GEODUCK (*PANOPEA ABRUPTA*) RECRUITMENT IN THE PACIFIC NORTHWEST: LONG-TERM CHANGES IN RELATION TO CLIMATE

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ABSTRACT

Investigation of climatic forcing on recruitment is often complicated by a scarcity of data at relevant spatial and time scales. Skeletal structures of long-lived sedentary animals can yield valuable long-term retrospective information, with fine spatial resolution. Geoducks are in that category: these gigantic and commercially valuable clams can reach an age of 168 years, and they aggregate in dense coastal beds from southeastern Alaska to Washington. Back-calculation of recruitment from age-frequency distributions compiled in 1979–83 in British Columbia and Washington shows a decades-long decline in recruitment over a vast geographical realm (British Columbia to Washington) that reached a minimum during the mid-1970s. Analysis of data collected between 1993 and 2002 confirms a large-scale pre-1970s decline and reveals a post-1975 rebound. Recruitment in British Columbia is correlated with coastal environmental indexes, such as river discharges (negatively) and coastal sea-surface temperature (positively).

INTRODUCTION

There has been a growing interest over the last decade to understand the effects of environmental variability on the dynamics of harvested marine populations (Hollowed and Wooster 1992; Clark et al. 1999; Zheng and Kruse 2000; Logerwell et al. 2003). Most of the search for connections between climate and recruitment (or year-class strength) has focused on oceanic ecosystems and mobile species (primarily finfish), and information has been aggregated at large geographical scales under assumptions of homogeneity. This emphasis reflects a scarcity of time-series data, both biological and environmental, that are informative at a spatial scale required to understand the complexity of processes in the intrinsically heterogeneous coastal ecosystems (Sinclair and Frank 1995). Evidence of climatic forcing, however, can be inferred from large-scale geographical coherence of year-class strength, even if the processes responsible for such effects are open to speculation (Orensanz et al. 1998).

Because of their life history and the distribution and spatial structure of their metapopulations, geoducks (*Panopea abrupta*) offer unique opportunities to investigate the effects of environmental factors on growth and recruitment along coastal ecosystems. They are among the longest-lived animals in the world (oldest recorded age is 168 years; Bureau et. al. 2002) and their shells contain a record of climate change (Strom 2002). They are also a convenient research material because of their size (largest infaunal bivalve, up to 5 kg in weight and 25 cm in shell length) and availability, as they support a very lucrative and widely spread commercial fishery. Back-calculation of relative recruitment based on age-frequency distributions compiled in 1979-83 indicates that by 1975 recruitment had been declining for decades over a large geographic range, from British Columbia to Washington (Orensanz et al. 2000). Suggestion of a rebound in recruitment during the 1980s and early 1990s, inferred from the post-harvest recovery of density in several tracts from Washington, could not be confirmed because no new age data became available for about 20 years.

New data became available in 2002 from an extensive ageing project conducted in British Columbia (Bureau et al. 2002). Preliminary analysis of these data revealed some significant features: recruitment was at a global minimum around 1975, and there was a post-1975 rebound in recruitment across all coastal zones of British Columbia (Orensanz et al. 2004). Geographical coherence in recruitment across British Columbia and Washington was observed both in the decline (pre-1975) and rebound (post-1975) phases. This large-scale spatial coherence suggests that coastwide climatic forcing may underlie the pattern. Several environmental variables have shown a major shift in the Pacific Northwest around 1975 (Ebbesmeyer et al. 1991). These changes have been referred collectively as regime shifts in the Pacific Northwest, and several studies have discussed their impact on the functioning at the ecosystem (Francis et al. 1998) and species level in the Pacific Northwest (Clark et al. 1999; Strom 2002). Prominent among the environmental variables capable of influencing the coastal zone at such large scales are coastal sea surface temperature (SST) and freshwater discharges by large rivers. Proximate effects aside, the latter integrates average climatic conditions on an annual basis. Here we explore the relationship between these two factors and geoduck recruitment from Washington to the Queen Charlotte Islands and discuss alternative hypotheses proposed to explain the decline in recruitment before 1975 and its subsequent rebound in the post-1975 era.

MATERIALS AND METHODS

Age-frequency distributions based on two large samples collected during the period 1979-82 in British Columbia (n = 2,276 specimens; Breen and Shields 1983) and Washington (n = 2,157 specimens; Goodwin and Shaul 1984), used by Orensanz et al. (2000) to back-calculate time series of an index of recruitment (here used as equivalent to year-class strength), were reexamined and compared to data that recently became available. The older samples are aggregates of small subsets of data (typically fewer than 200 specimens per site) spread over the entire Puget Sound Basin in Washington and the west coast of Vancouver Island and the Strait of Georgia in British Columbia.

Two ongoing ageing programs are yielding new age-frequency distributions after a period of almost 20 years during which little new data were gathered. Bureau et al. (2002) published a large data set based on biological samples collected from 34 sites throughout British Columbia between 1993 and 2000 (fig. 1). In order to avoid analytical difficulties resulting from pooling age distributions obtained during protracted periods, only samples collected between 1996 and 1998 (18 sites, 6,416 individuals aged) were used in the analyses. In Washington new data have been generated since 2000[1]; samples already processed and utilized in this study were collected in 2001 and 2003 from three nonharvested sites (n = 1,327 specimens; fig. 1). Harstene Island (n = 831, 47°40'N, 122°48'W, south Puget Sound) was sampled in 2001, and Quartermaster Harbor (n = 332, 47°22'N, 122°17'W, south Puget Sound) and Langley (n = 165, 48°03'N, 122°25'W, north Puget Sound) in 2003.

Age-frequency distributions were used to back-calculate time series of recruitment. Calculations of relative recruitment based on samples collected in 1979–82 followed Orensanz et al. (2000). In the case of the new samples from British Columbia (collected in 1996–98),

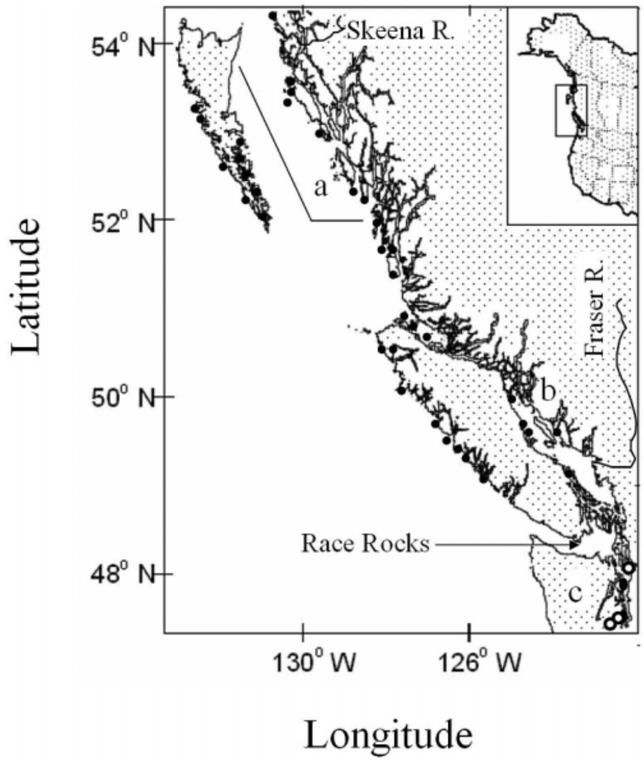

Figure 1. Geographic location of collections made during 1993–2003 in British Columbia (*black circles*) and Puget Sound, Washington (*white circles*). (*a*) North Coast, (*b*) Georgia Strait, (*c*) Puget Sound.

calculations were based on (1) the age-frequency distributions compiled by Bureau et al. (2002), (2) estimates of virgin (unfished) biomass (B_0) reported by Canada's Department of Fish and Oceans (DFO; estimation is based on density of unfished beds, total area of known beds, and mean weight; for details see Hand and Bureau 2000), (3) annual catch data for each bed (made available by DFO), and (4) a constant natural mortality coefficient, $M = 0.02$ yr^{-1}. The latter is close to the experimental estimate of Bradbury et al. (2000; 0.016 yr^{-1}) and to the value used by Washington Department of Fish and Wildlife (WDFW) (0.0226 yr^{-1}). In order to combine age-frequency distributions with catch data and estimates of B_0 (both reported in metric tons), biomass figures were converted to numbers using average weights estimated from the surveys, assuming that the harvest is nonselective; this is justified by the fact that geoducks virtually stop growing in weight over the range of ages of interest (Bureau et al. 2002). The back-calculated indexes of recruitment were aggregated at the geographical scales of the entire coast of British Columbia and the regions of Georgia Strait and the North Coast (fig. 1). Data from sites within a region were weighted by the estimated size of the population they represented. In the case of data from Washington (samples collected in 2001–2003) the back-calculations involved only natural

[1]J. Valero, D. Armstrong, and R. Hilborn, unpubl. data.

mortality, because samples were taken from unharvested sites. Relative recruitment was calculated for the 1940–90 year-classes in British Columbia and for the 1940–95 year-classes in Washington. These windows were chosen in order to avoid biases caused by the under-representation of younger ages in the samples (geoducks are fully recruited at an age of 8–10 years; Harbo et al. 1983; Bradbury et al. 1998), and of older age-classes because of poor representation.

Time series of the recruitment index obtained with samples collected over the last decade in British Columbia and Washington were used to explore correspondence with environmental variables. Time series based on data collected in 1979–82 are informative when integrated at the large geographical scale of the entire sample (Puget Sound, British Columbia), but they are difficult to use when the analysis requires adjustment of the spatial scale. Physical variables investigated as indicative of environmental forcing are sea surface temperature (SST) and the annual discharge of the Fraser and Skeena rivers (fig. 1). Long time series of SST have been collected in British Columbia through a network of lighthouses (http://www-sci.pac.dfo-mpo.gc.ca/osap/data/lighthouse/bcsop.htm; Hollister 1972; Mueter et al. 2002). The series from Race Rocks (fig. 1), in the Juan de Fuca Strait, is the longest (1922 to present; Hollister 1972) and has been previously used in other studies of the relation between climate and bivalve populations from the Pacific Northwest (Orensanz 1989; Strom 2002). The Fraser and Skeena rivers were selected because they drain the largest basins in British Columbia. Total annual (December–January) flows for the Fraser (Hope Station: 49°22.83'N; 121°27.08'W) and the Skeena (Usk Station; 54°37'50"N, 128°25'55"W) are available from http://www.msc-smc.ec.gc.ca/wsc/hydat/H2O/.

The time series of recruitment, SST, and river discharge were scaled to a maximum of 1 in order to allow comparisons between indexes with different units and ranges. In time-series analysis we are often interested in determining autocorrelations at different time lags (e.g., the relationship between SST on a particular year and SST at lag *t*). Partial autocorrelation is the relationship between the current state of the variable and the state of the variable at lag *t* when we have controlled for the correlations between all of the successive time steps between the current step and step *t* (Crawley 2002). Partial autocorrelations can be extended to two time series to determine if the patterns of ups and downs of the series are cross-correlated at different time lags (Crawley 2002). As a first quantitative exploration of the data we performed partial autocorrelations between SST, river discharge, and recruitment indexes. A more detailed formal analysis of high-frequency variability with higher spatial resolution and more refined temporal windows (e.g., intra-annual information on SST and river discharge instead of annual means or totals) is beyond the scope of this study, though it is the subject of forthcoming contributions.

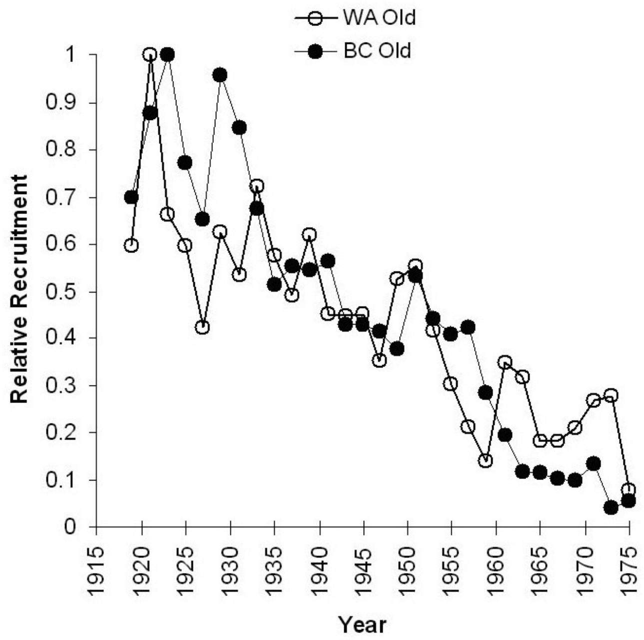

Figure 2. Trends in geoduck relative recruitment (1919–75) back-calculated from age-frequency distributions from British Columbia (data from Breen and Shields 1983) and Washington (data from Goodwin and Shaul 1984).

RESULTS

Time series of relative recruitment back-calculated from the old age-frequency distributions (1979–81) from Washington and south British Columbia (aggregated at the spatial scale of the two regions) show conspicuously similar patterns of decline during at least six decades (1920–75; fig. 2). The rate of decline of the indexes is comparable across these two large geographic domains, spanning nearly four degrees of latitude (47–51°N) of complex coastscapes. Relative recruitment calculated from age-frequency distributions of samples collected in British Columbia (54°N to 48°N) during the period 1996–98 shows a very similar pattern: a declining trend after 1940 and a minimum during the mid-1970s (fig. 3). The more recent data shows a consistent post-1975 rebound, reaching pre-decline levels during the early 1990s (fig. 3). In the case of Washington, new data are available from only three sites. Of these, Harstene Island is located in the southern part of Puget Sound (fig. 1), close to the Dougall site (n = 459, 47°19'N,122°50'W), sampled during the period 1979–82 (Goodwin and Shaul 1984). A comparison of the two series shows a similar pattern: while both show a distinct post-1940s decline, there is substantial high-frequency (year-to-year) variability (fig. 4). Both show,

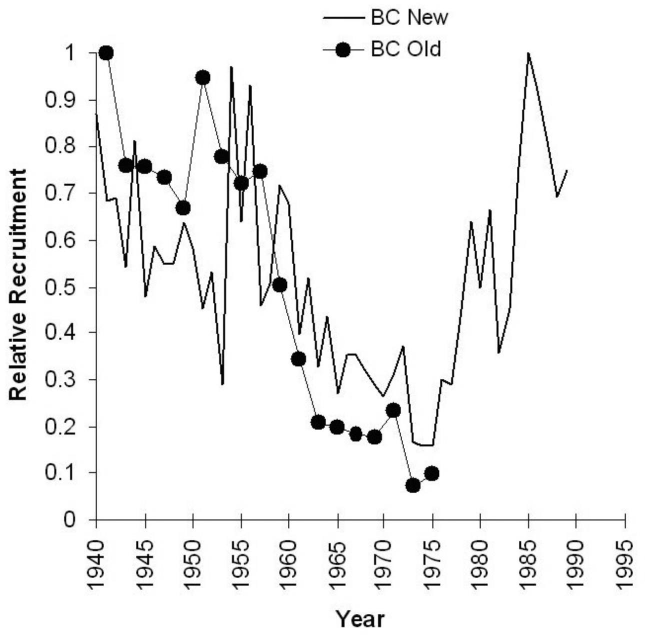

Figure 3. Trends in geoduck relative recruitment back-calculated from old (data from Breen and Shields 1983) and new (data from Bureau et al. 2002) age data from British Columbia.

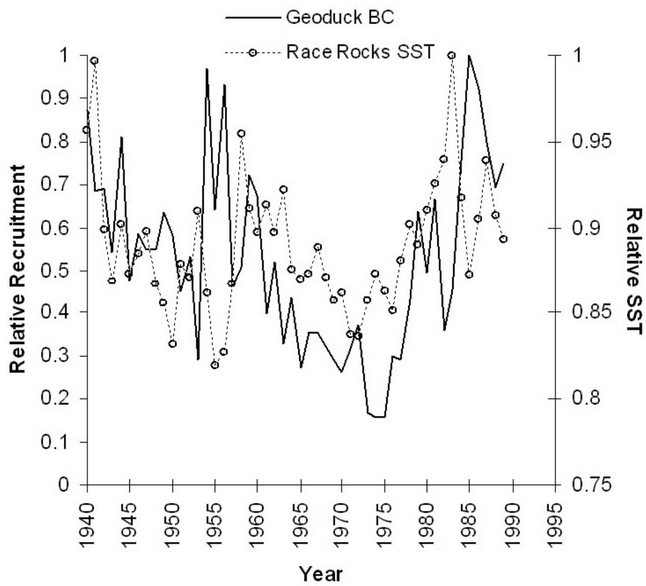

Figure 5. Time series of geoduck relative recruitment back-calculated from age-frequency distributions from British Columbia (data from Bureau et al. 2002) and relative sea surface temperature (SST) at the Race Rocks Station (data from Fisheries and Oceans Canada).

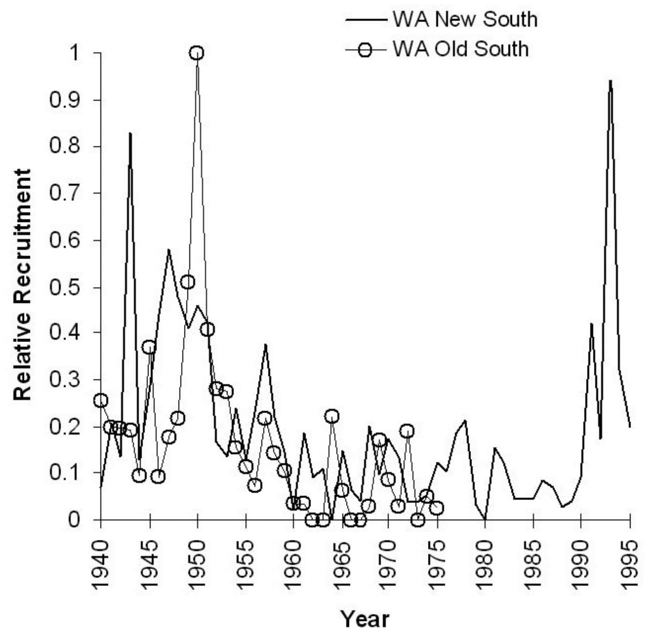

Figure 4. Trends in geoduck relative recruitment back-calculated from old (data from Goodwin and Shaul 1984) and new (data from this study) data collected from two closely located sites from Puget Sound: Dougall (sampled in 1979–81) and Harstene Island (sampled in 2001).

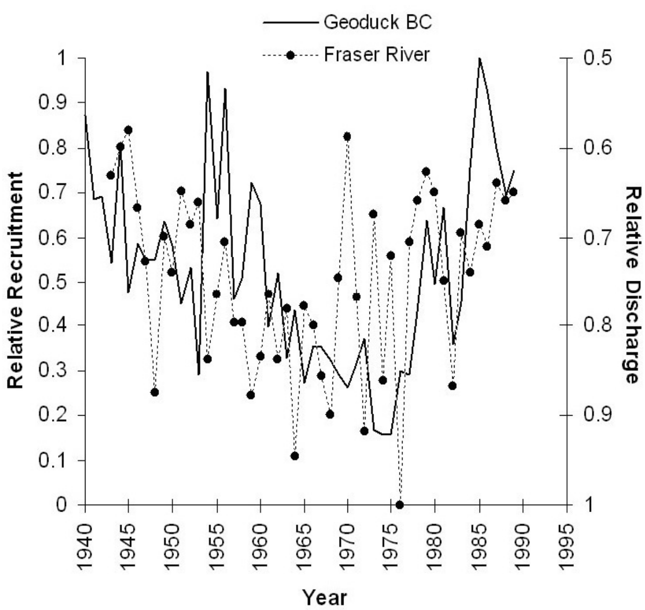

Figure 6. Time series of geoduck relative recruitment back-calculated from age-frequency distributions from British Columbia (data from Bureau et al. 2002) and relative Fraser River discharge at the Hope Station (data from Environment Canada).

on average, very weak year-classes during the 1960s and 1970s. The recent data shows a rebound of recruitment during the 1990s, reaching (as in British Columbia) pre-decline levels. Similar comparisons for the other two sites are precluded by the lack of comparable sampling sites in the earlier data series. Long-term trends of recruitment based on samples collected during 1996–98 in British Columbia are very consistent with long-term trends in SST recorded at Race Rock during the same period (fig. 5). Although there is considerable miss-match in year-to-year (high-frequency) fluctuations, there are significant positive cross-correlations at the 5% level at different lags.

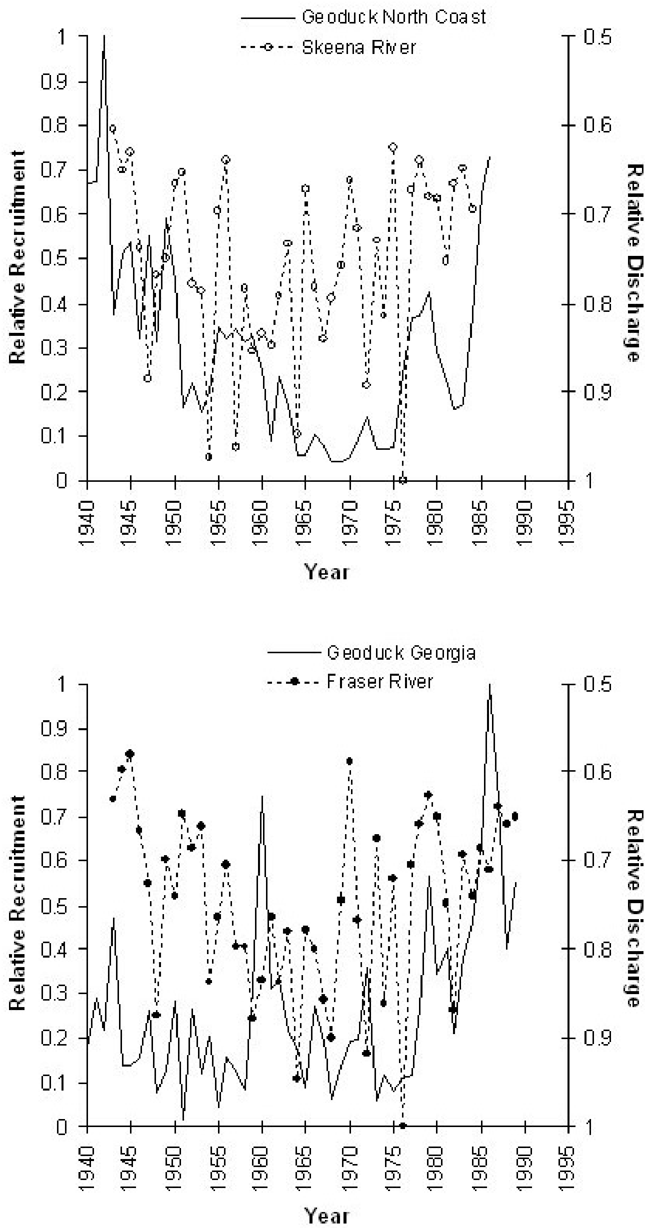

Figure 7. Time series of geoduck relative recruitment back-calculated from age-frequency distributions from the North Coast (*top panel, solid line*) and Georgia Strait (*bottom panel, solid line*; data from Bureau et al. 2002) and relative river discharge for the Skeena (*top panel, white circles*) and Fraser Rivers (*bottom panel, black circles*).

Discharge from the Fraser River showed an upward trend during the 1940s and 1950s. On average it remained relatively high during the 1960s and early 1970s (the maximum was reached in 1976), then during the 1980s it declined back to the level of the 1940s (fig. 6). In spite of strong year-to-year variability there is consistency between the long-term trends in flow discharge and geoduck recruitment (decreasing when river discharge increases, and vice versa). This is supported by significant negative cross-correlations at the 5% level at different lags.

The pattern seems to fade if the spatial resolution is increased to examine recruitment in the North Coast region in relation to annual discharge from the Skeena, and in the Strait of Georgia in relation to the annual discharge from the Fraser River (fig. 7). In spite of that, there are still significant negative cross-correlations at the 5% level. Year-to-year variation in the discharge from the Skeena River is very high, and the period of frequent high flows was more extended than in the Fraser, lasting from the mid-1950s to the mid-1970s. Recruitment in the North Coast region showed (as the aggregated British Columbia series did) a declining trend during the 1940s and 1950s and a rebound after 1975. By contrast, the period of low back-calculated recruitment is more protracted, extending over a decade (1964–75; fig. 7, *top*). Relative recruitment in the Strait of Georgia shows a post-1975 increase comparable to that observed in highly aggregated data, but there is no indication of a pre-1975 decline (fig. 7, *bottom*). In this region the back-calculation is based on two of the historically most heavily fished beds in British Columbia (Comox and Oyster rivers).

DISCUSSION

Orensanz et al. (2000, 2004) discussed a puzzling pattern in time series of year-class strength back-calculated for geoduck populations from the Pacific Northwest: a decades-long decline that reached a minimum during the mid-1970s, followed by a rebound to pre-decline levels during the 1980s and 1990s. Although subject to some regional variability, the general pattern appears very robust, showing up in data collected in various ways during 1979–82 and 1993–2001. While the pre-1975 decline (or at least a scarcity of young individuals in samples collected during the early 1980s) had been noticed in previous studies (Sloan and Robinson 1984; Bradbury et al. 1998), it was interpreted as an artifact created by patchiness (Breen and Shields 1983; Goodwin and Shaul 1984) or as the result of gear selectivity. The artifact of patchiness should disappear when data from many locations at a large geographical scale are pooled, but the pattern persists after pooling (Orensanz et al. 2000). With regard to gear selectivity, there is wide consensus that it can be assumed that geoducks are fully recruited by age 8–10 years (Harbo et al. 1983; Bradbury et al. 1998). It is interesting to notice that the only subset of the data in which the pre-1975 decline was not evident corresponds to the samples collected in 1996–98 from the Strait of Georgia. The two locations sampled correspond to the most intensely fished beds in British Columbia (the Comox and Oyster Rivers); this could cause errors in the back-calculation. Analysis of recent data (not included here) from an unharvested bed in the Strait of Georgia (South Round Island) may provide a valuable contrast.

Although the pattern appears robust, no attempts have been made to explain it. In the context of management it was noticed that the pre-1975 decline is not attributable to commercial harvesting (the decline started long before the onset of the fishery) or other anthropic influences (the decline was evident in pristine and in highly disturbed regions). Here we present evidence indicating that long-term trends in geoduck year-class strength in the Pacific Northwest parallel environmental indexes that indicate conditions prevailing in coastal environments at the regional scale. We show correspondence between time series of geoduck year-class strength, SST, and the discharge from the two largest rivers in British Columbia, the Skeena and the Fraser (no comparable rivers drain into the Puget Sound Basin). Trends in geoduck recruitment are coherent over a large geographic range, spanning approximately seven degrees of latitude (47–54°N; fig.1). River discharge integrates many environmental factors likely to have proximate local effects on a regional scale, including peripheral coastal zones (like Puget Sound) where there is no significant driver drainage. While many of the factors integrated are likely to influence the dynamics of populations of benthic sedentary organisms with pelagic larvae, the nature of the proximate operating mechanisms remains open to speculation.

The year-class strength minimum around the mid 1970s matches a period of low SST (the lowest in the post-1940 decades) and a high frequency of years with strong discharge from major rivers (figs. 5–7). Connections between environmental conditions and year-class strength in benthic organisms may involve temperature-related events in the reproductive calendar (e.g., Bonardelli et al. 1996), since sedentary organisms (unlike fish) cannot move to their preferred environment. Other sensitive processes are the advection/retention and survival of pelagic larvae. Delayed spawning during cold years or larval flushing off coastal environments during years of strong river discharge could possibly affect geoduck year-class strength. Extending the analysis to include additional variables such as wind, upwelling, and primary productivity should shed light on the processes responsible for the pattern described in this work.

Evidence of decadal climatic forcing of productivity in northeastern Pacific marine populations, ranging from plankton to marine mammals, has accumulated in recent years and has been widely discussed in the literature (Francis et al. 1998). One of the most conspicuous low frequency events of the last decades was a set of changes in environmental conditions that is referred to collectively as the 1976–77 regime shift (Ebbesmeyer et al. 1991; Francis et al. 1998; Hare and Mantua 2000). Phytoplankton and zooplankton productivity changed in response to the shift (Brodeur and Ware 1992; Polovina et al. 1995; Roemmich and McGowan 1995), with suggested cascading effects on survival of marine fish larvae (McFarlane and Beamish 1992). Year-class strength of groundfish (Hollowed and Wooster 1992; Clark et al. 1999) and salmon stocks (Hare and Francis 1995; Beamish et al. 1999) show coherence with environmental factors at decadal rather than annual scales. In the case of geoduck recruitment, long-term change appears to have been a gradual process that extended over decades.

Most studies of low frequency (decadal) forcing in marine systems have attended to mobile species in open oceanic ecosystems. Sedentary species from coastal ecosystems have attracted less attention, in part because of the difficulties posed by the spatial heterogeneity of such systems. Year-class strength of little neck clam (*Protothaca staminea*) in Garrison Bay (north Puget Sound, Washington) has been shown to be positively correlated with SST (Orensanz 1989) measured at Race Rocks, paralleling the pattern documented here for geoducks. There is indication of similar patterns in other bivalves of the Pacific Northwest, like butter and manila clams (A. Strom, pers. comm.). Previous work on climatic forcing on geoduck populations focused on patterns of growth rate, in which case the unit used to reconstruct a trend is an individual (Noakes and Campbell 1992; Strom 2002). In the case of year-class strength the detection of pattern is complicated by spatial heterogeneity. Strong year-classes should not be expected to be homogeneously distributed in space. Rather, a period of increasing year-class strength could consist of increasingly frequent but spatially localized pulses of settlement or recruitment, implying that series back-calculated for different locations can show little high-frequency spatial coherence. Interpretation of year-class strength data at different spatial scales requires aggregating the data at the appropriate scale.

The results presented here are exploratory. A detailed and formal analysis will require attention to (1) high-frequency (year-to-year) variability, (2) higher spatial resolution (analysis of the full data set with algorithms of hierarchical pooling) of both biological and environmental variables (e.g., Mueter et al. 2002), (3) more refined temporal windows (e.g., intra-annual information on SST and river discharge instead of annual means or totals), (4) potentially lagged responses, and (5) sequences of environmental events rather than events in isolation (e.g., Logerwell et al. 2003). These are beyond the scope of this study, but they are the subject of ongoing research by the authors.

Given geoducks' extreme longevity, the alleged stability of populations and the sustainability of the fisheries that they support could possibly be more apparent than real. Geoduck abundance changes slowly, the impact of recruitment variability being buffered by the large number of year-classes present in a population. Trends in abundance can be perceived only by examining long time series of data and understood only if placed in the context of long-term trends of climatic change.

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