Invaders in the open sea: Establishment of the New Zealand snail *Philine auriformis* in southern California coastal waters

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ABSTRACT - In late 1994, *Philine auriformis*, a clam predator from New Zealand, first appeared in Southern California Bight (SCB) coastal waters. This is one of a few documented exotic species introductions to shelf communities; most are reported from bays, harbors, or the intertidal zone. *P. auriformis* was first collected in California from San Francisco Bay in 1993, and spread within a year to Bodega Bay to the north. In the SCB, the *P. auriformis* invasion was tracked from its inception by outfall monitoring programs off the Palos Verdes Peninsula and San Diego, and regional monitoring programs that sampled throughout the Bight in 1994 and 1998. All four programs used trawls to indicate the occurrence and relative prevalence of larger individuals and benthic grabs to estimate population density, including small individuals. The first specimen in the SCB was collected in a trawl off Ventura in 1994. By the spring of 1995, specimens were abundant on the shelf off Los Angeles and were of very large size. Population density increased in 1995 and 1996, only to decline in 1997 and 1998. By 1998, the species was established at reduced density in much of the Bight and continues to date. The success of *P. auriformis* was likely due to its ability to efficiently feed on small bivalves, an underutilized resource, and switch readily to other prey in their absence. Declines in populations of small bivalves that are its preferred prey accompanied the invasion. The invasion was noticed and well documented because of the juxtaposition of monitoring programs and the size of the organism. Other coastal invasions are likely to pass unnoticed.

INTRODUCTION

As human influence has become more pervasive and our ability to recognize species as non-native has increased, the introduction of exotic animals to marine, terrestrial, and freshwater environments has been a growing concern. Introductions of exotic species, such as the Asian Clam *Potamocorbula amurensis* invasion of San Francisco Bay (Carlton *et al.* 1990, Nichols *et al.* 1990, Alpine and Cloern 1992), are often characterized by explosive increases in abundance. These increases may change community structure through elimination of native species and may alter the natural environment significantly (Ruiz *et al.* 1997, Grosholz *et al.* 2000, Grosholz 2002). As a result, the composition of biological assemblages is often changed irreversibly after exotic species are introduced.

Where food webs have been simplified through physical disruption, or where the habitat itself requires frequent species turnover and favors short-lived opportunistic species, exotic species have often been able to obtain a foothold in existing communities (Chapman 2000, Lohrer *et al.* 2000, Ruiz *et al.* 2000, Whitlach and Osman 2000). Such is the case in many bays and harbors, where fluctuating abiotic factors have led to communities composed primarily of eurytopic opportunistic species. Species optimally adapted to the preexisting natural physical and biotic regime are disfavored by anthropogenic change. In modified environments, we expect invasions to be more successful, and to be progressive as the presence of introduced species modifies the environment even further. This has been the case in California, particularly in heavily used commercial harbors such as San Francisco Bay (Cohen and Carlton 1995, Ruiz *et al.* 1997, Ruiz *et al.* 1999).

In contrast, most coastal marine food webs are complex, resulting in stable communities that are relatively resistant to the introduction of exotic species. Ecological theory holds that benthic communities on continental shelves are usually biologically

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accommodated, have very diverse food webs, and have little susceptibility to invasion by exotics (Ruiz *et al.* 1997, Chapman 2000).

Recently, an introduced exotic species, the marine snail *Philine auriformis*, successfully established itself in southern California coastal waters, calling this hypothesis into question. The success of *P. auriformis* is also an apparent contradiction of another paradigm: that invasive species are opportunists and generalists, able to quickly exploit disturbed areas. In New Zealand, *P. auriformis* is a specialist predator on small bivalves, particularly *Nucula hartvigiana* (Morton and Miller 1968, Rudman 1972b). Here, we document the history of the introduction and evaluate the validity of the theory based on the life history and habits of *P. auriformis*.

METHODS

Abundance data were obtained from four monitoring programs (Table 1). The Southern California Bight Pilot Project and Bight'98 regional monitoring programs provided snapshots of *Philine auriformis* abundance in the SCB in summer 1994 and summer 1998, while the Los Angeles County and City of San Diego wastewater outfall monitoring programs provided continuous records over more than 30 years for relatively small areas within the Bight. The Los Angeles County program sampled off the Palos Verdes Peninsula south of Los Angeles, while the City of San Diego sampled off Point Loma.

All four programs collected invertebrates by trawls and benthic grabs using identical sample collection and processing methods. Ten-minute hauls of a 25-foot Marinovich semi-balloon otter trawl and

0.1 m^2 Van Veen benthic grabs sieved through 1.0 mm mesh sieves were used to collect samples. Captured specimens were fixed and returned to the laboratory for identification and enumeration. The trawls and benthic grabs provide complementary information. Trawl data indicate the occurrence and relative prevalence of larger individuals over a large area while the benthic grabs provide quantitative population data that include small specimens. Although newly settled juvenile *P. auriformis* were probably not captured in the 1.0 mm mesh sieves used with the benthic grabs, they would be accurately assessed soon after metamorphosis. Trawls are only semi-quantitative because the actual time spent fishing on the bottom varies. Small individuals escape through the mesh of the trawl net.

A total of 428 trawls and 666 benthic grabs collected throughout the SCB were examined during the two regional monitoring programs. After *P. auriformis* was first encountered in July 1994, the contents of 447 trawls and 624 grab samples were examined off Palos Verdes as well as 318 trawls off Point Loma.

The Los Angeles County monitoring program at Palos Verdes collected additional data on *P. auriformis* depth distribution, length frequency distribution, and diet. Trawls and benthic grabs were collected at four depths (30, 61, 151, and 305 m) along several transects. Trawls were collected on four transects (Figure 1) while benthic grabs were collected along 11 transects in a 44-station grid (Figure 2). There are data from seven July and four January surveys between July 1995, when *P. auriformis* was first encountered on the Palos Verdes Shelf, and July 2001. During each July

Table 1. Data sources.

| Program	Collections	Duration	Frequency
Los Angeles County	Four trawl (Figure 1) and eleven benthic grab (Figure 2) transects at four depths (27, 61, 137, and 305 m) on the Palos Verdes Shelf	1971-2002	Quarterly trawls and semi-annual or annual benthic grabs
City of San Diego	Twenty-one or more sites in the vicinity of Pt. Loma up to 200 m deep. Different subsets sampled in different years	1972-2002	Variable: eight times a year to quarterly
Southern California Bight	Trawls at 114 sites and benthic grabs at 251 sites selected at random in the Southern California Bight from 10-200 m deep	August and September 1994	One episode
Bight'98 Regional Monitoring Program	Trawls at 314 sites and benthic grabs at 415 sites selected at random in the Southern California Bight from 10-120 m deep	August and September 1998	One episode
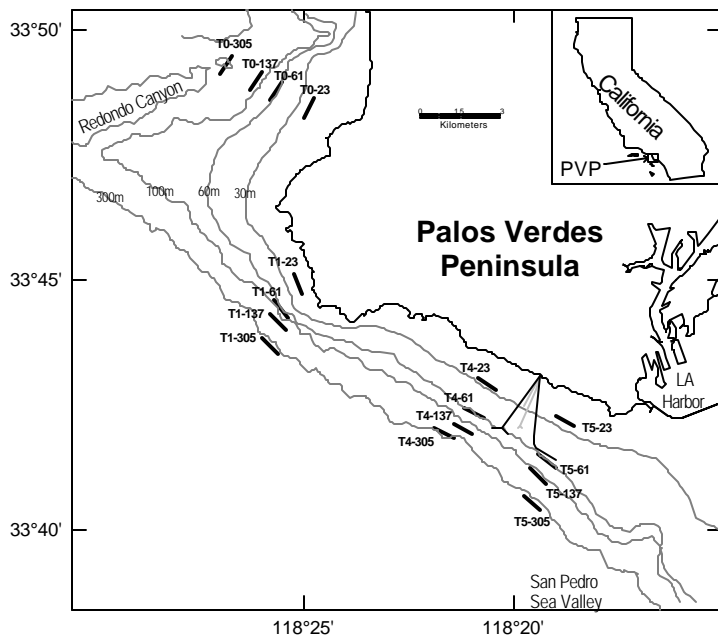
Figure 1. Los Angeles County trawl station locations.
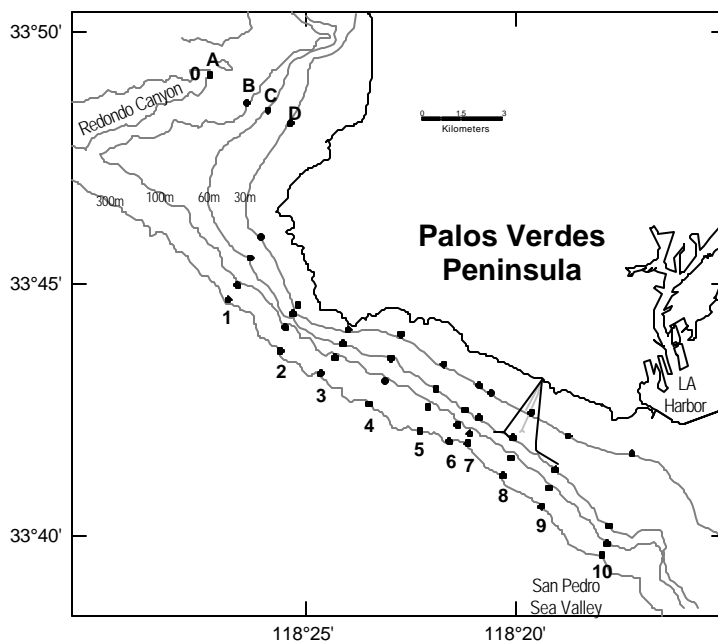

Figure 2. Los Angeles County benthic grab station locations.

survey, five replicate benthic grabs were taken at 61 m stations on transects 0, 1, 3, 6, and 8.

The length of animals collected from the Palos Verdes Shelf was measured from the middle of the head-shield to the margin of the pallial lobes after relaxing the organisms in isotonic magnesium sulfate solution. Where possible, freeze-killing was used rather than fixation with formalin.

To assess the diet, specimens of *Philine auriformis* collected in trawls and benthic grabs of all four programs were dissected and the gut contents were examined. Specimens were selected haphazardly, ensuring that the sizes of the organisms selected were representative of the size range in the collections.

RESULTS

No *Philine auriformis* were found in the thousands of trawls and benthic grabs collected by the Los Angeles County and City of San Diego programs prior to 1995. The first known *P. auriformis* was taken off Ventura in a Southern California Bight Pilot Project trawl in July 1994. At San Diego, the first specimens appeared in benthic grab samples in April 1995 and in trawls in July 1995.

1994 Southern California Bight Pilot Program

One specimen was taken in a July 1994 trawl off Ventura at a depth of 43 m. It was initially overlooked and later found misidentified among the trawl vouchers. None of the 251 benthic grab samples included *P. auriformis*, although other *Philine* species were encountered (Bergen *et al.* 1998).

Palos Verdes

P. auriformis appeared for the first time in trawls on the 27, 61, and 137 m isobaths in May 1995, with most individuals occurring at 61 m. It rapidly increased in numbers and maintained large populations at the 137 m isobath until the end of 1996 (Figure 3). Over 4,100 *P. auriformis* were captured in these samples with 83% (3,419) in the initial "boom" period from August 1995 to August 1996. After the end of 1996, *P. auriformis* populations decreased to relatively low levels at all isobaths (Figure 3).

The first *P. auriformis* appeared in grab samples at Palos Verdes in August 1995 (Figure 4), by which time they were already being trawled up in large numbers. Most individuals occurred at 151 m although, during most surveys, *P. auriformis* were taken at all four isobaths. Forty-five percent of the individuals were taken at 151 m sites, 25% at 61 m, 19% at 305 m stations and 12% at 30 m sites.
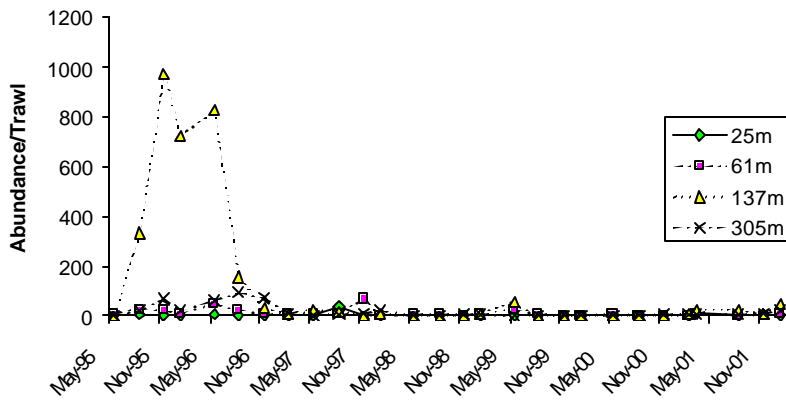
Figure 3. Abundance of *Philine auriformis* in trawls off Palos Verdes 1995-2002.

P. auriformis were encountered in grabs at 61 m on every sampling event since August 1995 except in January 2000; only two individuals were taken in that survey from the 151 m and 305 m isobaths. When densities were low, no individuals were encountered at inshore and, sometimes, deep stations.

P. auriformis were consistently taken in the grab samples after August 1995. They occurred in 155 samples (24.8%). Over the entire period, *P. auriformis* density averaged 15.2/m^2 in the grabs where it occurred. In July 1996, when abundances were highest, density averaged 18.3/m^2 for the 64 samples examined and *P. auriformis* occurred in 56% of samples; individual samples had up to 60 specimens/m^2. Summer densities initially rose, fell between 1996 and 1999, and then rose again. In July 2001, the maximum density was 30/m^2 and *P. auriformis* occurred in nearly 44% of samples.

A strong seasonal abundance pattern was observed, with few individuals captured in winter. January populations averaged only one-fourth of the July densities when compared with either the preceding or the following July. Winter density reached a new high in January of 2001 after declining from 1996 to 1997 and 1997 to 2000.

San Diego

The first *P. auriformis*, a single individual, was collected in a grab sample on April 6, 1995. By May 10, it was detected at two sites and by July, at twelve. These animals were initially too small to be caught in trawls, but were large enough by July

to be taken in trawls at eight sites, being abundant (108 individuals) at one.

Temporal abundance patterns were similar to Palos Verdes. Density of the population was generally low, averaging 14.5/m^2 at stations of occurrence and ranging from 10/m^2 (minimum detectable level) to 140/m^2 in one grab taken on April 10, 1991. A second grab collected simultaneously contained 50/m^2, and the average of 95/m^2 for the site is higher than the 60/m^2 maximum observed off Palos Verdes. In the period from the first detection in April 1995 to July 2001, *P. auriformis* was found in 147 benthic grabs. The seasonal pattern was also similar to Palos Verdes, with the winter population being much smaller than the summer.

Grab samples collected off San Diego were usually paired replicates, and inter-grab comparisons suggest the species distribution was not aggregated at grab scale. In most (80%) cases, *P. auriformis* was found in only one of the two grabs. When both grabs contained the species, density estimated from each was the same 56% of the time. In one case, the difference between replicates was particularly large, with none in one grab and 6 in the other (60/m^2).

Bight'98 Regional Monitoring Program

Philine auriformis specimens were collected in trawls throughout the SCB, with the largest catches in the Los Angeles/Long Beach Harbor complex (Figure 5). Despite peak abundance in harbor settings,
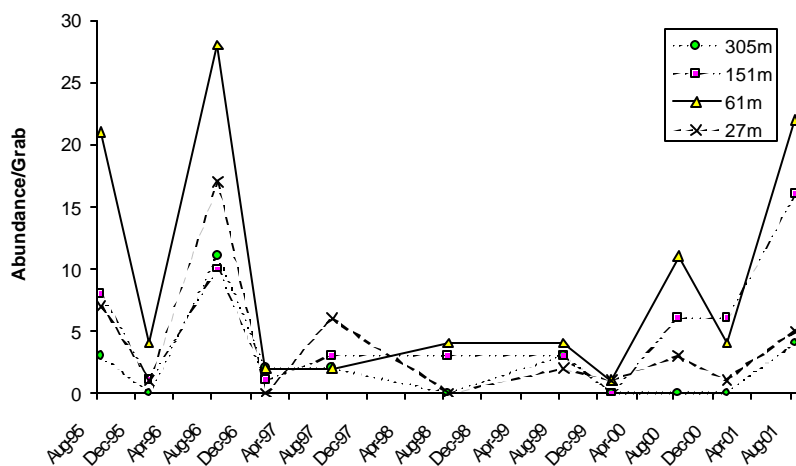

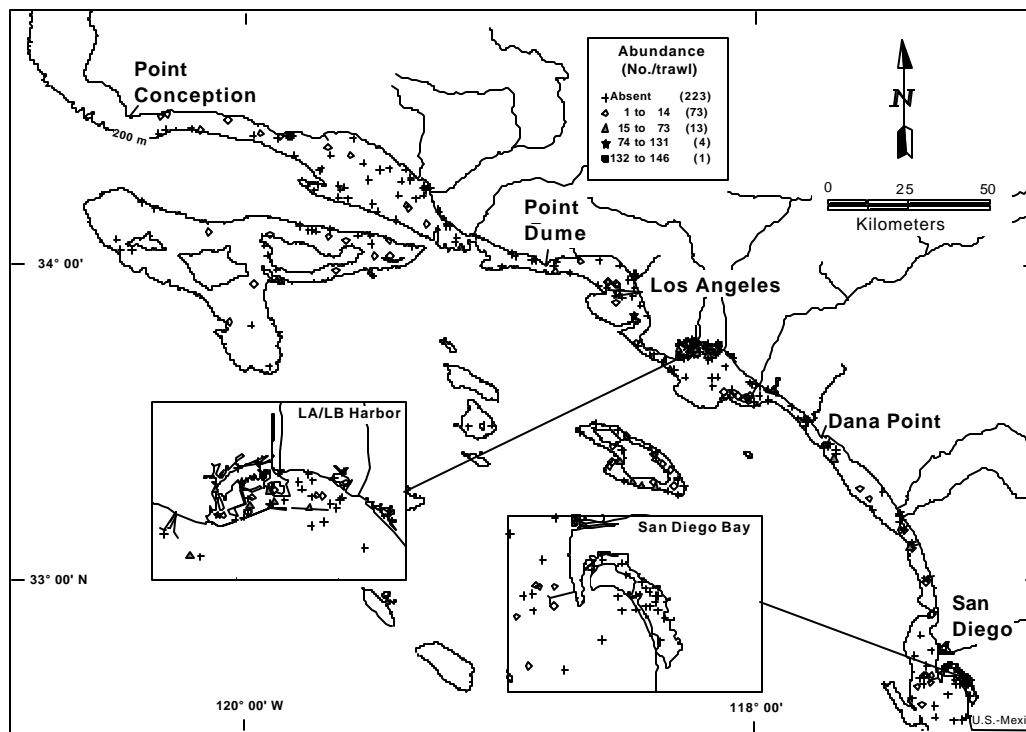**Figure 4. Abundance of *Philine auriformis* in grab samples off Palos Verdes 1995-2002.**

Figure 5. Abundance of *Philine auriformis* in Bight'98 trawl samples.

almost equal numbers were taken in bays and harbors (577) and mid-shelf depths (550). Far fewer were taken on the inner and outer portions of the mainland shelf (about 5% of specimens, in total), although both the mainland and island shelves yielded *P. auriformis*. It was taken in 29% of 314 trawls and, with 1,190 specimens, was the 7th most abundant trawl invertebrate.

It occurred in 39 (9.4%) of 415 benthic grab samples and only in the central and northern portions of the Bight (Figure 6) although, as described above, the species had previously been taken in benthic grabs at San Diego. The average density was 18.2/m² at stations where it occurred and 1.7/m² overall in the SCB.

Size Variation

Specimens obtained by trawling in 1995-1996 off Palos Verdes reached large sizes, but by August of 1996 the cohort of large individuals was gone and smaller specimens formed the entire catch. The largest collected specimens were 50 mm long (T4-137, February 1996; T1-137 May 1996), while many adults reached 40 mm (various sites starting in November 1995). Animals of this size were also taken as early as October 25, 1995, in additional samples collected near T4-137 (Figure 3). Nearly all samples with more than a few individuals showed

evidence of several cohorts with some large individuals and many of lesser size. Few very small individuals were seen in trawls as the net mesh truncated the lower end of the size distribution at around 10 mm.

Diet

Dissections of *P. auriformis* indicated a varied diet. Most animals, particularly those from off Palos Verdes, were filled with bivalves. Taxodont bivalves, the preferred prey in New Zealand, were uncommon at stations where *P. auriformis* were taken, and the consumed bivalves were usually small lucinids or thyasirids and the majority of individuals were *Parvilucina tenuisculpta* or *Axinopsida serricata*. While all *Axinopsida* were of a size appropriate as prey for *P. auriformis*, some *Parvilucina* were too large. In several dissections, large *P. tenuisculpta* were found completely blocking the esophageal opening to the gizzard. While the strong musculature and connective tissue sheath of the gizzard provides the force needed for the gizzard plates to crush thick-shelled prey, they render the entire structure relatively inelastic. In consequence, the gizzard opening cannot expand to allow passage of prey outside a set maximum size.

In the absence of bivalves, or at low bivalve population density, very little electivity was evident with prey in the gut at nearly the same proportions to
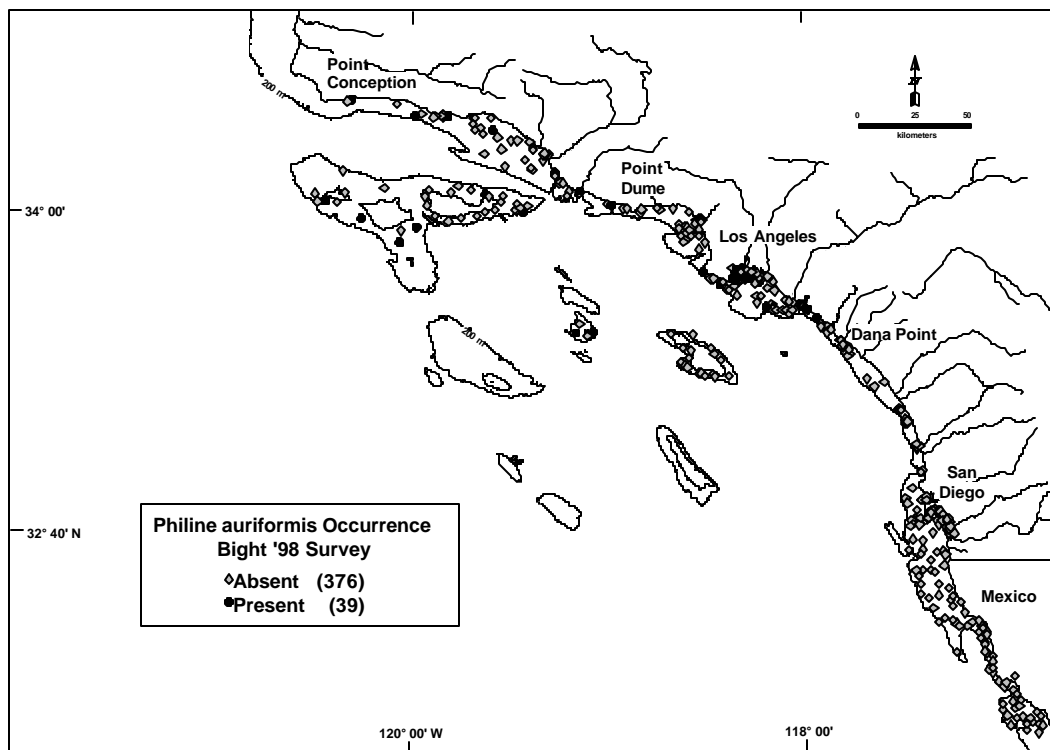
Figure 6. Occurence of *Philine auriformis* in Bight'98 grab samples.

their presence in the environment. On the upper slope in Santa Monica Bay, *P. auriformis* was found with guts full of *Rhizosolenia*, an arenaceous foraminifer abundant there. Other small mollusc carnivores such as *Cylichna* and *Rictaxis* were found in poorly filled guts, although not frequently.

DISCUSSION

Philine auriformis was originally described from the shallow waters of New Zealand (Suter 1909). The first California specimens were taken in July 1993 from San Francisco Bay (Gosliner 1995), and a second population was noted in Bodega Bay in April 1994. The first southern California specimen was detected in July 1994 and, more recently, the species spread farther northward and was reported from Coos Bay, Oregon (Jeff Goddard in Rudman 1998).

Our data present a compelling picture of an exotic species invasion with a classical "boom-and-bust" abundance pattern following establishment. It is fairly certain that the first individuals of *Philine auriformis* arrived in the SCB in 1994 since none were collected by the Palos Verdes and San Diego programs between 1971 and 1994 or in the 251 benthic grabs collected throughout the SCB by the

regional monitoring program in 1994. Discovery of the first specimen in 1994 was followed by sharp increases in abundances during 1995 and 1996, especially at its preferred depths of 61 m (Figure 4) and 137 m (Figure 3). After December 1996, abundances leveled off at lower, presumably sustainable, levels.

At first glance, the SCB is a physically and biologically stable environment that is an unlikely location for an invasion, and *Philine auriformis* is an unlikely invader. Most invasions occur in bays and estuaries with fluctuating physical environments and high natural and anthropogenic stress (Chapman 2000, Lohrer *et al.* 2000, Ruiz *et al.* 2000, Whitlach and Osman 2000). Stereotypic invaders are eurytopic opportunistic species able to establish themselves here rather than specialists like *P. auriformis*, with well-defined prey and habitat preferences that are ecologically integrated in its home range.

Several lines of evidence suggest that *Philine auriformis* succeeded in the SCB primarily by consuming populations of small molluscs that were an ecologically underutilized resource. Behind the food and habitat preferences were broad tolerances that enable *P. auriformis* to utilize a variety of foods and occupy a wide spectrum of bottom types. There was

also an apparent absence of predation on *P. auriformis* during the initial phase of the invasion.

The *P. auriformis* population and its individuals were an example of growth without constraint in the presence of adequate or excess food during the "boom" in 1995 and 1996. The 40-50 mm individuals present at Palos Verdes exceed the home range maximum by up to 30% and were present in large numbers. The size of *P. auriformis* in the type lot from New Zealand was 16 mm (Rudman 1972a) while Morton and Miller (1968) illustrate a 36 mm extended specimen from *Zostera* flats near Auckland. Gosliner (1995) lists living animals (presumably obtained from San Francisco or Bodega Bay) as between 15 and 30 mm in length.

Although the San Diego specimens were not measured, average size must have been smaller than off Palos Verdes because snails large enough to be retained in trawls were infrequent. While average density in grab samples where the species occurred was similar in the two areas, the catch and the effort-standardized catch were less than one-tenth of values at Palos Verdes in the same period. At San Diego, large *P. auriformis* were presumably lost through predation or unable to grow as large as at Palos Verdes.

The formidable gizzard of *P. auriformis* enables it to specialize as a carnivore on heavily shelled prey in New Zealand; few infauna carry shells heavy enough to escape crushing in the robust *P. auriformis* gizzard. We found that the predominant prey in the SCB, as in New Zealand, were small bivalves, although they were lucinids or thyasirids rather than toxodonts. In Bodega Bay, two small venerid clams, *Nutricola tantilla* and *Nutricola confusa* are the major prey of *Philine*, including *P. auriformis* (M. Chow in Rudman 1998). In San Francisco Bay, a large population of the small venerid clam *Gemma gemma* serves as the mainstay of its diet (Gosliner 1995). Other species of *Philine* have a similar diet. In its home range in Hong Kong, *P. orientalis* is known as a bivalve predator (Morton and Chiu 1990). The European *P. aperta*, which was also introduced into Bodega Bay, reportedly eats small bivalves while some populations are specialized on pectinariid polychaetes (Hurst 1965).

The powerful gizzard also allows *P. auriformis* to thrive in the absence of its preferred bivalve prey, consuming anything in its size range. When bivalves are absent or rare, the dietary flexibility indicated by shifts between nuculids in New Zealand, venerids in

northern California, and lucinids and thyasirids in the SCB progresses and it functions as a low-electivity opportunistic predator and scavenger that switches diet easily. We found *P. auriformis* gut contents with prey items in proportion to their occurrence in surrounding sediments when bivalves were absent or rare. Other snail-gut investigators found that foraminifera were prominent in the guts of dissected animals from San Diego (M. Lilly, personal communication) while ophiuroid arms were common where bivalves were few and ophiuroids formed much of the sample (T. Phillips, personal communication).

Philine occurs at relatively shallow depths in the sediments, presumably because its preferred prey has short siphons and is restricted to the upper inch of sediments (Morton and Miller 1968). On the mudflats and shallow water of Bodega Bay, specimens are found either at the surface or just beneath it and are not deeply buried (D. Cadien, personal observation). Rudman (1998) notes the animal is found only above the redox potential discontinuity in oxic sediments. Morton and Miller (1968) describe the species as burrowing readily in bare sand beaches or in sand between sea-grasses, while Rudman (1972a) indicates that it is often found at a depth of six inches in the sediments.

One of the reasons for the success of the *P. auriformis* invasion in the SCB may be that co-occurring carnivores are not direct competitors. The naticid gastropods *Euspira draconis*, *Neverita recluziana*, and *Calinaticina oldroydae* are bivalve predators, but usually target larger clams rather than the small bivalves that *P. auriformis* prefers. They drill with the radula rather than swallowing their prey. Dietary overlap between large *P. auriformis* and small *Calinaticina* is possible but probably infrequent. *Calinaticina* consume large-sized *Parvilucina tenuisculpta*, and *P. auriformis* smaller individuals. The prey size range utilized by both predators is narrow. Most *Calinaticina* prey are *Lucinoma annulata,* a larger lucinid species; large *P. tenuisculpta* are acceptable in their absence, but not preferred.

There is little dietary overlap with other carnivores. Other smaller carnivorous cephalaspids such as *Acteocina* and *Cylichna* primarily consume foraminifers (Shonman and Nybakken 1978), while *Rictaxis* harvests palps of polychaete worms. Amphipods (Ejdung and Elmgren 1998, Oakden 1984, Oliver *et al.* 1982) and crangonid shrimp (van der Veer *et al.* 1998) prey selectively on newly settling

larvae. Motile carnivorous polychaetes probably consume young bivalves (Fauchald and Jumars 1979). Asteroid echinoderms also feed on mollusks (Christensen 1970, Wurzian 1984, Franz and Worley 1982), consuming bivalves, gastropods, and scaphopods. Penaeid shrimp consume a wide variety of benthic infauna including mollusks (Dall *et al.* 1990).

There was no evidence of predation on *P. auriformis* and that is likely another reason for their success. None of the animals showed traces of unsuccessful attacks. In the months after their first appearance, the average size of individuals continued to increase. Guts of potential vertebrate predators taken along with *P. auriformis* yielded no evidence of their consumption.

Local carnivores either failed to recognize *P. auriformis* as potential prey or were effectively repelled by secretions of the mantle glands (Gosliner 1995). *P. auriformis* have limited defenses and are quite muscular, unprotected by an external shell and large compared to most macrofauna. The fragile internal shell does not provide protection from predators. Large *Philine* in Bodega Bay were sluggish and lacked behavioral defenses to predation. Such behavior in opisthobranchs usually accompanies well-developed camouflage or chemical defense. Since these large white animals were hardly camouflaged against the silty sands of Bodega Bay and were openly crawling at the surface during a daylight low tide, defensive secretions seem the most likely deterrent.

While direct evidence of predation is scant, changes in the size and density of the *P. auriformis* population at Palos Verdes over time suggest that predation has occurred in recent years. The decline of average size in benthic and trawl collections and the virtual absence of very large individuals suggest that the predator is large relative to the prey and is preferentially cropping large individuals. An anecdotal report of *Philine* in the stomachs of Pacific sanddab *Citharichthys sordidus* could not be confirmed. However, small juveniles of *P. auriformis* were recently taken from the guts of juvenile Dover Sole *Microstomus pacificus* off Palos Verdes. The predator of adult snails, if one exists, remains unidentified.

The longevity and life history of *P. auriformis* provide no compelling reasons for their success despite their effective dispersal and rapid spread in the SCB. In shallow water in California, the species appears to live for about a year (M. Chow, personal communication). In deeper waters offshore, and under the unusual circumstances of the initial invasion, some individuals survived for at least two years. The organisms are simultaneous hermaphrodites but apparently do not self-fertilize. After mating, each partner lays one or more egg masses that are about 2.5 cm long and attach by a long thin stalk to the bottom. Each egg mass contains many small eggs that hatch into small larvae with little reserve yolk and probably feed in the plankton (Gosliner 1995). Little is known about the length of larval life and factors that stimulate settlement and metamorphosis.

The rapid progress of this invasion may also have been influenced by zoogeography and the fluctuating oceanographic regimes of the SCB. The large cadre of species whose ranges end in the California Transition Zone are probably more significant than the endemic species present in this zone of faunal overlap and exchange (Newman 1979). The frequent oscillation between oceanographic regimes within the Bight (Hickey 1993) yields a large reservoir of unrealized biotic potential which includes endemic species, species whose distribution centers to the north, and species whose distribution centers to the south. Because of this flux between differing physical states, species with appropriate life-history attributes and properly timed production of propagules can establish themselves in the benthic community. From an even broader perspective, the coastline of the northeastern Pacific is subject to repeated invasion by introduced exotics because of the relatively constant water temperature (Chapman 2000).

Our ability to document the *P. auriformis* invasion of the SCB is the result of several factors including chance; this is probably not the first successful invasion of California coastal waters by an exotic species. The juxtaposition of spatially extensive regional monitoring surveys at and four years after the introduction with two point-source monitoring programs that lasted more than 30 years was a stroke of luck. Without the ability to combine data from the four monitoring efforts and the trawls and benthic grabs in each, our conclusions would be much less clear. The life spans of most macrofaunal species are so short that it is only coincidence if a population spike occurs during a bi-annual survey period. It is also unusual for an infaunal organism to be large enough to be caught in trawls as well as grabs. Monitoring programs usually track stable "normal" constituents of biological communities,
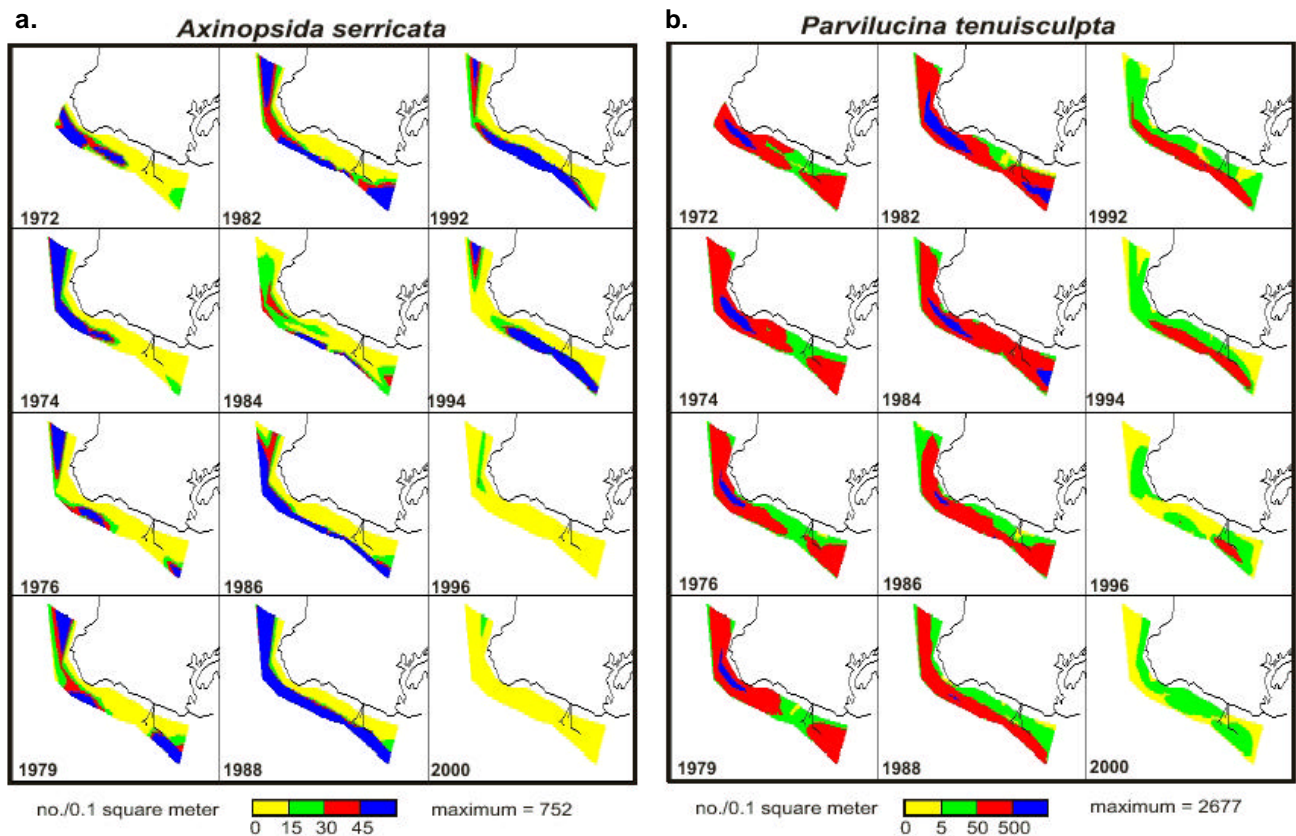
Figure 7. Density of small bivalve populations off Palos Verdes 1972-2000: (a) *Axinopsida serricata*; **(b)** *Parvilucina tenuisculpta* **(from Montagne 2001a).**

treating short-term opportunists as background noise to be avoided where possible; unfortunately, the background noise is where newly introduced taxa are likely to be found. Only where the temporary success of an introduction allows the invading population to reach high density (as with *Potamocorbula amurensis* in San Francisco Bay, Carlton *et al.* 1990; and *P. auriformis*) does it emerge into the foreground and demand attention.

Although there has been some controversy over the identity of the invading organism, after much study, the Southern California Association of Marine Invertebrate Taxonomists (2001) reports a single species *P. auriformis*. The taxonomy of *P. auriformis* remained confused until the type lot in New Zealand was reexamined and found to contain several species (Rudman 1970). Rudman examined the California specimens and concluded they were different from those from New Zealand. An on-line debate between Rudman and Gosliner (Rudman 1998) on the identity of these animals ensued and was never completely resolved. The debate was complicated by the presence of other externally similar

introduced *Philine* species in Bodega Bay (*P. aperta*, *P. orientalis,* and *P. japonica*). The Southern California Association of Marine Invertebrate Taxonomists (2001), agreeing with Gosliner, reports a single species *P. auriformis* because the differences from the New Zealand specimens are insufficient to separate the SCB material (and Gosliner's from San Francisco Bay) from *P. auriformis*.

The only known potential ecological effects of the invasion are declines in historically dense populations of small clams off Palos Verdes. The onset of the clam population decline corresponds with the *P. auriformis* invasion (Figures 7 and 8) and leads to the conclusion that the invasion is the cause of the decline. Populations of small bivalves off Palos Verdes have historically been dense, particularly in areas influenced by the discharge of the wastewater treatment plant. In addition to high densities, Hickman (1994) showed that individuals of the clam *Parvilucina tenuisculpta* were larger in this area than in other portions of the SCB. Fabrikant (1984) hypothesized that increased numbers and size were a response to outfall-derived nutrients.
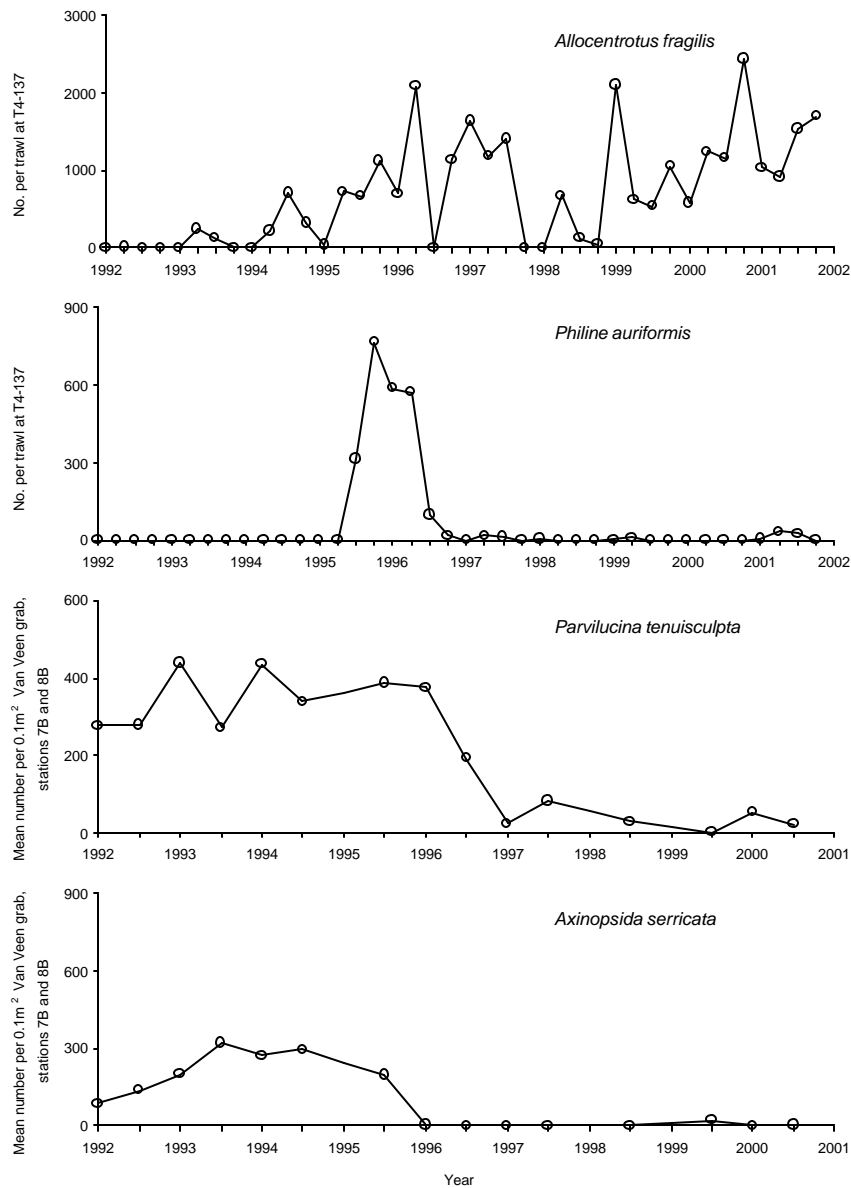
Figure 8. Comparison of trawl caught fragile sea urchin (*Allocentrotus fragilis*), and *Philine auriformis* at Station T4-137 with small bivalve populations at adjacent benthic Stations 7B and 8B (150 m), 1992-2001 (from Montagne 2001b).

In recent years, populations of most small clams off Palos Verdes, including *Axinopsida serricata* and *Parvilucina tenuisculpta*, have declined in abundance (Figures 7 and 8). Average individual size has declined to the norm for the SCB (Jones and Thompson 1984). The high-density areas of *Axinopsida* observed in 1994 were gone by the summer of 1996, when the P. auriformis boom was at its peak, and further reduced by 2000 (Figure 7). *Parvilucina* density dropped between summer 1994 and summer 1996 on much of the Palos Verdes Shelf and, by 2000,

no high-density areas remained (Figure 7). However, high *Parvilucina* abundances in the immediate vicinity of the outfall persisted into 1996, and intermediate density areas expanded subsequently. The apparent contradiction is probably because *Axinopsida* can be consumed by adult *P. auriformis* throughout its life while *Parvilucina* reaches a size refuge beyond effective predation. The persistent *Parvilucina* populations are individuals too large for *Philine* consumption. Both the pre-1994 *Axinopsida* and *Parvilucina* populations had their highest

abundances near the 150 m isobath, where *P. auriformis* abundances were highest. In Bodega Bay, *P. orientalis* decreased the density of the bivalve *Nutricola* by 63% during two-week caging experiments; however, *P. auriformis* did not significantly affect *Nutricola* sp. density (M. Chow, personal communication).

An alternate explanation for the reduced bivalve populations is related to predation by the fragile sea urchin *Allocentrotus fragilis,* which has increased in abundance (Figure 8). However, this animal is more likely a surface deposit feeder (Salazar 1970) than a predator-scavenger (Thompson *et al.* 1987, Lissner and Hart 1996) and, therefore, its increased abundance probably does not explain the declines.

The future course of the modified community is far from certain. During the initial *P. auriformis* boom period, there were fears of *P. auriformis* displacing and eliminating competing predatory species and concerns for the fate of prey populations. The initial high population density and large individual sizes did not persist. While prey populations have declined, these declines were localized in areas where populations were unnaturally dense due to organic enrichment. Potential competitor populations have not suffered declines. Despite the large number of individuals and occurrences of *P. auriformis* in the SCB, it remains uncertain if the invasion will ultimately succeed; both intentional and accidental introductions have failed in the past after initial success. It seems likely, however, that *P. auriformis* will become a permanent member of the local biota. It is well adapted to the vicissitudes of life in the SCB. Having survived through both particularly warm (1997-98) and particularly cool (1999) oceanographic periods, it must be able to reproduce successfully in the range of physical conditions that occur in the SCB. It may eventually settle into a pattern of swarm settlement into areas of high resource availability followed by declines to a lower "maintenance" density, and swarm settlement elsewhere as does *Listriolobus pelodes* (Stull *et al.* 1986).

The primary means of identifying introduced exotics such as *P. auriformis* is through specific high-intensity surveys of bays and harbors that are being performed throughout the nation's coastline. These studies have successfully documented the severity of the problem in different areas. However, such intense programs cannot be performed on open continental shelves. Regional monitoring efforts can supplement the introduced species surveys, but also cannot efficiently detect offshore introductions.

There is a gap in environmental monitoring through which exotic species pass; we can only detect them on the coastal shelf under unusual circumstances. *Philine auriformis* was recognized because it was large enough to be identified as an introduced exotic using the Chapman and Carlton (1991) criteria.

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