Population Dynamics of Razor Clams in Samut Songkram, Thailand

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We have measured the population density of razor clams, *Solen regularis*, as well as a related but economically less valuable species, *Solen vitreus*, at the same locations in the Don Hoi Lord mud flats in Samut Songkram, Thailand at monthly intervals from November, 1995 to March, 1997. The density of clams in each size class vs. time was fit by a simple population evolution model in terms of birth, growth, and death (e.g., by harvesting). The results indicate a growth rate of approximately 1 cm per month, the appearance of new clams during March-April and July-August, and intensive harvesting of larger clams during April-November. In addition to seasonal variations, a comparison with data from previous studies indicates a twelve-fold decline in the population of razor clams (*S. regularis*) since 1994-1995, while the population of *S. vitreus* declined only four-fold. We interpret this to indicate that environmental factors are responsible for a four-fold decrease in both clam populations, while intensive, selective harvesting of *S. regularis* has driven down its population by an additional factor of three.

Key words: Razor clams, *Solen regularis, Solen vitreus,* population dynamics.

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การเปลี่ยนแปลงประชากรหอยหลอดที่สมุทรสงคราม ประเทศไทย

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คณะผู้วิจัยได้หาความหนาแน่นประชากรของหอยหลอด *(Solen regularis)* และหอยหิน *(Solen vitreus)* ซึ่งมีลักษณะคล้ายกับหอยหลอดแต่มีมูลค่าทางเศรษฐกิจน้อยกว่า ณ ตำแหน่งเดิมที่ดอนหอยหลอด จังหวัดสมุทรสงคราม ประเทศไทย ประมาณเดือนละครั้งตั้งแต่พฤศจิกายน 2538 จนถึงมีนาคม 2540 ความหนาแน่นประชากรหอยในแต่ละกลุ่มขนาดต่อเวลาสามารถเปรียบเทียบกับผลจากแบบจำลองของการเปลี่ยนแปลงประชากรซึ่งพิจารณาภาวะเจริญพันธุ์ การเติบโต และการตาย (เช่น จากการเก็บหอยของมนุษย์) ผลการเปรียบเทียบนั้นแสดงว่า หอยหลอดมีอัตราเติบโตประมาณ 1 ซม. ต่อเดือน โดยเริ่มพบหอยขนาดเล็กในเดือนมีนาคม-เมษายน และกรกฎาคม-สิงหาคม และมีการเก็บหอยขนาดใหญ่ส่วนใหญ่ในเดือนเมษายน-พฤศจิกายน นอกเหนือจากการเปลี่ยนแปลงตามฤดูกาล การเปรียบเทียบกับผลจากการศึกษาในอดีตทำให้เห็นว่า ประชากรหอยหลอด *(S. regularis)* ลดลง 12 เท่าตั้งแต่ปี 2537-2538 แต่ประชากรหอยหิน *(S. vitreus)* ลดลงเพียง 4 เท่า เราตีความว่า ปัจจัยทางสิ่งแวดล้อมทำให้ประชากรของหอยทั้งสองชนิดลดลง 4 เท่า และการเก็บเฉพาะหอยหลอดโดยมนุษย์เป็นปัจจัยที่ทำให้ประชากรหอยหลอดลดลงเพิ่มขึ้นอีก 3 เท่า

คำสำคัญ หอยหลอด *Solen regularis* *Solen vitreus* การเปลี่ยนแปลงประชากร

INTRODUCTION

The mud flats found in certain river estuaries are alternately exposed and flooded by the tides, and host a unique type of ecosystem with a wide variety of specially adapted organisms. Among such organisms, razor clams (Figure 1) have received special attention because of their economic value as food for humans and for recreational harvesting [1]. The site in Thailand that is most famous for razor clams is the Mae Klong estuary in Samut Songkram Province, commonly known as Don Hoi Lord ("razor clam mud flats").

Figure 1. One of the largest razor clams found in this study (length ≈ 7 cm). Intensive harvesting in Samut Songkram does not allow many clams to reach this length.

In terms of scientific study, there are quantitative records of the population density of razor clams at Don Hoi Lord dating back to 1981 [2-6], which makes this species well suited for a study of population dynamics. In addition to their economic importance, it is believed that razor clams, and bivalves in general, provide sensitive indicators of any environmental degradation of an ecosystem. With this motivation, we undertook a new survey of the razor clam population at monthly intervals from November, 1995 to March, 1997; this record is complete except for weather-related data gaps in February and September of 1996.

The razor clams at Samut Songkram have been identified as belonging to the species *Solen regularis* [2], a member of the genus *Solen* originally classified by Linnaeus in 1758 [7] as part of Order Bivalvia and Phylum Mollusca. There is a closely related species, *Solen vitreus* (locally known as "hoi hin," or rock clam), which is indistinguishable from *S. regularis* to the untrained observer. They are physiologically very similar; both species are filter feeders that burrow into the mud in a river estuary environment. However, *S. vitreus* is somewhat smaller, and is generally not harvested by local fishermen, who say it is not tasty. This fortuitous

Figure 2. Map of the Don Hoi Lord Area of Samut Songkram Province.

circumstance gives us a way to separate the effects of specific harvesting of *S. regularis* from environmental effects that should affect both species in roughly the same way, given their close similarity; thus we have collected and analyzed samples of both species.

METHODOLOGY

During each month, at the time of the lowest tide, we took samples at 10 locations at 100-m intervals due south of the Krommaluang Chumporn Monument, completely transecting the nearest mud flat and with one sample on the mud flat to the south. Figure 2 shows a map of the region, and Figure 3 indicates the coordinates at which samples were taken. Three 1-m^2 quadrats (separated by 25 m East-to-West) were examined at each of 10 locations (separated by 100 m North-to-South), and we aimed to capture all razor clams within each quadrat (Figures 4 and 5). The three quadrats at any given latitude were taken to be three replicate samples for that location (latitude). There are major differences in the mean exposure, salinity, etc., depending on the height of each location on a mud flat, so we aimed to sample approximately the same locations each month. The primary means of location were using a compass (or the stars) and pacing off distances of 25 m or 100 m. A Global Positioning System (GPS) receiver was used only to determine the first position, to verify the 10 positions, and to guard against any cumulative error in the pacing.

Because we concentrated on these locations, strictly speaking our results only address the population dynamics of razor clams in these locations, i.e., across the nearest mud flat and on one part of the next mud flat to the south. However, during December, 1995 we did collect samples from a mud flat to the east of these, and found a population density almost identical to that on the nearest mud flat; therefore, this project has taken at least some data on 3 of the 5 mud flats [6] of the Mae Klong Estuary. Furthermore, as will be discussed later, anecdotal evidence from local fishermen, as well as market prices, support the qualitative applicability of our results to the Mae Klong Estuary as a whole.

RESULTS

Population of Razor Clams vs. Time

Estimates of the population density of razor clams at Samut Songkram from 1981 to 1997 are summarized in Figure 6, and data from the present work are shown for an expanded time scale in Figure 7. There were some differences in the data collection methods used at different times. For example, in 1981 the clams were collected according to the harvesting method commonly used by local fishermen, in which CaO is inserted into visible clam holes, and clams are harvested as they escape to the surface (Figure 4). However, in all later work (including the present work), the additional step was taken to dig out the mud in each 1-m^2 quadrat to a depth of ≈20 cm and search for additional clams within the dirt by hand (Figure 5). Therefore, it is possible that the 1981 data may underestimate the true population density at that time. Furthermore, previous studies collected samples from a variety of locations, whereas in the present study we used GPS technology to ensure that we revisited the same locations in each month. At any rate, the study of 1994-1995 [6] collected data from similar locations, so at least these results should be directly comparable to the present results.

Figure 4. The first stage of collecting clams in a 1-m^2 quadrat: according to the harvesting method commonly used by local fishermen, CaO is inserted into visible clam holes, and clams are harvested as they escape to the surface.

Figure 5. The second stage of collecting clams in a 1-m^2 quadrat: digging out the mud to a depth of $\approx$20 cm and searching for clams by hand.

Figure 6. Population density of razor clams *(Solen regularis)* in Samut Songkram during 1981-1997 as measured by previous work (solid circles; Refs. 2-4, 6) and the present work (open circles).

With these caveats in mind, several conclusions can be drawn from Figure 6. The razor clam population has been highly variable in recent years. Furthermore, there are strong intra-annual (seasonal) variations, which implies that at least a year's worth of data is necessary for a meaningful analysis of the population density. For quantitative analysis, we concentrate on the final two sets of data from 1994-1995 [6] and 1995-1997 (the present work), which were taken from similar geographic locations. In general, the population of razor clams was drastically lower in the later time period. More specifically, comparing a year's worth of data from April, 1996 to March, 1997 with data from June, 1994 to May, 1995, there was a 12-fold decrease in the average razor clam population density from 49.5 m^{-2} in 1994-1995 to 4.1 m^{-2} in 1996-1997 (Table 1). This sharp decline could be due to environmental factors, or due to harvesting by humans; in a later section we seek to distinguish between these two mechanisms.

Table 1. Mean population density of *Solen regularis* and *Solen vitreus* during June 1994 - May 1995 and during May 1996 - April 1997.

Species	Mean density per m^2	
	6/94 to 5/95	5/96 to 4/97
S. regularis	**49.5**	**4.1**
S. vitreus	**25.8**	**6.7**
Ratio	**1.92**	**0.61**

1 From Reference 6.

Regarding seasonal variations, in Figure 7 we see that the razor clam population rapidly increased during March-April and July-August of each year. A similar pattern was observed during 1994-1995. In the present work, the maximum population density was 10.7 m^{-2} and the minimum was 0.13 m^{-2}, representing an 80-fold variation. In contrast, the seasonal variations during 1994-1995 were only 15-fold. Note also the two points shown for December, 1995 in Figure 7 (see arrow), which indicate the (very similar) population density of razor clams measured at locations 1-4 on the nearest mud flat and measured on the next mud flat to the east.

Population of Razor Clams vs. Time and Length

Each individual clam's size (shell length) was measured, enabling us to analyze their size distribution at each sampling time (Figure 8). Similar data from a previous study during 1994-1995 are shown in Figure 9; note the 10-fold increase in the overall scale in population density. This type of data is analogous to the life table used in human population studies, the insurance industry, etc. Therefore, we aim to fit these data in terms of a mathematical model of the basic population processes affecting razor clams: fertility, growth, and mortality. We believe that any effect of migration can be neglected because razor clams and rock clams generally burrow in the mud and do not move much; we will present further justifications for neglecting this process in the Discussion section. For the present purposes, we consider fertility in terms of the number of clams that survive the larval stage and burrow into the ground to commence the adult stage of the life cycle. For growth, we assume a linear increase in length with time, because the lengths of clams that we found in the field are essentially all in the régime where the growth curve [4] is approximately linear. Finally, mortality, which includes harvesting, is assumed to be a time-independent function of length (representing the fact that larger clams are easier to harvest) multiplied by a time-dependent factor which represents seasonal variations in harvesting (for example, harvesting is less convenient in the winter of November to February, when the lowest tide occurs during the nighttime).

Figure 7. Seasonal variation of the population density of razor clams during 1995-1997.

Qualitatively, Figures 8 and 9 give a consistent picture in which it is possible to follow a cohort of razor clams as they grow from month to month. In both sets of data, a new cohort of small clams begins to appear in March-April and again in July-August, and the peaks in the density distribution move to longer lengths with time, representing the growth of individual cohorts. Presumably the seasons in which razor clams lay their eggs are shortly before these times of the year. The observation of peaks only at lengths of 2 cm or greater indicates that data collection was incomplete for the smaller clams, which are difficult to find in practice. For this reason, we only apply a quantitative analysis to clams of 3 cm in length or longer. It can also be seen that harvesting has been so aggressive that almost no clams have survived to a length of 7 cm, whereas razor clams can grow to much greater lengths in the absence of human interference.

We model the population dynamics of razor clams by using a transport equation in the form of a Fokker-Planck equation [8], a type of equation which is widely used in biology (Refs. 9, 10, and references therein) and in other fields such as physics and astrophysics [e.g., 11]:

$$\frac{\partial n(t,\ell)}{\partial t} = -G\frac{\partial n(t,\ell)}{\partial \ell} - M(t)m(\ell)n(t,\ell) \quad (1)$$

along with the boundary condition,

$$n(t,\ell=0) = B(t)/G, \qquad (2)$$

where n is the number of razor clams per m^2 per cm of length,
t is the time,
ℓ is the length,
G is the rate of growth (cm per

month),

Mm is the probability of death per unit time, and

B is the rate of young adult clams initially burrowing into the mud per m^2 per unit time.

Figure 8. Length distribution of razor clams at various times during 1995-1997.

In practice, because of the difficulty of measuring the population of clams smaller than 3 cm, we used the measured density of clams of 3.0-3.9 cm in length, $n(\ell = 3)$, and $n(\ell)$ for the first month of data (November, 1995) as the boundary conditions, and assumed that each cohort grows at a constant rate and each cohort's population changes further only due to mortality.

For a statistical comparison between the data and the model, we use a discrete form of the transport equation:

$$\begin{aligned} n(t+\Delta t, \ell) = n(t, \ell - G\Delta t) \\ - M(t)m(\ell)n(t, \ell - G\Delta t)\Delta t \end{aligned} \quad (3)$$

where Δt is the time between samplings. The values of $M(t)\Delta t$ and $m(\ell)$ were chosen empirically to fit the data, as was $n(\ell = 3)$ for times when data were not taken. We only fit data from the present study, for which we are confident the data were taken from the same geographical locations during each month, and we only fit data from November, 1995 to November, 1996, because the razor clam population was extremely low during December, 1996 to February, 1997, making a statistical analysis difficult. During some months the number of samples was lower than 30 because we were unable to collect more samples during the short time of the low tide.

Figure 9. Length distribution of razor clams at various times during 1994-1995 (data from [6]). Note the 10-fold change in the vertical scale as compared with Figure 8.

The data that were fit are shown in Table 2. In the model, we consider values of $G = 0.5$, 1, and 2 cm/month. It should be noted that we did not initially anticipate a 12-fold decrease in the average density of razor clams (compared with the previous study), and thus these data were in general of much poorer statistical quality than we had expected. Furthermore, the χ^2 values of the fits (calculated using the counting uncertainty $\sigma = \sqrt{N}$) were completely dominated by a few poorly-fit data points for which the measured number of clams was highly inconsistent with the model. The chi-squared values for $G = 0.5$ and $G = 1$ were similar, but we found that for $G = 1$ there is only one remaining data point (out of 50 data points that were fit) that is highly inconsistent with the model, i.e., for clams of 4.0-4.9 cm during July, 1996. Therefore, we conclude that the results are most consistent with a growth rate of 1 cm per month. The results of the fit are shown in Table 3.

Table 2. Measured length distribution of razor clams vs. time for shell lengths ≥ 3 cm. The number of 1-m^2 quadrats sampled is indicated by *N*. Blank cells indicate data gaps.

		Number of clams per m² in each size class					
Month	*N*	**3.0-3.9 cm**	**4.0-4.9 cm**	**5.0-5.9 cm**	**6.0-6.9 cm**	**7.0-7.9 cm**	**8.0-8.9 cm**
Nov. '95	30	0.13	0.63	0.97	0.67	0.07	0.00
Dec. '95	12	0.08	0.58	1.75	1.33	0.25	0.08
Jan. '96	30	0.47	0.20	0.47	0.27	0.00	0.00
Feb. '96							
Mar. '96	23	2.26	0.26	0.09	0.17	0.09	0.00
Apr. '96	30	5.73	1.33	0.77	0.47	0.10	0.00
May '96	30	2.10	1.60	0.10	0.07	0.00	0.00
Jun. '96	12	0.42	1.50	0.17	0.00	0.17	0.00
Jul. '96	10	1.70	2.60	0.70	0.10	0.00	0.00
Aug. '96	30	3.27	1.37	0.77	0.20	0.03	0.00
Sep. '96							
Oct. '96	25	1.94	0.67	0.83	0.22	0.00	0.00
Nov. '96	27	0.74	0.74	0.42	0.05	0.00	0.00

Population of Razor Clams and Rock Clams

Figure 10 shows the population density of rock clams, *S. vitreus*, during the course of this study, and can be directly compared with Figure 7, which shows analogous data for razor clams, *S. regularis*. One difference between the two time series is that *S. vitreus* exhibits less extreme depletions during the cool season: the minimum measured population density is only about 6 times lower than the maximum, in comparison with an 80-fold difference for *S. regularis*. This difference can be attributed to the harvesting of *S. regularis* by humans, even during the season of minimum population density. As mentioned earlier, local fishermen intentionally try not to harvest *S. vitreus* because of an apparent lack of market value. Aside from the different depletions during the cool season, the two species exhibit qualitatively similar seasonal variations, and seem to share the same hatching periods. Along with the close physiological and behavioral similarity between the two species, this justifies a direct comparison between the mean year-round populations of razor clams and rock clams as observed in this study and in previous work nearly two years earlier [6] (Table 1).

Table 1 indicates that the population density of *S. regularis* decreased by a factor of 12 from a one-year period of observations during 1994-1995 to a one-year period during 1996-1997. At the same time, the population density of *S. vitreus* decreased by only a factor of 4. Given the close biological similarity between the two species, it would seem that external, environmental factors should affect the two populations similarly.

Table 3. Model length distribution of razor clams vs. time based on equation 3 for $G=1$. Values of $M(t)\Delta t$ and $m(\ell)$ are also indicated.

Month	$M(t)\Delta t$	Number of clams per m^2 in each size class					
		3.0-3.9 cm	4.0-4.9 cm	5.0-5.9 cm	6.0-6.9 cm	7.0-7.9 cm	8.0-8.9 cm
Nov. '95	0	0.13	0.63	0.97	0.67	0.07	0.00
Dec. '95	0	0.08	0.13	0.63	0.97	0.67	0.07
Jan. '96	0.2	0.47	0.08	0.13	0.63	0.97	0.67
Feb. '96	0.05	0.26	0.44	0.07	0.11	0.51	0.77
Mar. '96	0	2.26	0.26	0.42	0.06	0.10	0.48
Apr. '96	0.7	5.73	2.26	0.26	0.42	0.06	0.10
May '96	0.6	2.10	4.59	0.84	0.08	0.13	0.02
Jun. '96	0.5	0.42	1.74	2.12	0.34	0.03	0.05
Jul. '96	0.4	1.70	0.36	0.96	1.06	0.17	0.02
Aug. '96	0.7	3.27	1.51	0.23	0.58	0.64	0.10
Sep. '96	0.8	0.75	2.61	0.56	0.07	0.17	0.19
Oct. '96	0.8	1.94	0.58	0.74	0.11	0.01	0.03
Nov. '96		0.74	1.50	0.16	0.15	0.02	0.00
$m(\ell)$			0.285	0.895	1	1	1

On the other hand, the extreme difference in market value implies very different harvesting patterns. During the time of this study, 1 kg of dried razor clams (without their shells) sold for 300 baht in Bangkok markets. This high market value (perhaps due to the low population of razor clams) can also explain the extreme depletion of razor clams that we observed during the cool season of 1996-1997. On the other hand, rock clams are reportedly not tasty and apparently have no market value unless they are mistakenly sold as razor clams. Also, the more marketable razor clams are the larger ones, and rock clams are rarely found to be longer than 5 cm.

All this explains why local fishermen, who can visually distinguish between the two species, intentionally select razor clams for harvesting. Therefore, we attribute the difference between changes in the population density of the two species to this difference in human harvesting behavior. Our interpretation of the data in Table 1 is that environmental factors can explain a 4-fold decrease in the mean population density of both species, and intensive harvesting explains the extra 3-fold depletion of razor clams, for a total 12-fold decrease.

Figure 10. Seasonal variation of the population density of rock clams *(Solen vitreus)* during 1995-1997.

DISCUSSION

The particularly drastic decline in the razor clam population density measured during January-February, 1997 represents a density nearly 100 times lower than ever observed in previous studies. The qualitative conclusion of an extremely low population density is supported by anecdotal evidence from local fishermen. They reported unusually intensive harvesting, including harvesting by non-locals, and the occasional use of unorthodox and destructive harvesting methods. One of them, aged about 30, said that time period had the fewest she had ever seen, having harvested clams ever since her childhood. Even before this time, the density of clams was so low that razor clam fishermen from Samut Songkram started looking for clams elsewhere, and when we went in July, 1996 for our pre-arranged field work, the fishermen who usually helped us had gone to harvest razor clams in Samut Prakan Province instead. Further evidence of the rarity of razor clams at that time came from the unusually high market price (which in turn helps drive further depletion of the population density). All this anecdotal evidence supports the qualitative applicability of our results on the average depletion of razor clams from earlier years to the Mae Klong Estuary as a whole.

Regarding environmental effects, to which we attribute a 4-fold decrease in the population density of rock clams, and part of the decrease in the population density of razor clams, there is less evidence for particular environmental damage during the time of this study. However, many harmful practices undoubtedly continue, and may contribute to a gradual environmental degradation. For example, during one of our field trips we saw a large boat, which the locals said had come to dump chemical waste from factories upriver. The presumably continued waste disposal practices of factories along the length of the Mae Klong River is a concern for the general environmental health of the estuary [6].

Populations of bivalves are generally able to rebound quickly from severe depletions [1], so we do not claim that the present trend of razor clam depletion at Don Hoi Lord in Samut Songkram Province will lead to their disappearance, and even if it did, there are other regions where razor clams are known to be present (e.g., Samut Prakan Province) or reported to be present (e.g., Trad Province). However, if the factors behind the depletion remain, the population density can be expected to remain low, and this does have implications for the ecosystem and for the economy of the region. The name Don Hoi Lord explicitly refers to the presence of razor clams, and numerous communities of fishermen rely on razor clam harvesting for much of their income. Don Hoi Lord is a well-known tourist destination within Thailand and as such is important to the economy of the province.

It is useful to consider in more detail the justification of the neglect of migration effects in our mathematical model of the population dynamics. First, it is widely believed that these organisms generally do not migrate substantially after initially burying themselves in the ground. Second, a systematic gradient in the razor clam density was observed within the nearest mud flat, and especially between there and the next mud flat. However, if there were a random (diffusive) migration process that substantially affected the population, it would affect the population in a way that removes local gradients, especially the sharp gradient between the nearest mud flat and the next one. Similarly, a systematic (advective) flow, if it significantly affected the population, would also not maintain that sharp gradient in one place. As our final justification, we note that the model is basically successful in its present form, as evidenced by the following features: a) cohorts with a high population density are evident as peaks in the length distributions which move to higher size classes as the clams grow, and b) the mortality parameters derived from the fit are consistent with known harvesting practices, as will be discussed shortly. If migration were substantially affecting the population dynamics, we would not expect such a clear cohort structure, with cohort mortality experiences correlating well with known harvesting habits.

Detailed modeling of the population dynamics of razor clams in their natural environment can provide useful information on their reproductive periods, growth rate, and the death rate as a function of size class and time, which is apparently strongly influenced by human harvesting. The present work has yielded such results, despite low statistics resulting from the record low abundance of razor clams. Our model of the dynamics of the population density of razor clams in each size class yields a best-fit growth rate of 1 cm per month. We treat the mortality rate as a product of two factors, one depending on the length of clams and one depending on time. Our inferred values for the length-dependent factor $m(\ell)$ (see Table 3) indicate much less harvesting of clams smaller than 5 cm. The time-dependent factor $M(t)\Delta t$ indicates little harvesting during the cool season of November, 1995 – March, 1996 and intensive harvesting during April, 1996 – October, 1996. (Note, however, that the record-low periods of January-February, 1997 were not included in the analysis due to poor statistics reflecting the extremely low population density.) This is consistent with the times of low tide being at night during November-March (making harvesting less convenient) and during the day in other months (making harvesting more convenient). These results regarding the mortality of razor clams are all consistent with the known habits of local fishermen. We hope that the type of modeling that we developed for this analysis will also prove useful for the analysis of other biological populations.

CONCLUSIONS

Measurements of the population density of razor clams, *Solen regularis,* in Samut Songkram Province, Thailand during November, 1995 – March, 1997 indicate the lowest population density ever documented. We have examined seasonal variations within the time period of this study in terms of a population dynamics model, verifying that seasonal population increases are due to the hatching of young (small) clams and that rapid population declines during certain times are due to intensive harvesting of larger clams by humans. The best fit is obtained for a growth rate of approximately 1 cm per month. We also find a twelve-fold decline in the yearly averaged population of *S. regularis* during April, 1996 - March, 1997 compared with that found in a previous study during June, 1994 - May, 1995 on the same mud flat [6]. Over the same time period, the population of a similar but economically non-valuable species, *S. vitreus,* decreased only four-fold. Our interpretation is that environmental effects are responsible for a 4-fold decrease in the mean population density of both species, while selective harvesting of razor clams explains their depletion by an extra factor of three, resulting in a total twelve-fold decrease.

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