	3	3
2011	PP-One Mile	18	5	0	6
2011	PP-One Mile	21	5	3	0
2011	PP-Minnesota	9	34	1	0
2011	PP-Minnesota	12	21	4	2
2011	PP-Minnesota	15	12	4	1
2011	PP-Minnesota	18	8	1	2
2011	PP-Minnesota	21	10	1	0
2011	SC-Center	9	21	1	0
2011	SC-Center	12	27	4	1
2011	SC-Center	15	12	2	1
2011	SC-Center	18	8	2	2
2011	SC-Center	21	5	4	10
2011	SC-South	9	12	3	1
2011	SC-South	12	34	9	1
2011	SC-South	15	5	1	0
2011	SC-South	18	10	2	4
2011	SC-South	21	3	4	2
2011	YI-Low	9	10	6	0
2011	YI-Low	12	7	1	1
2011	YI-Low	15	15	3	1
2011	YI-Low	18	22	3	0
2011	YI-Low	21	10	1	2
2011	YI-Yellow	9	41	0	0
2011	YI-Yellow	12	29	0	0
2011	YI-Yellow	15	43	2	1
2011	YI-Yellow	18	20	4	3
2011	YI-Yellow	21	36	3	2
2012	MP-Center	9	19	3	0

Year	Site	Depth (m)	Shrimp	Small fishes	Crabs
2012	MP-Center	12	64	3	0
2012	MP-Center	15	102	2	1
2012	MP-Center	18	60	2	0
2012	MP-Center	21	12	1	0
2012	MP-North	9	12	3	0
2012	MP-North	12	53	4	1
2012	MP-North	15	43	5	0
2012	MP-North	18	22	4	2
2012	MP-North	21	29	1	0
2012	NP-North	9	21	0	0
2012	NP-North	12	24	1	0
2012	NP-North	15	26	6	3
2012	NP-North	18	21	8	3
2012	NP-North	21	29	4	3
2012	NP-South	9	13	1	1
2012	NP-South	12	17	1	2
2012	NP-South	15	1	4	2
2012	NP-South	18	39	10	5
2012	NP-South	21	5	1	9
2012	PG-Center	9	3	1	1
2012	PG-Center	12	8	5	1
2012	PG-Center	15	7	6	3
2012	PG-Center	18	3	7	3
2012	PG-Center	21	6	2	2
2012	PG-South	9	31	1	0
2012	PG-South	12	8	2	0
2012	PG-South	15	12	2	2
2012	PG-South	18	16	4	0
2012	PG-South	21	17	4	2
2012	PP-One Mile	9	0	0	0
2012	PP-One Mile	12	1	1	1
2012	PP-One Mile	15	50	2	3
2012	PP-One Mile	18	41	4	8
2012	PP-One Mile	21	12	5	4
2012	PP-Minnesota	9	24	1	0
2012	PP-Minnesota	12	20	1	0
2012	PP-Minnesota	15	15	6	0
2012	PP-Minnesota	18	13	7	0
2012	PP-Minnesota	21	1	3	0
2012	SC-Center	9	21	1	0
2012	SC-Center	12	9	2	0
2012	SC-Center	15	25	5	0

Year	Site	Depth (m)	Shrimp	Small fishes	Crabs
2012	SC-Center	18	15	4	2
2012	SC-Center	21	17	3	2
2012	SC-South	9	32	3	1
2012	SC-South	12	27	7	0
2012	SC-South	15	6	4	0
2012	SC-South	18	12	3	2
2012	SC-South	21	11	4	1
2012	YI-Low	9	44	4	0
2012	YI-Low	12	20	2	0
2012	YI-Low	15	39	5	0
2012	YI-Low	18	76	3	3
2012	YI-Low	21	9	1	0
2012	YI-Yellow	9	61	2	0
2012	YI-Yellow	12	49	1	1
2012	YI-Yellow	15	31	2	1
2012	YI-Yellow	18	20	4	1
2012	YI-Yellow	21	31	2	0

Appendix C. Annual sessile epibenthos survey data. See Chapter 3, Table 1 and Figure 1 for location details, and Table 4 for species codes. Values are proportional cover.

Shallow sessile epibenthos:

Year	Site	AGFI	BARE	BARN	CCAP	DOCO	EALM	ENBR	ERCR	HBCO
2010	MP-Center	0.543	0.005	0.000	0.167	0.000	0.140	0.000	0.000	0.016
2010	MP-North	0.744	0.000	0.000	0.050	0.000	0.126	0.005	0.000	0.010
2010	NP-North	0.614	0.015	0.000	0.193	0.000	0.000	0.000	0.000	0.015
2010	NP-South	0.530	0.025	0.005	0.155	0.000	0.135	0.010	0.000	0.025
2010	PG-Center	0.548	0.000	0.000	0.126	0.005	0.206	0.005	0.000	0.030
2010	PG-South	0.365	0.042	0.000	0.255	0.000	0.198	0.000	0.000	0.026
2010	PP-One Mile	0.195	0.010	0.000	0.320	0.000	0.040	0.000	0.005	0.045
2010	PP-Minnesota	0.560	0.030	0.000	0.080	0.000	0.195	0.000	0.000	0.015
2010	SC-Center	0.615	0.000	0.000	0.165	0.000	0.060	0.000	0.000	0.010
2010	SC-South	0.545	0.016	0.000	0.225	0.000	0.147	0.000	0.000	0.005
2010	YI-Low	0.364	0.005	0.000	0.097	0.000	0.333	0.005	0.000	0.144
2010	YI-Yellow	0.693	0.000	0.016	0.047	0.000	0.047	0.000	0.000	0.021
2011	MP-Center	0.598	0.021	0.000	0.124	0.000	0.093	0.000	0.000	0.082
2011	MP-North	0.589	0.010	0.000	0.061	0.000	0.112	0.000	0.000	0.071
2011	NP-North	0.889	0.000	0.000	0.035	0.000	0.005	0.000	0.000	0.005
2011	NP-South	0.566	0.010	0.041	0.046	0.000	0.041	0.000	0.000	0.051
2011	PG-Center	0.533	0.010	0.000	0.086	0.000	0.132	0.005	0.000	0.086
2011	PG-South	0.337	0.015	0.000	0.138	0.000	0.204	0.005	0.000	0.214
2011	PP-One Mile	0.225	0.005	0.000	0.165	0.005	0.055	0.000	0.000	0.070
2011	PP-Minnesota	0.425	0.005	0.000	0.160	0.000	0.190	0.000	0.000	0.060
2011	SC-Center	0.684	0.005	0.000	0.107	0.000	0.015	0.005	0.000	0.087
2011	SC-South	0.438	0.010	0.000	0.139	0.000	0.155	0.000	0.000	0.227
2011	YI-Low	0.355	0.015	0.000	0.095	0.000	0.250	0.005	0.000	0.210
2011	YI-Yellow	0.751	0.000	0.005	0.021	0.000	0.026	0.000	0.000	0.109
2012	MP-Center	0.721	0.005	0.000	0.126	0.000	0.037	0.000	0.000	0.037
2012	MP-North	0.589	0.010	0.000	0.056	0.000	0.102	0.000	0.000	0.147
2012	NP-North	0.721	0.000	0.000	0.076	0.000	0.005	0.000	0.000	0.015
2012	NP-South	0.683	0.000	0.005	0.060	0.000	0.080	0.000	0.000	0.035
2012	PG-Center	0.609	0.000	0.000	0.112	0.000	0.152	0.000	0.000	0.071
2012	PG-South	0.284	0.005	0.000	0.173	0.000	0.264	0.000	0.000	0.193
2012	PP-One Mile	0.270	0.000	0.000	0.110	0.000	0.020	0.000	0.020	0.050
2012	PP-Minnesota	0.528	0.005	0.000	0.093	0.000	0.223	0.000	0.000	0.052
2012	SC-Center	0.605	0.000	0.000	0.115	0.000	0.055	0.000	0.000	0.100
2012	SC-South	0.387	0.000	0.005	0.257	0.000	0.094	0.000	0.000	0.110
2012	YI-Low	0.242	0.005	0.000	0.227	0.000	0.289	0.000	0.000	0.206
2012	YI-Yellow	0.756	0.000	0.000	0.010	0.000	0.015	0.000	0.000	0.020

Shallow sessile epibenthos, continued:

Year	Site	HYSP	KELP	META	PDMC	RFSP	SCUN	SPUN	TETR	TUSO	TWSO
2010	MP-Center	0.000	0.000	0.000	0.000	0.097	0.005	0.000	0.000	0.000	0.022
2010	MP-North	0.000	0.020	0.000	0.000	0.025	0.005	0.000	0.000	0.000	0.015
2010	NP-North	0.000	0.010	0.000	0.005	0.071	0.000	0.000	0.000	0.000	0.076
2010	NP-South	0.000	0.025	0.005	0.020	0.055	0.000	0.005	0.000	0.000	0.005
2010	PG-Center	0.000	0.025	0.000	0.005	0.025	0.000	0.000	0.005	0.005	0.015
2010	PG-South	0.005	0.016	0.000	0.000	0.052	0.000	0.000	0.000	0.000	0.042
2010	PP-One Mile	0.000	0.000	0.000	0.000	0.370	0.000	0.000	0.010	0.005	0.000
2010	PP-Minnesota	0.000	0.005	0.030	0.015	0.030	0.000	0.005	0.000	0.000	0.030
2010	SC-Center	0.000	0.050	0.000	0.005	0.050	0.005	0.005	0.000	0.015	0.020
2010	SC-South	0.000	0.000	0.000	0.021	0.000	0.000	0.000	0.000	0.010	0.031
2010	YI-Low	0.000	0.000	0.000	0.015	0.021	0.000	0.000	0.000	0.000	0.015
2010	YI-Yellow	0.000	0.047	0.000	0.000	0.125	0.000	0.000	0.000	0.000	0.005
2011	MP-Center	0.000	0.000	0.000	0.000	0.062	0.005	0.000	0.000	0.005	0.010
2011	MP-North	0.000	0.000	0.010	0.000	0.117	0.005	0.000	0.000	0.005	0.020
2011	NP-North	0.000	0.010	0.000	0.000	0.040	0.000	0.000	0.000	0.000	0.015
2011	NP-South	0.000	0.082	0.005	0.020	0.117	0.000	0.000	0.000	0.005	0.015
2011	PG-Center	0.005	0.046	0.000	0.010	0.066	0.000	0.000	0.010	0.000	0.010
2011	PG-South	0.000	0.046	0.000	0.010	0.026	0.000	0.000	0.000	0.000	0.005
2011	PP-One Mile	0.000	0.125	0.000	0.000	0.325	0.000	0.000	0.015	0.005	0.005
2011	PP-Minnesota	0.000	0.025	0.010	0.005	0.090	0.015	0.000	0.005	0.005	0.005
2011	SC-Center	0.005	0.036	0.000	0.005	0.031	0.000	0.005	0.005	0.000	0.010
2011	SC-South	0.000	0.000	0.000	0.000	0.026	0.000	0.000	0.000	0.005	0.000
2011	YI-Low	0.010	0.000	0.000	0.000	0.050	0.000	0.000	0.000	0.000	0.010
2011	YI-Yellow	0.000	0.057	0.000	0.000	0.031	0.000	0.000	0.000	0.000	0.000
2012	MP-Center	0.000	0.000	0.000	0.000	0.042	0.000	0.000	0.005	0.005	0.021
2012	MP-North	0.000	0.005	0.000	0.000	0.076	0.000	0.000	0.000	0.005	0.010
2012	NP-North	0.010	0.107	0.000	0.000	0.036	0.000	0.000	0.000	0.000	0.030
2012	NP-South	0.000	0.040	0.000	0.000	0.080	0.000	0.000	0.000	0.005	0.010
2012	PG-Center	0.000	0.025	0.000	0.000	0.025	0.000	0.000	0.005	0.000	0.000
2012	PG-South	0.000	0.000	0.000	0.000	0.051	0.005	0.005	0.000	0.000	0.020
2012	PP-One Mile	0.000	0.065	0.000	0.000	0.460	0.000	0.000	0.000	0.005	0.000
2012	PP-Minnesota	0.000	0.016	0.010	0.005	0.031	0.000	0.010	0.005	0.005	0.016
2012	SC-Center	0.000	0.070	0.000	0.005	0.020	0.000	0.000	0.000	0.005	0.025
2012	SC-South	0.000	0.000	0.000	0.010	0.120	0.000	0.000	0.000	0.016	0.000
2012	YI-Low	0.000	0.000	0.000	0.000	0.010	0.005	0.000	0.005	0.005	0.005
2012	YI-Yellow	0.000	0.132	0.000	0.000	0.061	0.000	0.000	0.000	0.000	0.005

Deep sessile epibenthos:

Year	Site	ABTI	AGFI	BAEL	BANU	BARE	BARN	BRBR	CCAP	CRGI
2010	MP-Center	0.000	0.025	0.013	0.000	0.000	0.000	0.000	0.177	0.000
2010	MP-North	0.000	0.005	0.000	0.000	0.000	0.099	0.000	0.042	0.000
2010	NP-North	0.000	0.000	0.021	0.000	0.000	0.000	0.000	0.176	0.000
2010	NP-South	0.000	0.005	0.011	0.005	0.000	0.000	0.000	0.158	0.000
2010	PG-Center	0.000	0.000	0.040	0.000	0.000	0.000	0.121	0.131	0.000
2010	PG-South	0.000	0.000	0.010	0.000	0.000	0.000	0.095	0.060	0.000
2010	PP-One Mile	0.000	0.000	0.005	0.000	0.005	0.000	0.000	0.165	0.005
2010	PP-Minnesota	0.000	0.000	0.005	0.000	0.010	0.000	0.000	0.045	0.000
2010	SC-Center	0.000	0.010	0.005	0.000	0.010	0.000	0.020	0.092	0.000
2010	SC-South	0.000	0.015	0.031	0.000	0.010	0.000	0.000	0.240	0.000
2010	YI-Low	0.000	0.005	0.000	0.005	0.005	0.005	0.000	0.141	0.000
2010	YI-Yellow	0.000	0.051	0.010	0.000	0.005	0.000	0.000	0.179	0.000
2011	MP-Center	0.000	0.039	0.006	0.006	0.000	0.000	0.000	0.089	0.000
2011	MP-North	0.000	0.000	0.000	0.005	0.000	0.010	0.000	0.036	0.000
2011	NP-North	0.021	0.000	0.011	0.000	0.005	0.000	0.000	0.080	0.000
2011	NP-South	0.038	0.000	0.016	0.000	0.005	0.000	0.000	0.076	0.000
2011	PG-Center	0.397	0.000	0.005	0.000	0.000	0.000	0.000	0.166	0.000
2011	PG-South	0.036	0.000	0.010	0.000	0.026	0.000	0.000	0.056	0.000
2011	PP-One Mile	0.270	0.000	0.015	0.000	0.000	0.000	0.000	0.235	0.000
2011	PP-Minnesota	0.020	0.005	0.025	0.000	0.000	0.000	0.000	0.080	0.000
2011	SC-Center	0.066	0.000	0.000	0.000	0.010	0.000	0.000	0.096	0.000
2011	SC-South	0.005	0.005	0.005	0.000	0.005	0.000	0.000	0.099	0.000
2011	YI-Low	0.045	0.000	0.005	0.005	0.005	0.000	0.005	0.040	0.000
2011	YI-Yellow	0.005	0.117	0.005	0.005	0.005	0.010	0.000	0.066	0.000
2012	MP-Center	0.000	0.000	0.011	0.000	0.011	0.005	0.000	0.115	0.000
2012	MP-North	0.000	0.000	0.000	0.000	0.016	0.059	0.000	0.059	0.000
2012	NP-North	0.017	0.062	0.006	0.000	0.006	0.006	0.000	0.085	0.000
2012	NP-South	0.072	0.000	0.015	0.000	0.005	0.000	0.000	0.133	0.000
2012	PG-Center	0.566	0.000	0.031	0.000	0.000	0.000	0.000	0.087	0.000
2012	PG-South	0.057	0.000	0.000	0.000	0.015	0.000	0.000	0.062	0.000
2012	PP-One Mile	0.370	0.000	0.015	0.000	0.000	0.000	0.000	0.135	0.000
2012	PP-Minnesota	0.030	0.015	0.020	0.000	0.005	0.000	0.000	0.045	0.000
2012	SC-Center	0.041	0.041	0.020	0.000	0.015	0.000	0.000	0.102	0.000
2012	SC-South	0.005	0.037	0.005	0.000	0.027	0.000	0.005	0.128	0.000
2012	YI-Low	0.015	0.000	0.005	0.000	0.010	0.000	0.000	0.030	0.005
2012	YI-Yellow	0.000	0.015	0.000	0.000	0.065	0.005	0.000	0.080	0.000

Deep sessile epibenthos, continued:

Year	Site	CRIS	DICA	DICL	EALM	ENBR	EUBI	HBCO	HEPA	HYSP
2010	MP-Center	0.000	0.006	0.000	0.278	0.038	0.000	0.095	0.000	0.019
2010	MP-North	0.000	0.000	0.000	0.251	0.031	0.084	0.099	0.000	0.183
2010	NP-North	0.000	0.000	0.139	0.021	0.059	0.102	0.166	0.000	0.155
2010	NP-South	0.000	0.000	0.147	0.026	0.032	0.137	0.084	0.000	0.158
2010	PG-Center	0.000	0.000	0.005	0.131	0.030	0.010	0.066	0.005	0.207
2010	PG-South	0.000	0.000	0.095	0.075	0.030	0.090	0.261	0.005	0.010
2010	PP-One Mile	0.000	0.000	0.085	0.030	0.045	0.030	0.120	0.005	0.310
2010	PP-Minnesota	0.000	0.000	0.100	0.115	0.130	0.045	0.295	0.000	0.050
2010	SC-Center	0.000	0.000	0.117	0.163	0.051	0.046	0.143	0.000	0.102
2010	SC-South	0.000	0.000	0.061	0.168	0.036	0.051	0.168	0.000	0.031
2010	YI-Low	0.000	0.005	0.000	0.146	0.060	0.226	0.121	0.000	0.060
2010	YI-Yellow	0.000	0.000	0.000	0.148	0.031	0.005	0.265	0.000	0.000
2011	MP-Center	0.000	0.000	0.000	0.168	0.006	0.011	0.430	0.000	0.011
2011	MP-North	0.000	0.000	0.000	0.172	0.005	0.026	0.245	0.000	0.146
2011	NP-North	0.000	0.000	0.176	0.032	0.005	0.032	0.369	0.000	0.091
2011	NP-South	0.005	0.000	0.162	0.027	0.000	0.059	0.292	0.005	0.092
2011	PG-Center	0.000	0.000	0.005	0.106	0.005	0.005	0.035	0.000	0.010
2011	PG-South	0.000	0.000	0.077	0.077	0.015	0.082	0.265	0.000	0.005
2011	PP-One Mile	0.000	0.000	0.055	0.030	0.015	0.005	0.075	0.005	0.015
2011	PP-Minnesota	0.000	0.000	0.090	0.170	0.015	0.075	0.255	0.000	0.045
2011	SC-Center	0.000	0.000	0.116	0.111	0.010	0.040	0.222	0.000	0.081
2011	SC-South	0.000	0.000	0.078	0.109	0.000	0.021	0.401	0.000	0.078
2011	YI-Low	0.000	0.000	0.000	0.091	0.040	0.111	0.379	0.000	0.071
2011	YI-Yellow	0.000	0.000	0.000	0.117	0.000	0.000	0.452	0.000	0.005
2012	MP-Center	0.000	0.000	0.000	0.181	0.000	0.000	0.396	0.000	0.000
2012	MP-North	0.000	0.000	0.000	0.155	0.000	0.053	0.230	0.000	0.267
2012	NP-North	0.006	0.000	0.102	0.011	0.017	0.023	0.311	0.006	0.113
2012	NP-South	0.000	0.000	0.256	0.010	0.000	0.031	0.159	0.000	0.123
2012	PG-Center	0.000	0.005	0.005	0.061	0.000	0.005	0.000	0.000	0.026
2012	PG-South	0.000	0.000	0.144	0.082	0.000	0.103	0.201	0.000	0.005
2012	PP-One Mile	0.000	0.000	0.110	0.035	0.000	0.040	0.035	0.000	0.015
2012	PP-Minnesota	0.000	0.000	0.070	0.170	0.005	0.060	0.205	0.000	0.120
2012	SC-Center	0.000	0.000	0.097	0.097	0.000	0.051	0.184	0.000	0.128
2012	SC-South	0.000	0.000	0.043	0.101	0.005	0.043	0.293	0.000	0.133
2012	YI-Low	0.000	0.000	0.000	0.131	0.010	0.131	0.338	0.000	0.096
2012	YI-Yellow	0.000	0.000	0.000	0.125	0.000	0.010	0.480	0.000	0.000

Deep sessile epibenthos, continued:

Year	Site	META	MOMD	PDMC	PSCH	RFSP	SCUN	SPUN	STYL	TETR
2010	MP-Center	0.000	0.000	0.013	0.000	0.019	0.032	0.006	0.000	0.006
2010	MP-North	0.000	0.000	0.000	0.000	0.094	0.000	0.005	0.000	0.016
2010	NP-North	0.000	0.000	0.027	0.005	0.027	0.005	0.005	0.000	0.011
2010	NP-South	0.000	0.000	0.000	0.000	0.105	0.021	0.026	0.005	0.047
2010	PG-Center	0.000	0.000	0.000	0.000	0.025	0.000	0.005	0.005	0.167
2010	PG-South	0.000	0.000	0.000	0.000	0.010	0.040	0.005	0.000	0.030
2010	PP-One Mile	0.000	0.000	0.000	0.000	0.020	0.000	0.000	0.000	0.150
2010	PP-Minnesota	0.000	0.000	0.000	0.005	0.020	0.010	0.130	0.000	0.020
2010	SC-Center	0.077	0.000	0.000	0.000	0.117	0.010	0.010	0.000	0.010
2010	SC-South	0.000	0.000	0.010	0.000	0.036	0.010	0.010	0.000	0.036
2010	YI-Low	0.000	0.000	0.025	0.000	0.060	0.000	0.030	0.005	0.015
2010	YI-Yellow	0.000	0.000	0.010	0.000	0.071	0.015	0.031	0.000	0.036
2011	MP-Center	0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.000	0.011
2011	MP-North	0.000	0.000	0.005	0.000	0.141	0.016	0.010	0.000	0.000
2011	NP-North	0.000	0.000	0.011	0.000	0.032	0.011	0.011	0.000	0.011
2011	NP-South	0.000	0.000	0.000	0.000	0.054	0.027	0.005	0.000	0.049
2011	PG-Center	0.000	0.000	0.000	0.000	0.080	0.025	0.005	0.000	0.075
2011	PG-South	0.000	0.005	0.005	0.000	0.051	0.010	0.026	0.000	0.041
2011	PP-One Mile	0.000	0.000	0.000	0.000	0.050	0.005	0.015	0.005	0.080
2011	PP-Minnesota	0.000	0.000	0.000	0.000	0.050	0.035	0.095	0.005	0.020
2011	SC-Center	0.106	0.000	0.000	0.005	0.071	0.015	0.015	0.000	0.020
2011	SC-South	0.000	0.000	0.016	0.000	0.047	0.000	0.021	0.000	0.021
2011	YI-Low	0.000	0.000	0.000	0.005	0.015	0.005	0.015	0.000	0.000
2011	YI-Yellow	0.000	0.005	0.000	0.000	0.081	0.010	0.010	0.000	0.010
2012	MP-Center	0.000	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.011
2012	MP-North	0.000	0.000	0.000	0.000	0.086	0.000	0.000	0.000	0.005
2012	NP-North	0.000	0.000	0.000	0.000	0.073	0.028	0.006	0.000	0.011
2012	NP-South	0.000	0.005	0.000	0.000	0.046	0.010	0.000	0.000	0.036
2012	PG-Center	0.000	0.000	0.000	0.000	0.010	0.005	0.000	0.000	0.071
2012	PG-South	0.000	0.000	0.000	0.005	0.010	0.062	0.000	0.000	0.062
2012	PP-One Mile	0.000	0.000	0.000	0.000	0.025	0.025	0.015	0.000	0.070
2012	PP-Minnesota	0.015	0.000	0.000	0.010	0.035	0.035	0.140	0.000	0.015
2012	SC-Center	0.092	0.000	0.000	0.000	0.041	0.010	0.020	0.000	0.036
2012	SC-South	0.000	0.000	0.005	0.000	0.043	0.032	0.005	0.000	0.037
2012	YI-Low	0.000	0.000	0.000	0.000	0.071	0.015	0.025	0.000	0.000
2012	YI-Yellow	0.000	0.000	0.000	0.000	0.060	0.010	0.025	0.000	0.010

Deep sessile epibenthos, continued:

Year	Site	TUBC	TUSO	TWCO	TWSO	ULVA	XEED
2010	MP-Center	0.000	0.032	0.000	0.234	0.006	0.000
2010	MP-North	0.000	0.010	0.000	0.079	0.000	0.000
2010	NP-North	0.000	0.021	0.000	0.053	0.005	0.000
2010	NP-South	0.000	0.026	0.000	0.005	0.000	0.000
2010	PG-Center	0.000	0.005	0.045	0.000	0.000	0.000
2010	PG-South	0.000	0.020	0.000	0.161	0.000	0.000
2010	PP-One Mile	0.000	0.000	0.000	0.000	0.000	0.025
2010	PP-Minnesota	0.000	0.000	0.000	0.020	0.000	0.000
2010	SC-Center	0.000	0.000	0.000	0.015	0.000	0.000
2010	SC-South	0.005	0.010	0.000	0.071	0.000	0.000
2010	YI-Low	0.000	0.050	0.000	0.035	0.000	0.000
2010	YI-Yellow	0.000	0.041	0.000	0.102	0.000	0.000
2011	MP-Center	0.000	0.011	0.000	0.190	0.006	0.000
2011	MP-North	0.005	0.057	0.000	0.120	0.000	0.000
2011	NP-North	0.005	0.027	0.000	0.070	0.000	0.000
2011	NP-South	0.011	0.065	0.000	0.011	0.000	0.000
2011	PG-Center	0.000	0.000	0.080	0.000	0.000	0.000
2011	PG-South	0.000	0.015	0.036	0.158	0.000	0.000
2011	PP-One Mile	0.000	0.010	0.095	0.000	0.000	0.020
2011	PP-Minnesota	0.000	0.005	0.000	0.005	0.000	0.000
2011	SC-Center	0.000	0.005	0.000	0.010	0.000	0.000
2011	SC-South	0.000	0.036	0.000	0.052	0.000	0.000
2011	YI-Low	0.000	0.061	0.000	0.101	0.000	0.000
2011	YI-Yellow	0.000	0.030	0.000	0.066	0.000	0.000
2012	MP-Center	0.000	0.022	0.000	0.236	0.000	0.000
2012	MP-North	0.000	0.005	0.000	0.064	0.000	0.000
2012	NP-North	0.006	0.017	0.000	0.090	0.000	0.000
2012	NP-South	0.010	0.072	0.010	0.005	0.000	0.000
2012	PG-Center	0.000	0.005	0.122	0.000	0.000	0.000
2012	PG-South	0.000	0.021	0.021	0.149	0.000	0.000
2012	PP-One Mile	0.000	0.005	0.055	0.000	0.000	0.050
2012	PP-Minnesota	0.000	0.000	0.000	0.005	0.000	0.000
2012	SC-Center	0.010	0.005	0.000	0.010	0.000	0.000
2012	SC-South	0.000	0.016	0.000	0.037	0.000	0.000
2012	YI-Low	0.005	0.015	0.000	0.096	0.000	0.000
2012	YI-Yellow	0.010	0.020	0.000	0.085	0.000	0.000

Appendix D. Annual mobile invertebrate survey data. See Chapter 3, Table 1 and Figure 1 for location details, and Table 5 for species codes. Values are counts per 40 m².

Shallow mobile invertebrates:

Year	Site	CFO	CHA	CST	DIR	DOR	FOR	HEN	LST	MKE
2010	MP-Center	1	3	0	2	1	0	3	3	0
2010	MP-North	1	0	1	1	0	1	1	0	0
2010	NP-North	0	0	1	0	0	0	2	0	0
2010	NP-South	5	0	1	0	1	0	2	2	1
2010	PG-Center	0	4	2	0	1	0	4	0	0
2010	PG-South	0	8	1	0	0	0	4	0	0
2010	PP-One Mile	0	2	12	0	2	0	0	0	0
2010	PP-Minnesota	0	0	2	0	0	0	1	0	0
2010	SC-Center	3	0	3	2	0	0	8	1	0
2010	SC-South	1	0	4	0	2	0	3	0	4
2010	YI-Low	0	0	0	0	2	0	0	4	2
2010	YI-Yellow	0	1	2	0	0	1	2	1	0
2011	MP-Center	1	0	0	1	0	1	0	2	0
2011	MP-North	0	0	1	0	1	1	3	0	0
2011	NP-North	3	0	2	1	0	0	6	1	0
2011	NP-South	5	0	2	0	1	0	13	2	1
2011	PG-Center	1	5	5	0	1	0	9	0	2
2011	PG-South	0	0	4	0	1	0	4	0	0
2011	PP-One Mile	0	0	11	0	1	0	3	0	0
2011	PP-Minnesota	0	0	4	0	0	0	1	1	0
2011	SC-Center	1	0	1	0	1	1	6	0	0
2011	SC-South	4	0	6	0	0	0	5	1	0
2011	YI-Low	1	0	3	0	4	0	4	3	0
2011	YI-Yellow	3	0	3	1	1	0	3	5	0
2012	MP-Center	0	0	2	1	0	0	7	1	1
2012	MP-North	0	0	0	0	2	1	6	0	1
2012	NP-North	0	0	3	1	0	0	2	2	0
2012	NP-South	8	0	2	1	0	0	4	1	0
2012	PG-Center	2	4	2	0	1	0	6	0	0
2012	PG-South	0	2	2	0	0	0	3	0	1
2012	PP-One Mile	0	0	20	0	1	0	4	0	0
2012	PP-Minnesota	0	0	4	1	0	0	0	0	1
2012	SC-Center	1	0	5	2	1	0	4	0	0
2012	SC-South	0	0	3	0	0	0	4	1	1
2012	YI-Low	2	0	2	0	2	0	4	3	5
2012	YI-Yellow	1	0	2	1	0	0	3	2	0

Shallow mobile invertebrates, continued:

Year	Site	NUC	PCA	PHE	STR	TCA	TLI
2010	MP-Center	13	23	1	58	0	0
2010	MP-North	1	15	0	31	0	0
2010	NP-North	0	2	0	0	0	0
2010	NP-South	18	2	2	59	0	0
2010	PG-Center	0	9	1	122	0	4
2010	PG-South	0	19	2	150	0	1
2010	PP-One Mile	0	0	0	0	0	0
2010	PP-Minnesota	0	0	0	80	0	1
2010	SC-Center	0	4	0	10	1	0
2010	SC-South	0	15	1	139	0	0
2010	YI-Low	1	12	0	44	2	1
2010	YI-Yellow	11	16	0	1	0	0
2011	MP-Center	5	10	0	75	0	0
2011	MP-North	0	20	0	47	0	0
2011	NP-North	0	2	0	2	0	0
2011	NP-South	67	8	0	42	0	0
2011	PG-Center	0	7	2	95	0	0
2011	PG-South	0	7	0	93	0	0
2011	PP-One Mile	0	1	0	0	0	0
2011	PP-Minnesota	0	1	1	165	0	0
2011	SC-Center	0	4	0	19	0	0
2011	SC-South	0	13	1	177	0	0
2011	YI-Low	0	18	2	38	0	0
2011	YI-Yellow	15	9	1	4	0	0
2012	MP-Center	2	14	0	57	0	0
2012	MP-North	2	8	0	48	0	1
2012	NP-North	0	7	0	0	1	0
2012	NP-South	1	2	1	17	0	0
2012	PG-Center	0	4	1	49	0	0
2012	PG-South	0	16	0	91	0	0
2012	PP-One Mile	0	1	1	1	0	0
2012	PP-Minnesota	0	1	0	107	0	0
2012	SC-Center	0	5	0	13	0	0
2012	SC-South	0	18	2	187	0	0
2012	YI-Low	0	19	1	57	0	2
2012	YI-Yellow	3	12	2	0	0	0

Deep mobile invertebrates:

Year	Site	CFO	CHA	DOR	DIR	DEN	FOR	HEN
2010	MP-Center	1	8	0	0	0	0	10
2010	MP-North	2	8	3	0	0	1	7
2010	NP-North	0	40	3	0	10	0	19
2010	NP-South	1	85	4	0	1	0	20
2010	PG-Center	0	9	12	0	0	0	14
2010	PG-South	0	13	2	1	2	0	9
2010	PP-One Mile	0	18	5	0	0	0	10
2010	PP-Minnesota	0	5	2	0	0	0	9
2010	SC-Center	1	2	2	1	2	0	13
2010	SC-South	0	1	5	1	1	0	3
2010	YI-Low	1	2	2	0	2	0	6
2010	YI-Yellow	0	10	0	0	0	0	10
2011	MP-Center	1	1	0	0	0	0	3
2011	MP-North	0	0	2	0	0	0	3
2011	NP-North	0	1	1	0	7	0	16
2011	NP-South	1	0	3	0	0	0	18
2011	PG-Center	0	2	0	0	1	1	8
2011	PG-South	1	25	1	0	2	0	12
2011	PP-One Mile	0	12	2	0	1	0	9
2011	PP-Minnesota	0	1	0	0	0	0	9
2011	SC-Center	0	2	1	0	1	0	15
2011	SC-South	1	4	0	1	0	0	10
2011	YI-Low	0	0	0	0	1	1	4
2011	YI-Yellow	0	1	0	0	0	0	7
2012	MP-Center	0	0	0	0	0	0	2
2012	MP-North	0	3	0	0	0	1	7
2012	NP-North	2	1	3	0	3	1	18
2012	NP-South	1	6	2	1	2	0	15
2012	PG-Center	0	5	2	0	0	0	11
2012	PG-South	0	5	0	0	0	0	8
2012	PP-One Mile	1	28	3	0	0	0	12
2012	PP-Minnesota	0	2	3	0	0	0	11
2012	SC-Center	4	9	0	2	0	0	13
2012	SC-South	1	0	0	0	0	2	7
2012	YI-Low	4	0	1	0	0	0	4
2012	YI-Yellow	0	0	1	1	0	0	4

Deep mobile invertebrates, continued:

Year	Site	MKE	LST	NUC	PCA	PHE	STR	TCA
2010	MP-Center	1	1	1	17	2	46	0
2010	MP-North	3	0	18	17	5	26	1
2010	NP-North	0	2	0	6	0	38	2
2010	NP-South	0	1	0	7	3	5	2
2010	PG-Center	0	1	0	3	0	3	5
2010	PG-South	3	0	0	6	0	36	0
2010	PP-One Mile	1	1	0	4	0	0	3
2010	PP-Minnesota	4	0	0	0	0	16	2
2010	SC-Center	0	0	0	4	0	0	1
2010	SC-South	0	1	0	7	0	55	0
2010	YI-Low	0	9	0	15	1	8	0
2010	YI-Yellow	0	3	1	6	2	28	2
2011	MP-Center	0	1	0	10	3	89	0
2011	MP-North	3	2	3	18	0	4	0
2011	NP-North	0	0	0	5	1	64	0
2011	NP-South	0	2	0	7	0	0	3
2011	PG-Center	0	0	0	0	0	1	0
2011	PG-South	0	0	0	9	0	44	0
2011	PP-One Mile	0	0	0	0	0	0	0
2011	PP-Minnesota	3	1	0	0	0	26	0
2011	SC-Center	0	1	0	3	1	2	1
2011	SC-South	0	0	0	7	0	26	0
2011	YI-Low	0	2	0	19	2	8	0
2011	YI-Yellow	0	1	2	7	3	23	0
2012	MP-Center	0	1	0	8	0	43	0
2012	MP-North	2	0	0	20	0	3	0
2012	NP-North	0	2	0	3	0	69	0
2012	NP-South	0	2	0	11	0	1	0
2012	PG-Center	0	0	0	1	0	3	0
2012	PG-South	0	0	0	2	0	36	0
2012	PP-One Mile	0	0	0	7	0	0	5
2012	PP-Minnesota	1	1	0	1	1	33	0
2012	SC-Center	1	1	0	6	0	4	4
2012	SC-South	0	1	0	8	0	24	0
2012	YI-Low	0	0	0	16	0	7	0
2012	YI-Yellow	0	2	0	1	0	38	0

VITA

Kevin Turner was born on 21 February 1982 in Seattle, Washington. He attended Garfield High School in Seattle, graduating in 2000. Kevin received a B.S. in Zoology and a B.S. in Aquatic & Fishery Sciences from the University of Washington in 2005. In 2015, Kevin completed his Ph.D. degree in Biology with Kenneth P. Sebens at the University of Washington.