

# A spatial gradient in the potential reproductive output of the sea mussel *Mytilus californianus*

Nicole E. Phillips

Received: 9 August 2006 / Accepted: 13 December 2006 / Published online: 6 January 2007  
© Springer-Verlag 2007

**Abstract** Spatial variation in reproductive output from different populations within a region could have important consequences for recruitment, and cascading effects on populations and communities of marine species, but is rarely examined over meso-scales (i.e., tens to hundreds of kilometers). In this study, reproduction in the dominant mid-intertidal mussel, *Mytilus californianus*, was examined from sites spanning Point Conception, California over a 6-month period (March–August 2000). There was a dramatic geographic pattern in the relationship between size and potential reproductive output that was qualitatively similar across all 6 months sampled. Increases in allocation to reproductive tissue with increasing body size occurred at all sites, but the slope nearly doubled at sites south of Point Conception compared to northern sites. The spatial variation in size-specific reproductive output, coupled with additional spatial gradients in mussel density and size distributions, combined to increase total reproductive output by over eightfold at southern relative to northern sites. This study highlights the need to explicitly examine spatial patterns of reproductive output at these meso-scales, in order to

better understand connectivity and source–sink dynamics in marine systems.

## Introduction

Across a region, spatial variability in reproductive output may influence larval supply and, if predictable spatially or temporally, may generate cascading effects on benthic populations and communities (Bertness et al. 1991). Depending on the patterns of larval transport and mixing, spatial variation in production may result in some sites that contribute disproportionately to the regional larval pool. This may have important implications for the genetic structure of populations, and regional dynamics of populations may be driven by the relative frequencies of source and sink sites. Or, if dispersal is more limited, spatial variation in reproductive output may drive corresponding spatial variation in larval settlement and, ultimately, spatial variation in population and community dynamics (Bertness et al. 1991). Although identifying variation in reproductive output is key to understanding source–sink dynamics in marine systems, and has important implications for management and conservation (i.e., siting of reserves or protected areas), relatively few studies have been published that examine variation in reproductive output at the scale of tens to hundreds of kilometers (Leslie et al. 2005).

Here, I examine spatial patterns of potential reproductive output in the dominant mid-intertidal species on the West Coast of the USA, *Mytilus californianus*, from sites spanning Point Conception, California. This region includes sharp gradients in ocean conditions that could generate correspondingly large gradients in

---

Communicated by S.D. Connell.

---

N. E. Phillips  
Department of Ecology, Evolution and Marine Biology,  
University of California, Santa Barbara, USA

*Present Address:*  
N. E. Phillips (✉)  
School of Biological Sciences,  
Victoria University of Wellington,  
P. O. Box 600, Wellington, New Zealand  
e-mail: Nicole.Phillips@vuw.ac.nz

filter-feeder feeding success. North of the point, upwelling is frequent and strong, and the water is generally cold, whereas south of the point, in the Santa Barbara Channel, upwelling is weaker and infrequent (Sverdrup 1938; Hickey 1979, 1993). As a result, the ocean is warmer and has fewer nutrients (Hickey 1993; Blanchette et al. 2002) in the Santa Barbara Channel.

Earlier work (Phillips 2005) has demonstrated strong geographic variation in organismal growth rates among benthic populations spanning Point Conception. Mussels and barnacles grow substantially faster at sites south of Point Conception than at sites further to the north. With such strong responses in growth rates, this is an ideal setting to examine the possibility of corresponding geographical variation in investment in reproduction.

Given the potential energetic trade-off between growth and reproduction, the patterns of covariation between the two could take a number of forms. If resource acquisition is constant among populations, classic life history theory would predict negative covariation between the two life history traits (Williams 1966; Sibly and Calow 1986; Stearns 1992). Alternatively, since the pattern of growth may be driven by changes in the physical setting or availability of resources, growth and reproduction may positively covary as individuals in some localities experience consistently better conditions, or are able to acquire more resources than individuals in others (van Noordwijk and de Jong 1986).

There are a number of possible scales at which variation in reproduction might vary. In this paper, I focus on the level of individuals and the level of sites. At the individual level, the key question is whether the fecundity–size relationship and allocation to reproduction vary geographically. Do individuals of similar size have similar reproductive output at different sites? At the site level, total reproductive output from a location depends on the size-specific pattern of fecundity as well as site-level attributes such as the proportion of individuals reproducing, the density of individuals, and the frequency distribution of sizes. Although each of these components could vary with microhabitat (e.g., across tidal zones), here I focused solely on individual and site level patterns for the mid-intertidal zone.

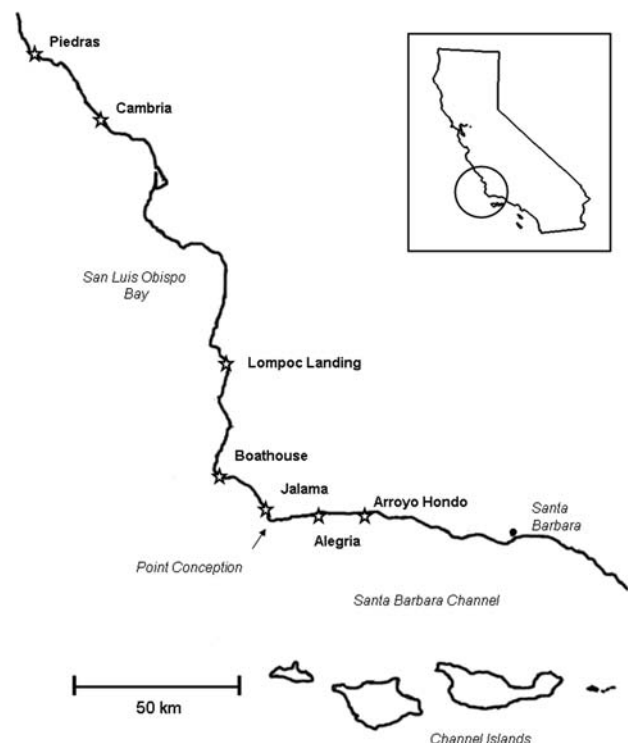
## Methods

### Estimating size-specific reproductive output

Approximately 50–70 *M. californianus* were collected from the mid-zone (i.e., intermediate tidal level) of

each of seven sites in southern and central California monthly from March to August 2000. The sites were (from south to north) Arroyo Hondo, Alegria, Jalama, Boathouse, Lompoc Landing, Cambria and Piedras (Fig. 1). Jalama is the closest site to Point Conception, approximately 2 km north of the point. They were all haphazard collections, followed by targeted additional collections to obtain individuals in the largest size classes. Care was taken not to collect individuals in close proximity to each other, and to collect over a wide spatial scale, spread out over the site. The scale over which sampling occurred was similar across sites.

In the laboratory, the mantle tissue, where the gonads reside, and the body tissue were dissected from each individual separately. Some mussel species (e.g., *Mytilus edulis*) store not only their reproductive tissue, but also glycogen in the mantle during non-reproductive periods, making it difficult to assess when they are reproductive without histological preparations (Seed 1969). However, Elvin (1974) reported that there was little glycogen storage in the mantle for *M. californianus*. Several researchers have used visual indices to estimate reproductive stages in this species that have been verified by comparison with histological preparations (e.g., Dittman and Robles 1991). For this study, I used a similar scale to estimate the ripeness of the mantle tissue visually using an index from 0 to 3 with the



**Fig. 1** Study sites in southern and central California, spanning Point Conception

following definitions: “0”: clear mantle tissue, “1”: mostly clear or mottled mantle tissue, with some but little development of reproductive tissue, “2”: thickened mantle tissue relative to 1, some gonoduct development, and some development of reproductive tissue around digestive organs and in mesosoma, “3”: thick mantle tissue with well-developed gonoducts and well-developed reproductive tissue in the mesosomal lobe and around the digestive organs.

As a conservative estimate, I defined any individual with a ripeness index of 2 or 3 as “ripe” and capable of spawning. I did not attempt to discriminate between the sexes, because sex is difficult to determine accurately without actually spawning the gametes. Other studies have found little difference among sexes in the weight of ripe reproductive tissue or the timing of spawning (Griffiths 1977; Sprung 1983; Okamura 1986). Mantle tissue and body tissue were dried at approximately 70°C for 48 h, and then weighed. I also measured the shell length of each mussel to the nearest 0.1 mm. For each month and site, I examined the effect of site on size-specific fecundity by quantifying the relationship between dry body weight and dry weight of the mantle tissue of ripe animals.

#### Estimating site-level reproductive output

Because reproductive output is sometimes related to body size non-linearly, I generated linear regression models and the best-fit exponential models for the relationship between body weight and mantle weight. Generally, the linear and non-linear models were very similar. In almost all cases, the linear model was most appropriate when both were compared with Akaike’s Information Criterion, so I used those. I examined the effect of site and month of collection on mantle weight in an ANCOVA, using body weight as a covariate.

To estimate aggregate reproductive output for each site, I combined the above individual data with population data from each site. Natural densities and size distributions of mussels from the mid-zone of each site were estimated by randomly placing four to six 0.25 × 0.25 m quadrats on a transect through the middle of the mid-zone parallel to the water line, and collecting all the mussels in each quadrat. All mussels over 40 mm shell length were counted and measured, as *M. californianus* smaller than 40 mm rarely had developed gonads in the mantle tissue (N.E. Phillips, personal observation). The total area of the mussel bed at each site was also estimated.

At each site, for each month, I used the regression equations between size and mantle weight for ripe mussels (derived from the monthly samples for estimating

reproductive output), to predict the mantle weights of each of the mussels collected from the field in the above random sampling design. First, for each site I used the relationship between mussel size and predicted ripe mantle weight to obtain a total estimated ripe mantle weight for all of the mussels in each quadrat. I calculated this separately for each month with the appropriate regression equation for that month. I then summed up the mantle weights for each replicate quadrat over all 6 months sampled, and estimated the mean predicted reproductive output (in g ripe mantle tissue) per m<sup>2</sup> of mid-intertidal mussel bed for the entire sample period. For example, for Arroyo Hondo: (reproductive output for *n* mussels in quadrat 1 (March) + reproductive output for *n* mussels in quadrat 1 (April)... + quadrat 1 (August)) × 4 = total reproductive/m<sup>2</sup> from quadrat 1 for the sampling period. I made this calculation for each of the four to six quadrats per site, and then calculated the mean total reproductive output/m<sup>2</sup> for each site by averaging across the replicate quadrats at each site. This final estimation of reproductive output therefore accounted for the natural size structure, ripeness, density, and size-specific reproductive output of mussels from the different sites in the study region.

I performed a one-way ANOVA on the effect of site on the mean total estimated reproductive output (as calculated above), and post-hoc Tukey tests to explore significant differences. To examine the spatial relationship further, I also examined the correlation between total estimated reproductive output for a site with distance along the coast from the southern-most site (Arroyo Hondo).

## Results

### Size-specific reproductive output

There was substantial variability among sites and months in the relationship between size and potential reproductive output (Table 1), with no clear seasonal or monthly trend. Although there was significant variability among months, there was a clear geographic trend with the slope of the relationship between reproductive output and body size decreasing moving north of Point Conception (Fig. 2). To demonstrate this relationship more clearly, and because there were no consistent patterns over time, I pooled the data from all of the months for each site (Fig. 3a). For all sites, there was an expected increase in the weight of mantle tissue with an increase in mussel size, but the slope of the relationship was on average twice as steep at the southern

**Table 1** ANCOVA results of site and month on mantle weight, with body weight as a covariate

Source	DF	SS	F	P
Site	6	2.76	22.89	<0.0001
Month	5	0.385	3.82	0.002
Site × month	30	2.18	3.61	<0.0001
Body weight	1	7.65	380.1	<0.0001
Site × body weight	6	9.94	82.27	<0.0001
Month × body weight	5	0.152	1.52	0.182
Site × month × body weight	30	6.79	11.25	<0.0001
Error	1,213	24.42		

sites (including Jalama) as at the northern sites (Fig. 3b). As a result, for example, a mussel that weighed approximately 3 g had more than double the weight of reproductive tissue at a southern site compared to the same sized mussel from a northern site.

#### Site-level reproductive output

Size distributions of mussels were heterogeneous among sites (Fig. 4). Most conspicuously, there was a complete absence of mussels over 80 mm in length from the two northern-most sites, and very few mussels this size or larger at Lompoc Landing as well (the third northern-most site, Fig. 4). Jalama, the site closest to Point Conception, had the greatest percentage of mussels in the largest size class, where 20% of all mussels were greater than 100 mm in length. Seventy to ninety percent of ripe mussels at the four northern-most sites were in the smallest size classes, whereas most of the ripe mussels at the three southern-most sites were in the largest size classes (Fig. 5). There were more ripe mussels from Jalama in the largest two size classes (65% of all the ripe mussels from this site) than any other site, likely in large part due to the high proportion of large mussels found there.

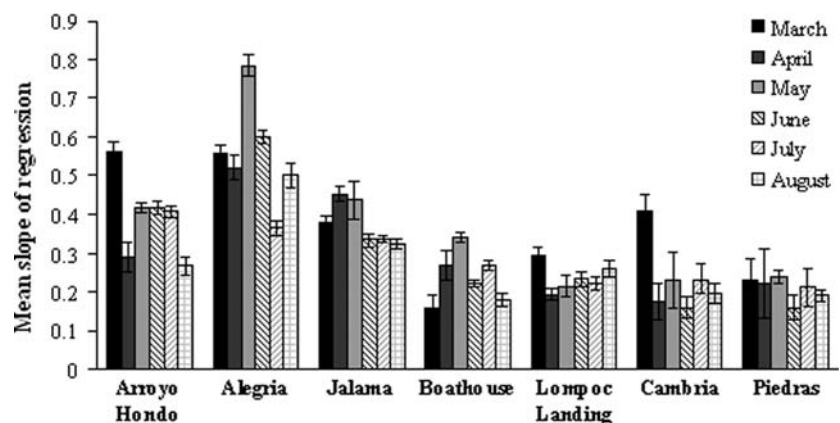
The parallel gradients in mussel density, size, and size-specific allocation to reproductive tissue create

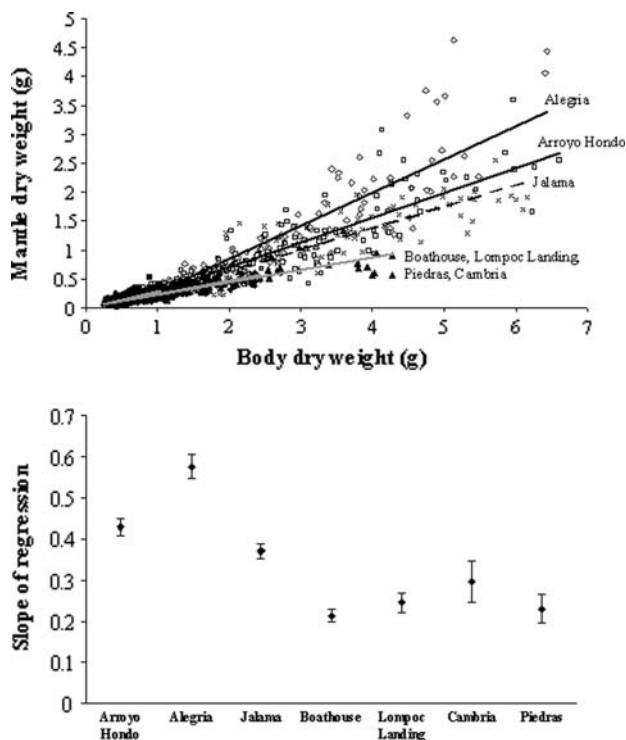
greater potential reproductive output (per m<sup>2</sup> of the mid-mussel bed) at southern sites compared to northern sites from this 6-month period (Fig. 6a). There was a significant effect of site on total estimated reproductive output ( $F_{6,25} = 11.4907$ ,  $P < 0.0001$ ), where Cambria and Piedras had significantly lower reproductive output than Arroyo Hondo, Alegria and Jalama, and Lompoc Landing also had lower reproductive output than Arroyo Hondo and Jalama (post-hoc Tukey tests,  $P < 0.05$ ). Further, there is a significant negative correlation between distance along the coast and total reproductive output per m<sup>2</sup> ( $R = -0.855$ ,  $P = 0.014$ , Fig. 6b). Finally, the areas of the mussel beds at the different sites would not compensate for these spatial patterns, if anything, they would exacerbate them (mid-zone mussel bed areas: Arroyo Hondo = 190 m<sup>2</sup>, Alegria = 210 m<sup>2</sup>, Jalama = 75 m<sup>2</sup>, Boathouse = 56 m<sup>2</sup>, Lompoc Landing = 224 m<sup>2</sup>, Cambria = 30 m<sup>2</sup>, Piedras = 60 m<sup>2</sup>).

#### Discussion

Results from this study demonstrate that spatial variation in potential reproductive output generally paralleled that of growth in the region spanning Point Conception. Mussels had highest potential reproductive output south of Point Conception, the same region where they have been found to have higher growth rates (Phillips 2005). Particularly interesting is the fact that similar to Phillips (2005), Jalama in this study appears more similar to southern sites than northern sites, despite the fact that is in fact a few kilometers north of Point Conception.

Limitations of this study include the fact that it covers only 6 months out of the year, and that mussels were only collected from the mid-zone. Reports of annual cycles of spawning in this species are varied, and mostly originate from areas much further to the

**Fig. 2** Slopes of regressions of mantle weight against body weight for ripe mussels ( $\pm 1$  SE) for each month at each site



**Fig. 3** The relationship between body weight and mantle weight for ripe *Mytilus californianus*. **a** Regressions for each site, data pooled over all 6 months sampled. The *black lines* are for the sites south of Pt. Conception, Jalama closest at 2 km north is a *dashed line*, the *gray lines* are sites north of the point. Symbols for each site are: *open square* Arroyo Hondo, *open diamond* Alegria, *crosses* Jalama, *filled triangle* Boathouse, *filled diamond* Lompoc Landing, *filled circle* Cambria, *filled square* Piedras. **b** Slopes of the above regressions ( $\pm 95\%$  CI)

south or north. For example, studies from San Diego, California (nearly 400 km south of the southern-most site in this study) have reported that *M. californianus* can reproduce year-round with peaks in spring and autumn (Coe and Fox 1942), but also that spawning is greatest October–February (Young 1942, although even in Young’s table there is as much spawning activity in March and April as January and February). From work done further north however, off the coast of Washington, *M. californianus* has been reported to possibly spawn year-round, with a peak of activity in late summer (Strathmann 1987). I have spawned this species from sites in this study area quite easily and successfully through out spring and summer (N.E. Phillips, in press and unpublished data). It is therefore, possible that *M. californianus* in this study region is reproductive in the other 6 months of the year that were not sampled here (September–February). However, given the natural size distributions and densities of mussels across these sites, and the spatial coherence in allocation to reproductive tissue over the 6 months

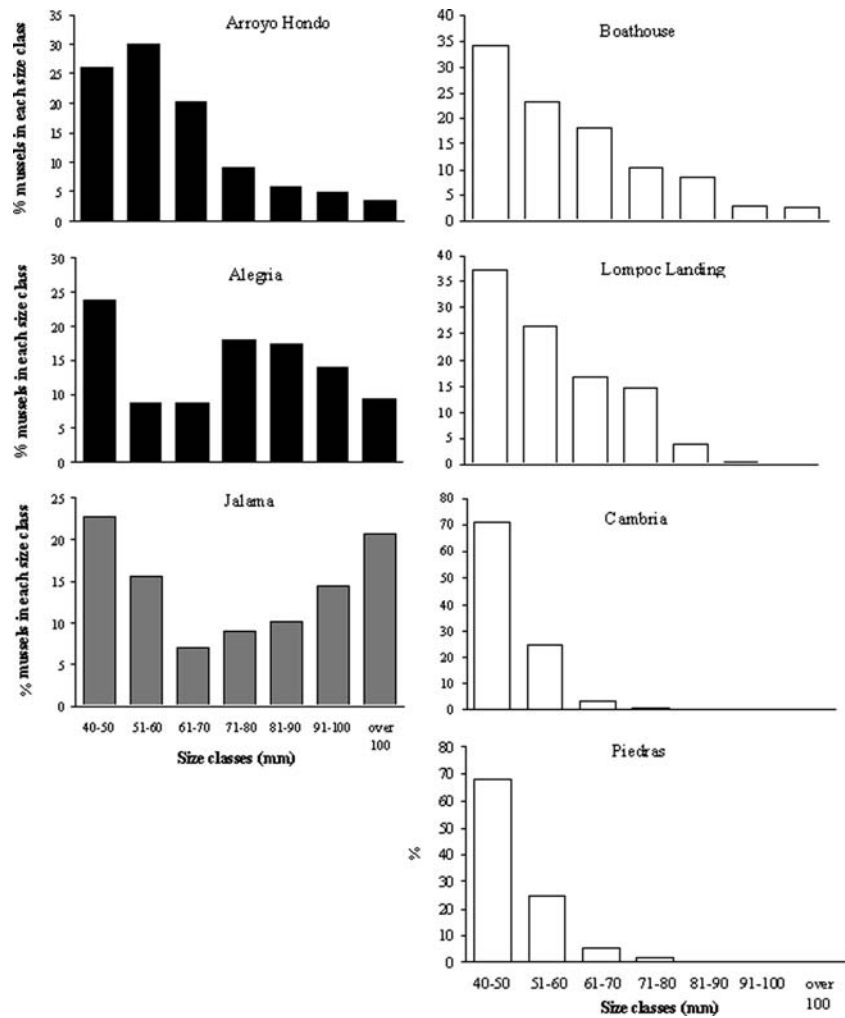
that were sampled, it seems unlikely that any potential temporal changes to allocation to reproduction at these sites could overcome the dramatic spatial patterns found here.

Reproductive output is generally greater for bivalves from lower in the intertidal compared to those living higher (Harvey and Vincent 1989; Borerro 1987; Harvey and Vincent 1991; Franz 1997). However, to compensate for the patterns found here in the mid-zone, there would have to be a dramatic switch such that high densities of large mussels were found in the low zone of northern sites and not at southern sites. Although densities and size distributions of mussels in the low zone were not quantified in this study, observations of the low zone strongly suggest this is not the case. In fact, if the opposite was true, and there were higher densities of large mussels in the low zone at southern sites, it would further exacerbate the patterns found here.

This geographic pattern in reproductive output may be driven by spatial variability in either available resources or resource acquisition. One hypothesis might be that differences in food availability among sites may explain this pattern. This hypothesis, however, is not supported by data from Phillips (2005), which shows no substantial spatial differences in the amount of planktonic food (measured as either particulate organic carbon or chlorophyll a) across these same sites for the same time period. Because north of Point Conception upwelling is generally persistent (rather than intermittent with periods of relaxation, Brink et al. 1984), phytoplankton produced from that upwelling may simply not be delivered back to shore in that region and become available to the filter-feeders. Immersion time is another factor that may play an important role in driving these patterns. In general, the mid-zone of the intertidal at northern sites lies at higher absolute tidal heights than southern sites, which may lessen the time mussels are immersed and therefore the time available for feeding. However, differences in tidal heights of these sites alone is not sufficient to explain the patterns here; for example, the mid-zone of the southern-most site Arroyo Hondo is at a similar tidal height to the northern site Boathouse (Phillips 2005).

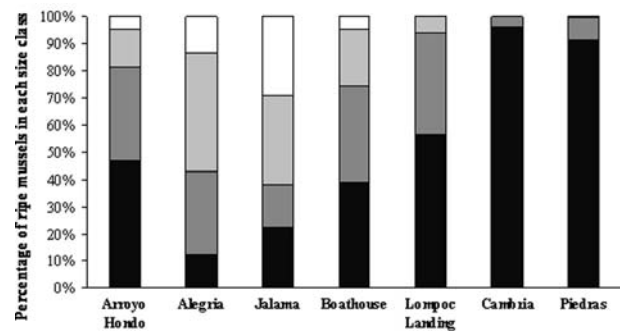
Finally, another hypothesis is that this spatial pattern in potential reproduction may be temperature driven. Water temperatures were consistently warmest at the most southern sites and decreased incrementally to the north (summer 2000 average water temperature was approximately 17°C in the south and approximately 13°C in the north, Phillips 2005). Physiological rates are temperature dependent, and although metabolic rates

**Fig. 4** Size distributions of randomly collected mussels from each site. Sites south of Point Conception have *black bars*, Jalama (closest to the point) has *gray*, and northern sites have *open bars*. Note the differences in the scales of the y-axes



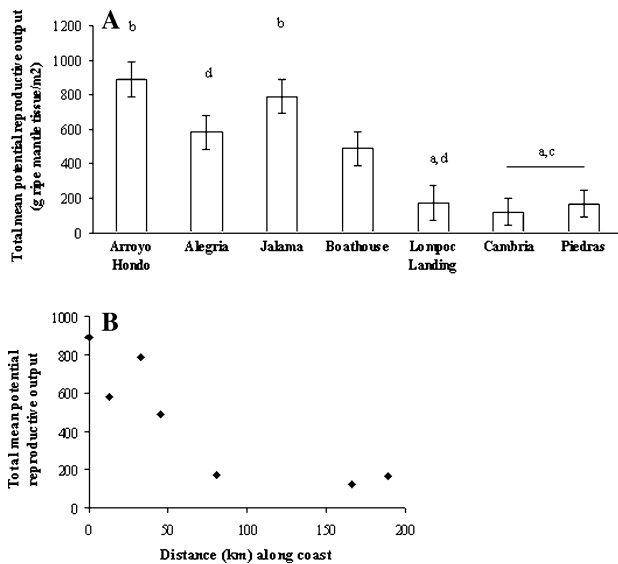
generally increase with temperature, rates of feeding for filter-feeding mussels increase with temperature as well (Bayne et al. 1976). If increases in feeding outweigh increased metabolic costs, adults at the smaller end of the size range could grow and reproduce at higher rates at southern sites than at northern sites. In support of this hypothesis, Bayne et al. (1976) found that oxygen consumption by *M. californianus* was largely independent of temperature over a range of laboratory temperatures similar to that found in this region (13–17.5°C). By contrast, the filtration rate increased at warmer temperatures with a  $Q_{10}$  greater than 1.8 over this same temperature range.

Although the maximum size of mussels was larger at southern sites, and there were greater densities of them, there were still some relatively large mussels (e.g., approximately 80–90 mm) at some of the northern sites. Why did large northern mussels invest so much less in reproduction than equivalent sized, and larger, southern mussels? If the increase in filtration rate increases with temperature and body size, then



**Fig. 5** The percentage of all ripe mussels from each site that fell into each of four size classes: *white bars* over 100 mm, *light gray bars* 81–100 mm, *dark gray bars* 61–80 mm, *black bars* 40–60 mm in length

large southern mussels may simply be able to acquire many more resources than large northern mussels. If metabolic rate also increases with body size, then large northern mussels may not be able to acquire more resources above those needed for maintenance. Wave exposure increases north of Point Conception, and



**Fig. 6** An estimate of total reproductive output for each site, summed over the 6-month sample period. **a** Plotted are means ( $\pm 1$  SE), based on predicted mantle weights of all mussels collected from four to six replicate quadrats per site (see [Methods](#) for calculation). Letters over the bars represented groups of means that are significantly different by Tukey test ( $P < 0.05$ ). **b** Correlation between mean estimated total reproductive output/m<sup>2</sup> for each site and the distance of the site along the coast (in km)

swell height increases as well (Blanchette et al. 2002). It is possible that northern populations must invest more in either production or maintenance of shell and/or byssal threads that keep them attached to the substrate, at the cost of reproduction. A better understanding of how energy is allocated to shell, byssal thread production, reproduction and somatic growth across these sites is an important area of future work. Other factors that may contribute to this geographic pattern in investment also include age, disease or parasitism, and genetic components. Future experiments and detailed studies designed to elucidate more clearly which factors, or combinations of factors, are driving this geographical pattern will be critical in allowing us to extrapolate to other systems.

In addition, to the fecundity–size relationship, the distribution of mussel sizes varied geographically. Large, ripe mussels were much more abundant at southern sites than northern sites, which amplified geographical differences in reproduction. The consequences of geographic variability in reproductive output for the benthic populations and communities in this region could be substantial. If larvae released in the region are sufficiently mixed that they effectively form a common larval pool, then larvae from southern parents would dominate the composition of the larval pool. Sites south of Point Conception would serve as a

source for northern populations and any gradients in natural selection would favor genotypes that performed well in southern populations. If, however, mixing of larvae from northern and southern sites is more restricted (as genetic evidence for barnacles from the region would suggest—Wares et al. 2001), then there may be orders of magnitude more larvae available for settlement at southern sites. This hypothesis seems more likely than the former, given what is known about the physical oceanography of the region.

In summary, the results of this study demonstrate a dramatic gradient in potential contribution to reproduction, which corresponds to other gradients across this same region in organismal performance and physical attributes of the nearshore ocean conditions. Depending on the transport and mixing of larvae, these spatial differences in reproductive output could influence recruitment dynamics in this region, or contribute to further spatial patterns in genetic structure, population, and community dynamics.

**Acknowledgments** For generous field and laboratory help I thank: C. Galst, M. Meyers, N. Hernandez, C. McGary, and E. Fikre; and for logistical support of field work: C. Svedlund and C. Blanchette. This research was supported by funds from an NSF graduate fellowship to the author, also in part by NSF BIR94-13141 and NSF GER93-54870 to W. Murdoch, and the David and Lucile Packard Foundation to S. Gaines. This is contribution number 232 from PISCO, the Partnership for Interdisciplinary Studies of Coastal Oceans, funded primarily by the Gordon and Betty Moore Foundation and David and Lucile Packard Foundation. The experiments reported here comply with the current laws of the USA.

## References

- Bayne BL, Bayne CJ, Carefoot TC, Thompson RJ (1976) The physiological ecology of *Mytilus californianus* Conrad I. Metabolism and energy balance. *Oecologia* 2:211–228
- Bertness MD, Gaines SD, Bermudez D, Sanford E (1991) Extreme spatial variation in the growth and reproductive output of the acorn barnacle *Semibalanus balanoides*. *Mar Ecol Prog Ser* 75:91–100
- Blanchette CA, Miner BG, Gaines SD (2002) Geographic variability in form, size and survival of *Egretta menziesii* around Point Conception, California. *Mar Ecol Prog Ser* 239:69–82
- Borerro FJ (1987) Tidal height and gametogenesis: reproductive variation among populations of *Geukensia demissa*. *Biol Bull* 173:160–168
- Brink KH, Chausse D, Davis RE (1984) Observation of the coastal upwelling region near 34°30'N off California: spring 1981. *J Phys Oceanogr* 14:378–391
- Coe WR, Fox DL (1942) Biology of the California sea-mussel (*Mytilus californianus*). I. Influence of temperature, food supply, sex and age on the rate of growth. *J Exp Zool* 90:1–30
- Dittman D, Robles C (1991) Effect of algal epiphytes on the mussel *Mytilus californianus*. *Ecology* 72:286–296
- Elvin DW (1974) Oogenesis in *Mytilus californianus*. PhD Dissertation. University of Oregon

- Franz DR (1997) Resource allocation in the intertidal sal-marsh mussel *Geukensia demissa* in relation to shore level. *Estuaries* 20:134–148
- Griffiths RJ (1977) Reproductive cycles in littoral populations of *Chromomytilus meridionalis* (Kr) and *Aulacomya ater* (Molina) with a quantitative assessment of gamete production in the former. *J Exp Mar Biol Ecol* 30:53–71
- Harvey M, Vincent B (1989) Spatial and temporal variations in the reproduction cycle and energy allocation of the bivalve *Macoma balthica* (L.) on a tidal flat. *J Exp Mar Biol Ecol* 129:199–217
- Harvey M, Vincent B (1991) Spatial variability of length-specific production in shell, somatic tissue and sexual products of *Macoma balthica* in the Lower St. Lawrence Estuary. I. Small and meso scale variability. *Mar Ecol Prog Ser* 75:55–66
- Hickey BM (1979) The California Current system—hypotheses and facts. *Prog Oceanogr* 8:191–279
- Hickey BM (1993) Physical oceanography. In: Dailey MD, Anderson JW, Reish DJ, Gorsline DS (eds) *Ecology of the Southern California Bight: a synthesis and interpretation*. University of California Press, Berkeley, pp 19–70
- Leslie HM, Breck EN, Chan F, Lubchenco J, Menge BA (2005) Barnacle reproductive hotspots linked to nearshore ocean conditions. *Proc Natl Acad Sci USA* 102:10534–10539
- Okamura B (1986) Group living and the effects of spatial position in aggregations of *Mytilus edulis*. *Oecologia* 69:341–347
- Phillips NE (2005) Growth of filter-feeding benthic invertebrates from a region with variable upwelling intensity. *Mar Ecol Prog Ser* 295:79–89
- Seed R (1969) The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores I. Breeding and settlement. *Oecologia* 3:277–316
- Sibly RM, Calow P (1986) *Physiological ecology of animals. An evolutionary approach*. Blackwell, Oxford
- Sprung M (1983) Reproduction and fecundity of the mussel *Mytilus edulis* at Helgoland (North Sea). *Helgol Meer* 36:243–255
- Stearns SC (1992) *The evolution of life histories*. Oxford University Press, Oxford
- Strathmann MF (1987) *Reproduction and development of marine invertebrates of the Northern Pacific coast*. University of Washington Press, Seattle
- Sverdrup HU (1938) On the process of upwelling. *J Mar Res* 2:155–164
- van Noordwijk AJ, de Jong G (1986) Acquisition and allocation of resources: their influence on variation in life history tactics. *Am Nat* 128:137–142
- Wares JP, Gaines SD, Cunningham CW (2001) A comparative study of asymmetric migration events across a marine biogeographic boundary. *Evolution* 55:295–306
- Williams G (1966) Natural selection, the cost of reproduction and a refinement of Lack's principle. *Am Nat* 100:687–690
- Young RT (1942) Spawning season of the California mussel, *Mytilus californianus*. *Ecology* 23:490–492