

Delta Regional Ecosystem Restoration Implementation Plan

CONCEPTUAL MODEL FOR *Potamcorbula amurensis*

Prepared by: Janet K. Thompson (jthomps@usgs.gov) and Francis Parchaso

U.S. Geological Survey

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For further inquiries on the DRERIP Conceptual Models, please contact Hildie Spautz at Hildegard.Spautz@wildlife.ca.gov

PREFACE

This Conceptual Model is part of a suite of conceptual models that collectively articulate the current scientific understanding of important aspects of the Sacramento-San Joaquin River Delta ecosystem. The conceptual models are designed to aid in the identification and evaluation of ecosystem restoration actions in the Delta. These models are designed to structure scientific information such that it can be used to inform sound public policy.

The Delta Conceptual Models include both ecosystem element models (including process, habitat, and stressor models) and species life history models. The models were prepared by teams of experts using common guidance documents developed to promote consistency in the format and terminology of the models
http://www.delta.dfg.ca.gov/erpdeltaplan/science_process.asp .

The Delta Conceptual Models are qualitative models that describe current understanding of how the system works. They are designed and intended to be used by experts to identify and evaluate potential restoration actions. They are not quantitative, numeric computer models that can be “run” to determine the effects of actions. Rather they are designed to facilitate informed discussions regarding expected outcomes resulting from restoration actions and the scientific basis for those expectations. The structure of many of the Delta Conceptual Models can serve as the basis for future development of quantitative models.

Each of the Delta Conceptual Models has been, or is currently being subject to a rigorous scientific peer review process. The peer review status of each model is indicated on the title page of the model.

The Delta Conceptual models will be updated and refined over time as new information is developed, and/or as the models are used and the need for further refinements or clarifications are identified.

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I. Introduction

Potamocorbula amurensis is a pest in the San Francisco Estuary (hereafter SFE) due to its ability to heavily graze pelagic food resources and its accumulation of toxic substances that are then moved into the food web through its predators. We begin by describing what we know of its life history and establish its life cycle within the framework of the ecological setting of the SFE. This model should be used within the context of a thought experiment, as there is not enough known about the species to design a strategy to control it in the SFE or Delta. The ultimate purpose of this conceptual model of *Potamocorbula amurensis* is to explore its weaknesses.

The geographic focus of the DRERIP models is the Delta. However we examine the life history patterns of *Potamocorbula amurensis* as far down bay as San Pablo Bay for two reasons. First, because some of the largest ecosystem effects attributed to *P. amurensis* are its consumption of pelagic carbon resources, it is necessary to include areas adjacent to the Delta due to the effects of tidal dispersion. Second, many of the life cycle patterns that are visible in San Pablo Bay are transferrable to upstream locations during drought periods.

Finally, we expect this model to evolve as a result of the many ongoing studies on *P. amurensis*. Some of the data shown in this discussion are the direct result of current CALFED studies being done jointly by California Department of Water Resources (EMP Program D. Messer and K. Gerhts) and the USGS (Analysis of Archived Samples to Assess Patterns of Historic Invasive Bivalve Biomass). Our co-investigators on that study have been gracious in allowing us to show some of that data here, before it has been published.

We start the model discussion with a brief description of the taxonomic status of this bivalve because the utility of the literature available to us is based on assumptions of

the correct identification. We also very briefly describe its introduction into the SFE as a reminder of the facts about its invasion.

A. A note on *Potamocorbula amurensis* taxonomy and nomenclature

Potamocorbula amurensis (Schrenck, 1861) was first identified by Carlton et al. (1990) with the aid of A. Matsukuma (National Science Museum, Tokyo) who was starting a revision of the genus at that time. Coan (2002) in his analysis of Eastern Pacific Corbulidae revised the identification to *Corbula amurensis* but he warned that it may be changed again once the Asian *Corbula* group is revised. Since that time The World Register of Marine Species (<http://www.marinespecies.org/aphia.php?p=taxdetails&id=397175&allchildren=1>) has listed *Corbula amuensis* as “unaccepted” and cites Huber (2010) as the source for reverting to *Potamocorbula amurensis*.

We do not believe the taxonomy question has been fully resolved. A PCR assay has been developed for the *Potamocorbula* species found in the SFE and the test has been shown to be successful in detecting both the *Potamocorbula* from SFE and *Potamocorbula.c.f. laevis* collected by S. Sato from southern Japan (Smith et al. 2012). In their 2002 publication, Sato and Azuma, refer to the southern species as a newly invasive *Potamocorbula* species found in the Ariake Sea and they state that it is different than the native *Potamocorbula amurensis* seen in northeast Japan. Sato and Azuma (2002) did not identify the new bivalve as *Potamocorbula c.f. laevis* at the time of publication but they may have since provisionally identified it as such. They did say that it was not seen in Japan before 1990 and that it probably arrived from China or Korea with shipments of *Corbicula*. If it is the same species as found in SFE, it would be the second invasion location for the species. The species identification remains elusive and will likely only be resolved with further genetic studies

B. Status and invasion of Potamocorbula amurensis in San Francisco Estuary

Carlton et al. (1990) hypothesize that *P. amurensis* (hereafter *Potamocorbula*) was introduced into the SFE in ballast water, most likely originating from an Asian port. The first specimen was discovered in late 1986, when juveniles were collected in the northern estuary. Within a year the species had spread throughout the northern estuary, and within 18 months had become the dominant bivalve in the northern estuary (Nichols et al., 1990). It spread to the southern estuary within two years where it has been a dominant bivalve (Thompson, et al. 2008) during years when bivalves occur in South Bay (Cloern et al. 2007). *Potamocorbula* is on the alert list for ISSG (Invasive Species Specialist Group) where it is listed as among the 100 World's Worst Invaders, is listed as a pest by NIMBUS (National Introduced Marine Pest Information System) (Hewitt et al., 2002), and has been classified as one of "six exotic high impact species" included in an early detection surveillance system in New Zealand (Global Invasive Species Database, 2005). Its presence on these lists is due in part to its ecosystem effects in the SFE.

II. Biology

Potamocorbula amurensis is a dioecious (sexes are separate), broadcast spawning bivalve with external fertilization (Figure 1). The fall and summer periods of gametogenesis usually last 1-2 months although Parchaso (1993) reported animals in San Pablo and South Bays to be almost continuously reproductively active in 1989-1990 during the 1987-1992 drought.

Females produce 45,000-220,000 oocytes. The oocytes (Table 1) are not buoyant and are fertilized near the bed (Nicolini and Penry 2000). Males produce sperm that are active for up to 12 hours in 15°C water. Non-mobile, non-feeding trochophore larvae develop within 24 hours of fertilization. Suspension feeding veliger larvae develop

24 hours later and swim actively to day 7; thereafter they swim intermittently until they settle at day 17-19.

Juvenile clams become reproductively active at about 5mm in length (Parchaso and Thompson 2002) which can occur within 2 months of recruitment. *Potamocorbula* lives 2- 2.5 years at most locations and commonly reproduces twice a year but can continuously reproduce if conditions permit. Recruitment variability is a function of the availability of adults to produce larvae and site specific environmental conditions. Thus recruitment timing varies within the estuary. Recruitment usually occurs in the western Delta (Chippis Island) in fall, in the northern estuary (Grizzly Bay) in early spring through fall, and in San Pablo Bay in late spring/early summer (Figures 2a, b, and c). Recruitment occurs over several months (Figure 2d) and a second recruitment period may occur at all locations although it is most common in the Grizzly Bay/Suisun Bay populations (Parchaso and Thompson 2002).

Potamocorbula populations have wide ranges in abundance within years and between years (Table 2). The maximum *Potamocorbula* abundance, observed thus far was in San Pablo Bay, and the maximum biomass was seen in Carquinez Strait. The examples shown in Figure 3 of *Potamocorbula* abundance, biomass, and mean shell length at two locations in SFE are representative of three types of variability observed in the estuary: (1) The lack of a predictive relationship between biomass and abundance is shown at the freshest channel station (near Chippis Island) in Figure 3a and 3b; note the similarity in biomass in the drought years (1987-1992) and the most recent years (1999-2006) despite much higher abundance in recent years. The relative increase in biomass during the drought when phytoplankton biomass was uniformly low (Alpine and Cloern 1992) is driven by different year class structure (older year classes during the drought, Figure 3c) and changes in clam condition (weight for a specific length of clam was also greater during the drought). (2) *Potamocorbula* populations in the shallow Grizzly Bay water (Figure 3d, 3e) have the most consistent seasonal patterns with biomass peaking in late fall/winter and abundance peaking in

summer and early fall. (3) The higher values of biomass in winter in Grizzly Bay during the drought years (1987-1992, Figure 3e) than was observed in later years occurred because of the near continuous recruitment of *Potamocorbula* and larger size of bivalves (Figure 3f) during this period.

III. Distribution

A genetic study of *Potamocorbula* in SFE (Duda 1994) found differentiation among populations to be low with all populations showing a high degree of variability. This is a genetic characterization of a species equipped to adapt to a large number of environments which we have found is true for *Potamocorbula*. Based on the few physiological studies that have been completed, the primary limiting environmental factor on *Potamocorbula*'s distribution is likely to be low salinity during the early stages of reproduction (Table 1, fertilization and spawning are limited to salinity of 5-25). Neither distribution nor reproduction appears to be temperature limited within the range of temperatures commonly found in the estuary (5-25° C). If the species identification is accurate, *Potamocorbula*'s native range is from 22° to 55° N latitude in the western Pacific and thus it is unlikely that the temperature regime in SFE would be limiting. The salinity range for adult animals, 0.1-32 (Werner and Hinton 2000 and Carlton et al. 1990), and recruits, 2-30 (Nicolini and Penry 2000), is sufficiently broad to encompass most of the northern estuary in most seasons and years (Figure 4). *Potamocorbula* is the dominant species in the salinity range of 1-18 and occur in salinities that range from 0-23.5 in the Amur River estuary (Kamenev and Nekrasov 2012). They occur in the warmest part of that relatively cold estuary and are believed to be limited by the cold temperatures there; they are found in a temperature range of 7.5-15.8° C.

Potamocorbula's distribution in the SFE has changed very little since its initial invasion with the exception of a broader distribution in the southern estuary (Thompson et al. 2008). The similarity in *Potamocorbula*'s distribution in the spring and summer of wet (1995, 2006) years and dry years (2007) (Figure 4a-4d) is

indicative of the intrusion of some salt in spring beyond the confluence of the rivers in most years or the persistence of older bivalves that settled during more favorable periods. . *Potamocorbula*'s distribution in fall is more variable and reflects the saltwater intrusion up the rivers and into the western Delta with the reduced flow during the drought (1990) (Figure 4e) and during the latter part of 2006 when management restricted fall outflow (Figure 4h). The latter observation shows the variability of salinity between the seasons as 2006 was a wet year but with very low freshwater flow in late summer and fall which allowed *Potamocorbula* to move up river late in the year (Figure 4h). The distribution during the falls of wet years (1995, Figure 4e) and above normal year (1993, Figure 4g) show *Potamocorbula* being moved down bay within Suisun Marsh, down bay of the confluence at most stations, and mostly kept out of the San Joaquin River during these years. Fall 2006 was unique in that *Potamocorbula* were found to have settled up the San Joaquin River as far as was the samples were collected.

Potamocorbula is capable of living in brackish marshes as shown by its presence in Suisun Marsh in 1990 (Figure 4eb). Its distribution in the marsh declines with increased freshwater flow as seen in the fall 1995 distribution. *Potamocorbula* and *Corbicula fluminea*, a freshwater/brackish water bivalve, overlap at a salinity range of about 2. This is consistent with the distribution for the same species on the Yangtze River where they overlap and are the transition species between two benthic communities dominated by *Potamocorbula* downstream and *Corbicula fluminea* upstream (Chao et al. 2012). It is unknown if *Potamocorbula* can live within *Egeria densa* beds; limited sampling within the beds by the U.S.G.S. in 2001 and 2003 revealed only *Corbicula fluminea* (U.S.G.S. unpublished data). However the salinity tolerances of *Potamocorbula* and *Egeria densa* overlap, so it is possible that they could co-occur.

Potamocorbula has been observed in all habitats except epifaunal (i.e. attached to hard substrate) habitats in the SFE. It prefers mid-intertidal to subtidal ranges but

large populations can be found in the high intertidal. Individuals have been collected in silt, clay, hard-pack clay, sand, gravel, peaty mud, and shell hash. They occur in fluid mud, high sedimentation, and high erosion rate areas in the Yangtze River estuary so it is apparent that sediment type rarely limits their distribution (Chao et al. 2012). They maintain their position in hard-pack clay or high velocity areas with a single byssal thread that passes through the anterior end of the shell and attaches to a piece of debris in the sediment. Animals were observed to live with one-half to two-thirds of their shell exposed while in a laboratory flume. This observation was verified by the presence of live barnacles on the posterior end of many collected animals.

IV. Ecology

Potamocorbula spends most of its 2-3 year life in the sediment and spends about 3 weeks as a larva in the water column (Figures 1 and 5) when it can disperse and expand the population distribution. Thus environmental conditions, predators, and food quantity and quality vary throughout the life cycle of the bivalve.

A. Ecological Influences on *Potamocorbula's* Life Cycle

1. Gametogenesis

The salinity range needed for the initiation of gametogenesis (0.1-28) is quite wide (Parchaso and Thompson 2002) and thus most of the adult bivalves present in the northern estuary are reproductively active. Almost 100% of the adult bivalves in a population are reproductive at the initiation of gametogenesis in each year.

Gametogenic activity has been linked to food availability by Parchaso and Thompson (2002). Although chlorophyll *a* concentrations (used as a measure of phytoplankton biomass) were quite low during the Parchaso and Thompson (2002) study, they did not observe non-reproductive populations; this fact is most likely a reflection of the lack of data on other food sources used by *Potamocorbula* such as bacteria (Werner and Hollibaugh 1993).

2. Spawning and Fertilization

Potamocorbula can be induced to spawn in the laboratory by withholding food and stressing the animals (Nicolini and Penry 2000) but it is unknown if these triggers apply to field animals. One of the few identified environmental limits on *Potamocorbula*'s reproduction and thus potentially on its distribution, is the salinity limit (5-25) at which spawning and fertilization can occur (Figures 5 and 6). It should be noted that although Nicolini and Penry (2000) found animals did not spawn at 2 and 32, they did not test salinities >2 and <5 , and salinities >25 and <32 so the range may be broader than 5-25. Within the 5-25 salinity range, both eggs and sperm are quite resilient and can tolerate a 10 step salinity change. Similarly, two hour old embryos that develop in a salinity of 15, tolerate salinities ranging from 10-30 in laboratory tests.

Like all broadcast spawning animals with external fertilization, successful reproduction is a result of a favorable chemical and physical environment at the time of spawning and fertilization (Figure 6). Nicolini and Penry (2000) found that the eggs settled to the bottom on release and that the sperm were free swimming, so it is unclear what percentage of fertilization occurs at the bed and what percentage of fertilization occurs in the water column with re-suspended eggs. In either case, the near-bed hydrodynamics and currents are a major determinant of reproductive success and the geographic position of the embryo as it develops into a larva.

3. Pelagic Larvae

Potamocorbula has two pelagic larval stages with broad salinity tolerances (Figure 5, 2-30). The short lived trochophore larvae are non-swimming and non-feeding and thus are vulnerable to transport and mixing into non-hospitable water (Figure 6). The veliger larva is not a dynamic swimmer but can move vertically in the water column and thus may be able to control some of its environment. Veliger larvae of this size mostly eat cyanobacteria and small autotrophic flagellates (Raby et al. 1997). Predators on both larval forms are likely to be the same as those on other zooplankton in the estuary.

Transport of embryos and larvae with the currents is a factor in the successful maintenance and spread of this species' populations and is most likely a factor in the timing of recruitment in the northernmost estuary (Figures 2a and 3). Even if the salinity is acceptable in spring, the residual flow during the spring outflow period is down-estuary throughout spring of most normal freshwater outflow years. Thus the largest number of larvae settles into this reach of the estuary during fall when both currents and salinity are favorable. In contrast to this pattern, Thompson et al. (2008) show that the 2-3 weeks that *Potamocorbula* larvae are pelagic are sufficient for larvae produced in the northern estuary to travel 40+ km and settle in the southern estuary. Thus, it is probable that populations throughout the estuary co-mingle and populations that are eliminated by mortality and inhospitable water quality conditions during one season are re-established by larvae from non-local populations. Because of the hydrologic variability in the estuary, the elimination of populations in the shallow water in most years (Thompson 2008), and the species' short life span, the repopulation of an area by non-local larvae is a critical component of the success of this species in the estuary.

4. Recruitment

As the veliger larva begins its transformation to become a benthic organism it swims less frequently and depends on the turbulence to transport it to the bed. Once there it has a short period of time to attach and burrow or to remain passive and be moved back into the water column (Crimaldi et al. 2002). There are several factors that determine the larva's transition from pelagic to benthic organism. First the water quality has to be acceptable and the salinity must fall in the 2-30 range. For this reason the abundance of recruits at a location can be related to the position of X2 in this estuary, as it is the bottom salinity that determines the success of the settling larvae (Figures 6 and 7). Recruitment therefore varies with location and freshwater outflow. A comparison of average monthly recruitment during wet/above normal, below normal, dry, and critically dry water years for a channel stations near Chipps Island (Figure 8a-d) and a shallow water station in Grizzly Bay (Figure 8e-h) shows

the effect of varying outflow on recruitment. The upstream station has one fall/winter recruitment, and few, if any recruits, from May through July in any water year. Wet/above normal outflow reduces the recruit abundance throughout the year. The below normal water year results in the highest number of recruits, with both the dry and critically dry years having fewer recruits than the below normal years. Recruits at the downstream, Grizzly Bay station are similar to those at the upstream station in that the wet/above normal years have low recruitment in summer and overall have a lower recruitment than in the other water years (Figure 8e). Below normal water years appear to be the most conducive to recruitment at this station with that year type being the only one with two distinct recruitment periods, in spring/summer and fall. The dry and critically dry years have one peak recruitment in summer although there are recruits available all months of the year.

The second factor that determines a larva's transition to a benthic organism is the physical environment, where the time to attach to the bottom is too short before the turbulence re-suspends the larvae. One factor shown to affect the time for attachment is the density of adult *Potamocorbula* at a location (Crimaldi et al. 2002). Additionally, *Potamocorbula* may also limit their own success by filtering their larvae out of the water column in a manner similar to that described for copepod nauplii (Kimmerer et al. 1994). The combination of these factors results in a density dependant threshold of adult *Potamocorbula* beyond which *Potamocorbula* recruits are less likely to settle. Our data show that at one location (shallow water Grizzly Bay) adult densities above about 100 m⁻² greatly limit the success of recruits (Figure 9a). Density dependent influences on settlement are not limited to intra-species effects. If conditions allow the estuarine amphipod *Ampelisca abdita* or some other surface tube-dweller to invade, we see a threshold effect on the *Potamocorbula* recruits as was seen with adult *Potamocorbula*. Nichols and Thompson (1985) reported a similar relationship between the bivalve *Macoma balthica* (now recognized as *M. petalum*) and *A. abdita* in the southern estuary. Although high abundances of adult *Potamocorbula* can co-occur with *A. abdita*, recruits appear to be limited either

by the flow disturbance of the tubes (Friedrichs et al. 2000) or the feeding activities of the suspension-feeding amphipod (Figure 9b).

The number of recruits is highly variable and, in addition to the intra- and interspecific competition noted above, predation and environmental variability are likely responsible for much of the variability (Figure 6). We have observed that the number of recruits in the shallows of North Bay is only reduced by freshwater outflow when we have prolonged, high outflow events as were seen in 1995 and 1998 (Figures 3a and 3d). When a high outflow event is followed by extremely low freshwater flow in summer and fall (e.g. 2006) we have observed near record number of recruits (reflected in the fall abundance in Figure 3a). Such patterns may be related to the removal of most benthic organisms during these flood events, thereby leaving a depauperate benthic community that is available to an opportunist like *Potamocorbula* (Nichols et al. 1990). The increase in fall abundance could also be due to a change in the freshwater fall pumping schedule in 1999 that resulted in salt water moving further up the rivers. Because this change occurs during the fall recruitment period, the recruits began settling further upstream than in the past.

Although there have been few studies on the predation on juvenile *Potamocorbula*, we observed in the 1980's that a remarkable number of clams 10+ mm in length from Carquinez Straits showed signs of being handled but not successfully eaten by a crustacean (Carlton et al 1990). Smaller clams did not show the chips along the edge of the valve, and we interpreted that as a sign that if they were picked up by the predator they were successfully consumed. We have since learned that *Cancer magister*, the Dungeness crab, occurs in this part of the estuary and preys on *Potamocorbula* (Stewart et al. 2004). Other likely predators on juvenile *Potamocorbula* include demersal fish, diving ducks in the shallow water, shrimp, and the exotic opisthobranch *Philine auriformis* in the more saline portion of the estuary (e.g. San Pablo Bay, Gosliner 1995).

Once settled to the bottom, recruits continue to feed on smaller sized pelagic food sources due to their small size (Table 1). We have observed growth to be more than 5mm in length within two months of recruitment in the southern estuary (Thompson et al. 2008), so the recruits likely graze on an increasing variety and size of algae and bacteria within a month of settling. Achieving reproductive size (Figure 10) is dependent on growth rate that varies between years and is likely a result of environmental stressors and food quantity and quality. Preliminary estimates of growth rate of Grizzly Bay *Potamocorbula* range from a peak of 3-4 mm/month in spring to <1-2 mm/month in fall (analyses by J. Thompson).

Juvenile and adult *Potamocorbula* are capable of being transported as bedload and within the water column. Small clams 5-8mm have been “sampled” using zooplankton nets in the deep water of the estuary (William Bennett pers. comm., University of California Davis). These individuals had a byssal thread still attached and we believe that like other bivalves they use the byssal thread for lift and subsequent transport (Beukema and Vlas 1989). Transport can result in individuals being both removed and deposited at a location (Figure 10).

5. Adult *Potamocorbula*

Adult *Potamocorbula* (>5mm in length) are remarkably tolerant of salinity changes and their wide distribution in the SFE reflects that tolerance (Table 1, Figure 11). *Potamocorbula* is an osmo-conformer that can adapt to changes in salinity within 48 hours. Adults can tolerate very low salinities (0.1) in the laboratory but was reported to die with prolonged freshwater exposure by Werner et al. (2003). Miller and Stillman (in journal review) found metabolic rates varied seasonally with the lowest rates in spring and highest rates in fall, but they were not able to relate metabolic variability to salinity, temperature, or food. *Potamocorbula* hyperosmoregulated in low salinity but the costs of that physical adjustment were not reflected in the metabolic rate or energy stores. They conclude that *Potamocorbula*'s distribution is not a result of energy costs due to osmoregulation. *Potamocorbula* may pay some metabolic price for this tolerance. Pagannini et al. (2010) observed that

Potamocorbula had 40% lower oxygen consumption rates (VO₂) at salinities fluctuating between 4 and 14 than the VO₂ observed at high (28) and low (2) salinities. Glycogen was reported as low by Werner et al. (2003) and high by Miller and Stillman (in journal review), and lipid stores were generally lower in *Potamocorbula* than in other bivalves (Richman and Lovvorn 2004). Therefore it appears *Potamocorbula* cannot or does not depend on energy stores during periods of stress. Canuel et al (1995) in examining the fatty acids in *Potamocorbula* suggested that they are “capable of rapid assimilation and incorporation of algal-derived organic matter into their tissues during periods of high phytoplankton abundance.” Such rapid assimilation could account for the differing glycogen results, i.e. glycogen concentration may reflect recent events.

The only oxygen tolerance data is an observation by Kamenev and Nerasov (2012) that *Potamocorbula* live in areas in the Amur River estuary with oxygen concentrations in the 3.2 to 6.3 ml L⁻¹ range and have the largest populations in the 3.9-6.3 ml L⁻¹ range. Although the data are not shown in their report, McEnulty et al. (2001) report that *Potamocorbula* “has a high tolerance to low oxygen and is found in polluted or eutrophic areas”. A similar statement is made by Sato and Koh (2004) who state that *Potamocorbula* “survived in a (the) bad aquatic condition for a long time” following the isolation of an embayment by dikes and its eventual dewatering.

Potamocorbula is a suspension feeder that can filter and assimilate both phytoplankton and bacteria (<1.2 µm) from the water column (Werner and Hollibaugh 1993). Their high secondary production in areas with low phytoplankton biomass (Thompson 2005) suggests it depends on carbon sources other than phytoplankton. Retention efficiency for natural bacteria is lower (28% and 13 % for 1 and 2 cm long clams) than for phytoplankton (100%). Bacterial gross assimilation rates (73-75%: Decho and Luoma 1991, Werner and Hollibaugh 1993) are somewhat lower than measured for phytoplankton (78-90% for a range of phytoplankton species; Schlekot et al. 2002). Bacterial carbon also appears to be more quickly

metabolized than phytoplankton carbon (Werner and Hollibaugh 1993). Net assimilation rates have been estimated at 45% for bacteria and $\approx 85\%$ for phytoplankton (Werner and Hollibaugh 1993, Schlekot et al. 2002).

Known aquatic consumers of adult *Potamocorbula* in the SFE include the Dungeness crab (*Cancer magister*, Carlton et al. 1990, Stewart et al. 2004), the Sacramento Splittail (*Pogonichthys macrolepidotus*, Deng et al. 2007), White Sturgeon (*Acipenser transmontanus*, Adams et al. 2007, Urquhart and Regalado, 1991, Kogut 2008), and the Green Sturgeon (*Acipenser medirostris*) (Adams et al. 2007). It is likely that any bottom feeding fish with a sufficiently large mouth that feeds in areas occupied by *Potamocorbula* consume some quantity of the bivalves due to their large population. Birds known to consume adult *Potamocorbula* include the Greater and Lesser Scaup (*Aythya marila* and *A. affinis*, Poulton et al. 2002) and the Surf Scoter (*Melanitta perspicillata*, Hunt et al. 2003). Conchiolin layers, organic laminae in the shells that occur in bivalves in the Corbulidae family, act both to increase the strength of the shell against predation from mechanical crushing and to deter gastropods from drilling through the bivalve's shell (Kardon 1998).

Populations of *Potamocorbula* are reduced and in some cases locally decimated by migratory birds in fall and winter in all but the deep channel areas of the SFE (Poulton et al. 2002, Thompson et al. 2008). Therefore the shoal areas are mostly dependent on the adjacent deep water populations to supply recruits each year.

The combination of *Potamocorbula's* ability to respond to food quickly to initiate gamete production and to produce gametes and embryos that are tolerant of large changes in salinity is likely to be a good strategy for this species to maintain its present distribution, as well as to expand its distribution during seasonal salinity changes in the estuary. Individuals become reproductively active within their first year of life and in many cases, spring recruits are capable of reproducing by summer

and fall, so adults are present during most months of the year to respond to a cue to begin gametogenesis.

B. *Potamocorbula's* Control of Phytoplankton Biomass

The SFE is a high nutrient, high turbidity estuary that has low primary production due to a combination of light limitation and bivalve grazing (Cloern 2001, Thompson et al. 2008). The northern estuary has always had low primary production, but declines in primary production following the invasion of *Potamocorbula* lead many researchers to conclude that suspension feeding by *Potamocorbula* resulted in the decline in phytoplankton biomass and the elimination of the annual phytoplankton bloom in the estuary (Alpine and Cloern 1992, Kimmerer 2002). The annual primary production has been reduced to $<20 \text{ g C m}^{-2} \text{ yr}^{-1}$ from $\approx 100 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Alpine and Cloern 1992, Jassby et al. 2002).

Two copepods (*Acartia* spp, *Eurytemora affinis*), a rotifer (*Synchaeta bicornis*), and a mysid shrimp (*Neomysis mercedis*) concurrently declined with the phytoplankton, presumably due to food limitation (Kimmerer 2002, Feyrer et al. 2003). Some of the declines in copepods may also be due to direct filtration of juveniles by *Potamocorbula* (Kimmerer et al. 1994). Despite what appeared to be a collapsing foodweb within 5 years of the invasion of *Potamocorbula*, most of the species involved remain in the estuary today. The robustness of the foodweb may be due to (1) its complexity and therefore weak links (Kimmerer 2002), (2) the importance of microzooplankton and small phytoplankton that are not presently accounted for in the data, or (3) the migration of one important, competing filter feeder, the Northern Anchovy (*Engraulis mordax*), out of the northern estuary following the reduction in phytoplankton biomass (Kimmerer 2006). Although the cause of a recent decline in pelagic fish in the ecosystem (Sommer et al. 2007) is probably at least partially due to changes in the pelagic foodweb, there is no conclusive evidence that food is the primary or only cause for the decline of the fish species.

Potamocorbula's pumping rate (a physiologically controlled rate), estimated in a flume with varying velocities, was found to range from 100-575 L (g dry weight)⁻¹ d⁻¹ with a mean of ~400 L (g dry weight)⁻¹ d⁻¹ or 1-5 L d⁻¹ clam⁻¹ for the phytoplankton *Chroomonas salinay* (Cole et al. 1992). Clearance rates (a physiologically controlled rate that varies with filtrate character) estimated in beaker experiments are similar: 4 L d⁻¹ for a 1 cm clam {filtration rate = -40+199 x shell length (cm)} for phytoplankton (*Isochrysis galbana*) and 45 ml hr⁻¹ clam⁻¹ (independent of shell size) for bacteria (Werner and Hollibaugh 1993). We can estimate the effect of *Potamocorbula*'s grazing rate (our estimate of a field rate) in two ways. First, *Potamocorbula*'s maximum effect on the phytoplankton biomass can be estimated by using pumping rates and assuming a vertically well mixed water column. The second method estimates a minimum effect of clam grazing on the phytoplankton by (a) assuming that a concentration boundary layer (CBL) forms within a bed of clams and (b) that not all clams feed at once (66% active clams at a time). In this case the phytoplankton removed by the bivalves is not replaced by vertical mixing which results in a vertical gradient in phytoplankton concentration (i. e.. the clams downstream of other clams have less food). The CBL method and a more thorough explanation of the estimation technique can be found in Thompson et al. (2008).

Potamocorbula's consumption of phytoplankton is likely a function of environmental factors such as temperature and suspended sediment in addition to the biomass of bivalves and vertical mixing rates (Figure 12). The effect of many of the environmental factors is not yet well defined. Table 3 shows grazing rates using the two methods. Note that the median grazing rate varies by a factor of 4 between stations for both methods. This range reflects the larger biomass of *Potamocorbula* observed in the deep water (Table 2). Vertical turnover time, or the time that the clams need to filter the water column over them, assuming the water column is vertically well mixed, is a reflection of the potential impact that *Potamocorbula* has on the phytoplankton standing stock and its capacity to achieve a bloom biomass. Turnover time using the median grazing rate is about 2-4 days for the shallow water

population in Grizzly Bay and 4-8 days for the channel populations. These turnover times are shortest in fall when biomass and grazing rate peak; *Potamocorbula* could theoretically clear the water column once every 8-16 hours in Grizzly Bay and every 8-24 hours in the channel during this period. Minimum biomass and therefore minimum grazing rates have consistently occurred in spring and early summer at all shallow water locations and most channel stations; the biomass time series shown in Figures 3b and 3e are representative of this seasonality.

The rapid turnover of the water column by the shallow water bivalves, in conjunction with the relatively slow phytoplankton growth rate (0.25 d^{-1} in the shallow water, Cloern et al. 1985) highlight the importance of shallow water *Potamocorbula* as one of the factors determining system-wide phytoplankton biomass. The high grazing rates in the channel may also influence phytoplankton biomass, but the negative growth rate of phytoplankton in the channel due to the poor light climate (i.e. limited illumination in the water as determined by incident light, absorption, scattering, and turbidity) (Cloern et al. 1985) is likely to be the primary factor controlling phytoplankton biomass in the deep water. Therefore the only locale in the northern estuary where the light climate allows phytoplankton to grow is in the shallows. Historically, a slow growing, 4-5 month long phytoplankton bloom began in the shallows and spread to the channels in the northern estuary (Cloern et al. 1985). Today, high *Potamocorbula* grazing rates in conjunction with relatively high water column vertical mixing rates challenge the potential for phytoplankton biomass increase in these shallow systems except during spring. The phytoplankton consumption rates reported here for *Potamocorbula* in the northern estuary will affect adjoining areas through tidal dispersion. Therefore the *Potamocorbula* filtration in the northern estuary may have a significant effect on the phytoplankton in the western Delta as reported by Jassby et al. (2002).

C. Negative Influence of the Trophic Transfer of Contaminants

The near-surface growth position of *Potamocorbula* makes them more available to predators than the deep-burrowing bivalve that previously dominated the northern

estuary (*Macoma petalum*, previously known as *Macoma balthica*). The caloric content of the two bivalves is similar (Richman and Lovvorn 2004). Thus the invasion of *Potamocorbula* might be an advantage to bottom feeding predators if not for the propensity of *Potamocorbula* to accumulate selenium at near toxic levels for consumers (Stewart et al. 2004). Since its arrival in the estuary, predators on *Potamocorbula* that now have selenium concentrations in their liver in excess of the toxicity threshold include the Sacramento Splittail (*Pogonichthys macrolepidotus*), the Dungeness crab (*Cancer magister*), the White Sturgeon (*Acipenser transmontanus*) (Stewart et al. 2004) and diving ducks (Scoter: *Melanitta perspicillata* and Scaup: *Aythya* spp) (White et al. 1987, 1988, 1989, Urquhart and Rigelado 1991, Linville et al. 2002). Although *Potamocorbula* also bioaccumulates heavy metals (Brown and Luoma 1995), hydrocarbons (Pereira et al. 1992), butyltins (Pereira et al. 1999), and pesticides (Gale et al. 2003), there is no literature on the effects of these toxins on *Potamocorbula*'s predators.

D. Constraints on Restoration

Potamocorbula invaded the SFE after a 100 year flood event that greatly reduced the diversity and abundance in the benthic community at the invasion location (Nichols et al. 1990). Although *Potamocorbula* then invaded other parts of the estuary in the following two years, and did so within a normally diverse community (Thompson 2005), its ability to monopolize the depauperate benthic community in the northern estuary signifies its likely response to newly restored habitat. *Potamocorbula* has invaded and dominated the benthic community following a dike being built in Korea (Ryu et al. 2011) and in Japan (Sato and Koh 2004). Ryu et al. (2011) attributed the order of magnitude increase in biomass with *Potamocorbula*'s invasion to their ability to live in the high organic area which developed with the reduction in current velocity behind the dike. *Potamocorbula* either became dominant (Sato and Koh 2004) or invaded following the dike construction which led Ryu et al (2011) to call *Potamocorbula* an opportunistic bivalve. This opportunistic ability, in combination with *Potamocorbula*'s prodigious grazing rates and ability to accumulate and transfer contaminants may limit our restoration options in the northern estuary.

The decline of fish that prey on zooplankton and shrimp, which depend on primary producers, has resulted in a primary restoration goal of increasing the production of phytoplankton. Because *Potamocorbula* grazing can restrict the net growth rate of phytoplankton, it has been suggested that control of *Potamocorbula* biomass in some select areas might allow phytoplankton to grow and be transported out of these areas. As the major control on *Potamocorbula* distribution appears to be salinity at fertilization and spawning, it has been discussed if increasing freshwater outflow during peak reproductive periods would limit their distribution. The low salinity stress on the eggs, embryos and pelagic larvae in combination with their transport out of the area with high flows (large flood events like 1995 and 1998) might reduce the population size and distribution of *Potamocorbula* in localized areas for short time periods. It takes very large, prolonged outflow events to reduce the estuary-wide population (Figure 3) over an extended time period, as local and non-local adults can respond quickly and produce new larvae as long as food is available. Increased outflow periods would need to be maintained for this to be a long term solution, as depauperate periods such as was seen in 2006 can be followed by an increase in the population size of *Potamocorbula* during subsequent years with normal salinity distributions. Therefore, sustained reduction in grazing would require the water for controlled floods most if not all years.

Potamocorbula's ability to accumulate toxins and its place in the food web as prey is also an important consideration in restoration plans. Without the elimination of *Potamocorbula* from the estuary, the best that can be done for protecting predators is to identify sources of contaminants and try to eliminate their availability to *Potamocorbula*. Any restoration action that increases the concentration of contaminants in *Potamocorbula* may result in an increase in the contaminant concentration in their predators, although the predictability of the amount transferred is contaminant and species specific.

Climate change may make *Potamocorbula* population biomass distribution less consistent between years as the frequency of high and low freshwater outflow events are predicted to increase. In addition to this “natural” population variability is that caused by declining freshwater resources. If there is an overall decline in freshwater available to the estuary as the need for freshwater is increased in California for human consumption, *Potamocorbula* will expand into the western Delta as the salinity increases. This will further complicate restoration in the western Delta.

V. Future research

The immediate research needs include (1) resolution of taxonomic questions in the family, (2) incorporation of biomass estimates in the DWR monitoring program, and (3) examination of the physiological characteristics of the species.

Potamocorbula amurensis has apparently not spread to intra-coastal ports nor has it been introduced to other Eastern Pacific locations. The wide distribution of *P. amurensis* in the Western Pacific leads us to question if the species is correctly identified. It seems unlikely that adults and larvae have not been included in ballast water that has been released in other ports. The only explanations we have at present for the lack of spread are that (1) there is something in its physiology that limits its transport and or settlement in most situations, (2) the balance of trade today reduces the number of ships arriving fully in ballast from Asia and thus there has been less opportunity for release of ballast water, or (3) it has invaded elsewhere but in localities without monitoring programs. All of these explanations would be influenced by finding that the taxonomy is incorrect; a genetic study may be needed to fully understand the Corbulidae taxonomy.

The second research need is to incorporate estimates of biomass of the major species as part of the routine analysis of DWR’s Environmental Monitoring Benthic Program. As seen in Figure 3, our understanding of ecosystem effects cannot be facilitated using abundance alone. The inclusion of biomass in the analyses would allow the

benthos to be defined as carbon, the common currency used in food web analyses. In addition, an estimate of biomass would give us the data needed to estimate grazing rates on phytoplankton and zooplankton, growth rates (i.e. how much carbon are they consuming), and the mass and contaminant content available to predators.

We cannot confirm many of our assessments of possible controls on the temporal and spatial distribution described in this document until more basic physiological measurements of *Potamocorbula* are done in the laboratory. The Miller and Stillman (in review) and Paganini et al. (2010) studies have helped but many questions have been raised by their studies and those have yet to be resolved. To thoroughly understand the distribution potential of *Potamocorbula* in a restored area we need to know how salinity and temperature co-vary, i.e. when does temperature narrow *Potamocorbula*'s salinity tolerance and when does salinity limit *Potamocorbula*'s ability to withstand high temperatures that may occur in high-residence time restored embayments. Understanding *Potamocorbula*'s low oxygen tolerance will help explain distribution anomalies in Suisun Marsh where low oxygen has been concurrently observed with dead *Potamocorbula* and help us understand the length of time necessary for *Potamocorbula* to die in low oxygen water. Finally, grazing rates are very important if we are to understand *Potamocorbula*'s effects on the estuary, but we know nothing about how its pumping rates are related to suspended sediment concentration, temperature, and food concentrations.

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VII. Tables

Table 1. *Potamocorbula* Life-Stage by Biological Measures.

		A	B	C	D	E	F	G	H	J	K	L	M	N
	Habitat (<i>life stage</i>)	Dates	Age (Days post hatch)	Weight	Length	Optimum Temp (Celsius)	Maximum Critical Temp (Celsius)	Min Salinity	Max Salinity	Min DO Limits	Water Velocity	pH	Turbidity	References
1	Benthic (<i>Eggs/Sperm</i>)	Jan- Dec	-1	UNK		UNK	UNK	5	25	UNK	UNK	UNK	UNK	Nicolini & Penry 2000
2	Benthic (<i>Fertilization of Egg</i>)	Jan- Dec	-1	UNK	60+ μm	UNK	UNK	5	25	UNK	UNK	UNK	UNK	Nicolini & Penry 2000
3	Pelagic (<i>Trochophore Larvae</i>)	Jan- Dec	0-1	UNK	70 μm	UNK	UNK	2	30	UNK	UNK	UNK	UNK	Nicolini & Penry 2000
4	Pelagic (<i>Veliger Larvae</i>)	Jan- Dec	1-19	UNK	75-135 μm	UNK	UNK	2	30	UNK	UNK	UNK	UNK	Nicolini & Penry 2000
5	Benthic (<i>Recruit</i>)	Jan- Dec	19~120		300 μm - 5 mm	UNK	UNK	2	32+	UNK	UNK	UNK	UNK	Nicolini & Penry 2000 Parchaso & Thompson 2002
6	Benthic (<i>Reproductive Adult</i>)	Jan- Dec	Maximum >3 years <4 years		>5mm	UNK	UNK	.1	32+	UNK	UNK	UNK	UNK	Parchaso & Thompson 2002

Table 2. *Potamocorbula* Population Characteristics.

			A	B	C	D	E	F	G	H	J	K	L	M	N	N
	Geographic Location	Station ID Source	Station depth at MLLW (m)	Maximum Biomass		Maximum Abundance		Abundance Range (#/m ²)				Biomass Range (gC/m ²)				Years Examined
				gC/m ²	mo/yr	#/m ²	mo/yr	max	yr	min	yr	max	yr	min	yr	
1	Colinsville	D4* DWR	11	5	4/91	3000	10/00	0-3000	2000	0	2002	0-5	1991	0	2002	1987-1988, 1991, 1998, 2000, 2002, 2004
3	Chippis Island	4.1 USGS	9	22	10/07	12,000	11/00	400-12,000	2000	10-500	1996	2-22	2007	0-0.7	1999	1988-2007
5	Carquinez Strait	8.1 USGS	17	80	5/88	30,000	4/07	1600-26,000	2006	10-800	1998	10-80	1988	0.2-1	1998	1988-2007
6	Honker Bay	433 USGS	2	4	7/90	5700	10/06	100-5700	2006	10-300	1995	0.2-3	1993 2007	<0.1-0.3	1996	1988-2003 2006-2007
7	Grizzly Bay	D7* DWR	2	5	12/05	17,000	6/87	300-16,000	2006	100-600	1995	0.2-5	2005	<0.1-0.6	1995	1987-2002 2006-2007
8	Grizzly Bay	417 USGS	<1	3	8/07	15,000	9/06	not enough data								2006-2007
9	San Pablo Bay	D41A* DWR	2	16	9/89	39,000	5/00	200-39,000	2000	400-1000	1994	0.3-16	1989	0.2-1	1994	1987-2002 2006-2007

* Data for D4, D7 and D41A Courtesy of DWR CALFED Biomass Study

Table 3. *Potamocorbula* Grazing Rates

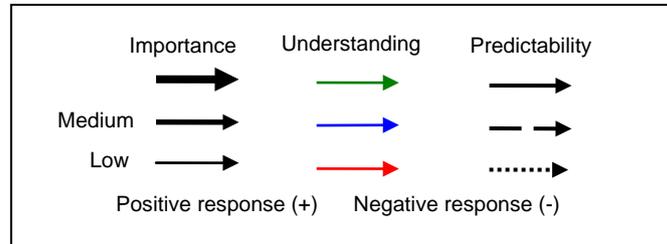
		A	B	C	D	E	F	G	H	I	J	K	L
	Habitat (life stage)	Dates	Water Column Depth (m)	CBL Corrected, 67% Feeding (m ³ m ⁻² d ⁻¹)					Pumping Rate (m ³ m ⁻² d ⁻¹)				
				mean	median	max	min	Turnover Time (day)*	mean	median	max	min	Turnover Time (day)*
1	Benthic Shallow D7 DWR**	1988-2006	2	1	0.5	3	0	4	1	1	6	0	2
2	Benthic Deep 4.1 USGS	1988-2006	8	1	1	10	0	8	2	1	20	0	8
3	Benthic Deep 8.1 USGS)	1988-2006	17	3	2	15	0	6	7	4	50	0	4

* using median grazing rate

** Data for D7 Courtesy of DWR CALFED Biomass Study

VIII. Figures

Figures 6, 10, 11 and 12 are matrices showing transitions from one life stage to the next. Negative and positive effects of processes on transition survival are designated by (-) and (+). Levels of importance, understanding and predictability of each process are given in the key below.



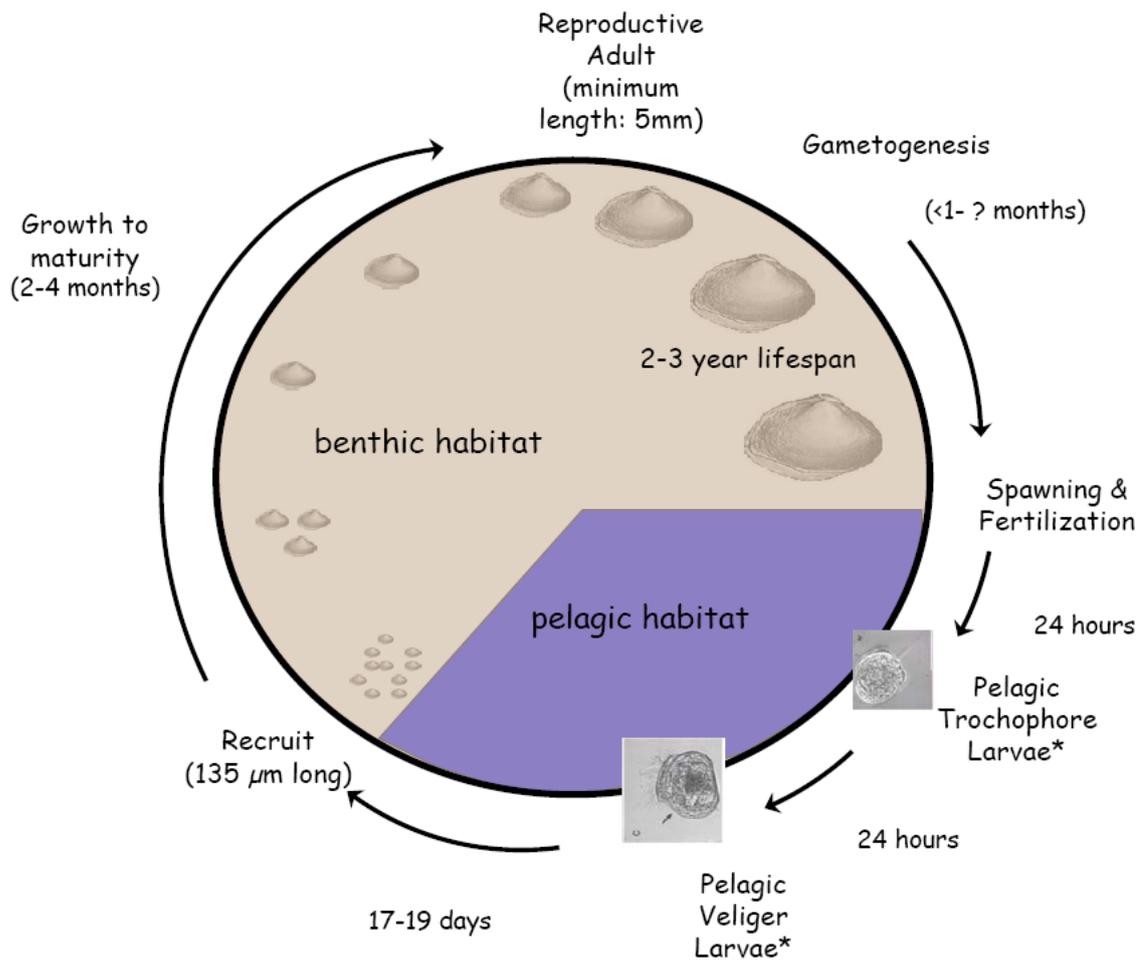


Figure 1. Life cycle of *Potamocorbula amurensis* in San Francisco Estuary. (Adapted from Nicolini, MH and DL Penry. 2000. Spawning, fertilization, and larval development of *Potamocorbula amurensis* (Mollusca: Bivalvia) from San Francisco Bay, California. Pacific Science: 54(4):377-388 NO PERMISSION FOR PUB.)

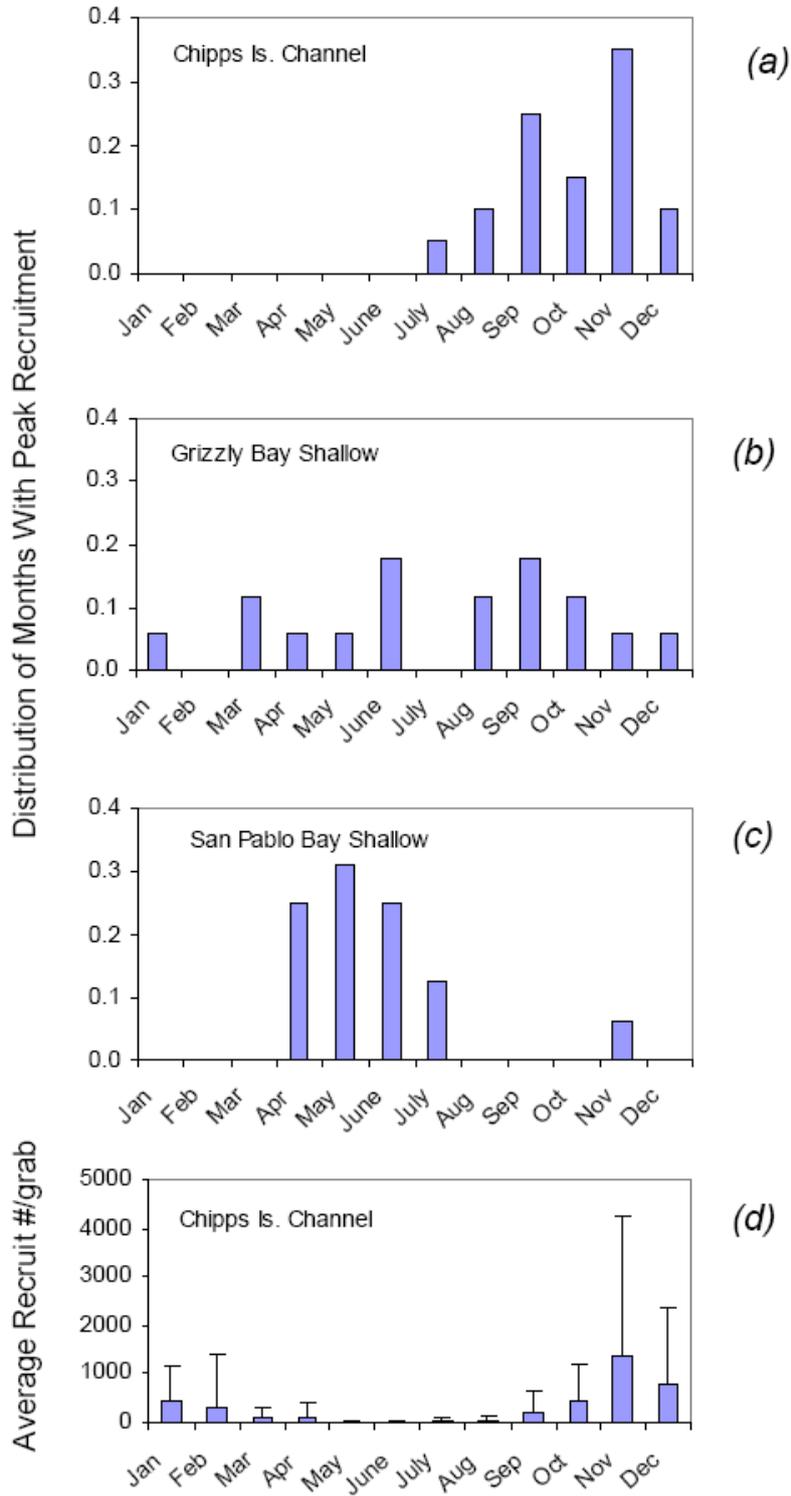


Figure 2. Distribution of months with peak *Potamocorbula* recruitment in (a) the western Delta, (b) Grizzly Bay, (c) San Pablo Bay. Average recruits occurring each month in the western Delta over the period of 1988 through 2006 (d). Grizzly Bay data courtesy of DWR CALFED Biomass Study.

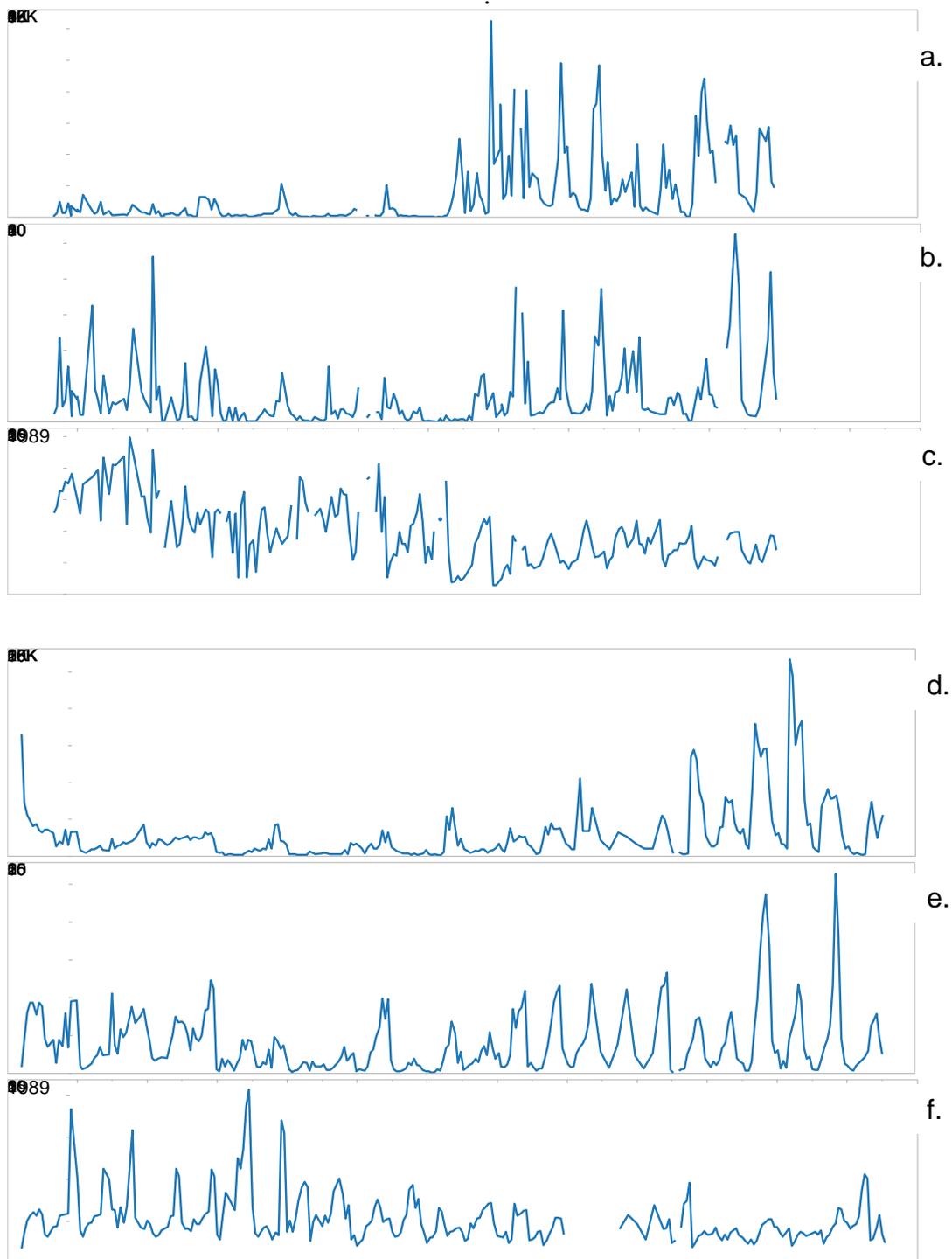


Figure 3. Density, biomass, and average shell length of *Potamocorbula* at the western Delta (a, b, c) and in Grizzly Bay (d,e,f). Grizzly Bay data courtesy of DWR CALFED Biomass Study.

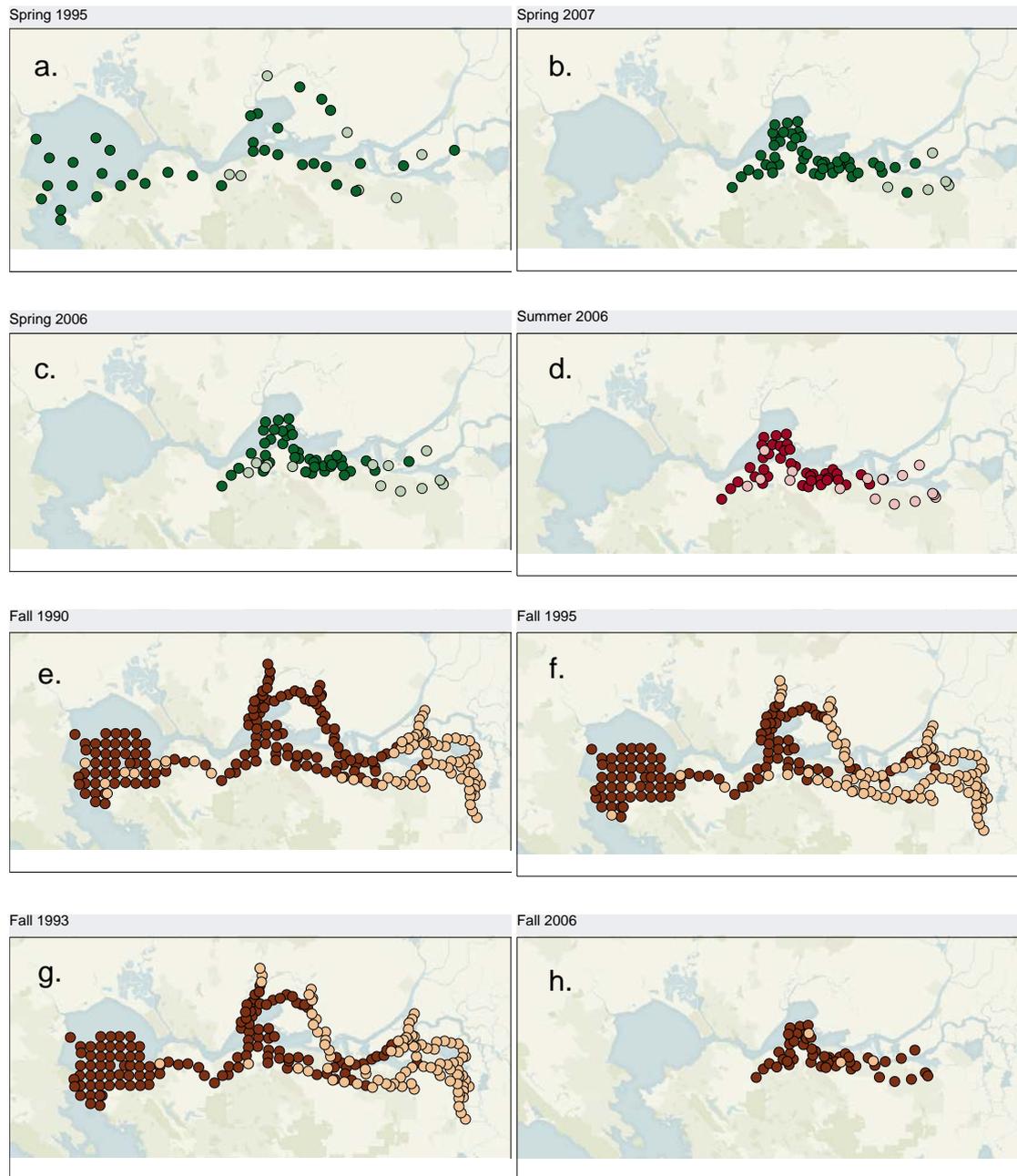


Figure 4. Distribution of *Potamocorbula* in SFE during (a-d) spring and summer months and (e-h) fall months. 1990 data from Hymanson (1991). 1995 data courtesy of DWR. Light colored symbols represent stations sampled but with no *Potamocorbula*.

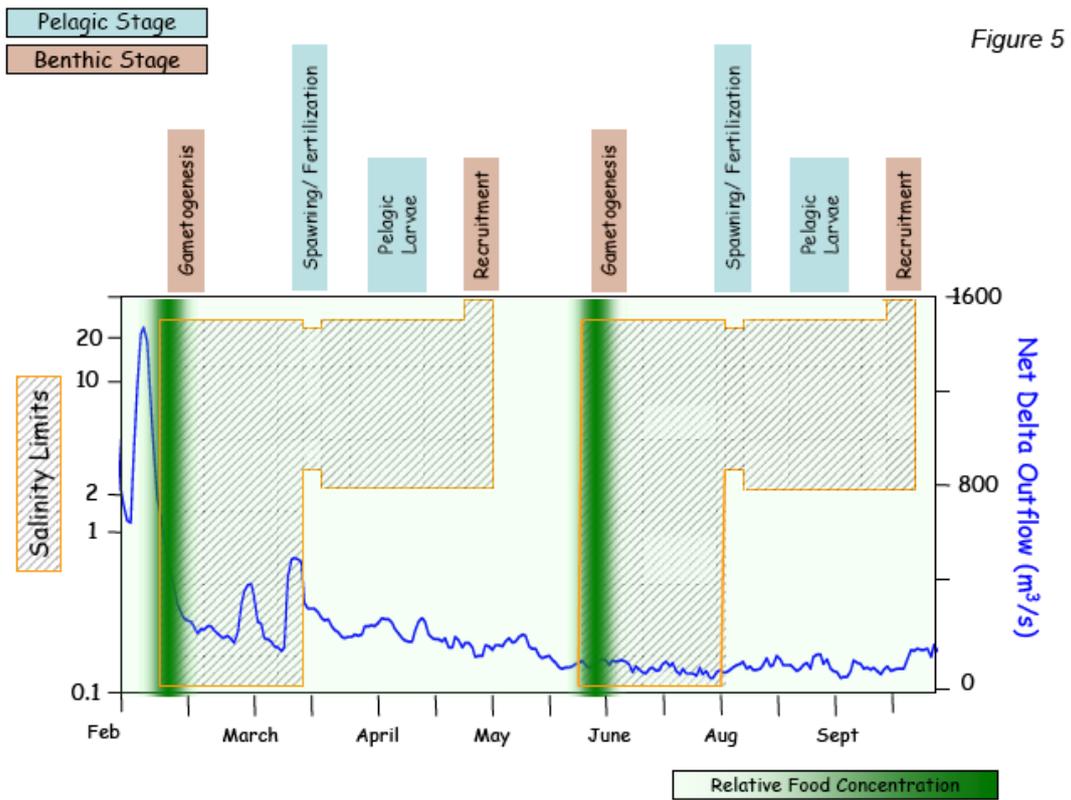


Figure 5. Life Cycle and habitat conceptual model for *Potamocorbula*.



Transition Matrix: Corbula

■ Biotic ■ Abiotic

Figure 6

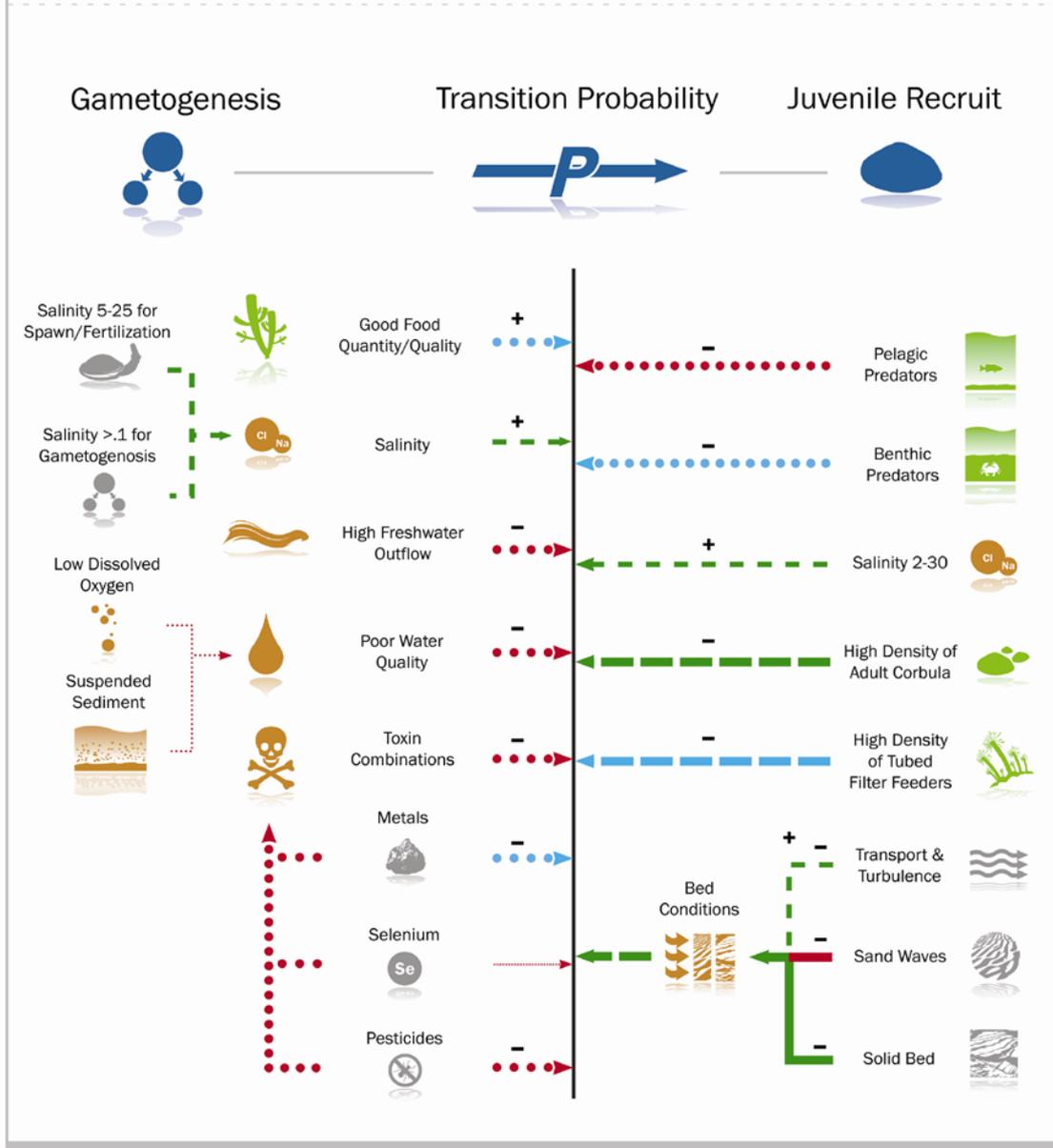


Figure 6. Transition probability of *Potamocorbula* gametogenesis to recruit.

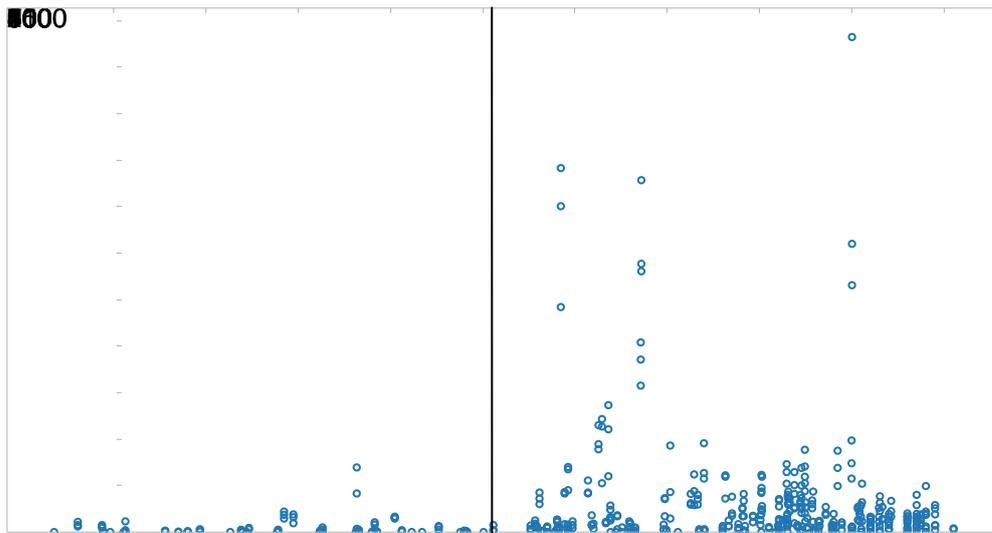


Figure 7. *Potamocorbula* recruit density in cores collected from station located at X2 km 64 (line on graph). Recruits are limited when the maximum excursion of X2 is downstream of the station, i.e. when salinities are less than 2 at the station the previous month prior to the sampling.

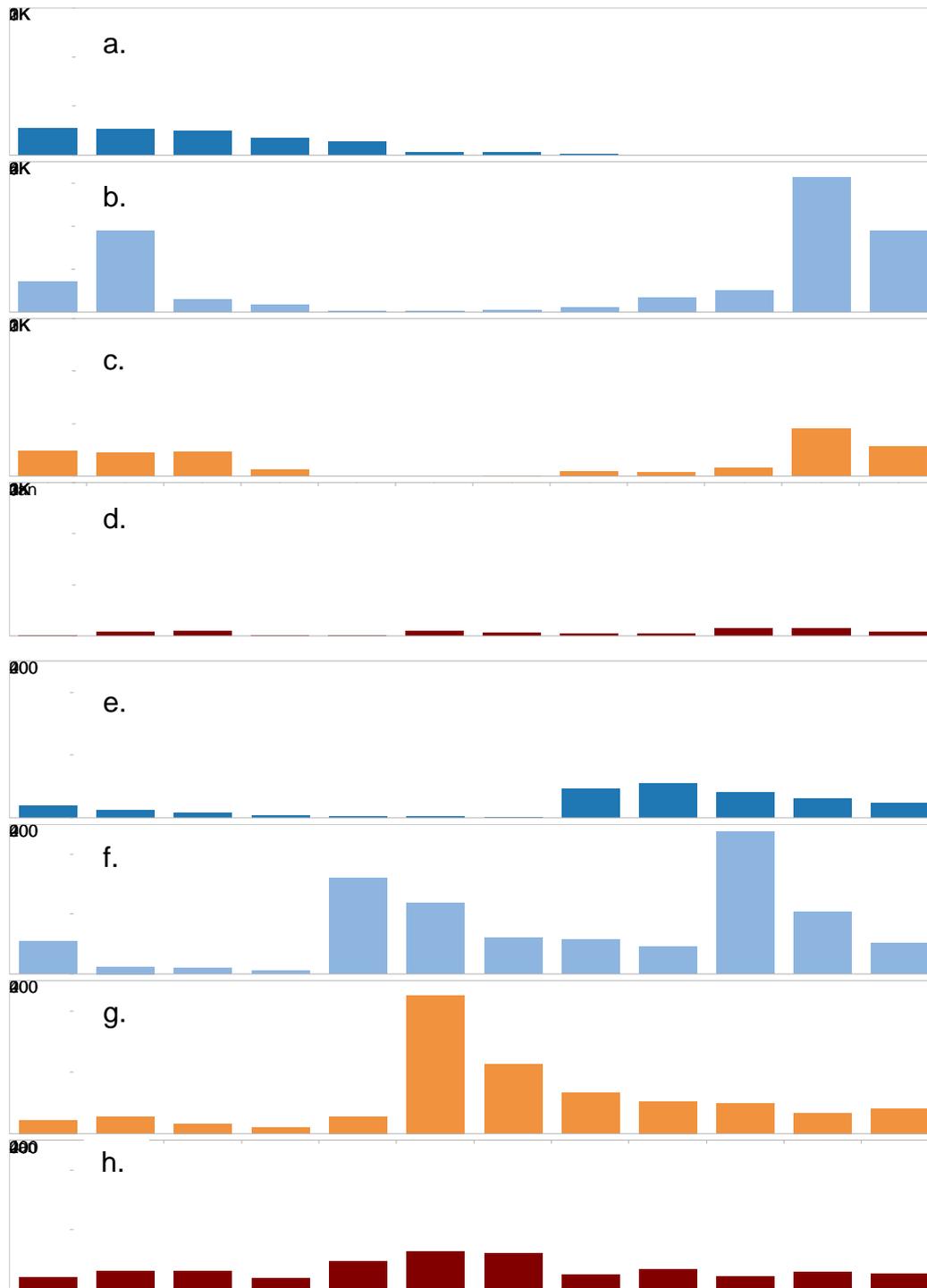
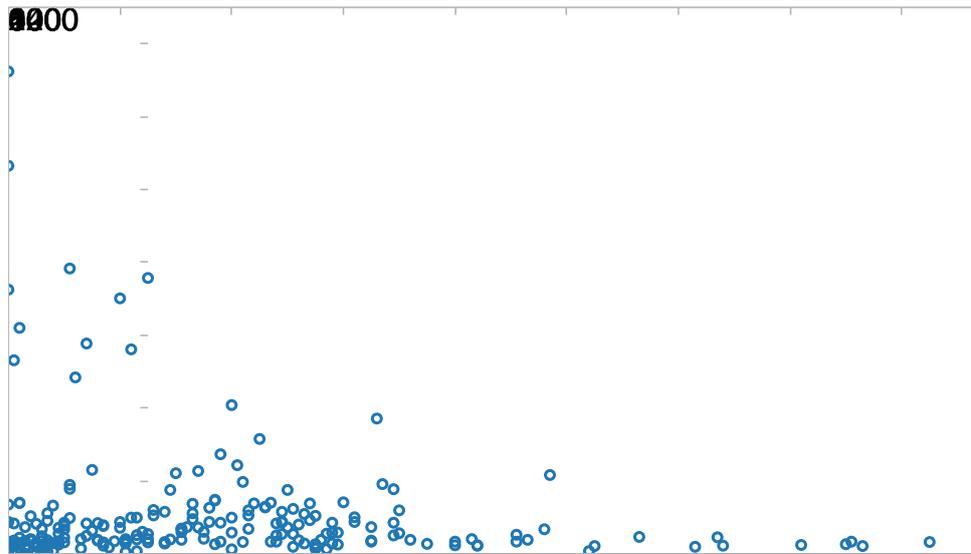
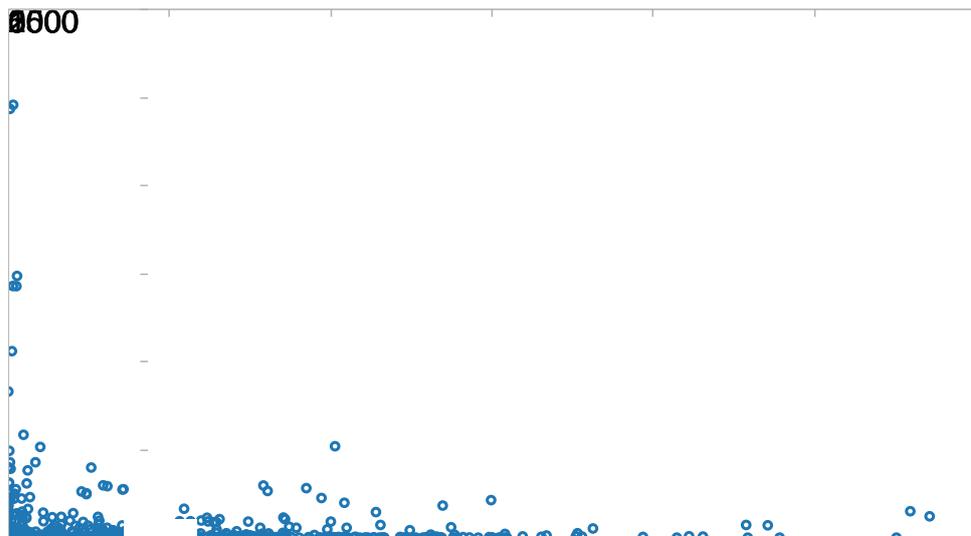


Figure 8. Abundance of *Potamocorbula* recruits in the western Delta for wet/above normal water year (a), below normal water year – note scale change (b), dry water year (c), critically dry water year (d) and in Grizzly Bay for wet/above normal water year (e), below normal water year (f), dry water year (g), critically dry water year (h). Grizzly Bay data courtesy of DWR CALFED Biomass Study.



a.



b.

h.
h.

Figure 9. *Potamocorbula* recruit density as a function of (a) adult *Potamocorbula* density and (b) *Ampelisca abdita* density.



Transition Matrix: Corbula

■ Biotic ■ Abiotic

Figure 9

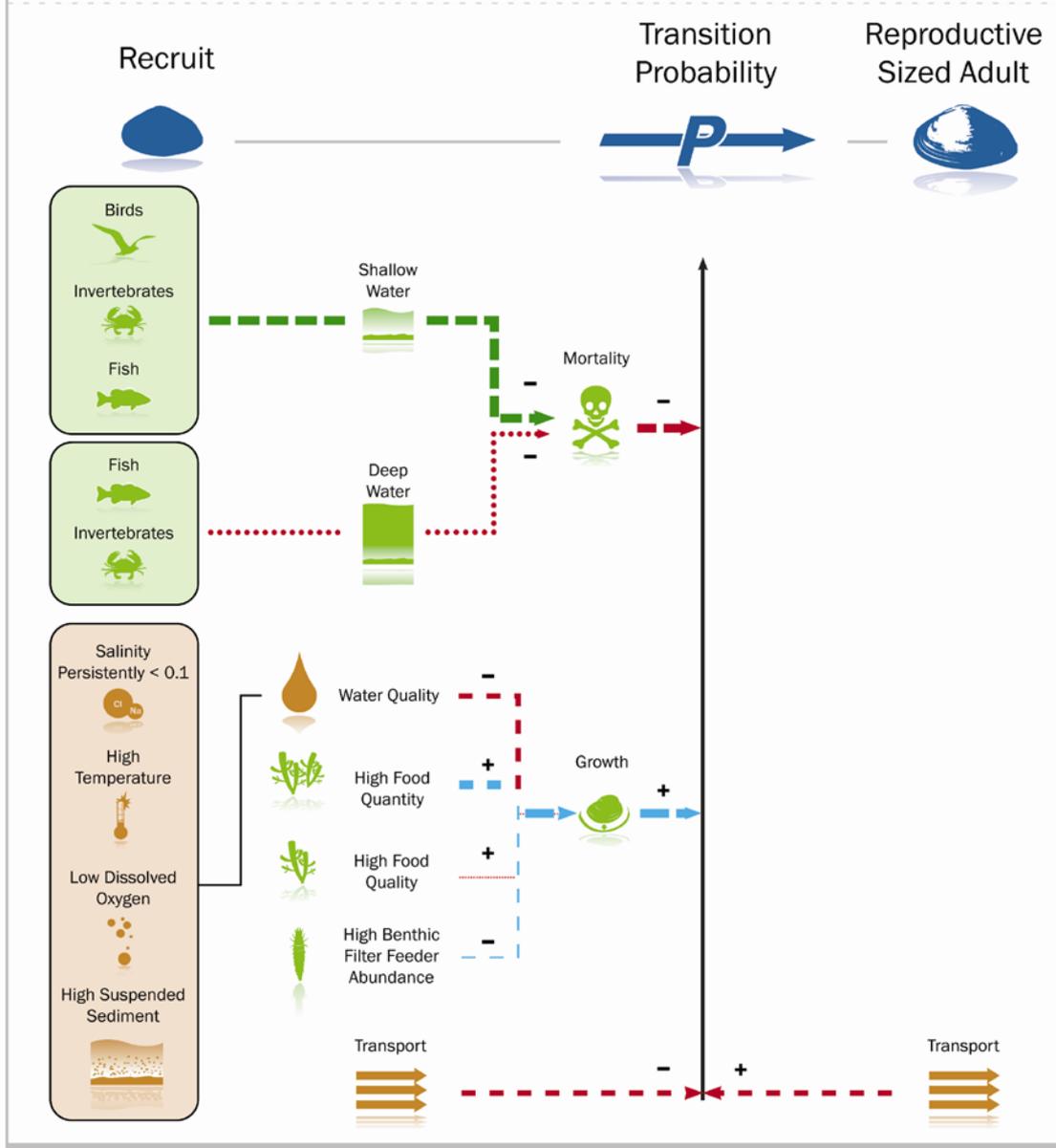


Figure 10. Transition probability of *Potamocorbula* recruit to reproductive adult.

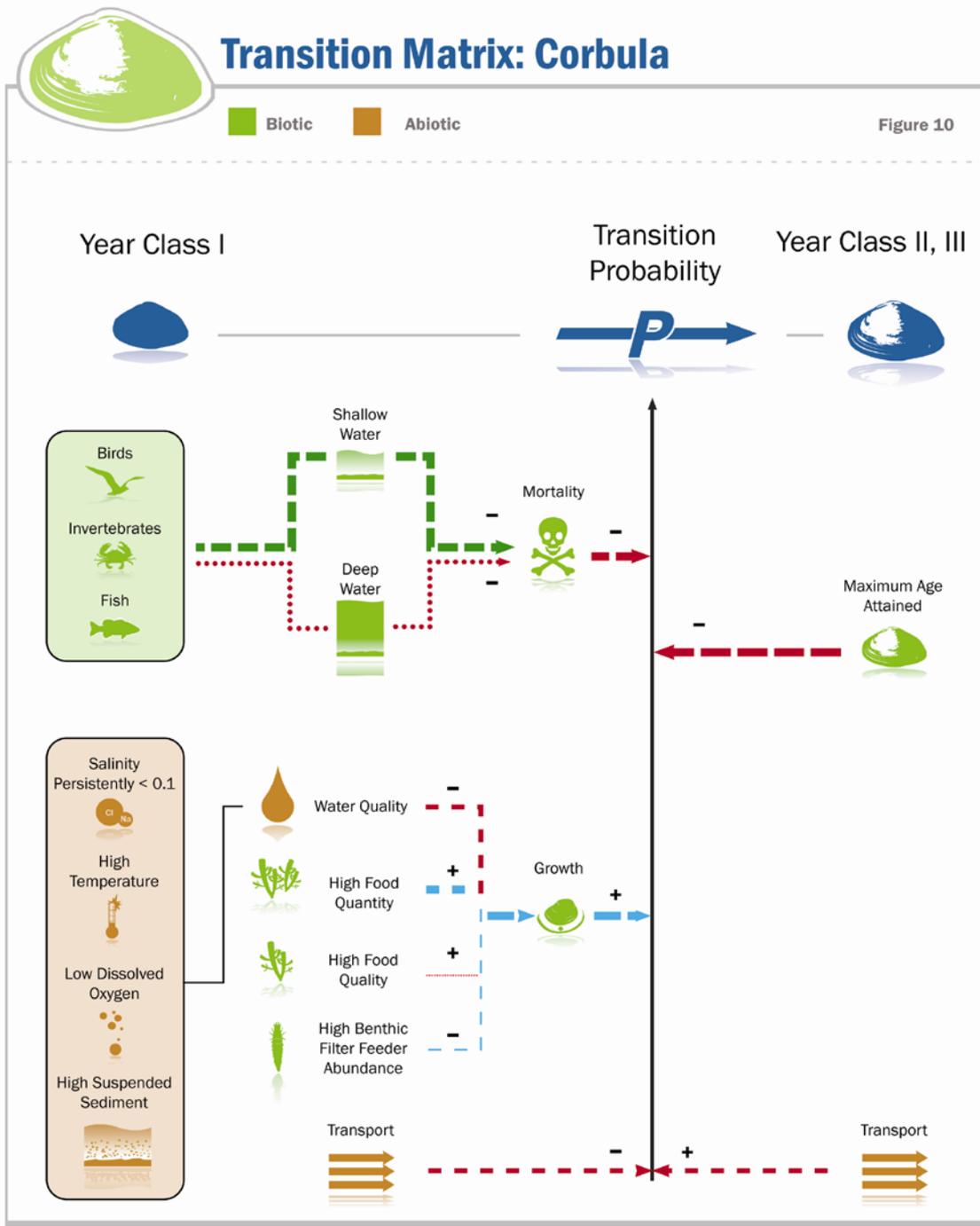


Figure 11. Transition probability of *Potamocorbula* one year old to a two year old or greater.



Transition Matrix: Corbula

■ Biotic ■ Abiotic

Figure 11

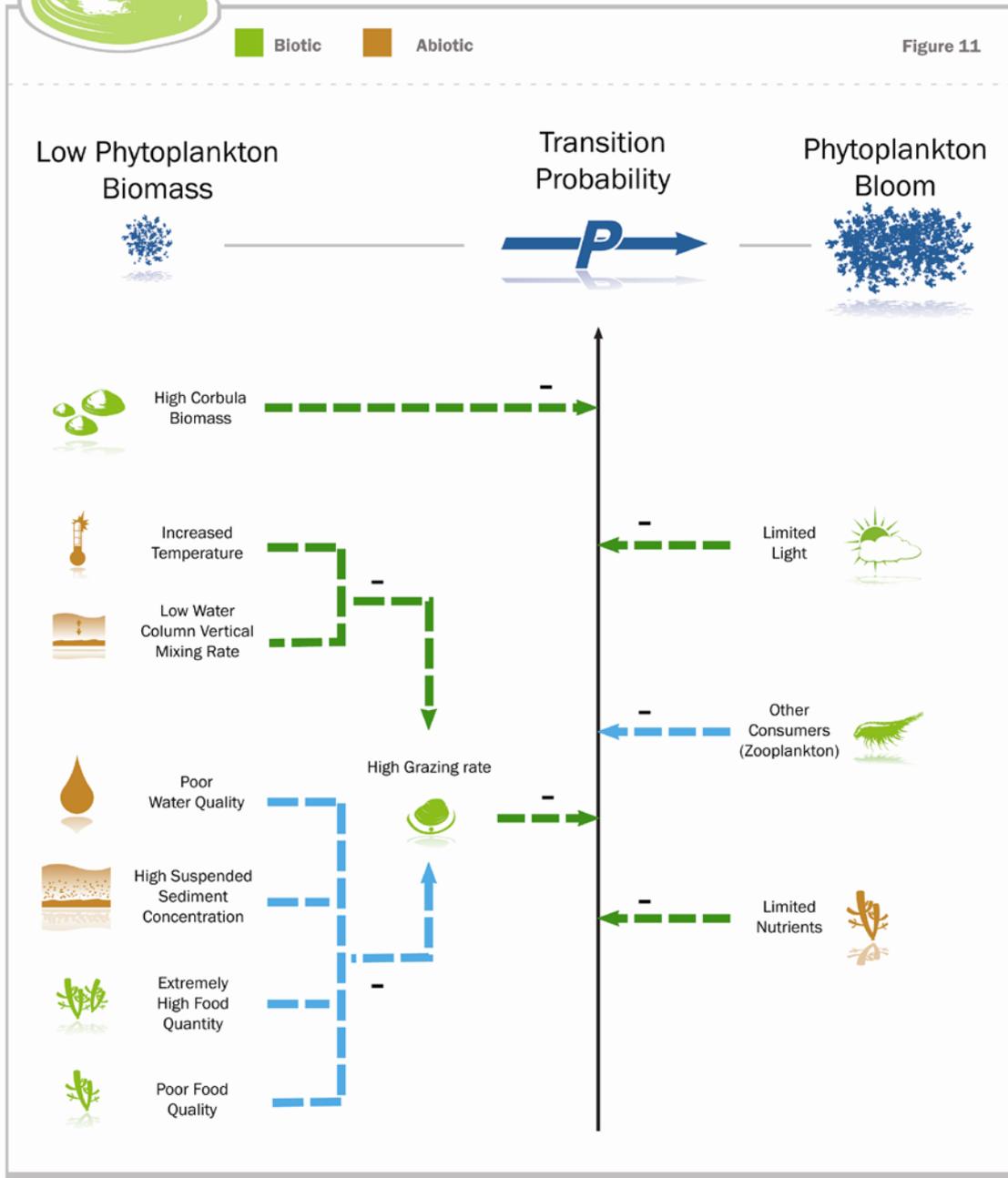


Figure 12. Transition probability of phytoplankton to bloom status.