

Variability in the accumulation and persistence of tar in four intertidal communities along the Central and Southern California Coast

Final Technical Summary

Final Study Report



U.S. Department of the Interior
Minerals Management Service
Pacific OCS Region

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Southern California Educational Initiative

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Minerals Management Service
Pacific OCS Region

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FINAL TECHNICAL SUMMARY

STUDY TITLE: Effects of an oil spill on multispecies interactions that structure intertidal communities.

REPORT TITLE: Variability in the accumulation and persistence of tar in four intertidal communities along the central and southern California coast

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KEY WORDS: tar, central California coast, barnacles, *Endocladia*, *Silvetia*, mussels, rocky intertidal, intertidal zones, intertidal communities, natural tar seeps, experimental

BACKGROUND AND OBJECTIVES: Our goal was to couple long-term monitoring data with experimental studies to better assess the impacts of oil spills. We combined long-term data from the Shoreline Inventory Program (currently funded by the Minerals Management Service and primarily an inventory of intertidal populations), which includes a number of sites in San Luis Obispo and Santa Barbara Counties, with experimental studies of tar accumulation and persistence, as part of an effort to improve the ability to assess the impacts of potential oil spills in this region. The central California coastline is vulnerable to oil spills

because of offshore oil drilling and a high amount of tanker traffic. Additionally, the central California coastline is characterized by numerous natural subtidal oil seeps, which have been documented as far back as 1792 (Foster *et al.* 1970). The oil from these seeps frequently washes ashore and the rocky intertidal in this region often has a large amount of oil (tar) on it. These factors make this an ideal location to (1) assess where tar accumulates and persists within different species zones and (2) determine what factor(s) are important to the accumulation and persistence of tar in the intertidal. To our knowledge no studies have been done using natural tar to mimic the effects of oil spills. Variability in tar accumulation and persistence may result from both physical and biological factors. Physical factors include temperature, tidal height and wave exposure. The major biological factor of importance depends on the characteristics of the species tar lands on. These factors not only contribute to the weathering (degradation) of tar, but may also have an effect on where the tar accumulates. We developed short-term experiments that use naturally occurring tar as a proxy for oil to evaluate those species that would potentially be most susceptible to an anthropogenic oil spill along the central California coastline. Since our study relies on tar accumulation and persistence as a proxy for oil accumulation and persistence, this method simulates a small-scale oil spill.

DESCRIPTION: Our study sites were in central California from North to South; Point Sierra Nevada, Shell Beach and Boat House. Slides from the Shoreline Inventory Program were scored to assess where tar was accumulating and to estimate the percent cover of tar in permanent plots within different intertidal communities, across many sites and over the course of several years. We performed thorough visual surveys in 4 intertidal zones: barnacle (primarily *Chthamalus*), *Endocladia* (a red alga), *Silvetia* (a brown, fucoid alga), and mussel zones in the fall of 1999 at Point Sierra Nevada, Shell Beach and Boat House. Based on the results from the slide data and our visual surveys we established permanent plots in the barnacle and *Endocladia* zones in the Fall of 1999 at Point Sierra Nevada, Shell Beach and Boat House to assess the accumulation and persistence of tar in different species zones. The permanent plots were sampled twice annually (Spring and Fall) to estimate the percent cover of tar in the different zones. Experiments were designed to measure variability in tar patch accumulation and persistence by removing the effect of substrate. We made identical casts of barnacles with a urethane material that mimics the texture of barnacles which allowed us to standardize the substrate. We placed sixty 10x10cm barnacle casts in the intertidal at each of our three sites (from north to south: Point Sierra Nevada, Shell Beach and Boat House) in April 2000. At each site, we placed fifteen casts into each “zone” (the barnacle zone (control), *Endocladia*, *Silvetia* and mussel zones for a total of 60 casts per site; 15 per zone). The casts were then checked monthly for 18 months (May 2000 to October 2001) for the presence or absence of tar. Because our visual surveys showed tar accumulating in higher zones, we tested the idea that variability in tar patch accumulation and persistence may be a function of tidal height and exposure. In an attempt to determine the relationship between temperature and the accumulation and persistence of tar, in March 2001 we measured the surface temperature of all the casts, nearby rock and permanent plots in the barnacle, *Endocladia*, *Silvetia*, and mussel zones at both Point Sierra Nevada and Boat House. We then compared the mean temperature of the cast vs. rock substrate for each community, at both Point Sierra Nevada and Boat House. To insure that we were not making any false generalizations, we placed Tidbit temperature loggers at the mean tidal height for each zone

(at both Point Sierra Nevada and Boat House) for a full month (April 24, 2001 to May 25, 2001).

SIGNIFICANT RESULTS AND CONCLUSIONS: Tar accumulation and persistence varied among as well as within sites. Results from the visual surveys suggest tar does not persist long in the mussel zone. While we have documented tar stuck to *Silvetia*, mussels and rock in the mussel zone, it does not reside long (observed less than two weeks). Results from the permanent plots show that tar accumulates and persists in the barnacle and *Endocladia* zones. At Point Sierra Nevada and Shell Beach tar accumulated more in the barnacle zone. In contrast, at Boat House more tar accumulated in the *Endocladia* zone. Results from the substrate experiments show that tar is likely to be deposited in all 4 zones. With the exception of the mussel zone, once tar accumulated on a standard surface it persisted. We found that the permanent plots highest on the shore accumulated the most tar, regardless of site. This suggests that in the event of an oil spill, the zones most likely to be affected are those highest on the shore. Our results showed that at Point Sierra Nevada, while there was a significant difference between the communities there was no difference between the rock and cast temperatures within communities. However, at Boat House we did find a difference between the rock and cast temperatures within the *Silvetia* zone. The rock temperature in this zone was several degrees cooler than the cast temperature. The results from our Tidbit temperature loggers suggest that temperature could play an important role. The results ranked by zones from highest temperature to lowest temperature: barnacle, *Endocladia*, *Silvetia* and mussels.

It appears that for different species different mechanisms are important, likely due to differences in life history traits. For example, in the *Silvetia* zone, tar was found on the casts, but not on the rock. Biological factors may be more important than physical factors in this zone. In the mussel zone we documented (occasionally) tar sticking on the rock, mussels and casts. However, tar does not persist long in this zone. In the mussel zone, physical factors may be more important than biological factors. For both the barnacle and the *Endocladia* zone, tar seems to accumulate and persist roughly the same on the cast and rock substrate. For barnacles and *Endocladia* it may be that physical and biological factors are working in concert. It also appears that aside from the natural process of weathering, that barnacles and *Endocladia* have no mechanism for tar removal. Once tar accumulates in these zones, it persists.

Overall, our findings are valuable for predicting the impacts of small to moderate oil spills. Moreover, we believe that some of our results may be extendable to a large-scale oil spill. In the short-term, the upper zones barnacles and *Endocladia* are likely to be most affected; our results show that once larger sized tar patches accumulate in these zones, they persist. However, results from other studies suggest that acorn barnacles are likely to be the species most able to recover quickly via recruitment. By contrast, mussels and fleshy algae are more resistant (for different reasons) to oiling but are much less likely to recover quickly if damaged via an oil spill.

STUDY PRODUCTS:

Forde, S.E. 2002. Modelling the effects of an oil spill on open populations of intertidal invertebrates. *Journal of Applied Ecology* 39: 595-604

Roe, C.A and Raimondi, P.T. 2001. Variability in the accumulation and persistence of tar in four intertidal zones. Western Society of Naturalists Meetings, Ventura, CA.

Forde, S.E. 2000. Assessing the individual and population level effects of a disturbance using a dynamic state variable model. Ecological Society of America Meetings, Snowbird, UT.

FINAL STUDY REPORT

Introduction

To date much of the information we have regarding shoreline oiling has, been in large part, the result of major oil spills, such as, the 1969 Platform A blowout in Santa Barbara, California, followed 20 years later by the *Exxon Valdez* Spill in Alaska. However, it is difficult to generalize about the effects of oil spills, due to the spatial and temporal variability of spills (Nelson 1982; Foster *et al.* 1988; KLI 1992) and because information is often gathered “after the fact” (Neushul 1970). If a community has not been monitored prior to a spill, assessment requires using data collected after the spill and an estimation of the community prior to the spill to determine the resulting magnitude of the impact. Typically, it is difficult to determine if the condition of the community prior to the spill was estimated accurately (Neushul 1970; Nelson 1982; Foster *et al.* 1983; Jackson *et al.* 1989; KLI 1992; Paine *et al.* 1996). As a result, postdictive studies of oil spill impacts maybe unable to provide estimates of the disturbance caused by oil spills or conclusively demonstrate that the oil spill was responsible for any presumed change. Thus, there is need to couple monitoring with experimental studies of impacts, particularly those of oil and gas production (Paine et al. 1996; Forde 2002).

Our goal was to couple long-term monitoring data with experimental studies to better assess the impacts of oil spills. We combined long-term data from the Shoreline Inventory Program (currently funded by the Minerals Management Service and primarily an inventory of intertidal populations), which includes a number of sites in San Luis Obispo and Santa Barbara Counties, with experimental studies of tar accumulation and persistence, as part of an effort to improve the ability to assess the impacts of potential oil spills in this region. The central California coastline is vulnerable to oil spills because of offshore oil drilling and a high amount of tanker traffic. Additionally, the central California coastline is characterized by numerous natural subtidal oil seeps, which have been documented as far back as 1792 (Foster *et al.* 1970). The oil from these seeps frequently washes ashore and the rocky intertidal in this region often has a large amount of oil (tar) on it. These factors make this an ideal location to (1) assess where tar accumulates and persists within different species zones and (2) determine what factor(s) are important to the accumulation and persistence of tar in the intertidal. To our knowledge no studies have been done using natural tar to mimic the effects of oil spills. Variability in tar accumulation and persistence may result from both physical and biological factors. Physical factors include temperature, tidal height and wave exposure. The major biological factor of importance relates to characteristics of the species tar lands on. These factors not only contribute to the weathering (degradation) of tar, but may also have an effect on where the tar accumulates. Thus, we developed some short-term experiments that use naturally occurring tar as a proxy for oil to evaluate those species that would potentially be most susceptible to an anthropogenic oil spill along the central California coastline. Since our study relies on low levels of tar accumulation and persistence as a proxy for oil accumulation and persistence, this method comes close to simulating a small-scale oil spill.

Methods

Species Descriptions

We looked at four communities characterized by the following species: acorn barnacles, *Endocladia*, *Silvetia* and mussels. Information about natural history is important for assessing the potential impacts of oil spills.

Balanus glandula and *Chthalamus fissus/dalli* (acorn barnacles) dominate upper intertidal zones. *Balanus* out competes *Chthalamus* through crowding, but *Chthalamus* is found higher in the intertidal due to increased resistance to desiccation (Ambrose et al. 1995). *Balanus* individuals have 2 to 6 broods during the Winter and Spring (Morris et al. 1980). 1,000 to 3,000 nauplii are released per brood, and peak settlement occurs during Spring and Summer (Morris et al. 1980). *Chthalamus* spp. have up to 16 broods per individual, primarily during Spring through Fall (Morris et al. 1980). 200 to 300,000 nauplii are released per brood, and settlement peaks in March and February (Morris et al. 1980; Strathman 1992). Juvenile barnacles preferentially settle near adults.

Endocladia is characteristic of the upper intertidal, and may be associated with *Mastocarpus*. Turfweed carpets form a microhabitat for small organisms and an attachment site for juvenile mussels (Ambrose et al. 1995). Mussels often displace *Endocladia* as patches grow, but *Endocladia* can grow on mussel shells.

Silvetia compressa (formerly *Pelvetia compressa*) is found in the high intertidal, below *Endocladia*/*Mastocarpus* associations. *Silvetia* also serves as shelter for invertebrates and algae, and as attachment sites for sessile organisms (Ricketts et al. 1985). Recruitment varies depending on adult densities. Studies have shown that dispersal (of new individuals from adults) is limited, probably on the order of meters or less (De Vogelaere et al. 1994). Therefore, abundance is highly variable, with a maximum in Summer and a minimum in Winter (Foster et al. 1991). Population fluctuations are often related to abiotic conditions.

Mytilus californianus is found in the mid- to low intertidal. Mussel associations provide food and shelter for a number of invertebrates and algal species. Mussels spawn year round, with peaks in July and December (Morris et al. 1980). Mussels settle preferentially to existing beds and growth is variable depending on physical factors (Ambrose et al. 1995). Recovery from disturbance varies depending on the size of the clearing and the number of mussels still present (KLI 1992; Ambrose et al. 1995).

Study Area

Our study sites were determined by the following criteria; 1) sites where long term data had been collected under the Shoreline Inventory Program, 2) sites in proximity to natural subtidal tar seeps, 3) sites where tar was known to be present on the shore, 4) sites with limited public access and 5) sites that would provide good spatial inference. From North to South; Point Sierra Nevada (N35° 43.512' W121° 19.264') near San Simeon, Shell Beach (N35° 10.118' W120° 41.795') near San Luis Obispo and Boat House (N34° 33.243' W120° 36.689')

located on the south base of Vandenberg Air Force Base (Fig. 1). Point Sierra Nevada (Fig. 2a) has a sloping bench, Shell Beach (Fig. 2b) has a gradually sloping bench and Boat House (Fig. 2c) has hogbacks that run parallel to the incoming waves.

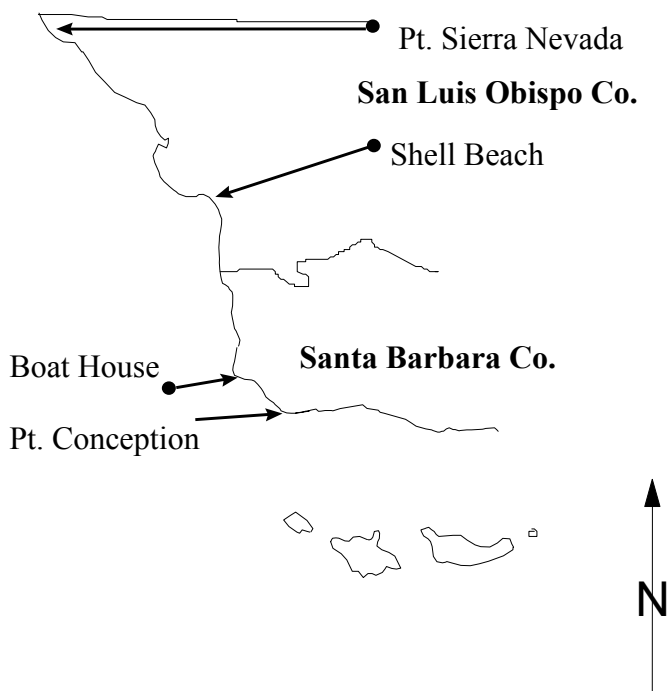


Figure 1. Location of study sites (Pt. Sierra Nevada, Shell Beach and Boat House) With Pt. Conception and the Channel Islands added for reference.

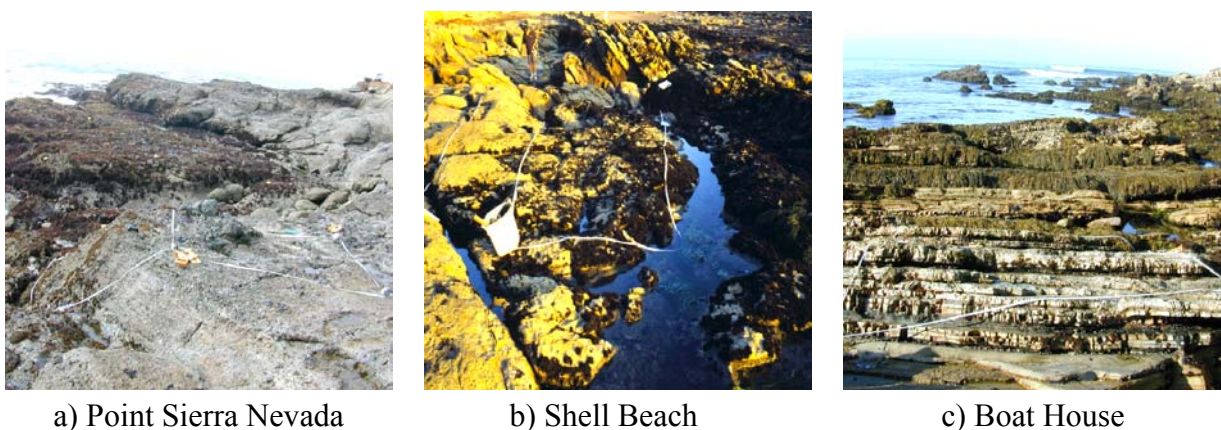


Figure 2. Study sites from North to South

Data from long-term monitoring program

Slides from the Shoreline Inventory Program were scored to assess where tar was accumulating and to estimate the percent cover of tar in permanent plots within different communities, across many sites and over the course of several years (Fig. 3). Following this, a subset of the slide data was used for the analysis (slides from; 7 biological communities, 6 sites and 6 years (two seasons (Fall and Spring) per year, totaling 12 seasons). This information was also useful for selecting which communities to assess and field study sites. Univariate and multivariate repeated measures ANOVAs were run to determine if site, season or community affected where tar accumulated and persisted.

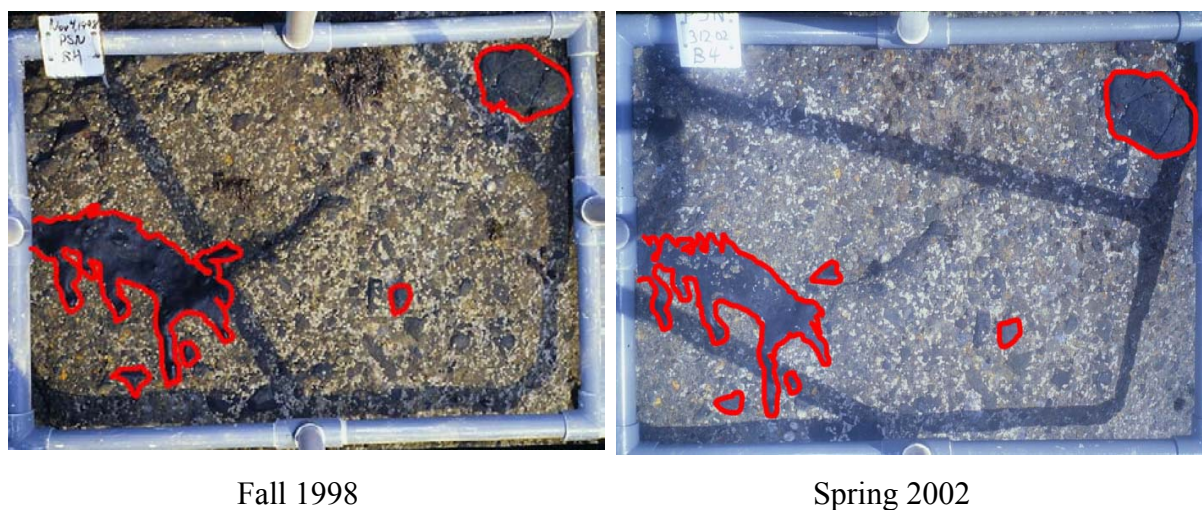


Figure 3. Slides from the Shoreline Inventory Program. Photo's are of Barnacle plot 4 at Point Sierra Nevada. Tar patches are outlined.

Visual Surveys

To further assess where tar was naturally accumulating, we performed thorough visual surveys in 4 intertidal zones: barnacle (primarily *Chthamalus*), *Endocladia* (a red alga), *Silvetia* (a brown, fucoid alga), and mussel zones in the fall of 1999 at Point Sierra Nevada, Shell Beach and Boat House. This also helped us select sites for our experiments assessing tar accumulation and persistence.

Permanent Plots

Based on the results from the slide data and our visual surveys we established permanent plots in the barnacle and *Endocladia* zones in the Fall of 1999 at Point Sierra Nevada, Shell Beach and Boat House to assess the accumulation and persistence of tar in different species zones. These plots were set up to provide a representative sample of tar accumulation and persistence in each zone at each site. Thus, the number of plots and the area sampled varied from site to site (2-3 plots per zone; area of individual plots between 5sq meters (Point Sierra Nevada and

Boat House) and 20sq meters (Shell Beach)). However, the number of plots per zone and the area sampled in each zone within a site were roughly the same (Fig. 4a). The permanent plots were sampled twice annually (Spring and Fall) to estimate the percent cover of tar in the different zones. [Although, permanent plots were not established in the *Silvetia* and mussel zones, we continued to do visual surveys for tar in these zones twice annually (Spring and Fall)]. Using a grid we were able to estimate the size of individual tar patches (Fig. 4b). These surveys allowed us to calculate the percent cover of tar in two different zones (barnacle and *Endocladia*), to determine the rate of accumulation in these zones and to do within and among site comparisons of tar accumulation and persistence. At each site, the number, size and relative freshness of tar patches per marked plot were recorded. Univariate and multivariate repeated measures ANOVAs were run to determine if there was an effect of site, time (season) or community on tar accumulation and persistence.



a) Permanent Plots

b) Sampling Method

Figure 4. a) shows an example of a permanent *Endocladia* plot (foreground) and a barnacle plot (background) at Point Sierra Nevada, b) shows how the plots are sampled to determine the percent tar cover.

Experimental substrate

Experiments were designed to measure variability in tar patch accumulation and persistence by removing the effect of substrate. We knew from our earlier work that tar accumulates and persists in the barnacle zone longer than any other zone. This may be due to a longer exposure to air (the tar has a chance to stick) or it may also result in part from the texture of barnacles. In contrast, tar does not accumulate and persist in the algal zones, which may be due to a shorter exposure period or it may also be biological in nature since many alga produce mucilage that may inhibit tar from sticking. To test these ideas we (1) made identical casts of barnacles with a urethane material that mimics the texture of barnacles (See, Appendix A) which allowed us to standardize the substrate and (2) placed sixty 10x10cm

barnacle casts in the intertidal at each of our three sites (from north to south: Point Sierra Nevada, Shell Beach and Boat House) in April 2000. At each site, we placed fifteen casts into each “zone” (the barnacle zone (control), *Endocladia*, *Silvetia* and mussel zones (Fig. 5a) for a total of 60 casts per site; 15 per zone). The casts were then checked monthly for 18 months (May 2000 to October 2001) for the presence or absence of tar (Fig. 5b). For greater resolution in October 2000 we began recording the presence of tar, the number of patches, the relative location of the tar on the cast and the diameter of individual tar patches. We only measured tar patches $\geq 2.0\text{mm}$. ANOVAs were run to determine if site, time (monthly) or community affected tar accumulation and persistence. Multivariate within subject tests could not be run because there were more temporal periods than replicates, hence the Greenhouse-Geisser Epsilon (GG) correction on Univariate stats are presented (Quinn and Keough 2002). Due to human interference, the barnacle cast experiments at the Shell Beach site were abandoned in October 2000.

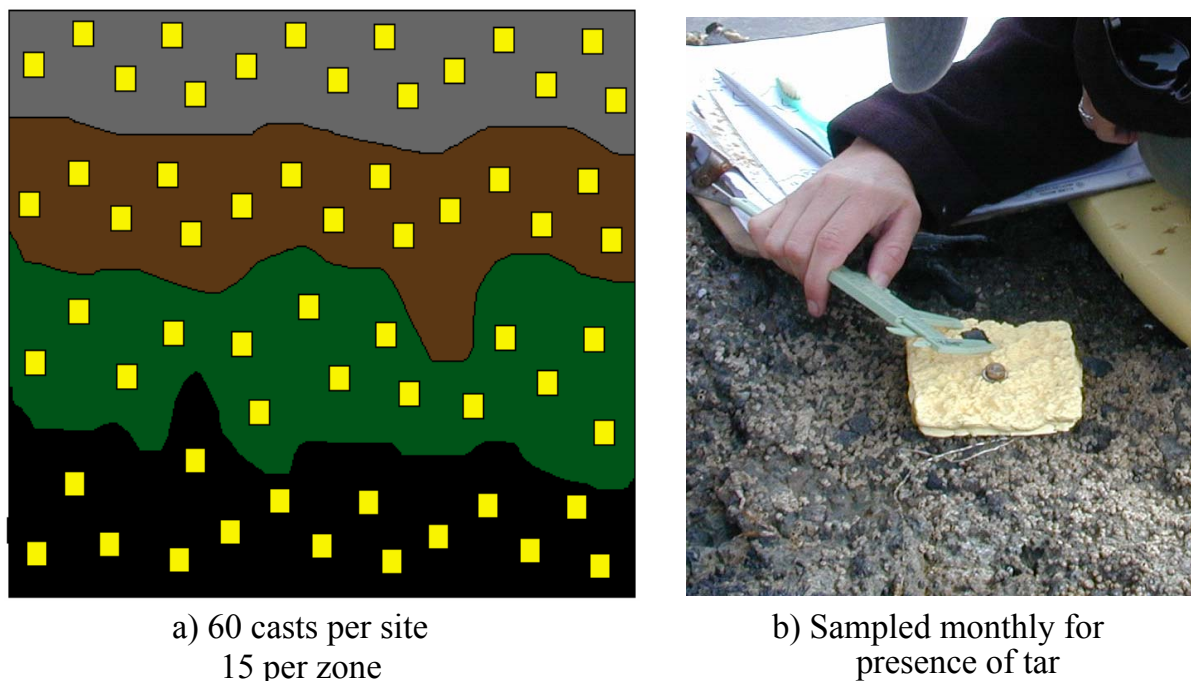


Figure 5. a) shows layout of casts in the field: grey represents barnacle zone, brown represents the *Endocladia* zone, green represents the *Silvetia* zone and black represents the mussel zone. b) photo shows how the casts were sampled.

Tidal Height

Because our visual surveys showed tar accumulating in higher zones, we tested the idea that variability in tar patch accumulation and persistence may be a function of tidal height and exposure. Using a tide height computer program we were able to create a model specific to the conditions near Boat House. Using 10-minute intervals of all outgoing tides during a one-year period (January 1, 2000 to December 31, 2000) we were able to calculate the proportion

of time the tide was at a given point on the shore. Using a laser leveler, in February 2001, we measured the tidal height of all of the barnacle casts and permanent plots at both Point Sierra Nevada and Boat House. We then compared the approximate vertical distributions of the four zones at Boat House, within which the barnacle casts were placed. ANOVAs were run to determine if tidal height affected where tar accumulated and persisted.

Temperature

In an attempt to determine the relationship between temperature and the accumulation and persistence of tar, in March 2001 we measured the surface temperature of all the casts, nearby rock and permanent plots in the barnacle, *Endocladia*, *Silvetia*, and mussel zones at both Point Sierra Nevada and Boat House (we used an Omega HH21 handheld microprocessor digital thermometer with a type T thermocouple model # TJFT72 special purpose transition joint thermocouple with a fine tip probe). Approximately 300 temperature measurements were taken at each site during single days while the casts were exposed to air (we followed the tide out and back in). We then compared the mean temperature of the cast vs. rock substrate for each community at both Point Sierra Nevada and Boat House. To insure that we were not making any false generalizations, we placed Tidbit temperature loggers at the mean tidal height for each zone (at both Point Sierra Nevada and Boat House) for a full month (April 24, 2001 to May 25, 2001). The Tidbit temperature loggers were fixed to a PVC plate and then bolted to the substrate. The Tidbit temperature loggers recorded the temperature at 10-minute intervals. Then, for our analysis we were able to go back and only look at the temperatures during times of exposure and daylight (during submersion and night time the temperature does not fluctuate between tidal heights). ANOVAs were run to determine if temperature was related to where tar accumulated and persisted.

Results

Data from long-term monitoring program

Results from the multivariate repeated measures analysis suggest that the interaction between community type and time (season) was significant (Table 1). The mean percent tar cover across all sites for each community over several seasons is presented graphically (Fig. 6). Note that *Pollicipes* plots are only sampled at one site (while the other species are sampled at multiple sites), resulting in a lower sample size and thus a higher mean. Additionally, there was no data available for the *Pollicipes* plots in Fall 99. Thus, with the exception of *Pollicipes*, the barnacle plots had the highest percent tar cover followed by *Endocladia*. In contrast, the *Silvetia* and mussel communities had very little tar cover (Fig. 6).

Table 1. Results from repeated measures ANOVA testing for the effect of site, community type, and season on the deposition of tar in permanent photo plots.

Univariate Analysis Between Subjects					
Source	SS	df	MS	F	P
Site	27.699	5	5.534	1.889	0.101
Community	143.618	6	23.936	8.171	0.000
Error	345.653	118	2.929		

Multivariate Repeated Measures Analysis (Pillai Trace)					
Test of:	Value	Hypoth. df	Error df	F	P
Season	0.294	10	109	4.532	0.000
Season x Site	0.365	50	565	0.891	0.687
Season x Community	0.919	60	684	2.061	0.000

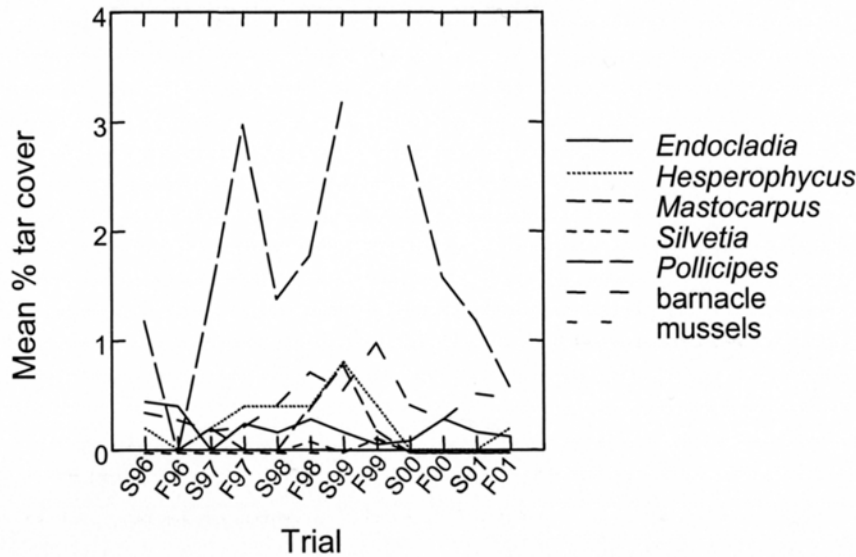


Figure 6. The mean percent tar cover from Spring 1996 to Fall 2001 for each community. Note that data for the *Pollicipes* plots were from one site, thus the mean is inflated due to lower sample size. No data were available for *Pollicipes* plots in the Fall of 1999.

Visual Surveys

In the fall of 1999 we performed visual surveys at Point Sierra Nevada, Shell Beach and Boat House. These surveys allowed us to qualitatively evaluate where tar appeared to accumulate within and among sites. Overall, we found more tar at both Point Sierra Nevada and Boat House and less tar at Shell Beach (personal observation). At all three sites, tar was found in the barnacle and *Endocladia* zones. During our visual surveys no tar was found in the *Silvetia* zone. Additionally at Point Sierra Nevada, four tar patches were found in the mussel zone (in contrast, no tar was found in the mussel zones at Shell Beach or Boat House). The four tar patches found at Point Sierra Nevada were marked and measured in late October 1999 and when we returned to this site in early December 1999 all four of the patches had disappeared. Because we were unable to find any tar in the *Silvetia* and mussel zones no permanent plots were established for these zones. However, during sample periods, we continued to search for tar in both the *Silvetia* and mussel zones.

Permanent Plots

In the fall of 1999, we established permanent plots at Point Sierra Nevada, Shell Beach and Boat House. These plots were surveyed in November 1999, May 2000, November 2000, May 2001 and November 2001 to: (1) assess the accumulation and persistence of tar within different species zones of different tidal heights and, (2) to determine which species would potentially be most susceptible to an oil spill. These surveys allowed us to calculate the

percent cover of tar in two different zones (barnacle and *Endocladia*), to determine the rate of accumulation in these zones and to do within and among site comparisons. Generally, we found more tar at Point Sierra Nevada and Boat House and less at Shell Beach (Fig. 7). The interaction between time (season) and community was significant (Table 2). We averaged the percent tar cover across all sites and found that over time, tar cover was higher in the *Endocladia* zone (Fig. 8). With the exception of the *Endocladia* zone at Boat House, we found the percent cover of tar to be fairly stable over time in both the barnacle and *Endocladia* zones (Fig. 7). At both Point Sierra Nevada and Shell Beach tar cover was consistently higher in the barnacle zone (primarily *Chthamalus spp.*) compared to the *Endocladia* zone (Fig. 7). This result was consistent with what we expected, based on the analyzed slides from our database and previous field observations. In contrast, at Boat House the percent tar cover was lower in the barnacle zone compared to the *Endocladia* zone (Fig. 7).

Table 2. Results from repeated measures ANOVA testing for the effect of site, community type, and season on the deposition of tar into permanent plots. Results of between subjects univariate analysis and multivariate analysis are presented.

Univariate Analysis Between Subjects					
Source	SS	df	MS	F	P
Site	47.096	2	23.548	0.957	0.424
Community	6.606	1	6.606	0.268	0.618
Site x Community	14.356	2	7.178	0.292	0.755
Error	196.892	8	24.612		

Multivariate repeated Measures Analysis (Pillai Trace)					
Test of:	Value	Hypoth. df	Error df	F	P
Season	0.750	4	5	3.756	0.090
Season x Site	1.073	8	12	1.736	0.187
Season x Community	0.843	4	5	6.719	0.030
Season x Community x Site	1.080	8	12	1.760	0.182

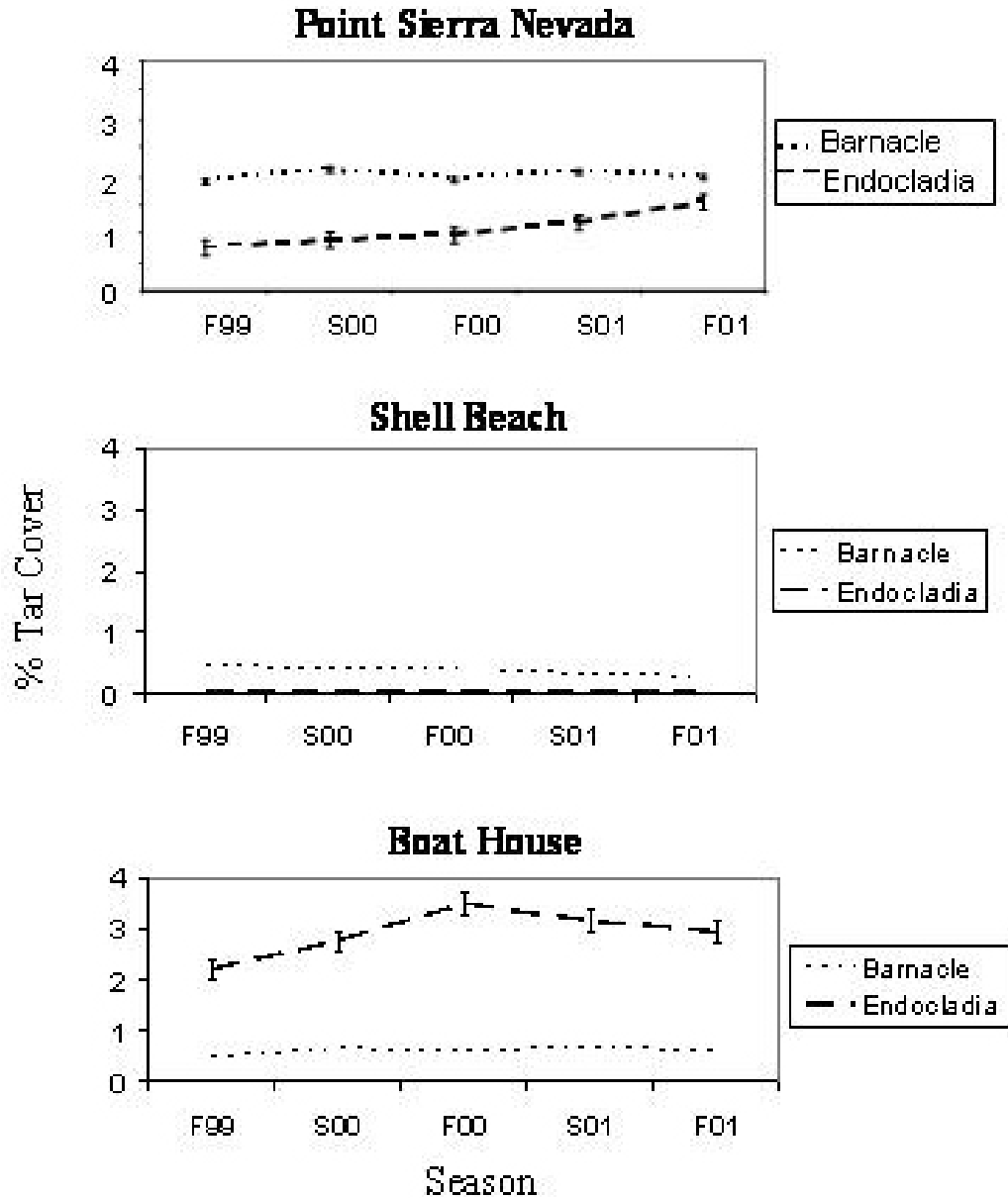


Figure 7. The percent tar cover (± 1 SE) in the barnacle and *Endocladia* plots at Point Sierra Nevada, Shell Beach, and Boat House from Fall 1999 through Fall 2001.

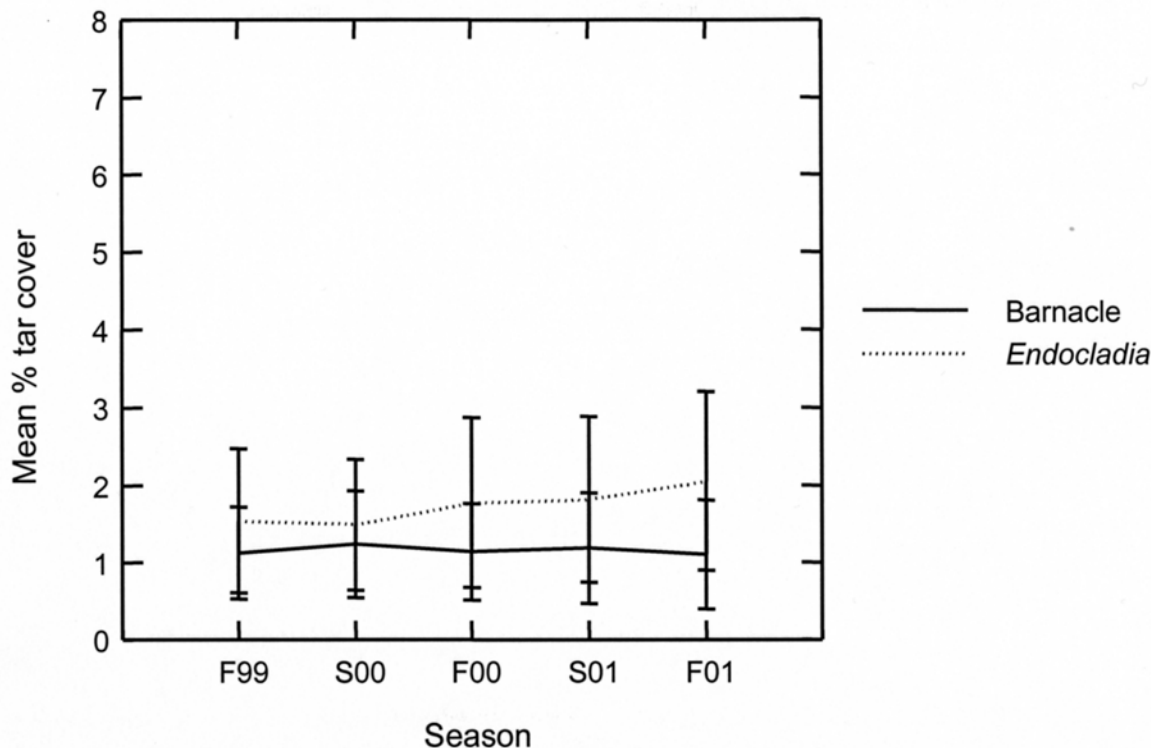


Figure 8. The mean % tar cover (\pm 1SE) by season (F=fall, S=Spring) for each community. Because site was not significant ($p=0.424$) the % tar cover was averaged across all sites. The error bars are large because the patterns are primarily driven by one plot at each site. For example, at Point Sierra Nevada, barnacle and *Endocladia* plots 3 have much more tar than plots 1 and 2. Additionally, at Boat House, *Endocladia* plot 1 has much more tar than plot 2.

Experimental Substrate

The barnacle casts that were put out at Point Sierra Nevada and Boat House in April 2000 were in the field for 18 months and were sampled monthly for the presence of tar (Fig. 9). While tar did not accumulate on the natural substrate in the *Silvetia* zone, it did accumulate on the standardized substrate in this zone. Additionally, there was little difference in the proportion of casts with tar in the barnacle zones compared to the casts in the *Silvetia* zone (Fig. 9). Results from repeated measures ANOVAs showed a strong temporal effect by site as well as by community on the deposition of tar (Table 3). Additionally, the interaction between site and community type also had a significant effect on the deposition of tar on casts (Table 3). To date, at Point Sierra Nevada tar accumulated on roughly 90% of the casts in the barnacle, *Endocladia* and *Silvetia* zones. Less than 7% of the casts in the mussel zone at Point Sierra Nevada had tar. At Boat House, tar accumulated primarily in the barnacle and *Silvetia* zone, 80% and 87% respectively. By contrast, only 53% of the casts in the *Endocladia* zone and 20% of the casts in the *Mytilus* zone (at Boat House) had tar (Fig. 9).

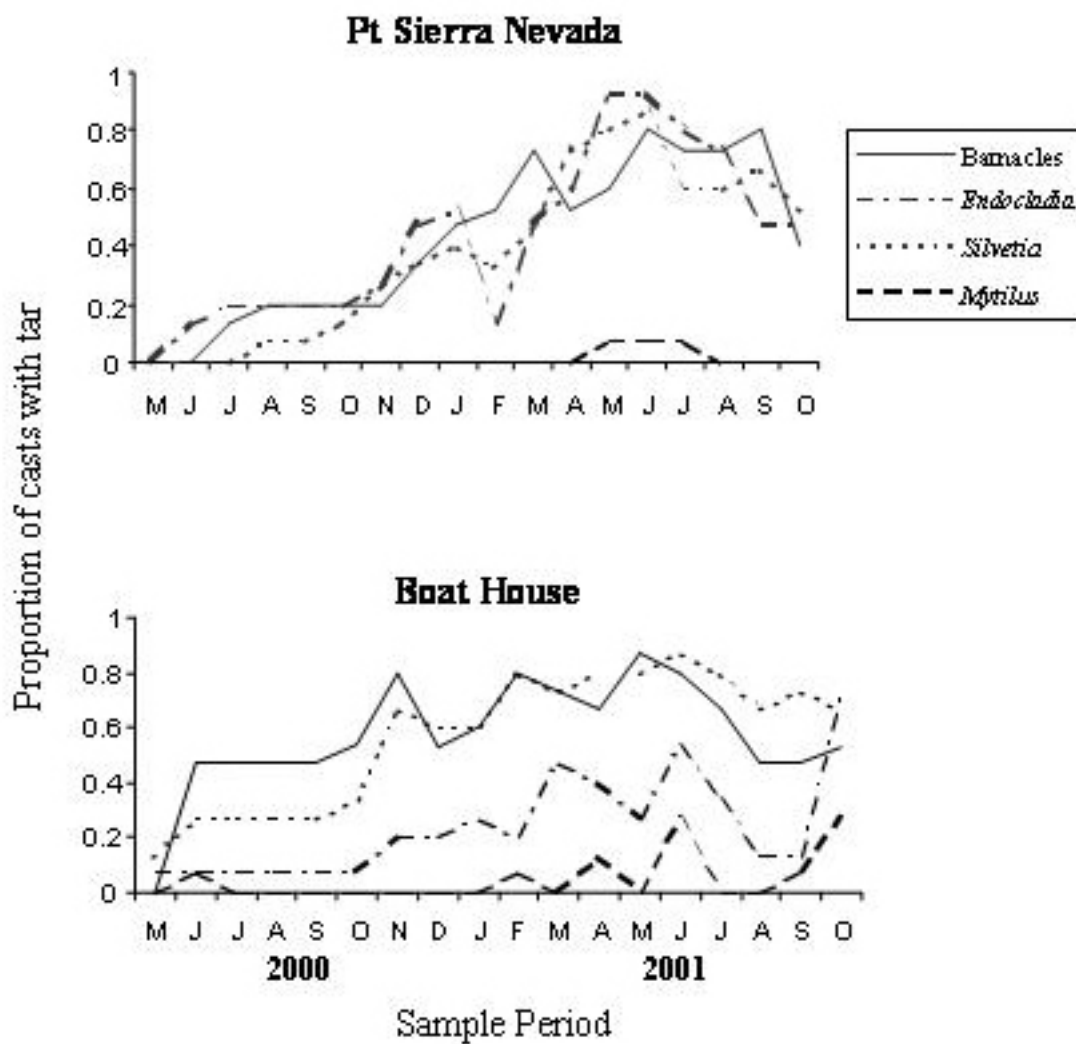


Figure 9. The proportion of casts with tar in four zones from May 2000 through October 2001.

Table 3. Effect of site, community type, and season on the deposition of tar on casts. Results shown are from repeated measures analysis where site and community were categorical, fixed variables. Multivariate within subject tests could not be run because there were more temporal periods than replicates; hence, GG correction on univariate stats are presented.

Between Subjects					
Source	SS	df	MS	F	P
Site	0.353	1	0.353	0.409	0.524
Community	57.026	3	19.009	22.012	0.000
Site x Community	9.298	3	3.099	3.589	0.017
Error	82.902	96	0.864		
Within Subjects					
Source	SS	df	MS	F	G-G
Season	56.115	17	3.301	29.713	0.000
Season x Site	4.739	17	0.279	2.509	0.008
Season x Community	20.832	51	0.408	3.677	0.000
Season x Site x Community	6.061	51	0.119	1.07	0.369
Error	181.303	1632	0.111		
Greenhouse-Geisser Epsilon:	0.5344				

Tidal Height

We tested the idea that variability in tar patch accumulation and persistence may be a function of tidal height and exposure. Our tidal model predicted that at Boat House, tar (which is transported in surface waters) should accumulate at tidal heights around 2.5-3.5 ft above MLLW: tidal heights where surface waters are most often in contact with the substrate (Fig. 10). Hence we predicted that tar should accumulate in the upper tidal zone. In February 2001, we measured the tidal height of all of the barnacle casts and permanent plots at both Point Sierra Nevada and Boat House. As expected, tidal heights varied as a function of site and community (Table 4). The substrate interaction was not included in the analysis because there was no difference in the tidal height between the casts and the adjacent rock. Overall, the mean tidal height for each community is higher at Point Sierra Nevada than Boat House (Fig. 11). Based on the tidal model and the mean tidal heights of each zone at Boat House, we expected that tar would accumulate in all four zones since the mean tidal height for each zone is within the 2.5-3.5 ft above MLLW range. We found no relationship between the mean vertical distributions of the four zones (at Boat House), within which the barnacle casts were placed to the accumulation of tar (Fig. 12).

Table 4. Results from ANOVA testing for the effect of tidal height as a function of community and site.

Analysis of Variance					
Source	SS	df	MS	F	P
Site	193.319	1	193.319	295.011	0.000
Community	61.625	3	20.542	31.347	0.000
Community x Site	19.755	3	6.585	10.049	0.000
Error	73.393	112	0.655		

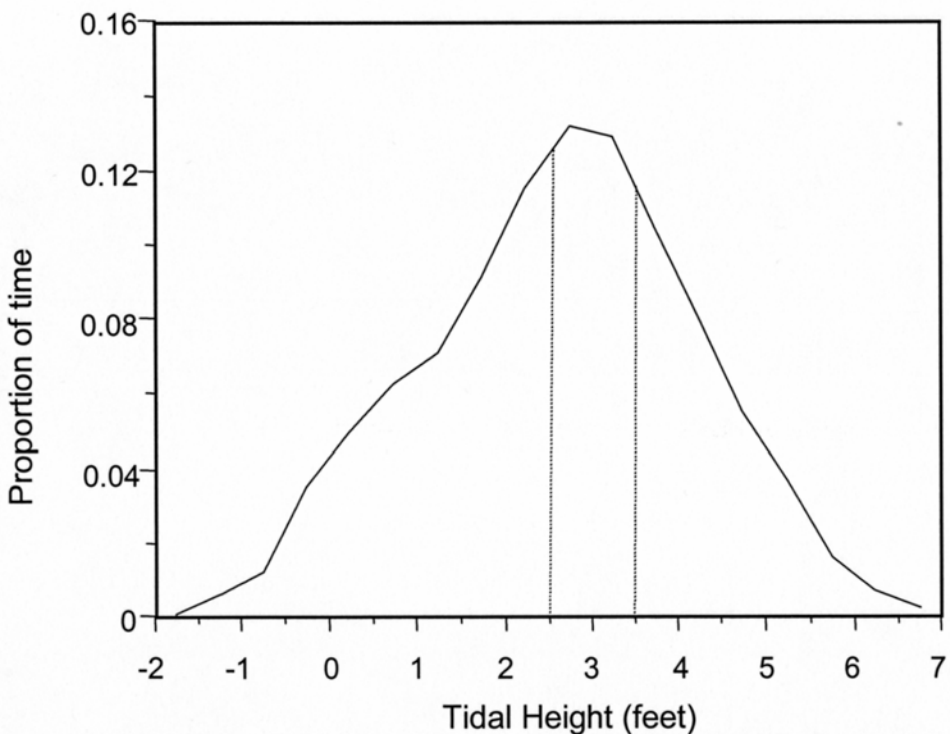


Figure 10. Proportion of time the surface waters were at a given tidal height on the shore. Model was based on tide data from Boat House taken at 10-minute intervals for 1 year (January 1, 2000 to December 31, 2000). Vertical lines represent the tidal range where tar should be deposited.

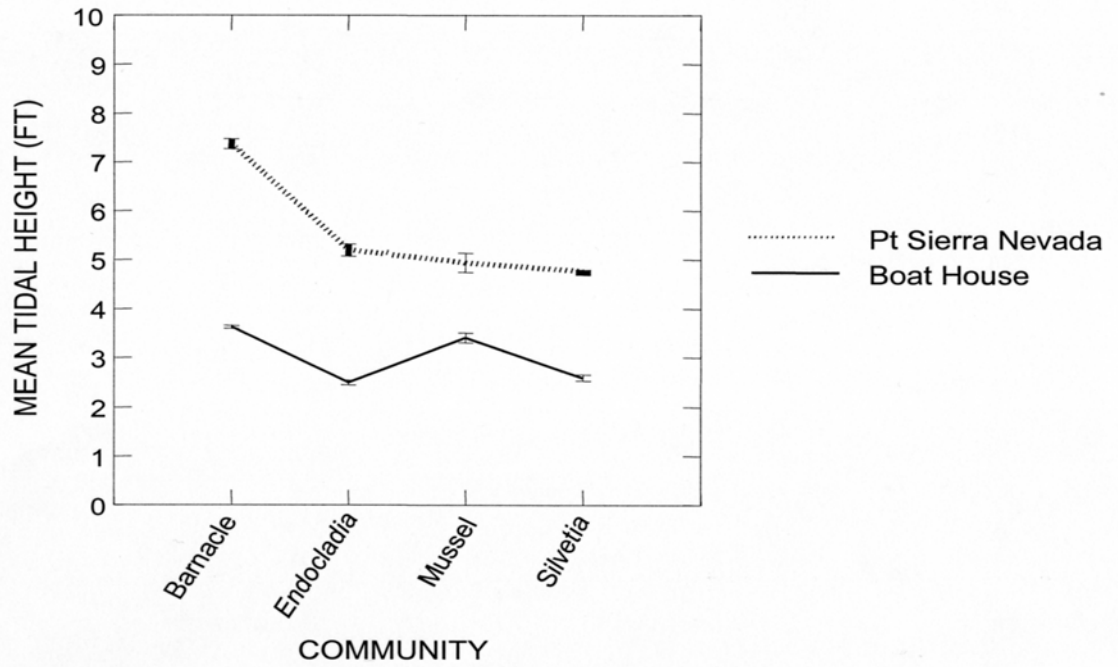


Figure 11. The mean tidal height (\pm 1 SE) of each community at Point Sierra Nevada and Boat House. The tidal height of all the casts and permanent plots in each zone were averaged.

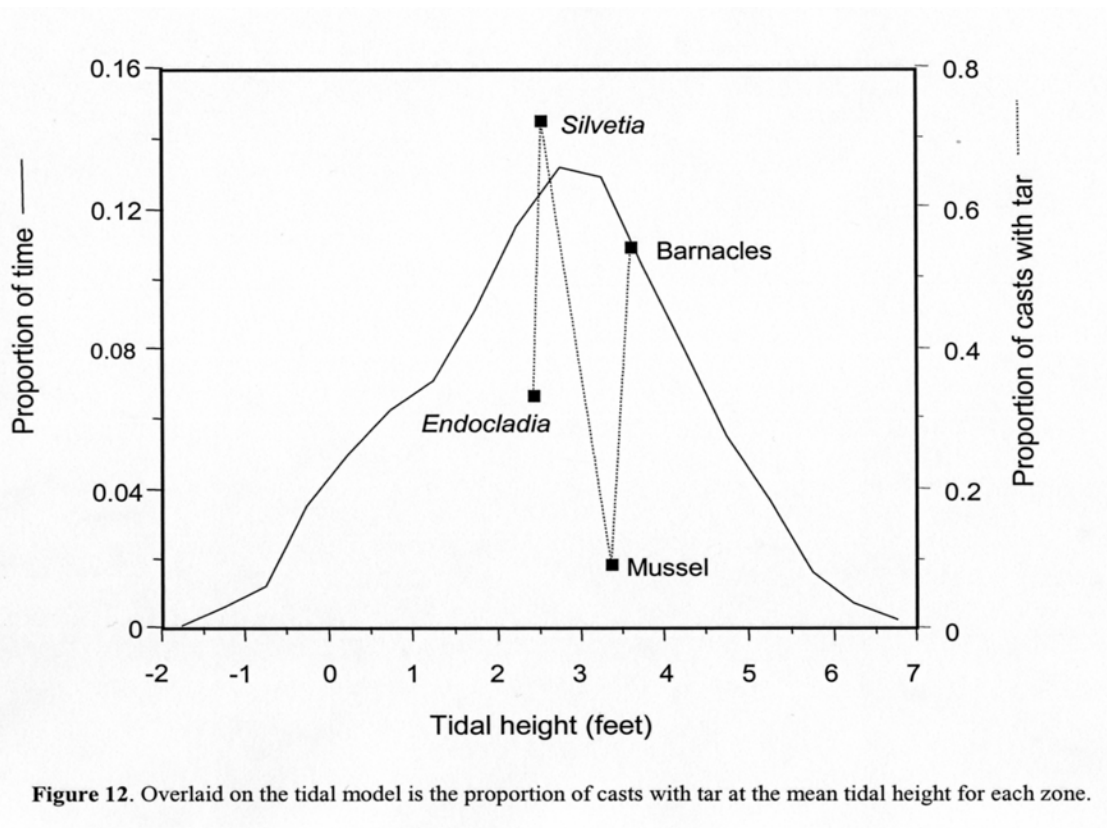


Figure 12. Overlaid on the tidal model is the proportion of casts with tar at the mean tidal height for each zone.

Temperature

The difference between the cast and rock temperatures at Point Sierra Nevada was not significant. However, there was a significant difference between the cast and rock temperatures at Boat House (Fig. 13). The results from the reduced model ANCOVAs showed that the interactions between community and site and between substrate and site were significant (Table 5). With the exception of the barnacle zone, temperatures at Boat House were warmer than Point Sierra Nevada (Fig. 14). Results from the Tidbit temperature loggers ANOVAs show significant interactions between community and site, time and site, and between time and community (Table 6). However, there was no significant correlation between tidal height and temperature. In contrast, these data also show that overall Point Sierra Nevada is warmer, with peak temperatures around 1pm (Fig. 15). Additionally, these data show that throughout the day regardless of site, that the barnacle zone is significantly warmer (Fig. 16).

Table 5. Results from reduced model ANCOVA testing for the effect of site, community type, substrate, and tidal height on temperature.

Analysis of Variance					
Source	SS	df	MS	F	P
Site	1.93996E+02	1	1.93996E+02	1.20508E+01	0.00055
Community	5.77370E+02	3	1.92457E+02	1.19552E+01	0.00000
Substrate	1.58892E+02	1	1.58892E+02	9.87024	0.00178
Tidal Height (ft)	2.72919	1	2.72919	0.16953	0.68071
Community x Site	8.41364E+02	3	2.80548E+02	1.74274E+01	0.00000
Substrate x Site	2.16872E+02	1	2.16872E+02	1.34719E+01	0.00027
Substrate x Community	4.75619E+01	3	1.58540E+02	0.98483	0.39964
Substrate x Community x Site	6.38997E+01	3	2.12999E+01	1.32313	0.26614
Error	7.63051E+03	474	1.60981E+01		

Table 6. Results from ANOVA testing for the effect of site, community type, and time on temperature.

Source	SS	df	MS	F	P
Site	135.235	1	135.235	3.916	0.048
Community	2179.861	3	726.620	21.042	0.000
Hour	31499.080	9	3499.898	101.355	0.000
Community x Site	1490.281	3	496.760	14.386	0.000
Hour x Site	1895.792	9	210.644	6.100	0.000
Hour x Community	1534.949	27	56.850	1.646	0.020
Hour x Community x Site	552.135	27	20.449	0.592	0.952
Error	64366.072	1864	34.531		

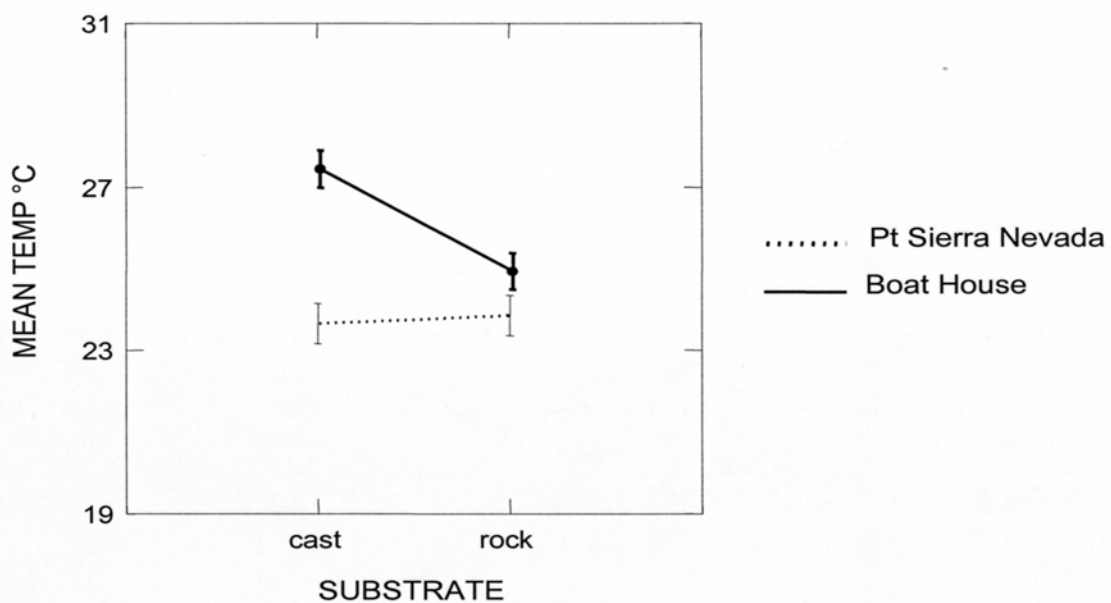


Figure 13. The mean temperature (± 1 SE) for each substrate type at Point Sierra Nevada and Boat House. Data were taken with a digital thermometer during the course of a single tide series.

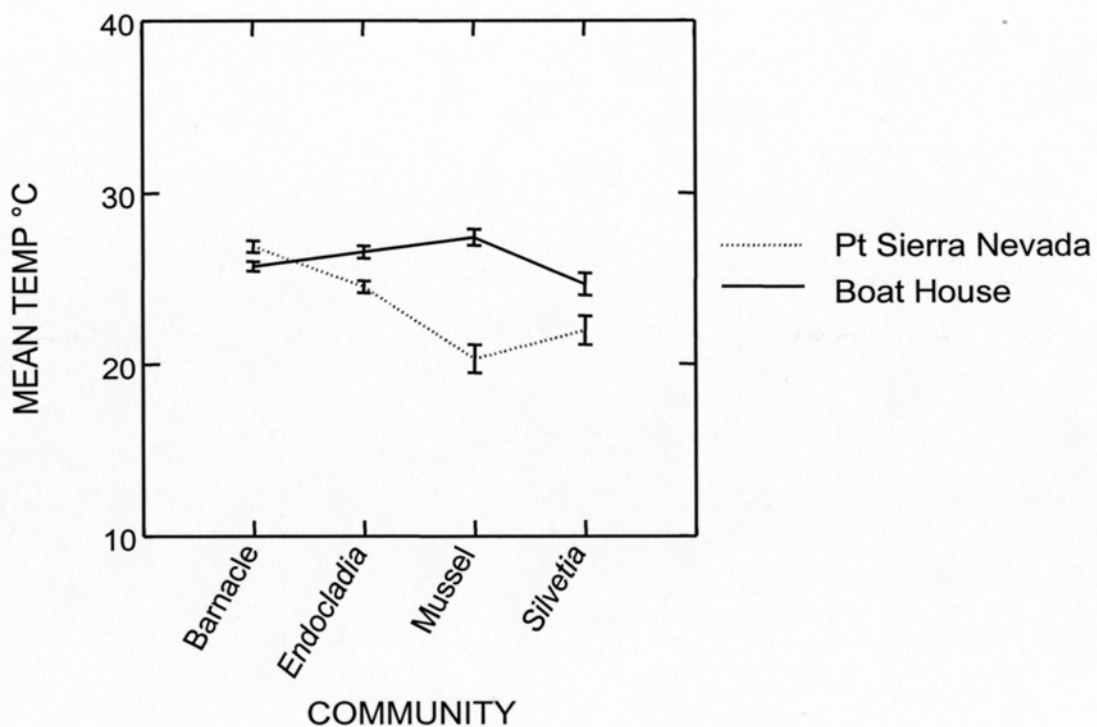


Figure 14. Mean temperature (± 1 SE) for each zone at Point Sierra Nevada and Boat House.

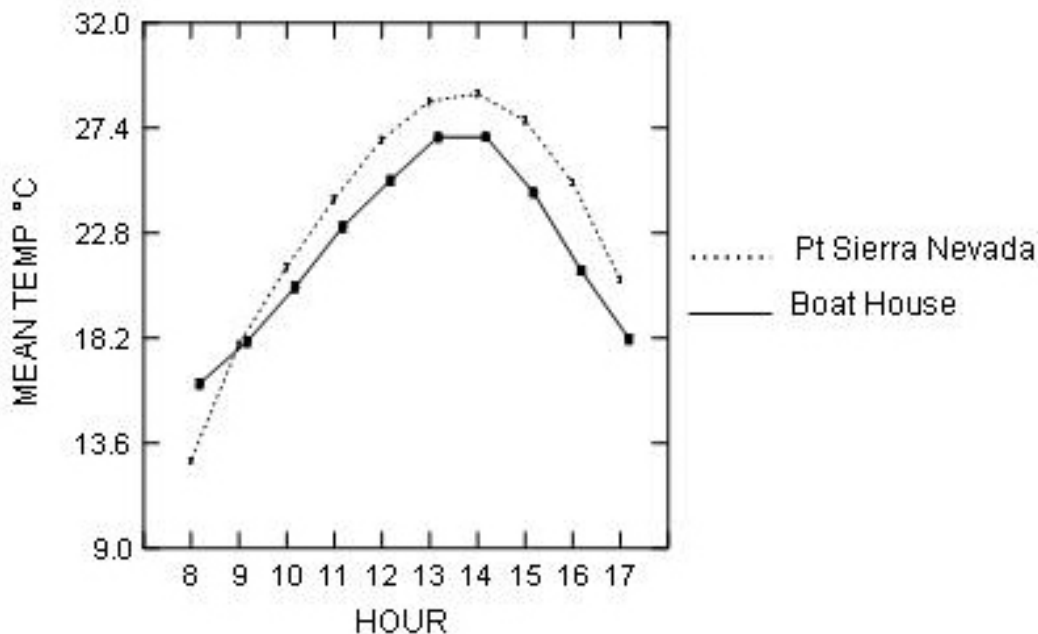


Figure 15. The mean temperature (± 1 SE) from 8am to 5pm at Point Sierra Nevada and Boat House. Data from the Tidbit temperature loggers were averaged for a one month period March 2001 to April 2001. Hour is shown in military time.

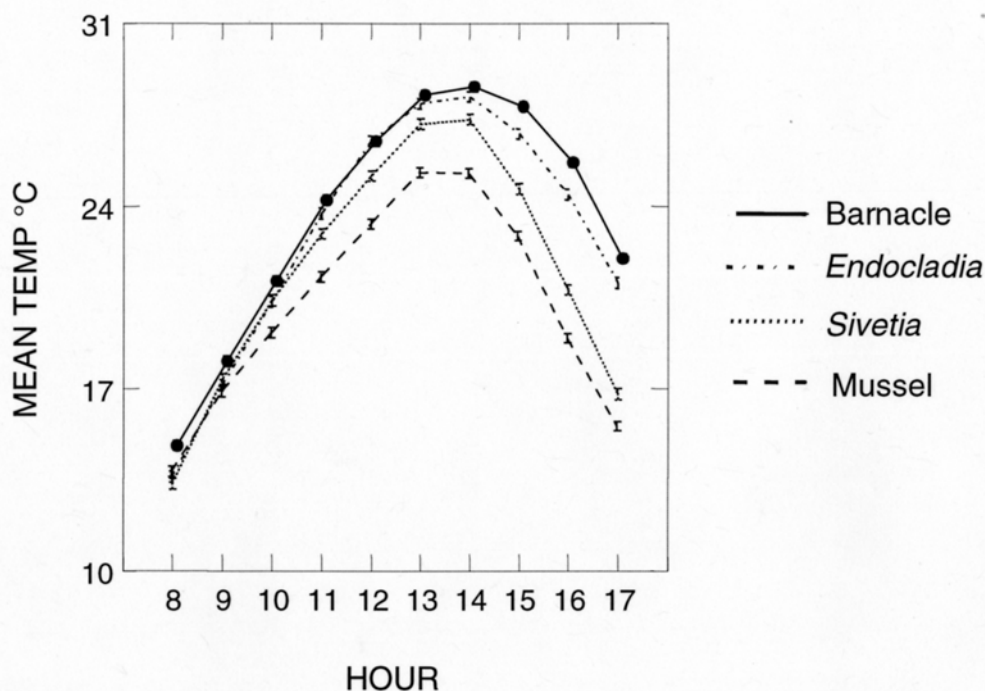


Figure 16. The mean temperature (± 1 SE) from 8am to 5pm for each community. Data from the Tidbit temperature loggers were averaged for a one month period March 2001 to April 2001. Hour is shown in military time.

Discussion

Tar accumulation and persistence varied among as well as within sites. Intertidal oil cover resulting from a spill is patchy in both space and time, resulting in variability in exposure duration, dosage, and weathering (Straughan 1982; Foster *et al.* 1988; Jackson *et al.* 1989; KLI 1992). Therefore there are variable effects on individual species in the community. Data from slides also show variability in tar accumulation and persistence among biological communities. Like oil, natural tar comes ashore in pulses and thus, not all communities are equally affected. Thus far, the slides from the Shoreline Inventory Program have been a valuable tool for accessing where tar is accumulating and persisting (at least for large tar patches). In the event of an oil spill the slide archive from the SIP will prove to be invaluable.

Results from the visual surveys also suggest tar does not persist long in the mussel zone. While, we have documented tar stuck to *Silvetia*, mussels and rock in the mussel zone, it does not reside long (observed less than two weeks). Since we sampled on a monthly basis (rather than more frequently) we do not have a true sense of the shorter periods of accumulation and persistence of tar in the mussel zone. In order to get to get a more accurate idea of accumulation and loss in this zone, we would need to sample more regularly during periods of low tides. In support of our observations, Straughan (1970, 1971) reported that at exposed sites oil was removed from the low intertidal zones by wave action within three weeks of the Platform A blowout in Santa Barbara. At both Point Sierra Nevada and Boat House the mussel zones are on benches with direct exposure to incoming waves.

Results from the permanent plots show that tar accumulates and persists in the barnacle and *Endocladia* zones. At Point Sierra Nevada and Shell Beach tar accumulated more in the barnacle zone. In contrast, at Boat House more tar accumulated in the *Endocladia* zone. This may be a result of the upward shift in species assemblages at this site, which at that point was unprecedented (Fig. 17). In 1999, when our permanent plots were initially set up, the *Endocladia* was growing on dead barnacles, by late 2001 the permanent plots in the *Endocladia* zone were reverting back to barnacle plots which indicates a shift in species zones. Additionally, it is important to note that not all tar that accumulated persisted. There was import and export of tar in these plots. However, once larger tar patches accumulate in the upper zones they persist for months to years (Nicholson and Cimberg 1970; Straughan 1970; Southward and Southward 1978). For example, in our study many of the tar patches that were found in October 1999 were still present in October 2001 with little change (personal observation). This result is also consistent with the slide data from the Shoreline Inventory Program (see Figure 2). The insight gained by determining where tar accumulated and persisted allowed us to predict which species would be most affected by an oil spill.

Results from the substrate experiments show that while tar is likely to be deposited in all 4 zones, it may not persist long in the mussel zone. Recall, that in our visual surveys very little tar was found in the mussel zone and no tar was found on rock beneath *Silvetia*, although on one occasion tar was found stuck to the fronds of *Silvetia*. This may support the idea that texture or biological processes are important (since casts are an abiotic mimic of the texture of barnacles). At Boat House, more tar accumulated on the casts (standardized substrate) in the barnacle and *Silvetia* zones than the *Endocladia* zone. This result was not expected based on

our permanent plot data at Boat House that showed that more tar accumulated in the *Endocladia* zone than the barnacle zone. Additionally, not only did tar accumulate on the casts in the *Silvetia* zone at each site, it also accumulated on casts in amounts nearly equal to that on casts in the barnacle zone. Further, not only did tar accumulate on the casts in the *Silvetia* zone, it also persisted. It appeared that, with the exception of the mussel zone, once tar accumulated on a standard surface it persisted. For example, 7% of the casts in the *Mytilus* zone at Boat House had tar in February 2001. Cast number 15 had the largest patch to date. It covered half of the plate and a portion of the surrounding mussel bed (390mm x 58.3mm). When sampled again in March 2001 the tar was not present. This was also the case in June 2000 when 7% of the casts in the *Mytilus* zone at Boat House had tar, but when they were sampled again in July 2000 the tar was absent. In support of our permanent plot and slide data, our cast data suggest that patches < 2mm degrade rapidly, while larger patches persist for many months. For example, *Silvetia* cast number 7 (at Boat House) had a tar patch that first appeared in May 2000 and was initially measured to be 14.7mm (diameter) and in October 2001 it was 13.7mm (diameter).



Spring 1993



Fall 1993



Fall 1995



Fall 1996

Figure 17. Slides from the Shoreline Inventory Program, showing the succession of *Endocladia* plot 1 (Spring 1993 to Fall 1996) at Boat House.

We found that, the permanent plots highest on the shore accumulated the most tar, regardless of site. For example, at Point Sierra Nevada barnacle plot 3 accumulated the most tar and it was also the plot highest on the shore, with a mean tidal height of 7.25ft above MLLW. This result was supported at Boat House where *Endocladia* plot 1 was highest on the shore, with a mean tidal height of 4.68ft above MLLW, it was also the plot that consistently had the highest percent tar cover. Additionally, when we looked at the average tidal heights of the plots at each site, the same pattern was found. At Point Sierra Nevada the average tidal height of the permanent; barnacle plots was 6.87ft above MLLW and the *Endocladia* plots was 5.96ft above MLLW. At Point Sierra Nevada the most tar accumulated in the barnacle zone. In contrast, at Boat House the average tidal height of the permanent plots in the barnacle zone was 3.69ft above MLLW and the average tidal height of the permanent *Endocladia* plots was 3.9ft. Once again, at Boat House tar accumulated primarily in the *Endocladia* zone. Jackson et al. (1989), found substantially more oil in the intertidal at tidal heights above MLW. This suggests that in the event of an oil spill, the zones most likely to be affected are those highest on the shore.

Our tidal height model for Boat House does not explain the pattern of tar accumulation and persistence on the casts. Based on the model we expected that tar would accumulate and persist approximately equally in all four zones, and while tar was deposited in all 4 zones, most tar accumulated on the casts in the barnacle and *Silvetia* zones. The model, didn't explain the pattern seen in the *Endocladia* or mussel zones. The casts were placed throughout the zones of each community. The *Endocladia* zone casts had a mean tidal height of 2.49ft slightly lower than the *Silvetia* zone casts, which had a mean tidal height of 2.59ft. However, the difference in tidal height between these two zones does not seem great enough to account for the differences in tar accumulation and persistence. Additionally, the *Silvetia* casts, which were lower on the shore accumulated tar at roughly the rate as the barnacle casts, which were higher on the shore. The differences seen between Point Sierra Nevada and Boat House may be due to the differences in the topography of the sites. Point Sierra Nevada has a much steeper vertical profile than Boat House, which is more up and down. Thus, other factors may be important.

If temperature was an important factor determining tar accumulation and persistence, it should accumulate in warmer zones, since warm tar is stickier. Additionally, we wanted to determine if there was a difference between the rock and cast temperature that could explain the pattern we saw in our cast experiments. Our results show that at Point Sierra Nevada, while there was a significant difference between the communities there was no difference between the rock and cast temperatures within communities. However, at Boat House we did find a difference between the rock and cast temperatures within the *Silvetia* zone. The rock temperature in this zone was several degrees cooler than the cast temperature. Recall, that in the *Silvetia* zone, tar was not found on the rock, but was found on the casts. It could be that in this zone the rock does not get warm enough for the tar to stick. It may also be that the *Silvetia* retains enough water and provides enough shade, which keeps the rock cooler. Another interesting result at Boat House was that there was no difference in the average cast temperature of the barnacle zone as compared to the average cast temperature of the *Silvetia* zone. Recall that these were the two zones that accumulated the most tar at Boat House, showing that temperature may be important at this site. Additionally, at Point Sierra Nevada, the similarity in rock and cast

temperatures suggest that the material of the cast is not significantly affecting the temperature in a way that would influence where tar accumulated and persisted in these zones. However, our study sites are characterized by different rock types: at Point Sierra Nevada its conglomerate and at Boat House the rock is Monterey formation. This may have an effect on where tar accumulates and persists since different rock types may have different thermal heat capacities (Raimondi 1988). It may also be that conglomerate behaves more similarly to the casts, with respect to temperature. However, we measured the substrate surface temperatures of the casts and rock at each site, on two different days during the same week. The air temperature at Boat House was between 15°C-23°C, while the air temperature at point Sierra Nevada was between 15°C-19°C. Overall, the difference was greater at Boat House (it was warmer) and this may have affected the results. Thus, data from the Tidbit temperature loggers may be more representative of the true patterns. The results from our Tidbit temperature loggers suggest that temperature could play an important role. Recall that the temperature loggers were placed at the mean tidal height of each zone and at each site where they recorded the temperature at 10-minute intervals for a one-month period. These data were then averaged over a month. The results ranked by zones from highest temperature to lowest temperature: barnacle, *Endocladia*, *Silvetia* and mussels.

Our findings, when coupled with natural history and previous studies, provide insight to potential impacts of oil spills along the central California coast. *Balanus glandula* and *Chthalamus fissus/dalli* (acorn barnacles) dominate upper intertidal zones and our study showed tar that accumulated in this zone persisted. Most studies show high mortality of barnacles following an oil spill (Foster *et al.* 1970; Neushul 1970; Nelson 1982; Southward 1982; Crothers 1983; Bokn 1993). For *Chthalamus*, there was an observed correlation between tidal height and mortality; at higher tidal levels there was higher mortality following the Santa Barbara oil spill (Cubit 1970). Further, higher mortality rates are seen in *Chthalamus* than *Balanus* (Nicholson and Cimberg 1970; Straughan 1970) due to smothering by oil. It is suggested that the taller height of *Balanus* may make it more resistant to oiling (Nicholson and Cimberg 1970). Acorn barnacles tend to recover quickly after an initial decrease in recruitment immediately following a spill (Bokn 1993, Ambrose *et al.* 1995). However, it appears that *Balanus* recovers more quickly (2 months) than *Chthalamus* (10 months) (Nicholson and Cimberg 1970; Straughan 1970), Nicholson and Cimberg (1970) suggested that the presence of a basal plate in *Balanus* (lacking in *Chthalamus*) may allow for earlier recolonization. Forde (2002) showed that recovery of acorn barnacles, which is dependent on recruitment, varies considerably due to individual variation in reproductive output. Thus, it appears that acorn barnacle recovery is dependent on the intensity of the spill, time of year (recruitment) as well as, the reproductive output of the source population (Forde 2002).

Endocladia is also found in the upper to mid intertidal zones and appears to be susceptible to tarring. In our study we found that once tar accumulated in this zone, it persisted. Additionally, there is evidence that *Endocladia* is susceptible to oiling and may take over 3 years to recover (KLI 1992).

While no studies have directly shown the effects of oiling on *Silvetia*, there is lots of evidence for other fucoids. For example, *Fucus gardneri* showed slow recovery after the *Exxon Valdez*

spill due to low recruitment, fewer reproductive adults and high desiccation rates (van Tamelen et al. 1997). *Hesperophycus harveyanus* also exhibited high mortality in the 1969 Santa Barbara oil spill (Straughan, 1971). Thus, we predict that recovery from a spill would be slow due to the high variability in reproduction and recruitment in intertidal fucoid species. During our study we occasionally found tar stuck to *Silvetia*, but it was not observed to stick long (less than 2 weeks). However, it seems plausible that in a large-scale spill, where *Silvetia* fronds were completely covered by oil, the increase in drag could lead to dislodgement.

Mytilus californianus is found in the mid- to low intertidal. Some studies have found no effect of oil spills on mussels, while others found evidence of mortality (Foster et al. 1970; Chan 1972; Southward 1982; Straughan 1982; Foster et al. 1988; Bokn et al. 1993). Recovery from disturbance varies depending on the size of the clearing and the number of mussels still present (KLI 1992; Ambrose et al. 1995).

It appears that for different species different mechanisms are important, likely due to differences in life history traits. For example, in the *Silvetia* zone, tar was found on the casts, but not on the rock. This provides evidence that biological factors are more important than physical factors in this zone. In this case, it is not the lack of input, but rather the lack of adherence. We know that *Silvetia* produces a mucilage that may act to inhibit tar from sticking. In addition, *Silvetia* also regularly sloughs cells, which may also lead to the lack of tar accumulation and persistence in this zone. In the mussel zone, we have documented (occasionally) tar sticking on the rock, mussels and casts. However, tar does not persist long in this zone. In the mussel zone, physical factors may be more important than biological factors. We think that as with *Silvetia*, it is not the lack of input, but rather the lack of adherence. Second, accumulation of tar in the mussel zone is lower both on casts and mussels – ruling out a biological process of removal (at least one related to mussels). Also the areas in which the mussel experiments were done are in open and exposed locations. While we did not directly test the effects of exposure we believe that it is an important factor. It is also possible that tar is present, but degrades very quickly in the mussel zone (causing our monthly samples to be too infrequent to detect the input). For the mussel zone, the mechanism is likely due to direct exposure to waves. It seems that in highly exposed areas, the waves regularly scour the tar off the rocks. Neushal (1970) suggested that the lower mortality rate of *Pollicipes polymerus* observed after the Santa Barbara spill may have resulted from “exposure to the cleansing action of the surf”.

For both the barnacle and the *Endocladia* zone, tar seems to accumulate and persist roughly the same on the cast and rock substrate. *Endocladia* neither sloughs cells or produces mucous. The barnacle and *Endocladia* zones are also less affected by wave intensity. For barnacles and *Endocladia* it may be that physical and biological factors are working in concert. It also appears that aside from the natural process of weathering, that barnacles and *Endocladia* have no mechanism for tar removal. Once tar accumulates in these zones, it persists.

Overall, our findings are valuable for predicting the impacts of small to moderate oil spills. Moreover, we believe that some of our results may be extendable to a large-scale oil spill. In the short-term, the upper zones barnacles and *Endocladia* are likely to be most affected; our

results show that once larger sized tar patches accumulate in these zones, they persist. However, results from other studies suggest that acorn barnacles are likely to be the species most able to recover quickly via recruitment. By contrast, mussels and fleshy algae are more resistant (for different reasons) to oiling but are much less likely to recover quickly if damaged via an oil spill.

Future Recommendations

There is a great need to investigate recruitment rates at a variety of sites to assess recovery by recruitment potential in order to more fully estimate effects of oiling – This work has just been partially funded by MMS. Further, post spill impact studies have concluded that surf grasses, limpets, gooseneck barnacles, sea star and abalone are all susceptible to oil spills (Cubit 1970; Foster *et al.* 1970; Neushal 1970; Nicholson and Cimberg 1970; Straughan 1970; Straughan 1971; Chan 1974; Southward and Southward 1978; Bokn *et al.* 1993; Ambrose *et al.* 1995; Dean *et al.* 1998). Therefore, we recommend that this project be followed with another that extended the survey and experimental work to other taxa including surf grass, *Lottia*, abalone and tide pool organisms (fish and others) that have not yet been evaluated for patterns and mechanisms of oil accumulation and persistence. In addition, we recommend increasing the spatial scale of the project to encompass sites all along the area of risk. We also recommend that the barnacle casts at Point Sierra Nevada and Boat House (4/zones, 15casts/zone, 60/site) be left in the field and completely covered with fresh tar (from a natural seep) and then sampled monthly to evaluate rates of weathering, recruitment, settlement and mortality. We recommend that these casts be followed until the tar completely degrades. It would also be interesting to determine the reproductive output (success) of those barnacles that settle on the tar compared to barnacles on unfouled adjacent rock. The information gained could then be coupled with this study to further our understanding.

Appendix A

Steps for making identical casts; 1) an impression of live barnacles in the intertidal was taken with a two part dental compound (often used for making molds of teeth) this became the master mold, 2) next using Alginate (another dental compound) 7 identical positives were made from the master, 3) next the positives were placed into square tupperware sandwich containers and then Synair's 2868 Por-A-Mold® was poured to cover them completely (see product guidelines for cure times), 4) once cured the positives were removed from the molds 5) the 7 identical molds now ready, were sprayed with Synlube 531 (a silicone release agent) and then dried with a hair dryer (to expedite the process), 6) finally the molds were filled with Synair's Mark II Por-A-Kast® (see product guidelines for cure times) and 7) identical casts were removed from the molds and the steps were repeated. It takes approximately 1 hour (steps 4-6) to make 7 casts.

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Literature Cited

- Ambrose, R.F., J.M. Engle, P.T. Raimondi, M. Wilson, J. Altstatt. 1995. Rocky intertidal and subtidal resources: Santa Barbara County mainland. Pacific OCS Region, Minerals Management Service, U.S. Department of Interior.
- Bokn, T.L., F.E. Moy, S.N. Murray. 1993. Long-term effects of the water-accomodated fraction (WAF) of diesel oil on rocky shore populations maintained in experimental mesocosms. *Botanica Marina* 36:313-319.
- Chan, G. 1972. The Effects of the San Francisco Oil Spill on Marine Life. College of Marin Kentfield, California. Part I.
- Chan, G. 1974. The Effects of the San Francisco Oil Spill on Marine Life. College of Marin Kentfield, California. Part II
- Crothers, J.H. 1983. Field experiments on the effects of crude oil and dispersant on common animals and plants of rocky sea shores. *Marine Environmental Research* 8:215-239.
- Cubit, J. 1970. The Effects of the 1969 Santa Barbara Oil Spill on Marine Intertidal Invertebrates. *Santa Barbara Oil Symposium* 131-136.
- Dean T.A., M.S. Stekoll, S.C. Jewett, R.O. Smith and J.E. Hose. 1998. Eelgrass (*Zostera marina* L.) in Prince William Sound, Alaska: Effects of the *Exxon Valdez* Oil Spill. *Marine Pollution Bulletin* 36 (3) 201-210.
- DeVogelaere, A.P. and M.S. Foster 1994. Damage and recovery in the intertidal *Fucus gardneri* assemblages following the 'Exxon Valdez' oil spill. *Mar. Ecol. Prog. Ser.* 106: 263-271.
- Forde, S.E. 2002. Modelling the effects of an oil spill on open populations of intertidal invertebrates. *Journal of Applied Ecology* 39, 595-604.
- Foster, M.S., A.C. Charters, M. Neushel, R. Zingmark. 1970. *Santa Barbara Oil Pollution, 1969*. Water Pollution Control Research Series. U.S. Department of the Interior.
- Foster, M.S., A.P. DeVogelaere, C. Harrold, J.S. Pearse, and A.B. Thum. 1988. Causes of spatial and temporal patterns in rocky intertidal communities of central and northern California. *Memoirs of the California Academy of Sciences* 9:1-45.
- Jackson, J.B.C., J.D. Cubit, B.D. Keller, V. Batista, K. Burns, H.M. Caffey, R.L. Caldwell, S.D. Garrity, C.D. Getter, C. Gonzalez, H.M. Guzman, K.W. Kauffman, A.H. Knap, S.C. Levings, M.J. Marshall, R. Steger, R.C. Thompson, E. Weil. 1989. Ecological effects of a major oil spill on Panamanian coastal marine communities. *Science* 243: 37-44.

- Kinetics Laboratories Inc. 1992. Study of recovery from an oil spill on the rocky intertidal coast of Washington. Pacific OCS Region, Minerals Management Service, U.S. Department of Interior.
- Morris, R.H., D.P. Abbott, and E.C. Haderlie. 1980. Intertidal invertebrates of California. Stanford University Press, Stanford, California.
- Nelson, W.G. 1982. Experimental studies of oil pollution on the rocky intertidal community of a Norwegian fjord. *J. Exp. Mar. Biol. Ecol.* 65: 121-138.
- Neushal, M. 1970. The Effects of Pollution on Populations of Intertidal and Subtidal Organisms in Southern California. Santa Barbara Oil Symposium 165-172.
- Nicholson, N.L. and R.L. Cimberg 1971. The Santa Barbara Oil Spills of 1969: a post-spill survey of the rocky intertidal. Biological and Oceanographical Survey of the Santa Barbara Channel Oil Spill 1969-1970. Ch 17 325-400.
- Paine, R.T., J.L. Ruesink, A. Sun, E.L. Soulanille, M.J. Wonham, C.D.G. Harley, D.R. Brumbaugh and D.L. Secord. 1996. Trouble on Oiled Waters: Lessons from the *Exxon Valdez* Oil Spill. *Annu. Rev. Ecol. Syst.* 27: 197-235.
- Quinn, G.P. and M. J. Keough 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press.
- Raimondi, P.T. 1988. Rock Type affects settlement, recruitment, and zonation of the barnacle *Chthamalus anisopoma* Pilsbury. *J. Exp. Mar. Biol. Ecol.* 123: 253-267.
- Raimondi, P.T., R.F. Ambrose, J.M. Engle, S.N. Murray and M. Wilson. 1999. Monitoring of Rocky Intertidal Resources Along the Central and Southern California Mainland. 3-Year Report for San Luis Obispo, Santa Barbara, and Orange Counties (Fall 1995-Spring 1998). Pacific OCS Region, Minerals Management Service, U.S. Department of Interior.
- Southward, A.J. 1982. An ecologist's view of the implications of the observed physiological and biochemical effects of petroleum compounds on marine organisms and ecosystems. *Phil. Trans. R. Soc. Lond. B* 297: 241-255.
- Southward, A.J. and E. C. Southward. 1978. Recolonization of Rocky Shores in Cornwall After Use of Toxic Dispersants to Clean Up the *Torrey Canyon* Spill. *J. Fish. Res. Board Can.* 35: 682-706.
- Straughan, D. 1970. Ecological effects of the Santa Barbara oil spill. Santa Barbara Oil Symposium 173-182.
- Straughan, D. 1971. What has been the effect of the spill on the ecology of the Santa Barbara Channel? Biological and Oceanographical survey of the Santa Barbara Channel oil spill 1969-1970 Ch 18. 401-426.

Straughan, D. 1982. Observations on the effects of natural oil seeps in the Coal Oil Point area. *Phil. Trans. R. Soc. Lond. B* 297: 269-283.

Van Tamelen, P.G., M.S. Stekoll and L. Deysher. 1997. Recovery processes of the brown alga *Fucus gardneri* following the 'Exxon Valdez' oil spill: settlement and recruitment. *Mar. Ecol. Prog. Ser.* 160: 265-277.

Modelling the effects of an oil spill on open populations of intertidal invertebrates

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Summary

1. Knowledge of the impact of oil spills on coastal communities, in California and elsewhere, is currently limited by a lack of long-term data, the inability to infer causality from monitoring studies, and the necessarily limited spatial and temporal scales of experimental studies.

2. This study therefore used a modelling approach to investigate the combined effects of different intensities of an oil spill and recruitment variation on a barnacle *Chthamalus fissus* population. The methodology and results are likely to apply to any similarly open marine populations with dispersive larval forms.

3. The model consisted of a source population comprising individuals that reproduced based on size and probability of mortality. Larvae from the source population entered a larval pool. A proportion of the larvae from the larval pool recruited to a focal population within the region.

4. The model was used to assess the effects on recruitment to the focal population of (i) the size structure of the source population, (ii) the intensity of oil spills in the source population, and (iii) recruitment intensity to the focal population.

5. Differences in the size structure of the source population had little effect on the reproductive output of the population relative to the intensity of the oil spill. Similarly, the intensity of the oil spill had a stronger influence on recruitment to the focal population than the size structure of the source population. Size structure of the source population was important, however, when evaluating the seasonal trajectory of the focal population.

6. Modelling provides a format in which questions about the effects of human impacts can be addressed that would be intractable using experiments. The results of this model suggest that recruitment variation, along with the processes underlying recruitment variation, are critical to predicting the effects of disturbance on open marine populations.

Key-words: barnacle, *Chthamalus fissus*, disturbance, individual-based model, life history, population model, rocky intertidal

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Introduction

As with most anthropogenic impacts, there is a need for well-designed research on the effects of oil spills on coastal marine habitats. The central and southern California coastline (USA) is susceptible to oil spills due to high amounts of tanker traffic and offshore oil drilling. Past experiments and monitoring programmes in this region have provided information and predictions regarding the effects of oil spills on

nearshore habitats in the region, particularly following the Santa Barbara oil spill in 1969 (Foster *et al.* 197). Further research assessing the consequences of spills for coastal marine habitats along the California coast, and world-wide, is needed because many of the conclusions that can be drawn from the results work to date are somewhat limited. This is due to lack of long-term data, the inability to infer causal relationships in monitoring studies, and the limited spatial and temporal scales of experimental studies as mentioned above.

If a nearshore community has not been monitored prior to a spill, recovery from the impact must be assessed by comparing an approximation of the

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abundance and distribution of resident species prior to the spill with similar data collected after the spill. It is often difficult to determine if species distributions and abundances were estimated accurately prior to the spill (Nelson 1982; Foster *et al.* 1988; Jackson *et al.* 1989; KLI 1992). As a result, studies conducted after an oil spill are often unable to provide accurate predictions of recovery from the disturbance caused by oil spills or conclusively demonstrate that the oil spill was responsible for any presumed change.

An alternative approach to monitoring programmes is to estimate the effects of an oil spill through extrapolation from controlled experimental field studies where oil is applied to small replicate plots (McGuinness 1990; Bokn, Moy & Murray 1993). Although such experimental studies of oil and gas impacts have been done, it is difficult to generalize from these results to any particular situation due to the spatial and temporal differences among oil spills (Foster *et al.* 1988; KLI 1992). Further, realistic results from experimental studies are often unattainable due to the constraints of designing an experiment that would encompass the spatial scale over which an oil spill occurs (Foster *et al.* 1988; Gilfillan *et al.* 1999).

Incorporating data from post-spill monitoring programmes and experiments into models strengthens the conclusions of impact assessments. Models can be parameterized to include 'pre-spill' data (e.g. measures of natural growth rates, reproductive output, size structure and population size). Data from actual oil spills can be used to parameterize variability in the amount of oil cover, the probability of mortality due to cover, etc. Further, the results of experiments done over small spatial or temporal scales can be incorporated into a model to address the effects of the disturbance over larger and more appropriate scales.

The acorn barnacle *Chthamalus fissus* (Darwin) was used as a model organism for this study. *Chthamalus fissus* is common in the high intertidal zone along the California coast and much is known about its life-history traits and population dynamics. Therefore, realistic biological parameters could be incorporated into the model. In general, *C. fissus* suffers high mortality following oil spills. However, oiling may also have sublethal effects, e.g. reduced growth and/or reproduction (Foster *et al.* 1970; Nelson 1982; Southward 1982; Crothers 1983; Bokn, Moy & Murray 1993). The recovery rate of acorn barnacle populations following oil spills depends on recruitment rates (Bokn, Moy & Murray 1993). *Chthamalus fissus* has life-history characteristics similar to many other intertidal invertebrates, so the predictions of the model can be applied to other open marine populations that are at risk of disturbance due to oil spills.

Individual variation in reproductive output was incorporated into a population model using a dynamic state variable model (Mangel & Clark 1988; Mangel & Ludwig 1992; Clark & Mangel 2000) in order to address three questions. First, given that individuals

within a population show considerable variation in reproductive output (Stearns 1992), what is the effect of this variation, conditional on size and the probability of mortality, on a population comprising different-sized individuals? Secondly, does the interaction between variation in reproductive output and subsequent recruitment affect population dynamics? Finally, how are these dynamics influenced by variation in recruitment, combined with different intensities of oil spills? The results of the model were also used to make general predictions regarding the effects of varying intensities of oil spills on intertidal and subtidal organisms with open population dynamics.

STUDY SYSTEM AND LIFE HISTORY OF *CHTHAMALUS FISSUS*

Chthamalus fissus occurs in the upper rocky intertidal zone along the coast of California. The life history of *C. fissus* consists of a sessile adult phase and a planktonic larval phase. Adult *C. fissus* live for about 2 years and are reproductive within the first year (Wetthey 1984). *Chthamalus fissus* is internally fertilized and an internal brooder. Therefore, the number of nauplii (the initial larval stage of barnacles) is correlated with adult size, measured as rostrcranial aperture (Morris, Abbot & Haderlie 1980; Wetthey 1984). *Chthamalus fissus* has up to 16 broods per individual per year, primarily from spring to autumn (Morris, Abbot & Haderlie 1980). Two-hundred to 3000 nauplii are released per brood (Morris, Abbot & Haderlie 1980). Barnacle larvae spend 4–6 weeks in the plankton before settling into the adult habitat, and settlement peaks in the spring.

AN OVERVIEW OF THE MODEL

The model progressed in two stages. First, it was necessary to identify the resource allocation strategy that would be predicted under natural disturbance and mortality schedules. This was done by calculating reproductive output and growth as a function of time and *C. fissus* size, given a baseline probability of mortality. Secondly, these results were incorporated into a population model by quantifying reproductive output of size-structured source populations to the larval pool, under different oil spill intensities (Fig. 1). A proportion of the larval pool recruited to a focal population elsewhere on the coast.

Methods

INDIVIDUAL REPRODUCTIVE OUTPUT

The state variables

Consider a sessile invertebrate characterized by a life-history trade-off between growth and reproduction. At a given point in time (t), an individual can either grow or reproduce under a certain probability of mortality

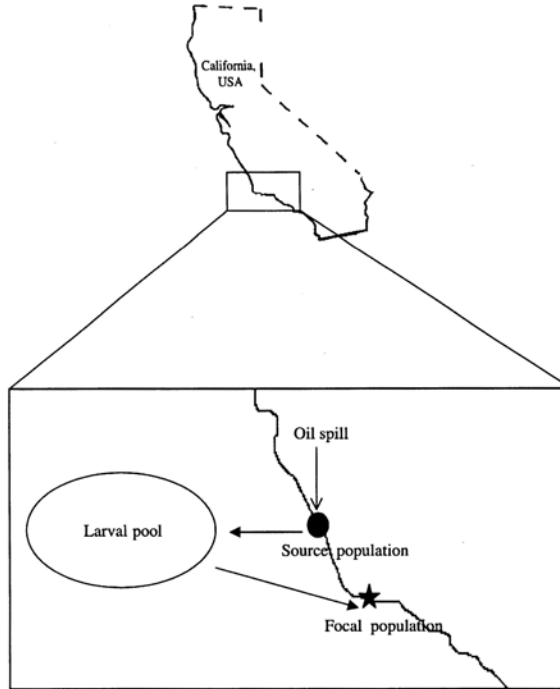


Fig. 1. The conceptual framework behind the model. The source population consists of 3000 individuals that each vary in their reproductive output. Oil spills of different intensities kill a certain percentage of the source population. Reproductive output from the source population, summed across all individuals, enters a larval pool. A proportion of the larvae from this larval pool recruits to a focal population elsewhere on the coast. The model assumes that benthic and pelagic processes are coupled on a regional scale, thus reproductive output from the source population is linked to the dynamics of the focal population through a regional larval pool.

due to natural causes, such as predation, competition and abiotic factors.

The state of the organism is defined by its size, here measured by the length of the rostrocranial aperture, $L(t)$, measured in millimetres. Time is divided into 104 weeks to represent the life span of *C. fissus* (2 years): the first year is represented by $t = 1-52$, and the second year by $t = 53-104$. At the end of each year (late autumn through early winter), individuals grew and did not reproduce, thereby incorporating seasonality into reproduction (Hines 1978).

Changes in the state variables

The state variable, length ($L(t)$), changes over time as follows:

$$L(t + 1) = L(t) + (k)(L_{\infty} - L(t))^q \quad \text{eqn 1}$$

where L_{∞} is the maximum length of *C. fissus*, and k and q are parameters in the equation used to fit an asymptotic curve that represents a realistic maximum growth function, assuming an individual grows rather than reproduces at each time step (Table 1 and Fig. 2).

A positive correlation between length and fecundity was assumed (Wethey 1984; Stearns 1992), such that if an individual reproduces (i.e. no growth) at a given time

step, reproductive output ($R(L)$) depends on length as defined by:

$$R(L(t)) = \beta(L(t)^3 - 1) \quad \text{eqn 2}$$

where β is a coefficient that converts rostrocranial aperture length into number of larvae as a function of test volume (Table 1).

Characterizing the trade-off between growth and reproduction

At each time step, there is a trade-off between present and future reproduction. On the one hand, the organism can continue to grow without reproducing but risks dying prior to reproduction, although, if it continues to grow, its future reproductive output should be greater. On the other hand, the organism can reproduce in the current time step, in which case it does not grow, possibly resulting in lower lifetime reproductive output but avoiding the potential loss of reproductive output in the future due to mortality.

Let $F(L, t)$ = the individual's maximum expected reproductive success (= value), at length L , from period t to T , where T is the maximum lifetime of an individual (2 years) eqn 3

Table 1. Parameters and values used in the model

Symbol	Value	Description
T	2 years	The maximum time that includes two reproductive periods in the life span of a barnacle
t		The current time, where $t < T$, in weeks
$L(t)$		The state variable (size in mm) at time t
L	11 mm	The maximum size (rostrcranial aperture length) of an individual barnacle
k	0.05	Parameter in growth equation
q	1.5	Parameter in growth equation
l		Size at time t in mm
$R(l)$		Reproduction at size l (number of larvae)
u	0.077	Mortality rate per week
p	0.074	The probability of mortality in 1 week, calculated as $1 - e^{-u}$
β	0.5 larvae mm ⁻³	Reproduction coefficient converting size to number of larvae
N_0	3000	The maximum number of individuals in the focal population
ϕ		Proportion of the larval pool recruiting to the focal population

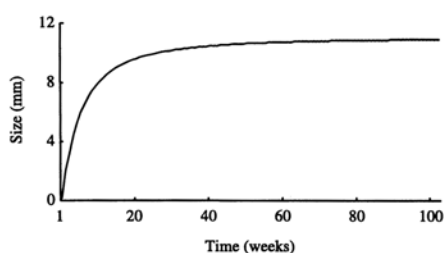


Fig. 2. The growth curve for an individual *C. fissus* over time, based on the equation: $L(t + 1) = L + (k)(L_{\infty} - L)q$, where l is the size at time t and k and q are parameters used to fit an asymptotic curve.

At the last time step ($t = 104$), maximum expected reproductive success ($F(L, T)$) is equivalent to reproductive output dictated by the individual's size $R(L(t))$.

The 'value' of growing at time t is:

$$F_{\text{grow}}(L, t) = (1 - p)F(L(t + 1), t + 1) \quad \text{eqn 4}$$

where p equals the probability of mortality (Table 1), based on survivorship data from Grantham (1997).

The 'value' of reproducing is:

$$F_{\text{reproduce}}(L, t) = R(L(t)) + (1 - p)F(L(t + 1), t + 1) \quad \text{eqn 5}$$

The maximum fecundity, at a given length (L), and time (t), is defined as the maximum 'value' given either growth or reproduction:

$$F(L, t) = \max(F_{\text{grow}}, F_{\text{reproduce}}) \quad \text{eqn 6}$$

A backward iteration of the model predicted the optimal behaviour for an individual of a given length at each time step under probability of mortality due to natural causes such as predation, competition and abiotic factors. $F(L, t)$ was calculated by working backwards in time from $t = T$. $F(L, T)$ is equal to the

reproductive output dictated by the individual's size at the last time step. $F(L, T - 1)$ was calculated for each value of L , using $F(L, T)$. This also gave the maximum value of growth or reproduction for each L . The procedure was repeated for $F(L, T - 2)$ using the values of $F(L, T - 1)$ calculated in the previous step. The same method was used for each time step ($T - 1, T - 2, T - 3$, etc.). For a given time step, an individual can either grow or reproduce.

The threshold length for reproduction indicated the optimal behaviour for a *C. fissus* at each length/time combination. The boundary on which the value of growing equals the value of reproducing dictated the threshold length for reproduction (Fig. 3). If the state of the individual at a given time was below the boundary, the optimal behaviour was to continue to grow, whereas if the state was above the boundary, lifetime reproductive output was greater if the individual reproduced. Again, this shows the optimal behaviour (i.e. to grow until a certain size and then reproduce), but an individual could reproduce in one time step and continue to grow in future time steps.

As time increased, the optimal size at reproduction decreased. In other words, maximum lifetime reproductive output for an 8-mm individual at 20 weeks would be achieved by continuing to grow and then reproducing at a larger size, whereas at about 80 weeks it would be achieved by reproducing at the current time step. These results were incorporated into the population model using a forward iteration of individual *C. fissus* behaviour based on different sizes at $t = 1$, which allowed for variation in reproductive output from the source population.

THE POPULATION MODEL

Individual differences in reproductive output were incorporated into an individual-based population model to investigate if these differences influenced the total reproductive output of the source population. The source population was defined as 3000 individuals. The reproductive output of the i th individual was

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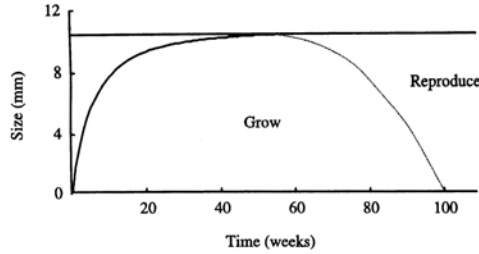


Fig. 3. The threshold length for reproduction vs. time, assuming the maximum growth rate. Values for growth and reproduction are biologically meaningless to the left of the maximum growth rate curve (i.e. an individual cannot be less than 0.2 mm at $t = 1$). The optimal behaviour for an individual is to grow until it reaches the threshold length for a given time (dashed line) and then to reproduce. See text for explanation.

determined by its size at time t , $L_i(t)$, and whether it reproduces or not. Size structures of natural *C. fissus* populations often vary spatially and/or temporally, depending on a variety of factors such as food availability, disturbance and recruitment rates (Roughgarden, Iwasa & Baxter 1985). Therefore, the size structure of

the source population was varied to investigate if there were differences in the total reproductive output of populations characterized by different size structures. Thus, in each iteration of the model, the population consisted of different proportions of individuals in each size class, and each of these individuals either grew or reproduced at each time step, based on the maximum fecundity at a given length and time, as calculated by equation 6.

At $t = 1$ the source population was dominated by small, intermediate or large individuals (Fig. 4). The size frequency distribution of the 3000 individuals consisted of a recruit class plus a normal distribution of adults, which was calculated using the Box–Muller algorithm (with a mean of 5 mm for the small size structure, 6 mm for the intermediate size structure and 7 mm for a large size structure, and a variance of 1 mm; Press *et al.* 1986). As mentioned above, because the size structure of *C. fissus* populations can depend on recruitment rates (Roughgarden, Iwasa & Baxter 1985), the number of recruits in each population structure was also varied. The small size structure consisted of 1000 recruits, the intermediate size structure consisted of

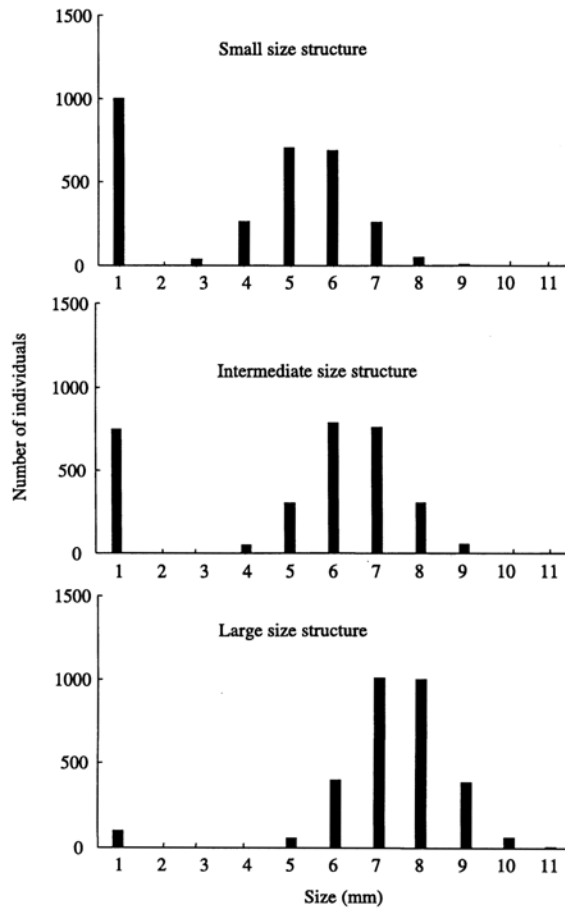


Fig. 4. The size structures of the source population. The source population is dominated by small, intermediate or large individuals (small: mean = 5 mm, 1000 recruits; intermediate: mean = 6 mm, 750 recruits; large: mean = 7 mm, 100 recruits).

750 recruits, and the large size structure consisted of 100 recruits. Thus, for each iteration of the model, the size structure of the source population was dominated by *C. fissus* of different sizes. This cohort of individuals was followed over the 2-year iteration of the model. The size structure of the source cohort changed over time due to growth and mortality, and therefore reproductive output changed over time. This model construction allowed the investigation of whether differences in size-based reproductive output at the individual level resulted in differences in the total reproductive output of the source population.

Theory and empirical work suggest that populations with obligate dispersive stages are defined as open on a small scale (i.e. metres to kilometres); larval supply is independent of local population and community dynamics (Gaines & Lafferty 1995; Connolly & Roughgarden 1999). In contrast, at a regional scale (tens to hundreds of kilometres), production of larvae is a major determinant of recruitment levels (Hughes et al. 2000). Thus, at larger scales, population sizes are determined in part by adult stock sizes, which are affected by benthic interactions such as competition, predation and disturbance (Connolly & Roughgarden 1999). In this model, the focal population is open; recruitment is not a direct function of local larval production. At a regional scale, benthic and pelagic processes are coupled. Reproductive output from the source population is linked to the dynamics of the focal population through a regional 'larval pool'.

Constructing the larval pool

Total reproductive output ($L_p(t)$) that enters the larval pool in the water column, is the sum of the reproductive output of the 3000 individuals in the source population:

$$L_p(t) = \sum \delta(i, t) \quad \text{eqn 7}$$

where $\delta(i, t)$ is the reproductive output of the i th individual at time t . Reproduction for each individual was calculated based on equation 5. Total reproductive output of the source population was then calculated for each size structure.

Recruitment and population dynamics

Recruitment at time t is equal to a proportion of the larval pool:

$$R(t) = \phi(L_p(t)) \quad \text{eqn 8}$$

By varying ϕ , the proportion of larval recruitment from the water column into the focal population was varied; thus ϕ accounts for various pre-recruitment factors that influence the proportion of larvae recruiting to the focal population (e.g. larval mortality in the plankton, the influence of current patterns, etc.).

The population size at time $t + 1$ depends on the population size at time t , and recruitment at time t :

$$N(t + 1) = e^{-\mu} N(t) + \min\{R(t); N_o - N(t)\} \quad \text{eqn 9}$$

N_o is the maximum number of adults in the focal population and μ is the mortality rate (Table 1). Therefore, $N_o - N(t)$ is a proxy for the amount of free space available for new recruits (Gaines & Roughgarden 1985; Possingham & Roughgarden 1990; Connolly & Roughgarden 1999).

The number of individuals killed by a disturbance, such as an oil spill, can be variable. For the purposes of this model, it was assumed that the focal population consisted of 10 individuals at $t = 1$. Thus, the population model predicts the growth trajectory of the focal population over 2 years (the same time span used when modelling individual variation in reproductive output), starting with only a few individuals. Oil spills of varying intensities (10% and 70% of the source population killed) were then incorporated into the model. Thus, the overall structure of the model consisted of three different size structures of the source population (small, intermediate and large), three different oil spill intensities in the source population (no spill, 10% killed and 70% killed) and three different recruitment intensities (low, intermediate and high). All possible combinations of these factors were iterated to assess (i) how differences in size structure affect the reproductive output of the source population; (ii) how different intensities of an oil spill interact with variation in size structure to affect reproductive output from the source population; and (iii) how the interaction between different oil spill intensities and recruitment variation influenced the dynamics of the focal population.

Results

REPRODUCTIVE OUTPUT OF THE SOURCE POPULATION

Differences in the size structure of the source population resulted in small differences in the cumulative reproductive output of the source population (Fig. 5), which was due to individual variation in the timing and magnitude of reproductive output (Fig. 3). For no spill and 10% killed, the cumulative reproductive output of the source population was about 10% greater when the source population was dominated by large individuals than when it was dominated by small individuals. When small individuals dominated the source population, fewer individuals reached the threshold length for reproduction than when large individuals dominated the population, resulting in slightly lower cumulative reproductive output.

Increased oil spill intensity resulted in a considerable decrease in total larval production (Fig. 5). The magnitude of the effect of oil spills far exceeded the effect of different size structures in the source population (note

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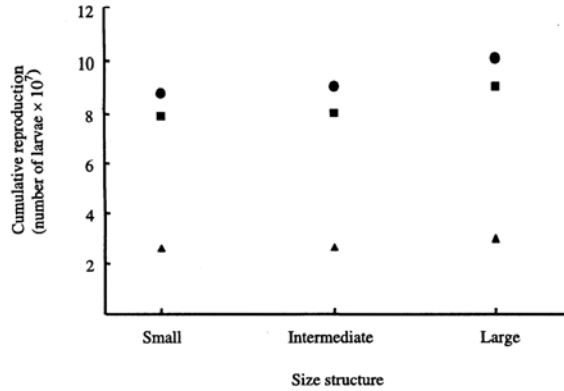


Fig. 5. Cumulative number of larvae, produced by the source population, entering the larval pool in the water column over 2 years under different intensities of an oil spill (● = no spill; ■ = 10% of the source population killed; ▲ = 70% of the source population killed).

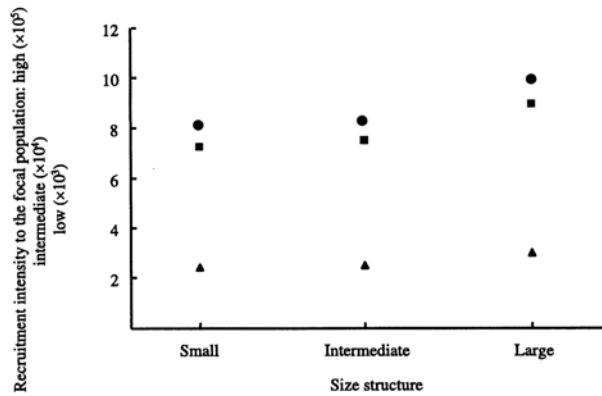


Fig. 6. Cumulative number of larvae entering the focal population over 2 years under low ($\phi = 0.0001$), medium ($\phi = 0.001$) and high ($\phi = 0.01$) amounts of recruitment and different intensities of an oil spill (● = no spill; ■ = 10% of the source population killed; ▲ = 70% of the source population killed). Note differences in the magnitudes of recruitment for each recruitment intensity on the y-axis.

y-axis). Thus, cumulative reproductive output to the larval pool depended more on the intensity of the oil spill than on the size structure of the source population.

RECRUITMENT AND DYNAMICS OF THE FOCAL POPULATION

Increased oil spill intensity in the source population resulted in a sizeable decrease in recruitment to the focal population (Fig. 6). The magnitude of recruitment was a direct product of recruitment intensity. Recruitment was slightly higher when the source population was dominated by large individuals than when it was dominated by small individuals for all oil spill and recruitment intensities. Therefore, as with reproductive output of the source population, recruitment to the focal population depended more on the intensity of the oil spill than on the size structure of the source population.

The size structure of the source population was important, however, when looking at the seasonal

trajectory of the focal population. The simple mathematical relationship between the intensity of the oil spill, the proportion of larvae recruiting and recruitment to the focal population disappeared when the focal population size was plotted over time. The seasonal dynamics of the focal population depended on the intensity of the oil spill, recruitment intensity and the size structure of the source population. The population size over time was plotted under no oil spill and when 70% of the source population was killed (Fig. 7). Under both oil spill intensities, seasonal declines in the focal population were greater under small and intermediate size structures than under a large size structure. In fact, there was no seasonal decline in the focal population when the size structure of the source population was large and recruitment intensity was intermediate or high. Differences in recruitment intensities resulted in time lags in increases in the focal population size (i.e. the rate of population increase was slower when recruitment was low than when it was high), particularly under small and intermediate size structures.

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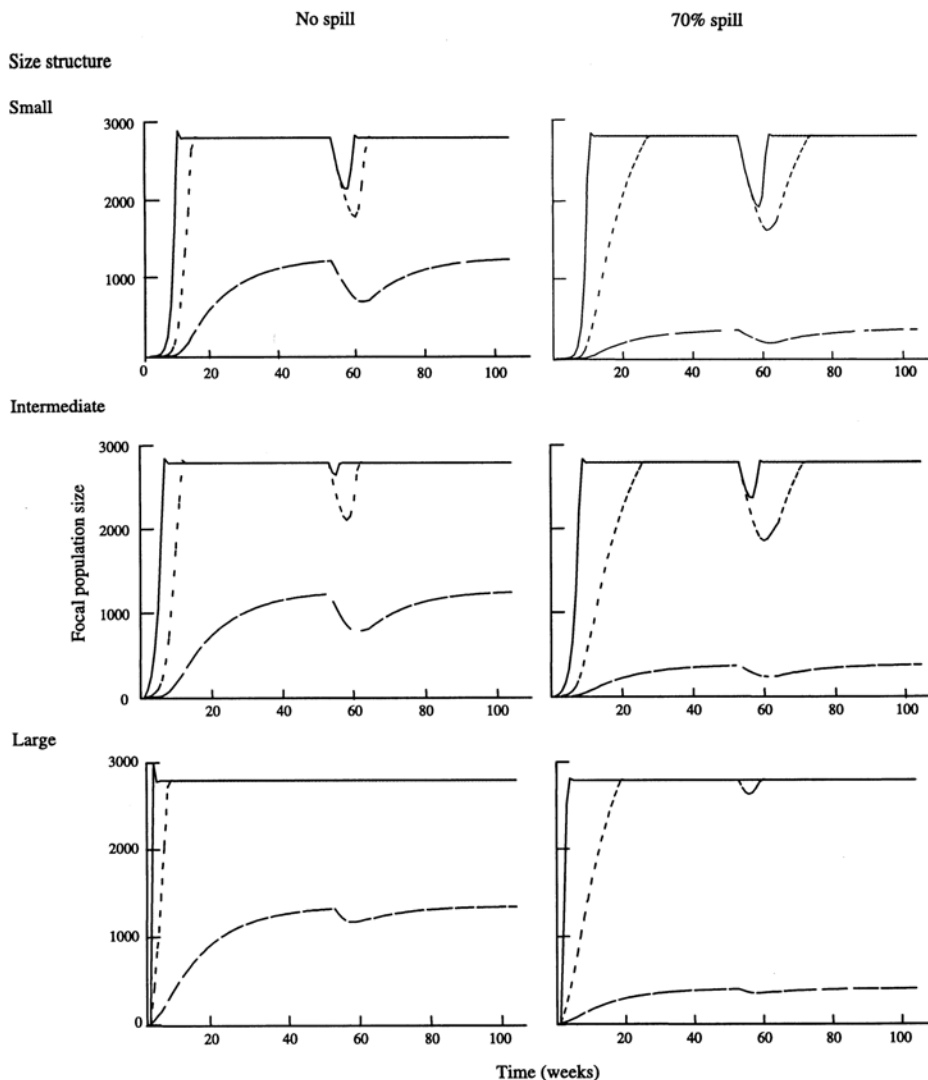


Fig. 7. Population dynamics under different proportions of recruitment from the larval pool, different size structures of the source population when there is no oil spill and 70% of the source population killed. Solid line, high recruitment; dashed line, intermediate recruitment; broken line, low recruitment.

Although the focal population reached similar maximum sizes under intermediate and high amounts of recruitment in all cases, it took 5–10 weeks longer for the population to reach the maximum size when recruitment intensity was intermediate than when recruitment intensity was high. The focal population did not reach the maximum size when recruitment intensity was low.

Discussion

The recovery of open populations from oil spills depends on the interactive effects of the size structure of the source population, the intensity of the oil spill (and the resulting adult mortality) and recruitment

intensity. Although the size structure of the source population had little effect on reproductive output and recruitment to the focal population, there was a considerable influence of size structure on the seasonal dynamics of the focal population. Source populations consisting of larger individuals were less likely to result in recruitment limitation on a regional scale in the face of disturbance and reduced survivorship of propagules than those consisting of small individuals.

The results of the model are consistent with past research on the relationship between recruitment and the dynamics of the adult population (reviewed by Caley *et al.* 1996). Under low amounts of recruitment and if resources are available, a population is defined as recruitment-limited. In the low-recruitment run of the

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model, the recovery rate of the focal population was slowest, the population size never reached the maximum (i.e. resources, specifically free space for recruitment, were still available) and seasonality in recruitment was apparent in the population dynamics.

At high amounts of recruitment, populations are defined as recruitment-unlimited. In recruitment-unlimited populations, recruitment is sufficiently high such that any further increase in the number of individuals entering a population does not result in a further increase in adult abundance (Raimondi 1990; Menge 1991; Caley *et al.* 1996; Connolly & Roughgarden 1998, 1999). Under intermediate and high levels of recruitment, whether the focal population was recruitment-limited or unlimited depended on the size structure of the source population and on oil spill intensity. More importantly, conclusions regarding recruitment limitation depended on seasonality in recruitment. When the source population consisted of large individuals, there was no oil spill and recruitment was intermediate or high, the population remained at a maximum size over time. In contrast, in all other runs of the model, conclusions regarding recruitment limitation depended on time.

The results of the model have implications for managing open populations because decisions are often based on whether or not a population is recruitment-limited. If a population was sampled at the maximum population size, managers might conclude that an anthropogenic impact resulted in little to no change in the population and recruitment was sufficiently high to allow for full recovery (Fig. 7; intermediate size structure, 70% spill at week 40). In contrast, if the same population was sampled at a different time of year, managers might conclude that the impact resulted in a change in the population size and further monitoring of the population was required to assess recovery (Fig. 7; intermediate size structure, 70% spill at week 60). Thus, the results highlight the importance of long-term monitoring of open populations in order to accurately assess both pre- and post-impact population dynamics.

Although this is a somewhat simplified model of an open marine population, it illustrates that recruitment variation is a critical factor in predicting the effects of disturbance on populations with dispersive larval phases. The model illustrates that size structure of a population is a key element in determining the degree to which recruitment variation will exert an effect at a regional scale. Past research has shown that recruitment (Caley *et al.* 1996) and disturbance, particularly due to oil spills (Foster *et al.* 1988; Jackson *et al.* 1989; KLI 1992; Gilfillan *et al.* 1999), can vary considerably in space and time. Further, empirical work has shown that colonization of free space depends on when a patch is created relative to seasonality in larval abundance (Kay & Keough 1981). Therefore, recovery from an oil spill will depend on the timing and intensity of the spill relative to the timing and intensity of

reproduction in the region and subsequent recruitment to the population in question. The results of the model suggest we need to understand stock–recruitment relationships and what processes underlie recruitment variability in populations with obligate dispersive phases. Without this knowledge, we cannot evaluate accurately the consequences of anthropogenic impacts on populations with dispersive phases.

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References

- Bokn, T.L., Moy, F.E. & Murray, S.N. (1993) Long-term effects of the water-accommodated fraction (WAF) of diesel oil on rocky shore populations maintained in experimental mesocosms. *Botanica Marina*, **36**, 313–319.
- Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P. & Menge, B.A. (1996) Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics*, **27**, 477–500.
- Clark, C.W. & Mangel, M. (2000) *Dynamic State Variable Models in Ecology: Methods and Applications*. Oxford University Press, New York, NY.
- Connolly, S.R. & Roughgarden, J. (1998) A latitudinal gradient in northeast Pacific intertidal community structure: evidence for an oceanographically based synthesis of marine community theory. *American Naturalist*, **151**, 311–326.
- Connolly, S.R. & Roughgarden, J. (1999) Theory of marine communities: competition, predation and recruitment-dependent interaction strength. *Ecological Monographs*, **69**, 277–296.
- Crothers, J.H. (1983) Field experiments on the effects of crude oil and dispersant on common animals and plants of rocky sea shores. *Marine Environmental Research*, **8**, 215–239.
- Foster, M.S., Charters, A.C., Neushel, M. & Zingmark, R. (1970) *Santa Barbara Oil Pollution, 1969*. Water Pollution Control Research Series. US Department of the Interior, Washington, DC.
- Foster, M.S., DeVogeleare, A.P., Harrold, C., Pearse, J.S. & Thum, A.B. (1988) *Causes of Spatial and Temporal Patterns in Rocky Intertidal Communities of Central and Northern California*. Memoirs of the California Academy of Sciences

- Number 9. California Academy of Sciences, San Francisco, CA.
- Gaines, S.D. & Lafferty, K.D. (1995) Modeling the dynamics of marine species: the importance of incorporating larval dispersal. *Ecology of Marine Invertebrate Larvae* (ed. L. McEdward), pp. 389–412. CRC Press, Boca Raton, FL.
- Gaines, S.D. & Roughgarden, J. (1985) Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. *Proceedings of the National Academy of Sciences*, **82**, 3707–3711.
- Gilfillan, E.S., Harner, E.J., O'Reilly, J.E., Page, D.S. & Burns, W.A. (1999) A comparison of shoreline assessment study designs used for the Exxon Valdez oil spill. *Marine Pollution Bulletin*, **38**, 380–388.
- Grantham, B.A. (1997) *Coastal upwelling, larval recruitment and the dynamics of upper intertidal barnacle communities*. PhD Dissertation. Stanford University Press Stanford, CA.
- Hines, A.H. (1978) Reproduction in three species of intertidal barnacles from Central California. *Biological Bulletin*, **154**, 262–281.
- Hughes, T.P., Baird, A.H., Dinsdale, E.A., Moltchanivskyj, N.A., Pratchett, M.S., Tanner, J.E. & Willis, B.L. (2000) Supply-side ecology works both ways: the link between benthic adults, fecundity and larval recruits. *Ecology*, **81**, 2241–2249.
- Jackson, J.B.C., Cubit, J.D., Keller, B.D., Batista, V., Burns, K., Caffey, H.M., Caldwell, R.L., Garrity, S.D., Getter, C.D., Gonzalez, C., Guzman, H.M., Kauffman, K.W., Knap, A.H., Levings, S.C., Marshall, M.J., Steger, R., Thompson, R.C. & Weil, E. (1989) Ecological effects of a major oil spill on Panamanian coastal marine communities. *Science*, **243**, 37–44.
- Kay, A.M. & Keough, M.J. (1981) Occupation of patches in the epifaunal communities on pier pilings and the bivalve *Pinna bicolor* at Edithburgh, South Australia. *Oecologia*, **48**, 123–130.
- Kinetics Laboratories Inc. (KLI) (1992) *Study of Recovery from an Oil Spill on the Rocky Intertidal Coast of Washington*. Pacific OCS Region, Minerals Management Service, US Department of Interior, Washington, DC.
- Mangel, M. & Clark, C.W. (1988) *Dynamic Modeling in Behavioral Ecology*. Princeton University Press, Princeton, NJ.
- Mangel, M. & Ludwig, D. (1992) Definition and evaluation of behavioral and developmental programs. *Annual Review of Ecology and Systematics*, **23**, 507–536.
- McGuinness, K.A. (1990) Effects of oil spills on macro-invertebrates of saltmarshes and mangrove forests in Botany Bay, New South Wales, Australia. *Journal of Experimental Marine Biology and Ecology*, **142**, 121–135.
- Menge, B.A. (1991) Relative importance of recruitment and other causes of variation in rocky intertidal community structure. *Journal of Experimental Marine Biology and Ecology*, **146**, 69–100.
- Morris, R.H., Abbott, D.P. & Haderlie, E.C. (1980) *Intertidal Invertebrates of California*. Stanford University Press, Stanford, CA.
- Nelson, W.G. (1982) Experimental studies of oil pollution on the rocky intertidal community of a Norwegian fjord. *Journal of Experimental Marine Biology and Ecology*, **65**, 121–138.
- Possingham, H.P. & Roughgarden, J. (1990) Spatial population dynamics of marine organisms with a complex life cycle. *Ecology*, **71**, 973–985.
- Press, W.H., Flannery, B.P., Teukolsky, S.A. & Vetterling, W.T. (1986) *Numerical Recipes: The Art of Scientific Computing*. Cambridge University Press, Cambridge, UK.
- Raimondi, P.T. (1990) Patterns, mechanisms, and consequences of variability in settlement and recruitment of an intertidal barnacle. *Ecological Monographs*, **60**, 283–309.
- Roughgarden, J., Iwasa, Y. & Baxter, C. (1985) Demographic theory for an open population with space-limited recruitment. *Ecology*, **66**, 54–67.
- Southward, A.J. (1982) An ecologist's view of the implications of the observed physiological and biochemical effects of petroleum compounds on marine organisms and ecosystems. *Philosophical Transactions of the Royal Society of London B*, **297**, 241–255.
- Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford, UK.
- Wetthey, D.S. (1984) Effects of crowding on fecundity in barnacles: *Semibalanus (Balanus) balanoides*, *Balanus glandula*, and *Chthamalus dalli*. *Canadian Journal of Zoology*, **62**, 1788–1795.

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The Department of the Interior Mission

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering sound use of our land and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.



The Minerals Management Service Mission

As a bureau of the Department of the Interior, the Minerals Management Service's (MMS) primary responsibilities are to manage the mineral resources located on the Nation's Outer Continental Shelf (OCS), collect revenue from the Federal OCS and onshore Federal and Indian lands, and distribute those revenues.

Moreover, in working to meet its responsibilities, the **Offshore Minerals Management Program** administers the OCS competitive leasing program and oversees the safe and environmentally sound exploration and production of our Nation's offshore natural gas, oil and other mineral resources. The **MMS Royalty Management Program** meets its responsibilities by ensuring the efficient, timely and accurate collection and disbursement of revenue from mineral leasing and production due to Indian tribes and allottees, States and the U.S. Treasury.

The MMS strives to fulfill its responsibilities through the general guiding principles of: (1) being responsive to the public's concerns and interests by maintaining a dialogue with all potentially affected parties and (2) carrying out its programs with an emphasis on working to enhance the quality of life for all Americans by lending MMS assistance and expertise to economic development and environmental protection.