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Effects of density dependence and environment on recruitment of coastal invertebrates

BY

CAROLYN JEAN LUNDQUIST
B.S. (University of California, Los Angeles) 1993

DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of
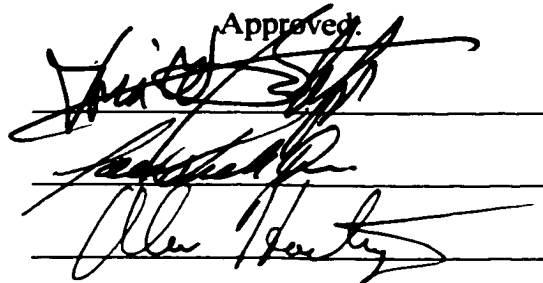
DOCTOR OF PHILOSOPHY

in

Ecology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

Davis

Approved:

Committee in Charge

2000

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Two roads diverged in a yellow wood,
And sorry I could not travel both
And be one traveler, long I stood
And looked down one as far as I could
To where it bent in the undergrowth;
Then took the other, as just as fair,
And having perhaps the better claim,
Because it was grassy and wanted wear;
Though as for that the passing there
Had worn them really about the same,
And both that morning equally lay
In leaves no step had trodden black.
Oh, I kept the first for another day!
Yet knowing how way leads on to way,
I doubted if I should ever come back.
I shall be telling this with a sigh
Somewhere ages and ages hence:
Two roads diverged in a wood, and I-
I took the one less traveled by,
And that has made all the difference.

Robert Frost

Reality is an illusion brought on by the temporary absence of beer.

North Coast Brewery, Fort Bragg, California

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And finally, to the beautiful blue ocean, thank you for never getting too nasty that I didn't make it home and for keeping the white sharks at bay.

Carolyn Jean Lundquist
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Ecology

Effects of density dependence and environment on recruitment of coastal invertebrates

Abstract

The processes influencing recruitment in sea urchins are poorly understood. To examine the depensatory density-dependent reproduction of broadcast spawning invertebrates, I created a simulation model of fertilization dynamics. The model described decreased fertilization success as density decreased, and increased fertilization as the aggregation of adult spawners increased. Highest fertilization success resulted from simulations with wide gamete dispersal distributions with an extended tail, representing low flow conditions. Surprisingly, the model did not predict a deterministic Allee effect or minimum threshold density of spawners for successful fertilization, but instead produced a gradual non-linear decline in larval production at low densities. A stochastic Allee effect was observed, as the variability in larval production increased substantially at low density.

To estimate current larval production of the red sea urchin *Strongylocentrotus franciscanus*, I applied this fertilization model to observed spatial distributions. Adult sea urchins were censused at eleven sites to determine density and local spatial distribution. Reserve sites generally had higher densities than fished sites. All sites were significantly aggregated, and aggregation increased as density decreased. Fertilization success was strongly influenced by both density and aggregation. Estimated current larval production was approximately one-third of estimated pre-fishery larval production,

with 75% of the decline attributable to declines in mean density, and the fertilization Allee effect responsible for the remainder of the decline.

To evaluate density-independent influences on recruitment, I examined settlement patterns of juvenile sea urchins and crabs in northern California. Prior research had determined an intra-annual pattern of settlement during local wind relaxation events. This pattern was present during the 1998 El Niño, resulting in high settlement of cancrid crabs and sea urchins. The 1999 La Niña lacked the typical upwelling/relaxation pattern, and low settlement was observed.

These results illustrate several aspects of population dynamics that should be considered in fisheries management and reserve design. Decreased adult density can have long-lasting effects if reproductive potential is affected. Local oceanographic transport of planktonic larvae can result in spatial and temporal variability in juvenile settlement. Researchers will need to consider both reproductive potential and settlement variability when designing reserve networks.

Introduction

Many fisheries in northern California show signs of collapse through severe declines in population size and density. While factors including overfishing, episodic recruitment, and density-dependent Allee effects have been implicated in these declines in density, little is known about the recovery potential of these populations. Determining the effect of this reduced density on population dynamics is essential for developing management plans for these fisheries. The spatial distribution of a population may influence reproductive dynamics, such as in red sea urchins which are broadcast spawners (Levitan et al. 1991, Levitan et al. 1992). Larval dispersal patterns of crab and sea urchin species can result in temporal and spatial variation in the number of juveniles settling at each location (Ebert & Russell 1988, Wing et al. 1995a, Wing et al. 1995b, Wing et al. 1998, Morgan et al. 2000b). An understanding of both density dependence in reproduction and variability in settlement patterns is particularly important when developing criteria necessary to identify candidate harvest refuge sites.

The objectives of this dissertation were to analyze the effect on larval production of reduced density of benthic invertebrates due to fishing and to examine temporal patterns of settlement of benthic invertebrates in northern California. Part I provides background information on the fishery and general biology of sea urchin and crab species in northern California, as well as a basic introduction to prior research on fertilization of broadcast spawners and larval settlement. Part II presents a model of fertilization efficiency of broadcast spawners with varying density and spatial distribution of adult spawners, and varying sperm dispersal distributions. Part III examines the local spatial distribution and current density levels of one benthic invertebrate, the red sea urchin in

northern California, and will adapt the fertilization model of Part II to estimate current and pre-fishery levels of larval production. Part IV examines temporal variation in juvenile sea urchin and crab settlement at one site in northern California to determine the influence of environment on population dynamics. Improved models of density dependent and density independent processes affecting benthic invertebrate population dynamics can assist management in the development of optimal strategies for both fisheries management and reserve design.

Part I. Fishery and general biology of the red sea urchin and cancrid crabs in northern California

The Red Sea Urchin *Strongylocentrotus franciscanus*

Relevant aspects of red sea urchin biology

The red sea urchin *Strongylocentrotus franciscanus* is found along the west coast of North America from Baja California to Alaska, and on the Asiatic coast as far south as Hokkaido Island, Japan (Kato & Schroeter 1985). Red sea urchins are typically found in mid to lower subtidal zones on rocky substrates near stands of giant kelp and other brown algae (Schroeter 1978).

Red sea urchins in northern California spawn annually in late spring and early summer. Sea urchins are broadcast spawners, releasing their gonads directly into the water column. Larval urchins spend 62-131 days in the plankton before settling (Strathmann 1978), at which time they are approximately 0.5 mm. Some growth studies indicate annual growth increments of approximately 13-25 mm attaining harvestable size in 4-5 years (Kato & Schroeter 1985). Other studies indicate much lower growth rates,

especially in colder waters of northern California, and show harvestable size to be obtained in approximately 12 years (Ebert et al. 1993, Morgan et al. 2000a). Red sea urchins are sexually mature at 30-50 mm (Bernard & Miller 1973).

Urchins in northern California do not have the same predators as central and southern California or British Columbia urchin populations. Southern California urchins have a variety of predators including spiny lobsters (*Panulirus interruptus*) (Tegner & Levin 1983) and California sheephead (*Semicossyphus pulcher*) (Cowen 1983). Sea otters (*Enhydris lutris*) are found primarily in Alaska and central California, with populations just begining to repopulate the central California coast and resume their position as important urchin predators. Northern California urchin predators include the sunstar *Pycnopodia helianthoides* (Mauzey et al. 1968, Moitoza & Phillips 1979, Duggins 1983), introduced green crabs (*Carcinus maenus*), cancrid crabs (*Cancer* spp.), leather stars (*Dermasterias* spp.), and rockfish (*Sebastes* spp.).

Fishery

The commercial fishery for the red sea urchin began in southern California in 1971 to satisfy a need for exports to Japan of sea urchin roe (Kato & Schroeter 1985). Japanese stocks of sea urchins were at low levels, and *S. franciscanus* is similar to the primary fished urchin of Japan *S. intermedius* in both size and quality of roe. The sea urchin is harvested for its roe, called 'uni', which is eaten raw as an expensive sushi delicacy. The red sea urchin is no longer the largest fishery in California in terms of total pounds harvested, but due to the high price obtained for this delicacy, it is still one of the most valuable of California fisheries (McIntyre 1995, Kalvass & Hendrix 1997).

Initial spread of the fishery was gradual until the mid-1980s at which time northern California stocks were heavily exploited and total state catch peaked at over 50 million pounds (approx. 24 metric tonnes) in 1988. Subsequent declines in catch in northern California were severe, decreasing from over 30 million pounds in 1988 to approximately 3 million pounds at the present time (Kalvass & Hendrix 1997). Southern California landings have remained fairly constant, fluctuating at levels of approximately 20 million pounds since the late 1970s (Kalvass & Hendrix 1997). Fishery managers in northern California have observed a decline in density from an average of 1.7 total sea urchins per m^2 in 1989 to 0.6 per m^2 in 1994 (Kalvass & Hendrix 1997). As densities are less than half of the pre-fished level, there is concern that fishing has decreased reproductive success and the red sea urchin is recruitment overfished (Kalvass & Hendrix 1997).

The primary ports in northern California are Bodega Bay, Point Arena, Albion, and Fort Bragg. Management measures include requiring fishing permits, minimum size limits of 89 mm, and a limited fishing season closed in July and open few days per week in other summer months in order to maximize gonad yield and provide for maximum reproductive output (Kalvass et al. 1993). Northern California fishery officials (California Department of Fish and Game) have declared the northern California fishery to be at a crisis stage (Kalvass et al. 1993) and strict management was deemed necessary to salvage the fishery.

Proposed reasons for red sea urchin fishery decline

Overfishing of this resource has been proposed, as stocks are in decline and recruitment into the population is both low and episodic in northern California. Many theories contribute to possible reasons as to why the fishery catch remains at low levels. In particular, both depensatory density-dependent behavior (Allee effects) and variability in recruitment likely have strong influences on population dynamics. However, it is unclear whether recruitment has declined due to the fishery, or if recruitment in northern California has always been low and sporadic.

Red sea urchins are hypothesized to exhibit Allee effects, or decreases in population growth rate when a population decreases below a certain level (Allee 1931). Two Allee effects are proposed for red sea urchins: 1) reduced spawner efficiency, and 2) reduced spine canopy protection for juveniles. As red sea urchins are broadcast spawners, higher densities of adults will provide for greater spawning success, while increased distance between spawning individuals decreases fertilization efficiency to almost zero (Pennington 1985, Levitan et al. 1992). Spine canopy protection is such that juveniles up to approximately 30 mm often reside beneath the adult spine canopy and receive both protection from predators and possibly drift kelp remnants caught by the adult urchins (Tegner & Dayton 1977, Tegner & Dayton 1981, Breen et al. 1985). Urchin divers often debate this theory (McIntyre 1995), but higher survival of urchins under spine canopies has been shown in laboratory experiments and inferred from long term *in situ* studies of juvenile survival (Sloan et al. 1987, Rogers-Bennett et al. 1995). The spine canopy Allee effect is also often inferred through observed bimodal size frequency distributions, which indicate differential mortality for smaller juveniles via a

size refuge under adult spine canopies (Tegner & Dayton 1977, Tegner & Dayton 1981, Breen et al. 1985).

Allee effects in reproduction are hypothesized for the red sea urchin due to increased gamete dilution as distance between spawners is increased at lower densities. Some aspects of the Allee effect of decreased fertilization success at reduced density in benthic marine invertebrates have been studied. Researchers have shown that fertilization declines as density decreases (Levitan 1991, Brazeau & Lasker 1992, Downing et al. 1993, Yund & McCartney 1994, Levitan & Young 1995, Yund 1995), as wave action increases (Pennington 1985, Denny & Shibata 1989, Epel 1991, Mead & Denny 1995), and as distance between spawners decreases (Pennington 1985, Grosberg 1987, Yund 1990, Brazeau & Lasker 1992, Levitan et al. 1992, Yund 1995). *In situ* studies for the red sea urchin have demonstrated the effects of density, abundance, and distance between adults on spawning success (Levitan et al. 1991, Levitan et al. 1992).

Another possible cause of the decline in sea urchin density is sparse recruitment. Conditions favoring settlement are rare and episodic, such that recruitment events may not occur often enough to sustain the high level of harvest in northern California. Southern California populations seem to have much more consistent settlement with less fluctuation in ocean conditions and are not expected to be recruitment-limited to the same effect as northern California populations (Tegner & Dayton 1981, Ebert et al. 1994). Settlement observations in northern California have elucidated some intra- and interannual patterns of settlement variability. On an intra-annual scale, larvae are concentrated offshore in the lee of headlands during upwelling events, and are transported onshore and alongshore during local wind relaxation events (Wing et al.

1995a, Wing et al. 1995b, Wing et al. 1998). Recruitment is strongest at headlands, and decreases with distance north from each headland structure, as these locations become more dependent on longer relaxation events for larval transport (Wing et al. 1995a). Differential larval settlement is also reflected in size frequency distributions (e.g. red sea urchins), which show larger percentages of juveniles at locations just north of headlands (Morgan et al. 2000b).

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Allee effects due to reduction of invertebrate density by fisheries

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Running Head: Allee effects at reduced density

Abstract

There has been widespread concern that reduction in density of broadcast spawners by a fishery can have severe effects on reproduction. As fishing decreases density, fertilization efficiency declines so that reproduction declines more rapidly than indicated by density, producing an Allee effect. Water flow conditions also affect fertilization by increasing dilution of gametes. Aggregative behavior can compensate for reduced fertilization at low density by decreasing nearest neighbor distances. While these factors are known, the nature of the potentially precipitous decline in reproduction with declining density or stock size is not well understood. We first used a simple analytical model of the reproductive dynamics of a broadcast spawning invertebrate to show that a strict threshold Allee effect is possible only when individuals are evenly spaced and sperm dispersal distribution is a constant out to a specified distance. Random spacing of individuals or a gradually decaying sperm distribution led to a more gradual departure from a linear relationship. We then used a simulation model to explore the combined effects of density, flow conditions, and aggregation of adult spawners. The model is based on a spatial distribution of spawning effectiveness empirically determined previously for *Strongylocentrotus droebachiensis*, the green sea urchin, under two flow regimes. The spatial distribution was broader under low flow conditions of < 0.2 meters/second than under high flow conditions of > 0.2 meters/second). Simulations over a range of commonly observed sea urchin densities (0.2-2.0 spawners/m^2) showed that average fertilization increased with density for low flow conditions, often reaching 100% within this range. High flow conditions produced much lower fertilization success,

with a maximum of less than 50% fertilization success. An extended tail of the distribution of spawning effectiveness resulted in higher fertilization success. Increasing the aggregation of adult spawners resulted in relatively small increases in fertilization success. A plot of the geometric mean of larval production versus density indicates a deterministic, gradual Allee effect for simulations with both a low flow and a high flow sperm dispersal distribution, but high flow larval production was lower at high density than the low flow case. Most simulations also showed a stochastic Allee effect of increased variability in larval production at low densities.

Key phrases: Allee effects at reduced density; effect of fishery on population dynamics

Key words: fertilization; broadcast spawner; external fertilization; Allee effects; aggregation; simulation model; individually-based model; sea urchin; *Strongylocentrotus droebachiensis*

Introduction

At the present time, over 60% of the world's fisheries are listed as overfished or utilized to their full extent (Garcia 1997). In this context, overfishing refers to recruitment overfishing, or lowering reproductive potential to a point such that recruitment declines. Fisheries are commonly managed on the basis of stock recruitment dynamics as described by a nonlinear relationship between stock and recruitment (Ricker 1954, Beverton and Holt 1957). A critical aspect of the uncertainty underlying these models is that very little is known about the shape of the stock recruitment curve at low stock abundance. At low stock abundance, most fishery models depict recruitment decreasing linearly to zero as stock decreases to zero. For some species, however, there may be an Allee effect, where recruitment decreases to zero below a threshold level of abundance or is severely reduced to levels below that which a linear decline would predict (Allee 1931, Dennis 1989). Unfortunately, in most cases the only way to determine the threshold stock size at which reproduction into the population will decline with fishing is to fish a population to low stock levels and determine when the population experiences reproductive failure. This is obviously not a biologically nor an economically desirable test. It would be preferable to be able to determine the abundance level at which the Allee effect takes place as well as the magnitude of this decrease in reproduction on the population through other means.

Fortunately, some populations demonstrate reproductive behavior that can be observed directly to determine the nonlinear dependence of reproduction on spawner density. Particularly good examples of populations with a directly observable relationship between population density and fertilization success are broadcast spawners

where the distances between spawning adults determine reproductive success. This relationship between distance and fertilization success has been observed in many invertebrate taxa, for example echinoderms (Pennington 1985, Levitan et al. 1992), asteroids (Babcock and Mundy 1992), octocorals (Brazeau and Lasker 1992, Coma and Lasker 1997), ascidians (Grosberg 1987, Yund and McCartney 1994, Yund 1995), bryozoans (Yund and McCartney 1994), and bivalves (Andre and Lindegarth 1995, Downing et al. 1993). This relationship is assumed for many fished invertebrate taxa with external fertilization, including scallops, giant clams, sea urchins, sea cucumbers, mussels and abalone (Braley 1984, Cameron and Fankboner 1986, Shepherd 1986, Tegner et al. 1989, Downing et al. 1993). Fertilization efficiency can be determined based on knowledge of the gamete dispersal distribution and spatial distribution of adult spawners. The fertilization dynamics of many of these benthic species could be directly observed and modeled to determine the stock-recruitment relationship of a population, without driving a population to low levels.

One behavioral mechanism that counteracts the negative effect of decreased density on fertilization is the aggregating behavior of many adult benthic invertebrates. Many sedentary invertebrate species have been observed aggregating in pairs or small groups for the purpose of spawning (e.g., abalone: Breen and Adkins 1980, Shepherd 1986, sea urchins: Kalvass 1991, Young et al. 1992, Unger and Lott 1993). However, less mobile species (i.e., giant clams) are unable to reposition themselves to increase likelihood of fertilization and may be too far from other spawners for successful fertilization to occur (Braley 1984). Those populations that do not reposition during the spawning season may have decreased fertilization if the ecological factors causing

observed spatial distribution patterns do not lead to individuals being in close proximity to one another. Downing et al. (1993) found fertilization rate in a freshwater mussel population to be correlated with local density and aggregation of adults. Brazeau and Lasker (1992) also observed higher rates of egg fertilization with closer distances between colonies of a Caribbean octocoral.

Fishery models of broadcast spawning species have considered Allee effects in various ways. Often, fishery managers propose a threshold density below which the spawning population is subject to Allee effects. Botsford et al. (1993) chose a critical threshold of spawner density for the red sea urchin *Strongylocentrotus franciscanus* in their model of a rotating harvest scenario for this fished invertebrate. Similarly, Pfister and Bradbury (1996) modeled a rotating harvest strategy with reproduction decreasing abruptly when the population dropped below 50% of pre-harvest levels. Investigators have expressed concern that threshold density levels would be higher in shallow, subtidal habitats due to decreased fertilization success at higher flows (Denny and Shibata 1989, Botsford et al. 1993, Quinn et al. 1993). Quinn et al. (1993) used a threshold density to investigate fishery management strategies and noted that the highest levels of fishing of *S. franciscanus* occur in the mid-depth subtidal areas where fertilization is likely optimal due to lower wave stress than shallowest areas and higher densities than deepest areas.

Allee effects may cause a population to be more susceptible to recruitment overfishing and have been implicated in the lack of recent recruitment of many abalone populations in California and the near extinction of the white abalone (Tegner et al. 1989, Tegner et al. 1996). Prince et al. (1987) attributed reduced recruitment of abalone in Tasmania in areas with experimentally reduced density to Allee effects. Abalone in

South Australia have been documented to have erratic or failed recruitment at fished densities and decreased levels of aggregation at low densities (Shepherd and Brown 1993, Shepherd and Partington 1995). Shepherd and Baker (1998) proposed management based on adult density for abalone subpopulations using an egg-per-recruit threshold. Additional abalone studies indicate a minimum critical threshold density of between 0.15 and 0.2 adult abalone per m^2 to maintain fertilization success (Shepherd and Partington 1995). The possibility that current densities of giant clams are below a critical threshold density has led to the suggestion that they be translocated to reserve areas to maintain high densities for spawning (Munro 1989).

To consider fertilization dynamics in fishery management, we need to know how they affect the stock recruitment relationship, i.e., where and how recruitment changes as fishing reduces density. It is clear from empirical and theoretical research on fertilization dynamics that aggregation, density, and water flow all significantly affect fertilization (Pennington 1985, Denny and Shibata 1989, Levitan et al. 1992). However, it is not clear whether a threshold Allee effect is representative of fertilization dynamics of broadcast spawners. The Allee effect is defined in most ecology texts (see, e.g. Begon et al. 1986), as a decrease in population growth rate (often to zero or negative population growth) below a threshold population size. To account for Allee effects in fishery management of broadcast spawners, we need to know how the spatial distribution of adult spawners affects fertilization success and how fishing affects spatial distribution patterns. We also need to understand how water flow conditions influence the consequent stock recruitment relationship of broadcast spawners (Pfister and Bradbury 1996, Quinn et al. 1993, Botsford et al. 1993). Here we explore the dynamic response of fertilization to different

combinations of density, flow, and spatial distribution patterns that might be present in invertebrate fisheries on broadcast spawners. Our ultimate goal is to determine the nature of the stock-recruitment relationship of broadcast spawners at low abundance levels for fished populations.

Modeling Approach

The basic mechanisms underlying the dynamics of reproduction in broadcast spawners are known. Both empirical and theoretical research has shown that fertilization decreases as gametes are diluted with increased distance from spawning adults (Pennington 1985, Denny and Shibata 1989, Yund 1990, Babcock and Mundy 1992, Levitan et al. 1992, Yund 1995). Other studies have demonstrated that increasing density or the number of spawning adults increases fertilization success (Pennington 1985, Levitan 1991, Yund and McCartney 1994, Levitan and Young 1995, Yund 1995). Models of fertilization dynamics in various flow fields have shown that in habitats with high wave action, turbulence increases the rate of dilution of gametes and decreases the probability of fertilization (Denny 1988, Denny and Shibata 1989, Epel 1991, Mead and Denny 1995). While most of these results were not obtained for the purpose of gaining insight into fishery dynamics, they provide useful information on the effect of reduced density on recruitment in broadcast spawning invertebrate populations.

Modeling studies of fertilization began with the theoretical approach of Vogel and colleagues who created a simplified model of fertilization describing the gamete kinetics of the European sea urchin *Paracentrotus lividus* (Vogel et al. 1982). Denny and colleagues included turbulent diffusion in a fertilization model (Denny 1988, Denny and

Shibata 1989. Mead and Denny 1995) to show the decrease in fertilization in environments with high water movement. Denny et al. (1992) also modeled fertilization within surge channels, and predicted fertilization to be at high levels due to low exchange rates between the channel and surrounding waters, leading to low dilution of gametes and high mixing rates. More recent models of fertilization have increased the scale and size of populations of spawning individuals (Levitan and Young 1995) and have used more accurate functions of gamete diffusion in three dimensional habitats (Babcock et al. 1994). Most of the prior theoretical studies have validated the models by comparison to empirical observations of egg fertilization at increasing distances from a spawning male (Denny and Shibata 1989, Levitan et al. 1992).

Here we extend these results by taking a slightly different approach to characterizing the Allee effect of decreased fertilization due to low adult densities in a fishery context. Our main purpose was to determine the effect of the fertilization process on standard fishery models. Our model is phenomenological in nature, without detailed mechanisms of turbulence and gamete kinetics. Specifically, we examined the effect of varying density on fertilization to determine how the decrease in density due to fishing would decrease recruitment in a broadcast spawning population. We first determined the effect of scale or size of the population in our model to determine a minimum population size that must be modeled in order to accurately represent the behavior of a population of hundreds of thousands of individuals. We then examined the effect of different observed levels of gamete dilution with distance to determine the potential effect of turbulent diffusion on population reproductive success. We explored the effects of aggregation of adults by varying spatial distribution patterns of the population. We summarize these

results in terms of deterministic and stochastic influences on the stock-recruitment relationship of broadcast spawning invertebrates.

Methods

Analytical Model

We first present a simple analytical model to demonstrate theoretical predictions of the behavior of Allee effects at reduced densities. This model includes two primary components: 1) the spatial distribution of adult spawners, and 2) the distribution of gametes with distance from a spawner. For this simple analytical model, we assumed no dispersal of female gametes. We calculated expected distributions of distance from a female spawner to the closest ten nearest male neighbors over a range of male densities for an evenly-spaced 'regular' spatial distribution and a uniform 'random' spatial distribution of adult spawners. Distances between neighbors for the regularly spaced distribution were calculated based on a computer-generated evenly-spaced distribution at different densities. For a random spatial distribution of individuals at density D, the probability distribution function of the n-th neighbor being found at a distance r is (Thompson 1956, Eberhardt 1967):

$$p(r) = 2\pi Dre^{-\pi Dr^2} \frac{\left(\pi Dr^2\right)^{n-1}}{(n-1)!}$$

We compare a sharply declining 'disk' sperm distribution, where fertilization of eggs is 100% successful for all male neighbors only within 1 meter of a female to a gradually decaying 'Gaussian' sperm distribution, where egg fertilization success is distributed normally (mean 0, variance 1) with distance from the female. Values from the Gaussian distribution were doubled so that fertilization approached levels of 100% as distance

decreased to zero. Total fertilization success for a female was calculated as the cumulative percent success of all male neighbors based on the sperm dispersal distance to the female spawner. A maximum of 100% fertilization success was assumed, and no decrease in fertilization due to high concentrations of gametes (sperm competition) was included. To calculate the relative number of larvae produced (i.e., recruitment) for a given density of male spawners, we multiplied fertilization success by total density (male density times two, assuming a 1:1 male:female ratio).

Simulation Model

We used an individual-based simulation model of broadcast spawners as our primary model to evaluate the effect on reproduction of reduced density due to harvest. These simulations determined the effects on reproduction of three variables: 1) density of adult spawners, 2) distances from a spawner over which competent gametes are distributed (i.e., the sperm dispersal distribution), and 3) degree of aggregation of adult spawners.

Density

To assess the effect of density on the fertilization process, we placed spawners randomly within a square grid. The gender of each spawner was determined randomly, using an equal sex ratio. The percentage of eggs fertilized for each female was calculated based on the cumulative percentage of sperm reaching each female from all males within the grid. Average fertilization was calculated for each simulation as the average fertilization percentage of all females in a given simulation. 100 simulations were

performed, varying the random placement of spawners within the grid, at each of the following densities: 0.2, 0.5, 0.7, 1.0, 1.2, 1.5, 2, and 5 spawners/m^2. These densities were chosen to span the range of typical spawner densities that have been observed in the field for fished invertebrate broadcast spawners. They encompass observed densities of *S. franciscanus* in fished northern California populations which at the present time vary between 0.1 and 2.0 urchins/m^2 (Lundquist et al. 2000). Abalone populations subject to harvest are found at similar densities (Tegner et al 1989). However, some unfished populations exist at much higher density levels. Urchin barren populations in central and southern California of both *S. franciscanus* and *S. purpuratus* and in Nova Scotia and Newfoundland of *S. droebachiensis* have been observed at densities exceeding 50 urchins/m^2 (Estes and Harrold 1988, Harrold and Reed 1985, Rowley 1989, Bernstein et al. 1981, Keats et al. 1984, Scheibling 1986, Himmelman 1986). We used a random (i.e., not aggregated) adult spatial distribution pattern and a decreasing exponential decline in sperm concentration with distance corresponding to low water flow conditions in our comparisons of fertilization success at varying density.

Scale of Numerical Experiment

To minimize computer simulation time while also retaining biological realism in our simulations we included only the total number of individuals necessary to exhibit fertilization dynamics. Previous theoretical models and empirical studies of fertilization have concentrated solely on one or just a few individuals in a population, examining the effects of water flow, density and distance between individuals on the fertilization success of one or a few individuals (Pennington 1985, Levitan et al. 1992). Empirical

studies have shown that fertilization increases as the number or density of individuals (and thus the number of gametes) in a fertilization scenario is increased (Pennington 1985, Levitan et al. 1992). Simulations of populations of the sea biscuit *Clypeaster rosaceus* have modeled fertilization success of populations of thousands of individuals and found that population abundance had a strong influence on fertilization (Levitan and Young 1995). We compared fertilization success with different spawner abundances to determine the minimum abundance that would fully encompass the fertilization dynamics of our population. This was determined to be the size of the grid beyond which fertilization percentage did not change appreciably. Simulations were performed at scales of 2 meters by 2 meters, 5 meters by 5 meters and 10 meters by 10 meters to determine the optimal area for this study.

Gamete Dispersal Distributions

The functional dependence of gamete dilution on distance has been shown to influence the fertilization process of broadcast spawners (Levitan et al. 1991, Levitan 1995, Levitan et al. 1992). While sperm cells are motile, their swimming speed is small relative to the velocity of water currents (Levitan et al. 1993). As such, the diffusion of both egg and sperm cells is primarily influenced by hydrodynamic processes including turbulence and advective flow (Pennington 1985, Denny 1988, Denny and Shibata 1989, Levitan and Young 1995). Model estimates of sperm diffusion rates with distance were based on empirical observations by Pennington (1985) on the green sea urchin, *S. droebachiensis*. Pennington measured fertilization percentage of stationary egg masses at increasing distances from the release point of a sperm solution. To keep the model as

simple as possible and consistent with empirical observations which show that fertilization is not sensitive to egg concentration (Levitan et al. 1991), simulations included only dispersal of male gametes.

Pennington (1985) made empirical observations of fertilization at two current speeds: 1) a low current speed for all trials with velocity of less than 0.2 meters per second (Figure 1a) and 2) a high current speed for all trials with velocity of greater than 0.2 meters per second (Figure 1b). We fit these empirical data using maximum likelihood estimates of parameter values for exponential, normal (Gaussian), gamma, and Weibull distributions (Mathworks 1997). Negative exponential distributions provided the best least squares fit to Pennington's observations of the percentage of eggs fertilized versus distance from a spawning male for both low and high current speeds (Figure 1a, 1b). Theoretical models of sperm dilution based on hydrodynamic conditions experienced in Pennington's empirical study predict a similar exponential decline in fertilization with distance (Denny and Shibata 1989). We simulated populations at both low flow (wide gamete dispersal distribution) and high flow (narrow gamete dispersal distribution) to determine the effects of flow on fertilization.

The negative exponential function did not accurately represent the non-negligible tail of the empirical data of fertilization percentage at relatively large distances from spawning individuals (Pennington 1985). Similar extended tails of gamete dispersal distributions have been observed in other broadcast spawning species (Babcock and Mundy 1992). In order to test the effect of this 'tail' on the resulting fertilization success for broadcast spawners, we generated two additional distributions by fitting a negative exponential decline to Pennington's empirical data for smaller distances and using a low

constant rate of fertilization for larger distances. The resulting two distributions were termed 'low flow with tail' and 'high flow with tail', corresponding to the strictly negative exponential decline distributions termed 'low flow, no tail' and 'high flow, no tail' (Figure 1a, 1b). We limited the total sperm distribution to 5 meters distance between spawners based on rates of sperm dilution and limiting concentrations of gametes for successful fertilization for similar species (Denny and Shibata 1989). Sperm dispersal distributions with tails were normalized to the corresponding distributions without tails to maintain a constant sperm supply.

Degree of Aggregation

Heterogeneity in the spatial distribution patterns and relative distances between individuals has been shown to affect fertilization success (Levitan et al. 1992, Levitan and Young 1995, Downing et al. 1993, Brazeau and Lasker 1992, Braley 1984, Yund and McCartney 1994, Yund 1990, Young et al. 1992, Babcock and Mundy 1992, Yund 1995). To quantify the effect of different degrees of aggregative behavior on the reproductive success of broadcast spawners, we investigated fertilization for four spatial distribution patterns (i.e., degrees of aggregation): 1) a uniform randomly generated distribution (R), 2) a slightly aggregated distribution (A1), 3) an aggregated distribution with many small clumps of adult spawners (A2), and 4) an aggregated distribution with few large clumps of adult spawners (A3) (Figure 2).

The uniform random distribution (R) was created by using a uniform random number generator to obtain x and y coordinates for each spawner within a square grid. The three aggregated distributions were created by first generating random positions for a

specified fraction of the total number of spawners simulated, then placing the remaining

spawners at random locations within a minimum threshold distance of these locations.

Varying the number of spawners initially placed uniform randomly (parameter α)

allowed us to vary the number of clumps of adult spawners, as the number of spawners

placed randomly represented the maximum number of clumps. Varying the minimum

threshold nearest neighbor distance (parameter β) allowed us to vary the aggregation

within each group of adult spawners, as lower minimum threshold nearest neighbor

distances created more tightly clumped groups of spawners. For distribution **A1** we used

values of 0.5 for both parameters α and β to create a slightly aggregated distribution. For

distribution **A2** we used values of 0.5 and 0.2 for parameters α and β, respectively, to

create a distribution with many small clumps of tightly spaced spawners. For distribution

A3 we used values of 0.2 and 0.5 for parameters α and β, respectively, to create a

distribution with few large clumps of adult spawners.

We used three measures of aggregation to compare the levels of aggregation of

each distribution (Table 1). Variance-to-mean ratios and standardized Morisita indices of

dispersion (MSID) were calculated using spawner position data binned into quadrats

within the model grid (Krebs 1989). For the quadrat size tested (0.5 x 0.5 meter^2), these

two methods show significant clumping for the **A2** and **A3** distributions, but have higher

levels of aggregation for the **A2** distribution, due to the large clump size within the **A3**

distribution often being split into more than one quadrat. Measures of aggregation based

on nearest neighbor distance (Krebs 1989) show increasing levels of aggregation as

predicted from our choice of parameters for the spatial distribution types, with significant

levels of clumping for all three aggregated distributions. We used both a boundary-less

nearest neighbor analysis and a boundary-corrected nearest neighbor analysis for these comparisons (Krebs 1989). Simulations with varying spatial distribution patterns were performed for the four levels of aggregation (**R, A1, A2, A3**) using both low flow and high flow sperm dispersal distributions.

Larval Production

We expressed the spawning efficiency resulting from combinations of density, aggregation and flow in terms of the implications for the relationship of interest to fishery biologists, the stock recruitment relationship. To relate the process of fertilization efficiency to recruitment, we calculated the relative number of larvae produced, equal to the density of spawners times the average percentage of eggs fertilized. This calculation allowed us to see the decrease in recruitment (number of larvae produced) due to this specific density-dependent process.

Results

Analytical Model

Results from the analytical model exhibited different non-linear declines in recruitment at low densities depending on adult spatial distribution and sperm dispersal distribution. Only the 'evenly-spaced, disk' case produced the classic sharp threshold decline to zero larval production at densities of approximately 2 spawners/m^2 (Figure 3a). Allowing either random spacing of adults or modifying the sperm dispersal distribution to one of a more gradual decay in fertilization success with distance (i.e., Gaussian (0,1)) led to a more gradual non-linear decline in larval production at approximately one third

of the threshold density for the 'evenly-spaced, disk' case (Figure 3b,c). Including both

random spacing and a gradually decaying sperm distribution produced an even less

severe non-linear decline at a density of approximately one-sixth of that seen in the

'evenly-spaced, disk' case (Figure 3d).

Simulation Model

Scale

Comparison of simulation results at three scales to determine the optimal

minimum simulation size for our fertilization trials indicated that 5x5 m^2 grids were

adequate for our study (Figure 4). Results from the 2x2 m^2 quadrats differed

significantly from results using larger scales. The 5x5 m^2 and 10x10 m^2 simulations were

very similar, with resulting average percent fertilization success differing by less than

10% in all but two of the 12 combinations of grid size, density, and sperm dispersal

distribution. In contrast, the 2x2 m^2 quadrats differed by more than 20% in average

percentage fertilization success from the 5x5 m^2 and 10x10 m^2 simulations in 7 of 12

combinations.

Density

Simulated distributions of fertilization success behaved as would be expected, in

the sense that fertilization of eggs increased as density increased for a random adult

spatial distribution and low flow conditions (Figure 5). Simulations at densities of 0.5

spawners/m^2 had low average fertilization success (44%) as well as high variance in the

distribution of fertilization percentages. Simulations at higher densities of 1.0 and 1.5

spawners/m^2 had higher average fertilization success, 75% and 90%, respectively, and decreasing variability in the distribution of simulation fertilization values. Fertilization at the highest density of 2.0 spawners/m^2 had the highest average fertilization value of 97%, with over 70% of the simulations having 100% fertilization of all females in the simulation. In summary, average egg fertilization rate increased with density, and the variability in the distribution of fertilization percentages for each set of 100 simulations decreased as density increased.

Sperm Dispersal Distribution: Width

Results from high flow simulations with a random adult spatial distribution differed markedly from those with low flow conditions (Figure 6). These high flow simulations all had average fertilization percentages of less than 10% fertilization success. The variance of all high flow simulation runs was much lower than that of the low flow runs, as all simulations had very low levels of successful fertilization. While there was a small increase in average fertilization as density increased, the range of fertilization rates even at the highest density level of 2.0 spawners/m^2 included no values above 20%. This low level of fertilization success is similar to that predicted by theoretical models based on the relatively high flow conditions seen in the Pacific Northwest (Denny and Shibata 1989) and suggests that invertebrates spawning in high flow conditions will have minimal chance of successful fertilization, regardless of density.

Sperm Dispersal Distribution: Tail

Comparisons of the modified (tailed) sperm dispersal distributions with the standard (tail-less) distributions showed increased fertilization success for the tailed distributions at all densities simulated, even though the overall sperm supply was equivalent for tailed and tail-less distributions. Increases in fertilization success for low flow distributions were highest at low densities, with a total increase of 14% at a density of 0.5 spawners/m^2, 20% at 1.0/m^2, 10% at 1.5/m^2 and 3% at 2.0/m^2 (Figure 7). High flow, tailed distributions showed increases in fertilization success of 6%, 12%, 18%, and 16% at 0.5, 1.0, 1.5 and 2.0 spawners/m^2 (Figure 8). Relative to the average fertilization success for the high flow, tail-less distributions, fertilization increased on average by a factor of 3 in the high flow, tailed distribution simulations. Relative increases for the low flow, tailed distributions were not as large, as fertilization was relatively high in the low flow, tail-less distributions.

Degree of Aggregation

Trials with different degrees of aggregation showed the advantages of aggregative behavior on fertilization. We present two cases to show the range of the effect of aggregation on reproduction (Figure 9, 10). Randomly distributed spawners had the lowest fertilization percentage in all trials (Figure 5, 6). For the low flow, no tail distribution, increasing the aggregation of spawners at low densities increased the fraction of eggs fertilized (Figure 9a,b,c). However, at densities of approximately 2.0 spawners/m^2, aggregation behavior was no longer effective as fertilization success was already at high levels. Aggregation during high flow conditions resulted in similar small increases in average fertilization, though the effect of aggregation did not decline at high

densities (Figure 10a,b,c). Increases in average fertilization in aggregated simulations with high flow conditions were accompanied by an increase in the variance of fertilization percentages from each simulation.

Fertilization versus density

The distribution of percent of fertilization success were plotted against density to determine the mechanism underlying the Allee effect. We present the case of a randomly distributed simulation with low flow, no tail sperm dispersal distribution to illustrate the general nature of the relationship (Figure 11a). Plots of the arithmetic mean of fertilization versus density showed a non-linear decline in mean fertilization as density declines. Stochasticity in fertilization success (i.e., increased variance in fertilization success) increased as density decreased, as shown by the increase in width of the distributions of mean fertilization for each simulation as density decreased. Plots of the geometric mean show a more abrupt decline to zero as density declines than do the plots of arithmetic mean versus density.

Plots of the stochastic behavior of the fertilization simulations for all 16 different cases of the fertilization model show the effect of varying degrees of aggregation and sperm dispersal distribution (Figure 11b). The pattern is generally similar for the eight plots at low flow conditions, with a non-linear decrease in mean fertilization as density declines and an increase in variance of fertilization at low density. The geometric mean of all low flow plots declines to zero prior to the arithmetic mean, reflecting the increased stochasticity as density decreases, as well as the likelihood of at least one simulation having a zero value increasing as density decreases. The eight 'high flow' plots had much

lower values of fertilization success, and showed an almost linear decline in fertilization as density declines (Figure 11b). While all 'low flow' simulations approached fertilization success of 100% as density increased, the 'high flow' simulations did not approach 100% success over the range of densities simulated. Fertilization in the 'high flow, tail' plots did increase to values of almost 50% fertilization success at high densities, while 'high flow, no tail' plots increased only to approximately 25% fertilization success at high densities. The 'high flow' simulations did not show the pattern of increased variation at low density seen in the 'low flow' simulations, due to an effect of a stronger decrease in fertilization percentage at low density and little variability in this low fertilization rate.

The geometric mean of fertilization showed a more pronounced decline in fertilization at low densities, suggestive of increased stochasticity at lower densities. A geometric mean of zero simply occurs when the distribution of fertilization percentages includes zero. We refer to the level below which the distribution of fertilization success includes complete fertilization failure (a zero value) as the critical geometric threshold. In particular, all simulation types had a geometric mean of zero at a density of 0.2 spawners/m^2, and 3 of the 4 high flow, no tail sperm dispersal distributions also had zero values for the geometric mean at 0.5 spawners/m^2. As average density of fished urchin populations as determined by California Fish and Game officials have ranged between 0.4 and 0.6 urchins/m^2 since 1990 (Kalvass and Hendrix 1997), we performed additional simulations at values of 0.3, 0.4 and 0.6 spawners/m^2 in order to determine the exact drop off point of the geometric mean at low density. Of the 16 simulation types (different combinations of the 4 levels of aggregation and 4 types of sperm dispersal distributions)

we tabulated the number of simulations with each critical geometric threshold value,

defined as the lowest density at which fertilization was non-zero. Two simulations had a

critical geometric threshold of 0.3 spawners/m^2, 7 simulations had a critical geometric

threshold of 0.4 spawners/m^2, 4 had a critical geometric threshold of 0.5 spawners/m^2, 2

had a critical geometric threshold of 0.6 spawners/m^2, and one had a critical geometric

threshold of 0.7 spawners/m^2.

Larval Production

The effects of these declines in spawning efficiency on larval production

determine the Allee effect resulting from broadcast spawning. A representative plot of

the relative number of larvae produced versus density for a randomly distributed spatial

distribution and low flow, no tail sperm dispersal distribution shows decreased larval

production at all densities (as compared to a model representing 100% fertilization)

(Figure 12a), reflecting the effect of fertilization success on the recruitment process

(Figure 11b).

However, when examining plots of relative number of larvae produced versus

density for the other low flow simulations (Figure 12b), we see that the Allee effect

demonstrated in Figure 12a is not as pronounced in most of the plots. Instead, the

relationship between larval production and density is almost linear in the low flow plots,

with very little demonstration of a density-dependent effect (Figure 12b). Only at very

low densities (< 0.5 spawners per meter^2) do we see any difference between larval

production and a 1:1 ratio between density and larvae produced (the 45° line). This effect

is only observed when larval production is calculated from the geometric mean rather

than the arithmetic mean. As variability in the distribution of fertilization success increases as density decreases, a stochastic Allee effect is present; however, neither the deterministic nor the stochastic Allee effect is very large for the low flow cases.

The 'high flow' simulations all demonstrated significant reductions in larval production as compared to the 'low flow' simulations (Figure 12b). Though larval production was low, the 'high flow with tail' simulations produced a non-linear decline in larval production with both an arithmetic and a geometric mean (Figure 12b). The high flow, no tail cases produced no evidence of an Allee effect, as larval production showed much lower larval production for all simulations, as well as a linearly declining slope with density. The linear decline in the relationship between larval production and density implies that larval production for the 'high flow, no tail' simulations is a density-independent process (Figure 12b).

Discussion

Adding the fertilization dynamics of broadcast spawners to fisheries models of the recruitment process gives somewhat unexpected results. Prior analyses have anticipated or assumed a threshold density level at which fertilization, and thus recruitment, would display a precipitous decline. However, our simulations rarely produced a strong non-linear Allee effect in the relative number of larvae produced at most density levels. In fact, a deterministic Allee effect in the larval production was only seen in the high flow, tail cases. Stochastic Allee effects, as demonstrated by increased variability in the distribution of larvae produced, did occur, and these effects were most significant at very low densities.

From the results of the simple analytical model, it is clear that randomness in adult spatial distributions and gradually declining gamete distributions are responsible for this lack of a threshold. A threshold would be observed only if spawners were evenly spaced with a constant, limited gamete dispersal distribution. However, if spacing was random rather than equal, the distance between neighbors is represented by a probability distribution rather than a specific distance. Variability in neighbor distances due to random spacing leads to variability in the range of fertilization values and the disappearance of the threshold decline. Random spacing at low densities also leads to an increase in variance of fertilization as density declines (a stochastic Allee effect).

An understanding of the stochastic aspects of the Allee effect requires careful consideration of what the variability in the model simulations represents. The interpretation of this variability, based on the model-generated spatial distribution of spawners, is that each simulation represents one possible spatial distribution at a given density and degree of aggregation. If there are behavioral rules that lead to each statistical configuration of the spatial distribution, but individuals reform this spatial distribution during each spawning season, then this variability would be seen as interannual variability in the spatial distribution of the population. The variability in our simulations could also represent uncertainty as measurement error due to incomplete knowledge of the position of each individual.

While there appears to be an Allee effect at both high and low flows, the behavior at higher density differs. For the narrower gamete distributions, the eventual linear increase in larval production with density does not return to the same high rates of fertilization over the range of densities tested in our model. The implied consequence of

increased water flow is that fertilization during high flow conditions will always be sub-optimal compared to low flow conditions at the same density. High flow locations (i.e., shallow, subtidal areas) would thus be less productive larval source populations. Low flow sites, however, are expected to have 90-100% fertilization (given synchronous spawning) if spawners are present at density levels of above 2 spawners/m^2 for a randomly distributed population. While most researchers assume that natural spawning events occur during periods of low wave action and minimal tidal flow (Pennington 1985, Oliver and Babcock 1992, Serrao et al. 1996), one can clearly see the effect of high water flow versus low water flow trials of this model. Red sea urchins in northern California are hypothesized to spawn during the upwelling season when wind conditions cause fairly consistent strong wave action (Wing et al. 1995), but it is not known whether urchins could detect and synchronously spawn during the few periods of relaxed flow during the spawning season. If urchins were capable of spawning during this relaxed flow, spawning success would be greater. However, if urchins spawn during other times when wave action was greater, clearly, as shown by our simple fertilization model, the success of their reproductive activity would be limited.

The presence of an extended tail of the sperm dispersal distributions leads to higher predictions of fertilization success than with the tailless distributions. This tail reflects fertilization occurring at very low sperm:egg ratios and high levels of sperm dilution, which is contrary to many laboratory experiments that indicate fertilization does not occur at these low sperm concentrations (Levitan et al. 1991, Pennington 1985, Andre and Lindegarth 1995). Extended distributions of fertilization success have been observed in many field studies of fertilization (Pennington 1985, Babcock and Mundy 1992).

Physiological mechanisms that may promote this higher fertilization at larger distances include sperm packaging and high levels of sperm stickiness, which result in higher sperm concentrations than would be expected with a simple random diffusion model of sperm dispersal (Thomas 1994a, b). Extended tails or leptokurtic distributions have also been shown to have a critical effect on the dynamics of processes, including the spread of introduced species (Lewis and Kareiva 1993, Kot et al. 1996), mammal, bird, and insect dispersal between habitat fragments for conservation purposes (Van Kirk and Lewis 1997), and seed dispersal curves (Portnoy and Willson 1993).

The lack of a strong effect of aggregation on fertilization, as compared to the effect of wave action, confirmed prior research describing the interaction between aggregation and density. Aggregation is not important for fertilization success at high densities, as there appears to be an upper level of density above which fertilization is maximized. Thus, increased aggregation will not increase fertilization at high density levels. Levitan and Young (1995) also demonstrated that aggregation is unimportant at high population density, but increases fertilization at low densities. For aggregation to be important at low densities, spawners must increase aggregating behavior when density declines. Researchers have shown that some abalone populations do not increase aggregative behavior at low densities (Shepherd and Partington 1995, Shepherd and Brown 1993). Research on red sea urchin populations has shown the opposite, with aggregation increasing at low densities (Lundquist et al. 2000).

Our model quite likely overstates reproductive success for some broadcast spawners because it assumes synchronous spawning. Some invertebrate populations exhibit large-scale mass spawning events synchronized by lunar periods and seasonal

cycles (Oliver and Babcock 1992, Harrison et al. 1984). However, synchrony is rarely observed in echinoderms, and many observations of *in situ* events have shown that not all members of populations participate in the few events observed to date (see Pennington 1985 for an early review). Recent evidence of a large event of echinoderm spawning in British Columbia (Levitan, pers. comm.) indicates that researchers have just missed observing these events, as was the case for coral mass spawning in the tropics until recent decades (Harrison et al. 1984). However, we must consider our model conservative until more evidence is provided on synchrony and the undiscovered cues in many populations that might synchronize all individuals to spawn. If partial synchrony or general asynchrony is more often the case for invertebrate reproductive behavior (e.g. *Diadema antillarum*, Levitan 1988), total adult density is no longer directly correlated with fertilization. Rather an effective density level given the expected percentage of a population spawning would be a more accurate measure of density for fertilization success. Clearly, at any level of synchrony less than complete synchrony, our model would show decreased estimates of fertilization compared to results assuming synchronous spawning.

An additional complexity omitted from our simple model is that of size differences in adults resulting in different amounts of gametes released. For most broadcast spawners, gonad size increases volumetrically with adult size. Fishing changes size distributions such that size distributions of fished populations generally have fewer individuals in larger size classes compared to unfished sites (Morgan et al., *in press*). The implications of this change in size distribution is that fished sites will have fewer

fertilized gametes as compared to higher density reserve sites that still contain the larger size classes of a population with large gonads.

We used the geometric mean rather than the arithmetic mean of fertilization success to determine a critical threshold density. The geometric mean is a better descriptor of average population processes when stochasticity is involved (Lewontin and Cohen 1969, Ludwig 1976). As many empirical distributions are often leptokurtic, the arithmetic mean is often biased high because of extreme values. Conservation biologists have shown that times to extinction and population growth rates often have lognormal distributions, and thus risk of extinction should be based on geometric rather than arithmetic means (Lewontin and Cohen 1969, Lande and Orzack 1988). We used the geometric mean of fertilization success to increase sensitivity to low ranging values of fertilization success.

Even though we did not find evidence for a strict threshold decline in average fertilization with decreasing density, our model does imply density levels at which fertilization declines from 100% and variability or uncertainty in fertilization success increases. Fishery managers have been hesitant to apply a threshold density strategy due to variability in growth rates, mortality rates, recruitment rates, and density of broadcast spawning invertebrates over large spatial scales (Kalvass and Hendrix 1997). However, we have shown that at some density, depending on flow conditions and aggregation, recruitment will decline nonlinearly and randomly, if not precipitously. This also indicates that marine reserves which maintain densities closer to natural levels could provide a source of larvae to surrounding populations.

Acknowledgements

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Table 1

Comparison of spatial distributions using standard methods for determining level of

aggregation.

Distribution	α	β	V-M[1]	MSID[2]	s.d.[3]	NND-1[4]	NND-2[5]
Random	1	NA	0.9931	-0.0291	0.2216	1.0636	0.1305
Aggregated #1	0.5	0.5	1.2903	0.3544	0.1775	-2.3380*	-2.6866*
Aggregated #2	0.5	0.2	2.1024	0.5127*	0.0127	-4.4197*	-4.4105*
Aggregated #3	0.2	0.5	1.7479	0.5045*	0.0256	-7.2739*	-6.7742*

Aggregated #1 = Slightly aggregated, Aggregated #2 many small clumps, Aggregated #3

= few large clumps

α=percent of urchins initially placed randomly within the model grid (see text)

β=minimum threshold nearest neighbor distance (see text)

*=aggregated at 95% degree of significance

[1]variance to mean ratio. A value of 1 signifies a random spatial pattern.

[2]Standardized Morisita Index of Dispersion. A value of 0 signifies a random spatial

pattern.

[3]Standard deviation of the Standardized Morisita Index of Aggregation.

[4]Nearest neighbor distance method for calculating aggregation, without correction for

boundary.

[5]Nearest neighbor distance method for calculating aggregation, with boundary correction.
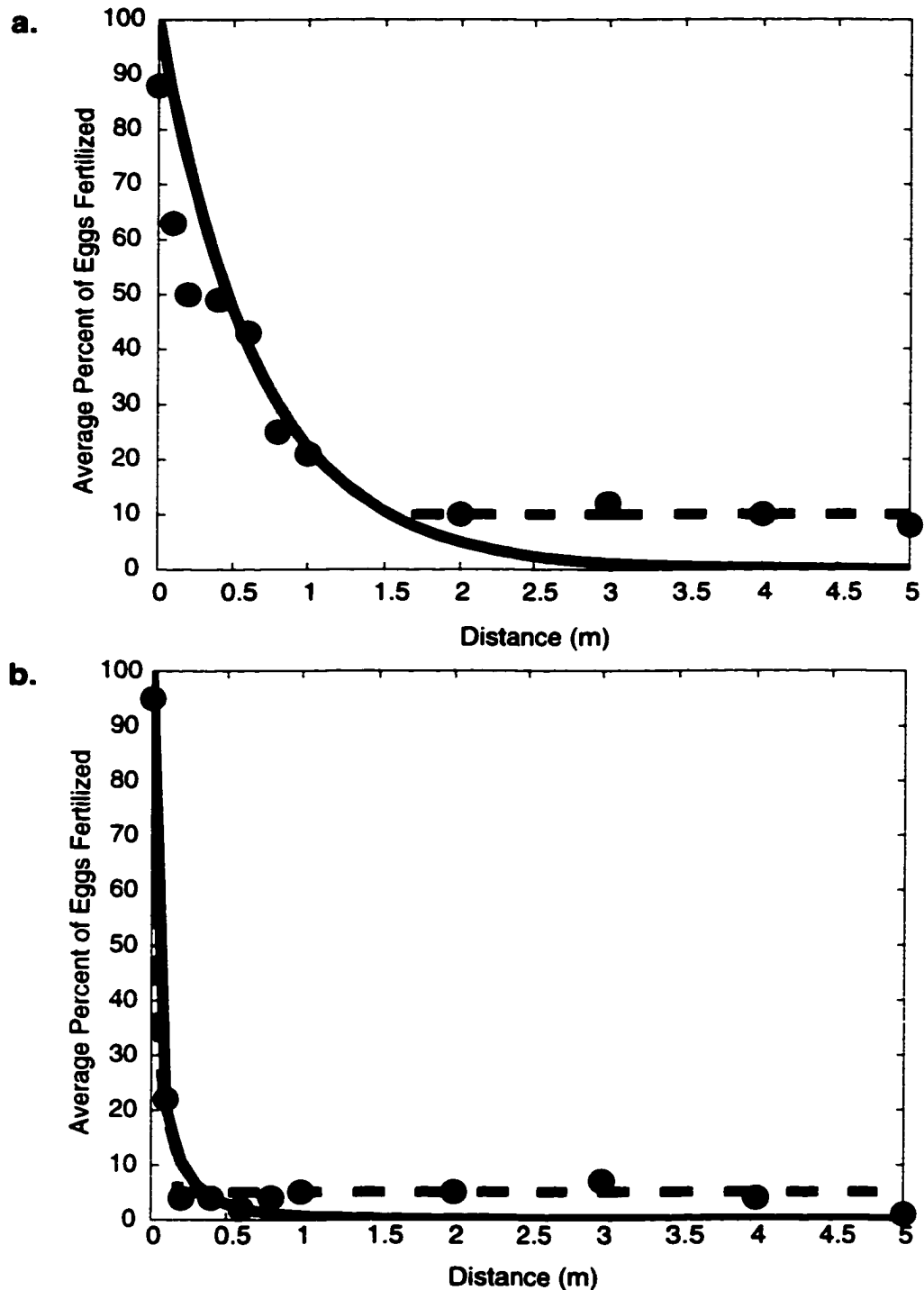
Figure 1. Sperm dispersal distributions for a) low flow conditions and b) high flow conditions. Bullets – Empirical data from Pennington (1985), solid line – negative exponential decline [low flow, no tail distribution (y=exp(-1.5x)); high flow, no tail distribution (y=exp(-5*sqrt(x)))], dashed line – modified negative exponential decline [low flow, tail (y=exp(-1.5x) for 0<x<1.5; y=0.10 for 1.5<x<5)); high flow, tail (y=exp(-5*sqrt(x)) for 0<x<0.18; y=0.05 for 0.18<x<5))].

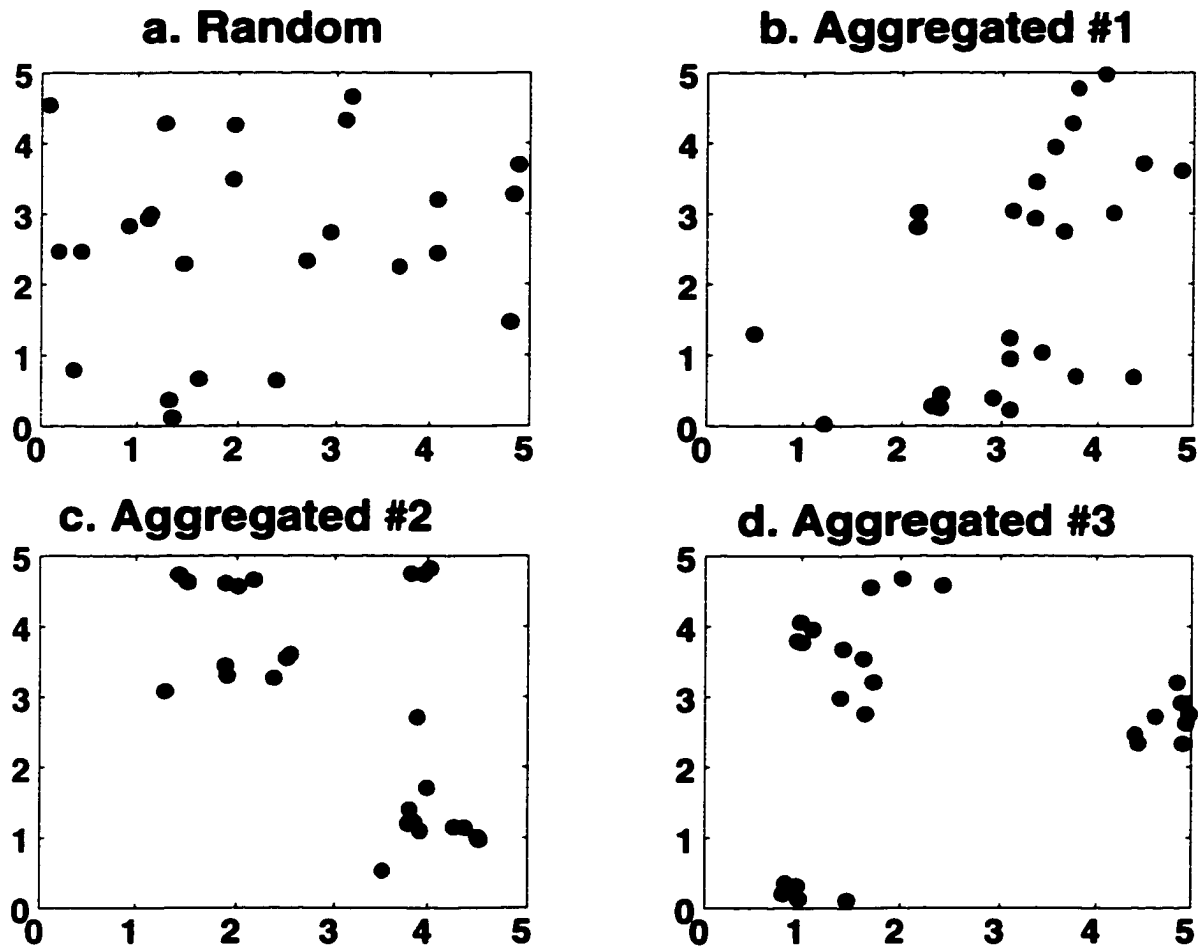Figure 2. Spatial distribution patterns used in the simulation model. a) Random Distribution (a=1.0), b) Aggregated Distribution #1 (slightly aggregated) (a=0.5, b=0.5), c) Aggregated Distribution #2 (many small clumps) (a=0.5, b=0.2), d) Aggregated Distribution #3 (few large clumps) (a=0.2, b=0.5). Parameters are as explained in text.
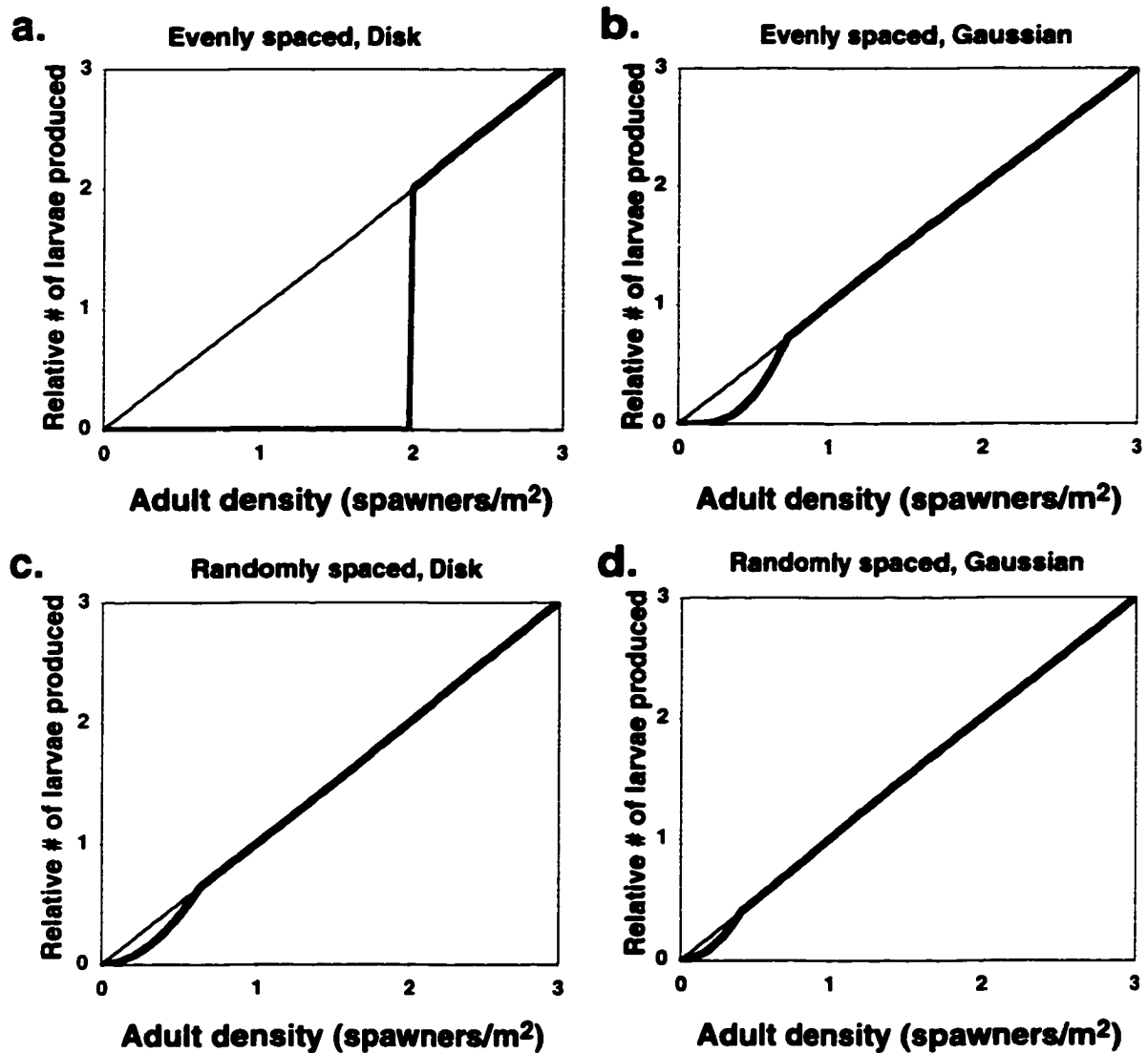
Figure 3. Relationship between density and relative larval production (total adult density * average percentage of eggs fertilized) for the simple analytical model. a) evenly-spaced (regular) spatial distribution with disk sperm dispersal distribution, b) evenly-spaced (regular) distribution with Gaussian sperm dispersal distribution, c) random spatial distribution with disk sperm dispersal distribution, and d) random spatial distribution with Gaussian sperm dispersal distribution.
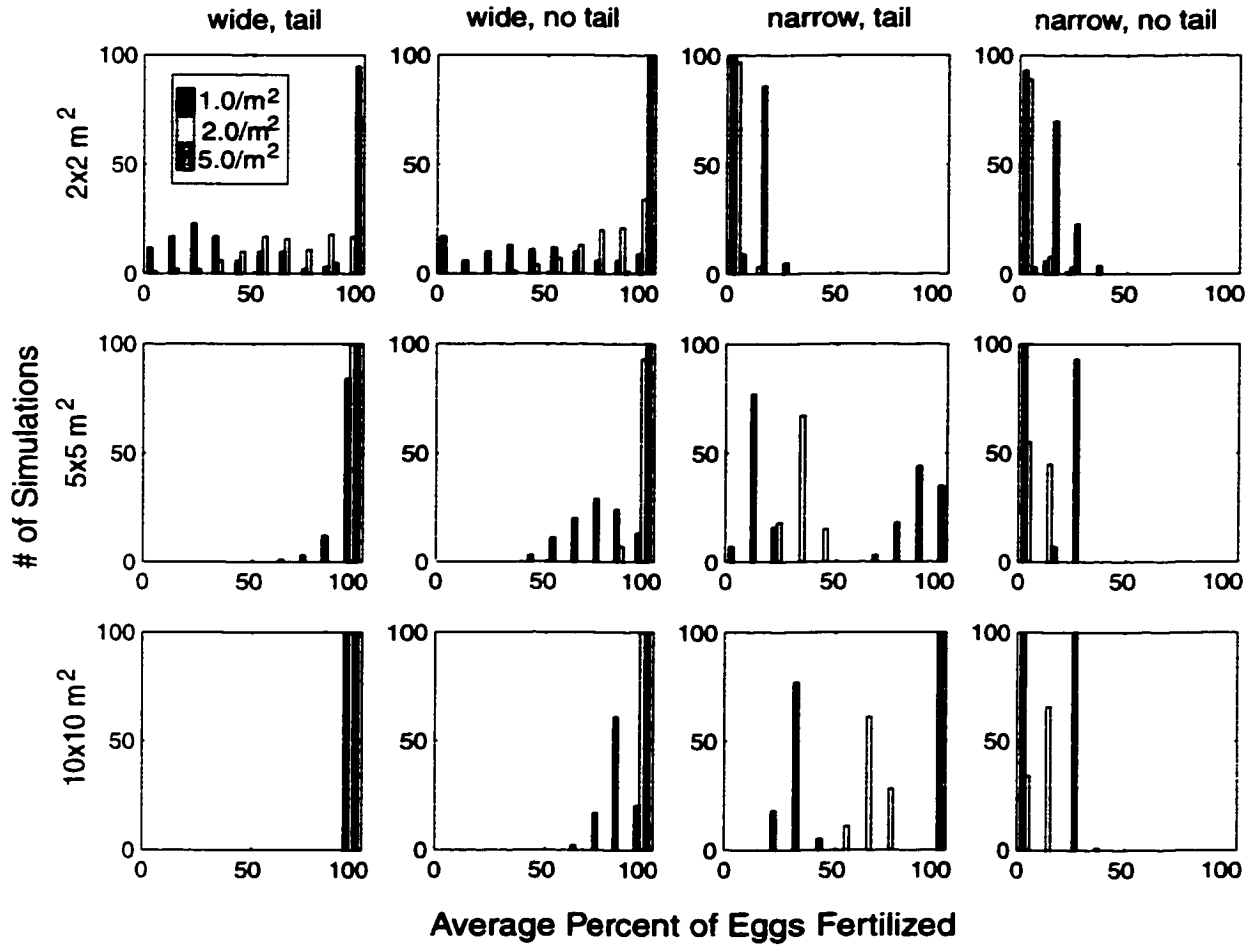
Figure 4. Average percentage of eggs fertilized at 1, 2 and 5 urchins/m2, with varying grid size of 2x2 m2, 5x5 m2, and 10x10 m2 and using all four gamete dispersal distributions.

Random Distribution, Low Flow, No Tail

Legend:
- ■ ■ ■ 0.5 spawners/m^2
- ı ı ı ı ı ı ı 1.0 spawners/m^2
- ı ■ ı ■ ı 1.5 spawners/m^2
- ▬▬▬ 2.0 spawners/m^2

Y-axis: Number of Simulations
X-axis: Average Percent of Eggs Fertilized
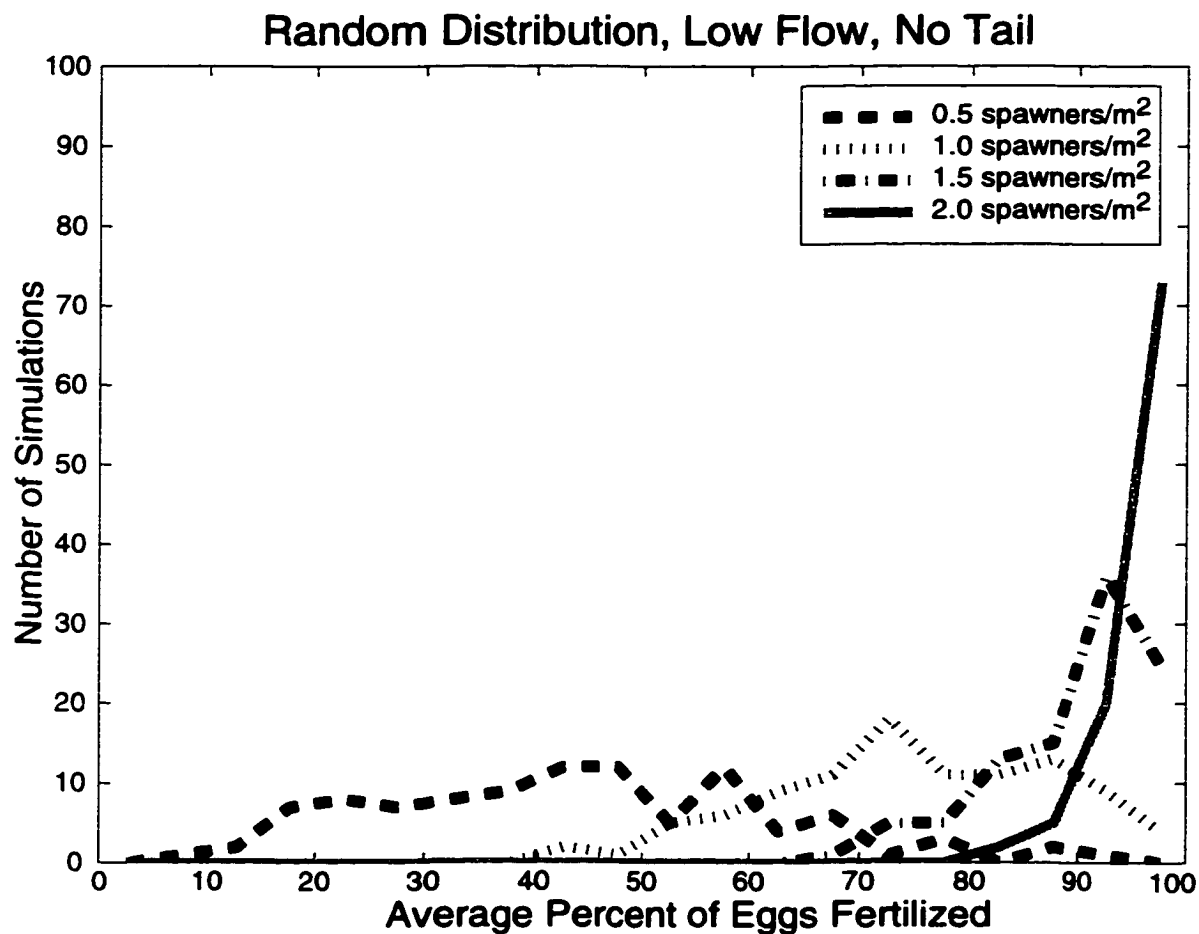
Figure 5. Distribution of average fertilization percent at density level of 0.5, 1.0, 1.5 and 2.0 urchins/meter^2 for a random adult spatial distribution pattern, using a low flow sperm dispersal distribution without a tail.

Random Distribution, High Flow, No Tail
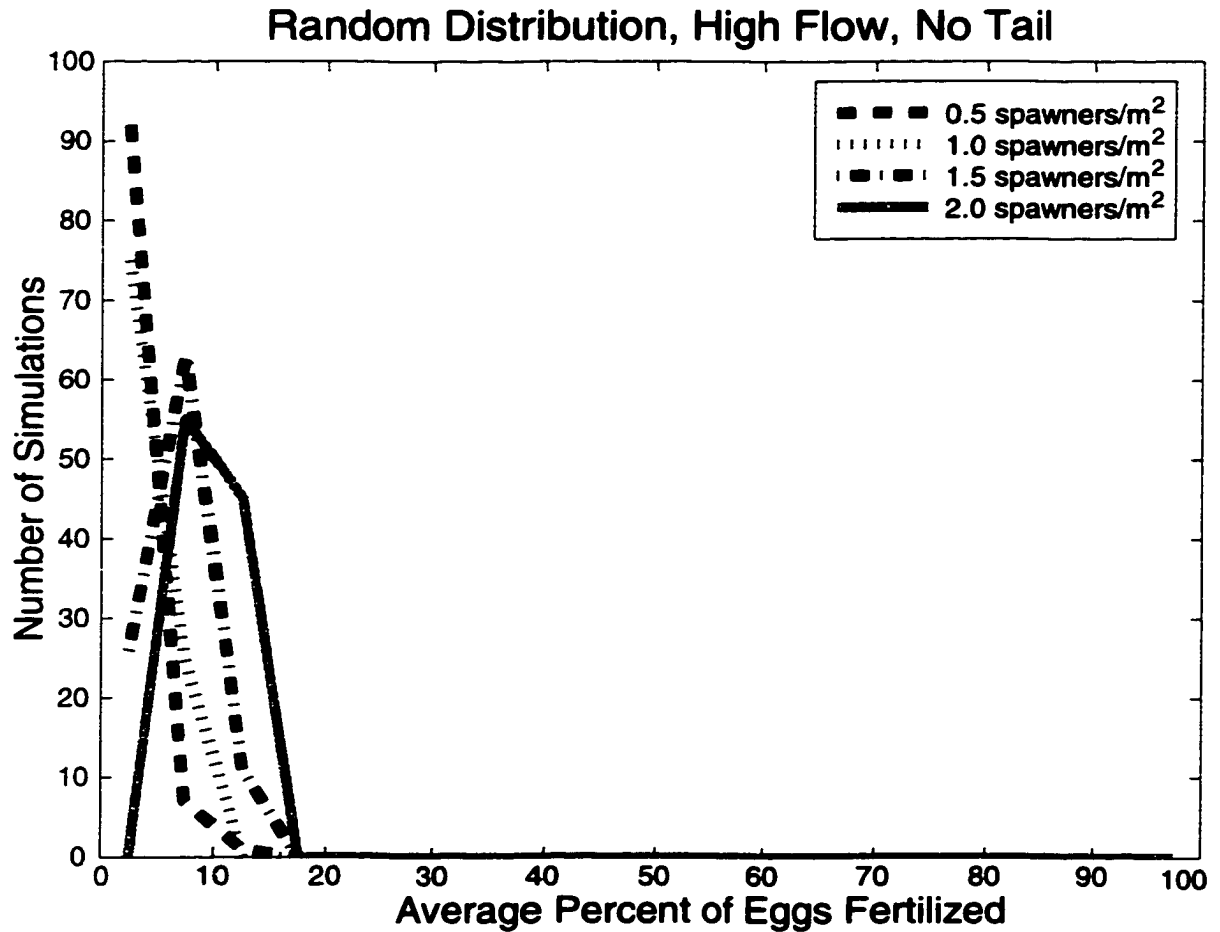
Figure 6. Distribution of average fertilization percent at density level of 0.5, 1.0, 1.5 and 2.0 urchins/meter^2 for a random adult spatial distribution pattern, using a high flow sperm dispersal distribution without a tail.

Random Distribution, High Flow, Tail
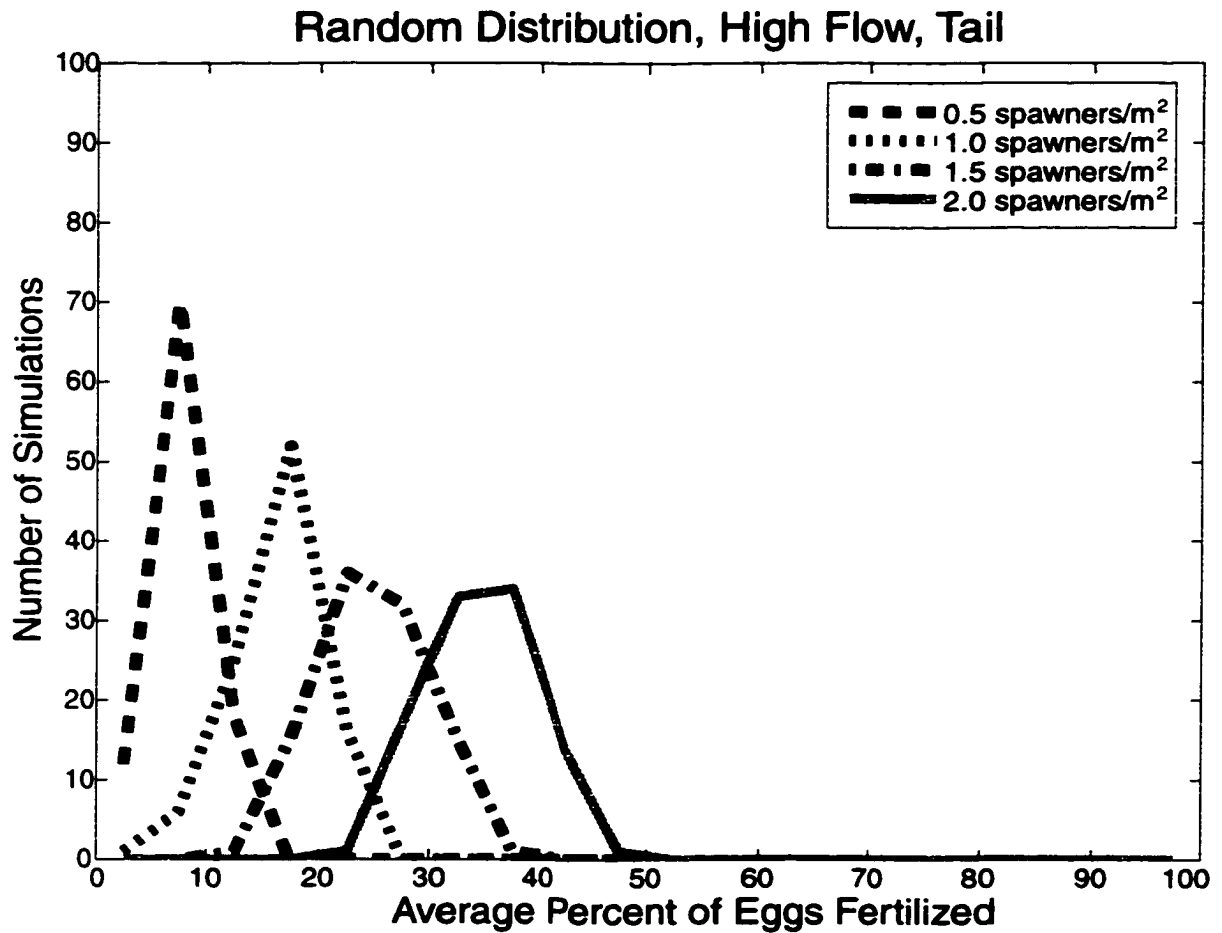
Figure 7. Distribution of average fertilization percent at density level of 0.5, 1.0, 1.5 and 2.0 urchins/meter^2 for a random adult spatial distribution pattern, using a low flow sperm dispersal distribution with a tail.

Random Distribution, Low Flow, Tail

Figure 8. Distribution of average fertilization percent at density level of 0.5, 1.0, 1.5 and 2.0 urchins/meter^2 for a random adult spatial distribution pattern, using a high flow sperm dispersal distribution with a tail.
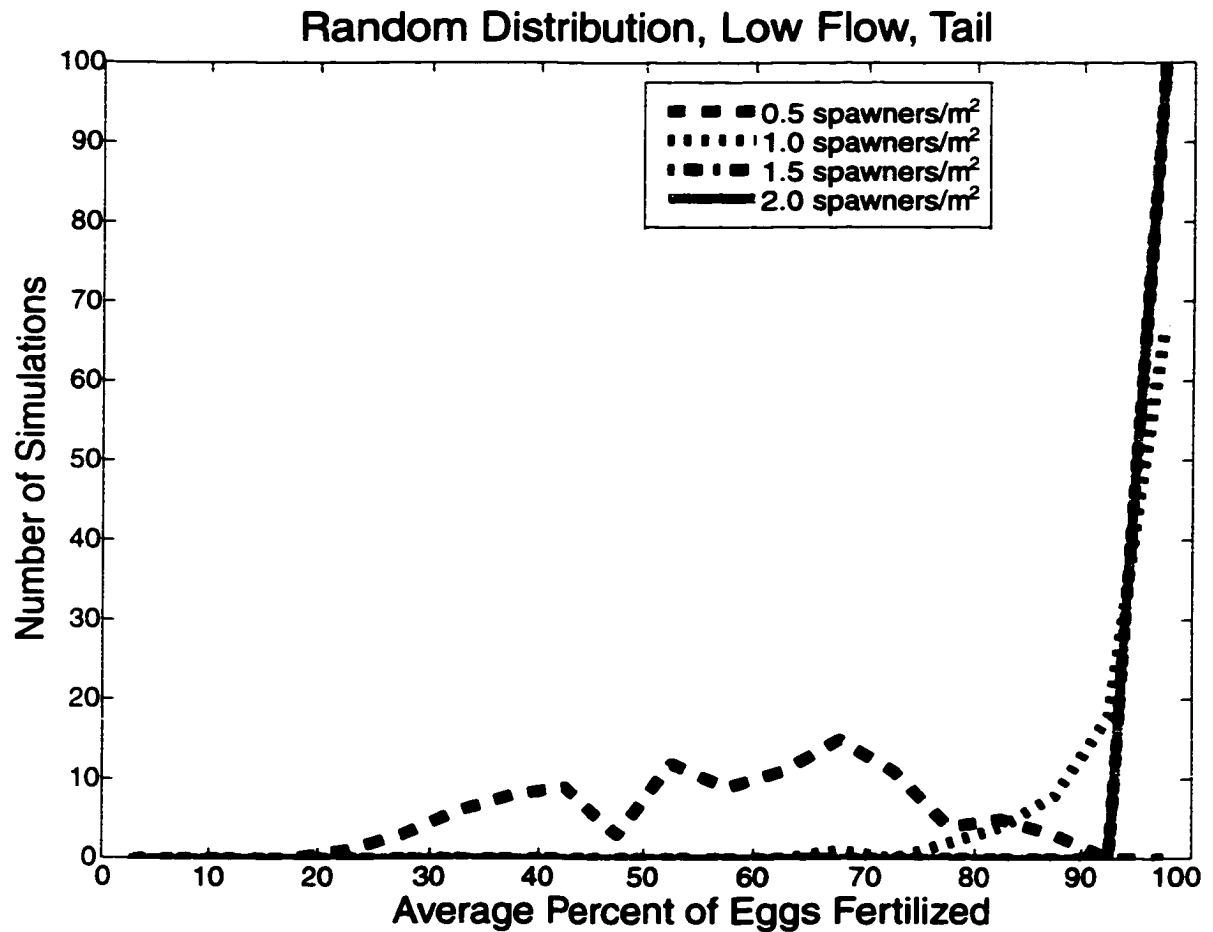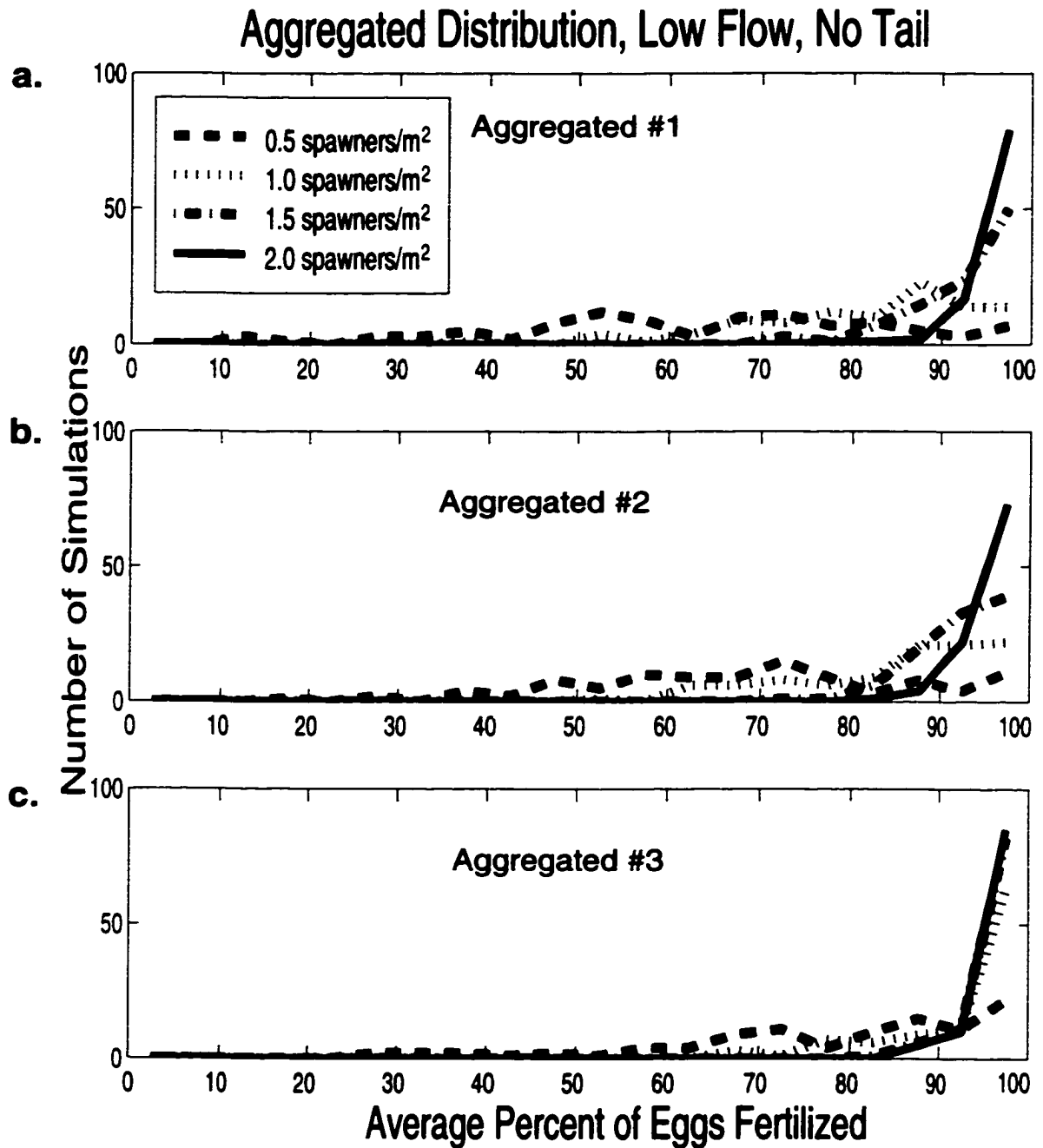
Figure 9. Distribution of average fertilization percent at density level of 0.5, 1.0, 1.5 and 2.0 urchins/meter² for a) Aggregated Distribution #1 (slightly aggregated), b) Aggregated Distribution #2 (many small clumps), and c) Aggregated Distribution #3 (few large clumps), using a low flow sperm dispersal distribution without a tail.
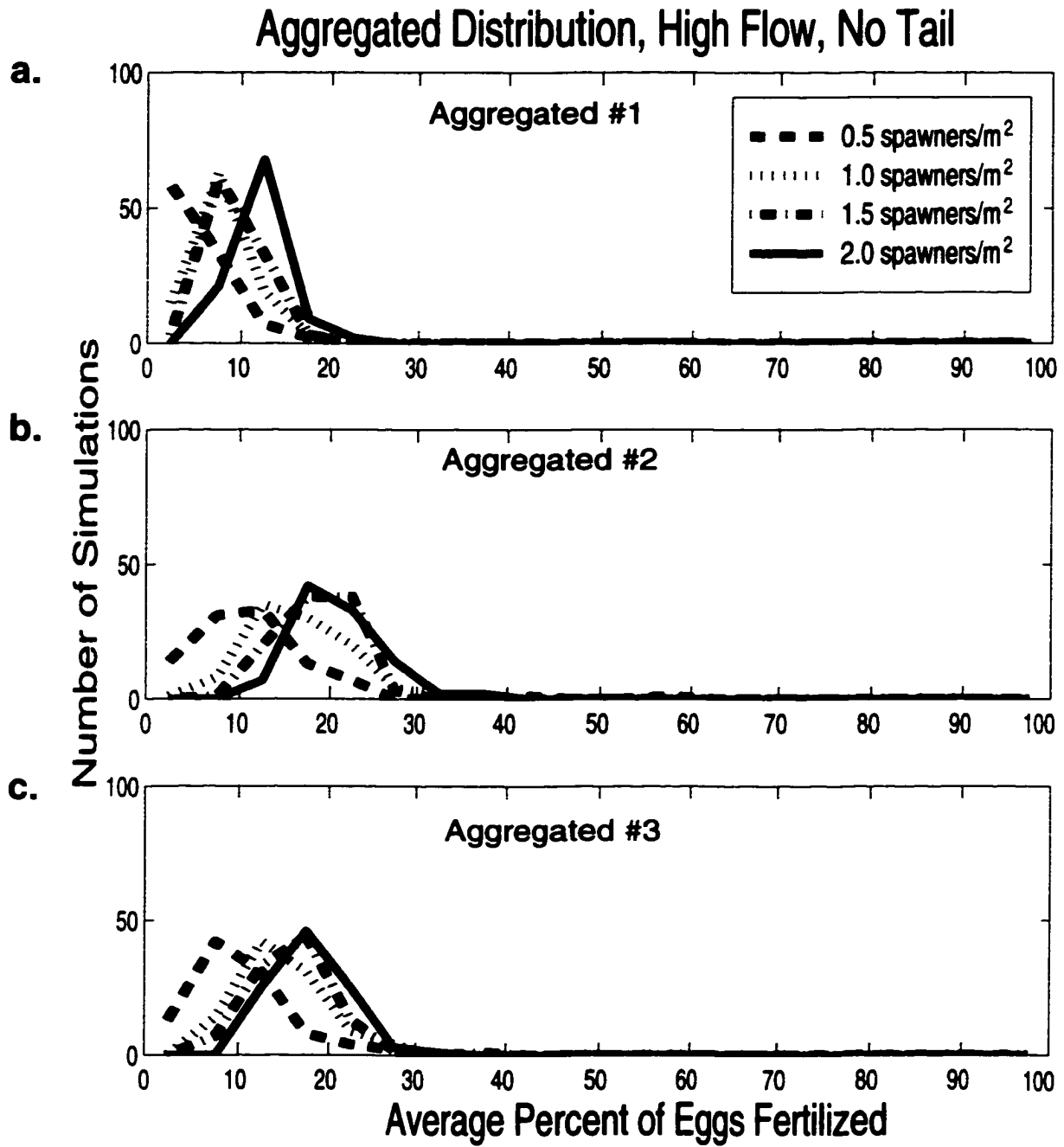
Figure 10. Distribution of average fertilization percent at density level of 0.5, 1.0, 1.5 and 2.0 urchins/meter^2 for a) Aggregated Distribution #1 (slightly aggregated), b) Aggregated Distribution #2 (many small clumps), and c) Aggregated Distribution #3 (few large clumps), using a high flow sperm dispersal distribution without a tail.

a. **Random, Low Flow, No tail**
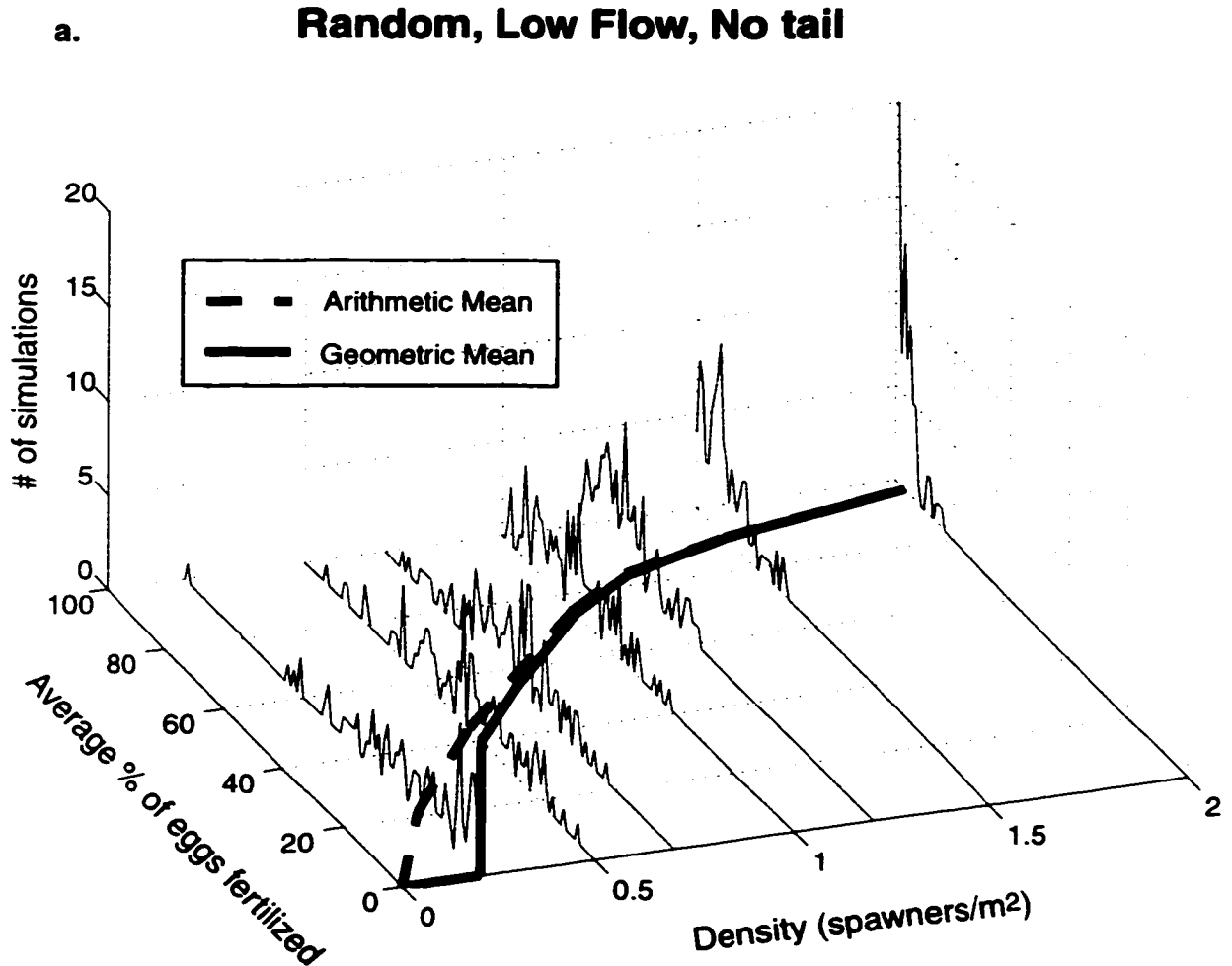
Figure 11a.   Average percent of eggs fertilized at varying density for a random adult
spatial distribution pattern, simulated with a low flow sperm dispersal
distribution without a tail.

b.
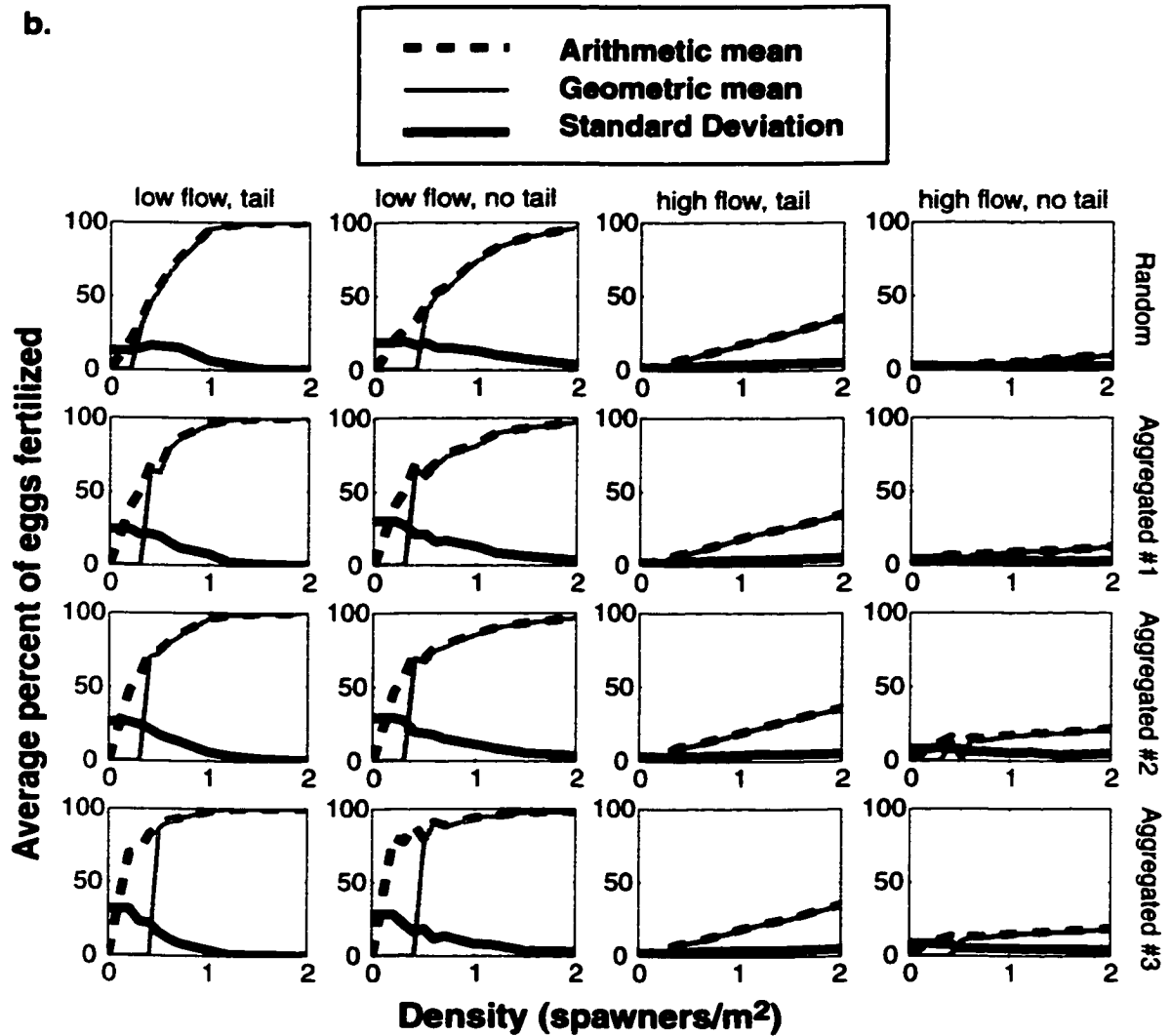
Figure 11b. Arithmetic mean, geometric mean, and standard deviation of average percent of eggs fertilized at varying density for combinations of the four types of spatial distribution patterns and the four types of sperm dispersal distributions.

a. **Random, low flow, no tail**
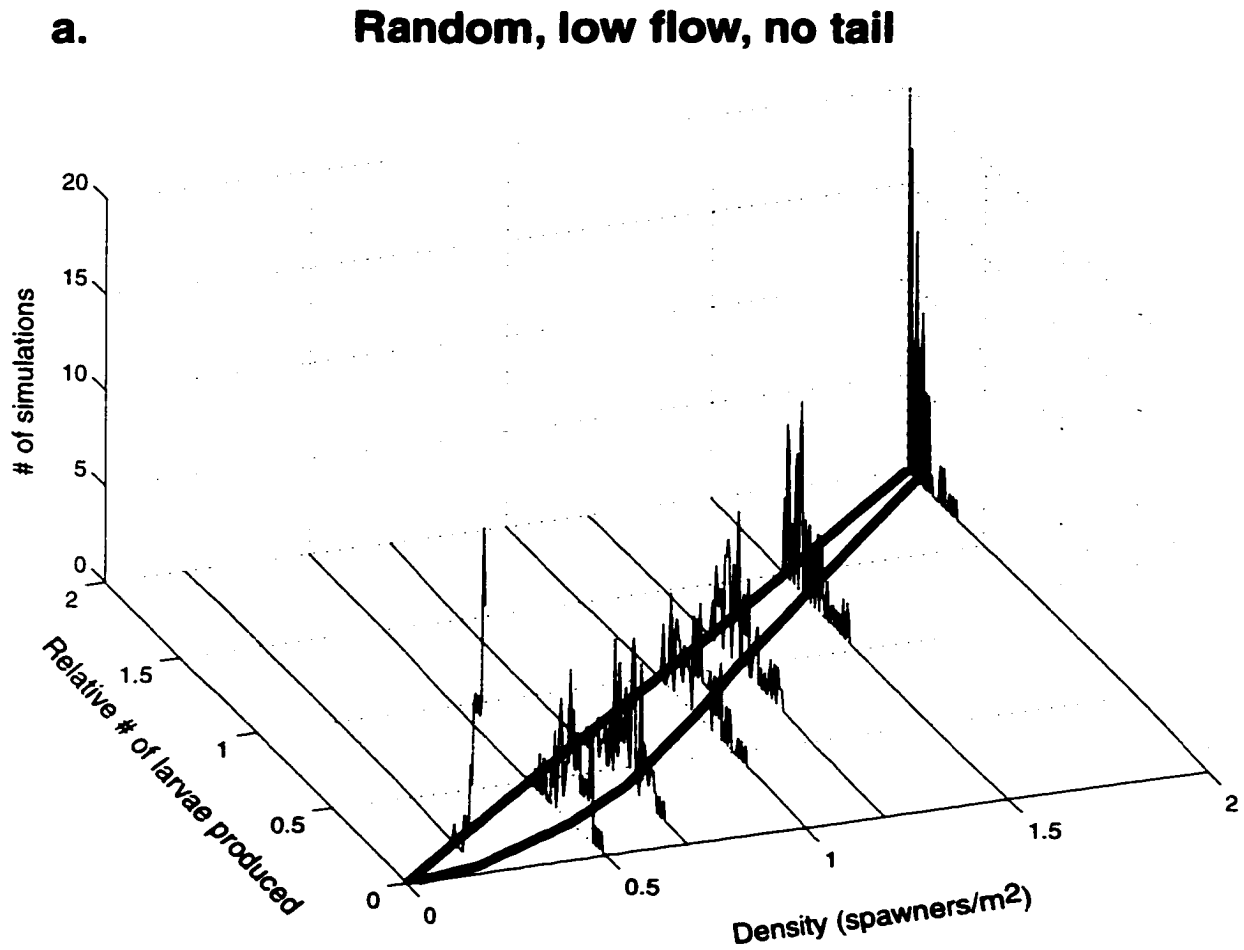
Figure 12a. Relative larval production (density * average percent of eggs fertilized) at varying density for a random adult spatial distribution pattern simulated with a low flow sperm dispersal distribution with no tail. The z axis shows the distribution of simulation values. A 45 degree line is shown to emphasize the decrease in the production of larvae relative to a model assuming 100% fertilization.

b.

▬ ▬ ▬	Arithmetic mean
———	Geometric mean
— — —	45 degree line

Low flow, tail   Low flow, no tail   High flow, tail   High flow, no tail

Relative Number of Larvae Produced

Random

Aggregated #1

Aggregated #2

Aggregated #3

Density (spawners/m2)
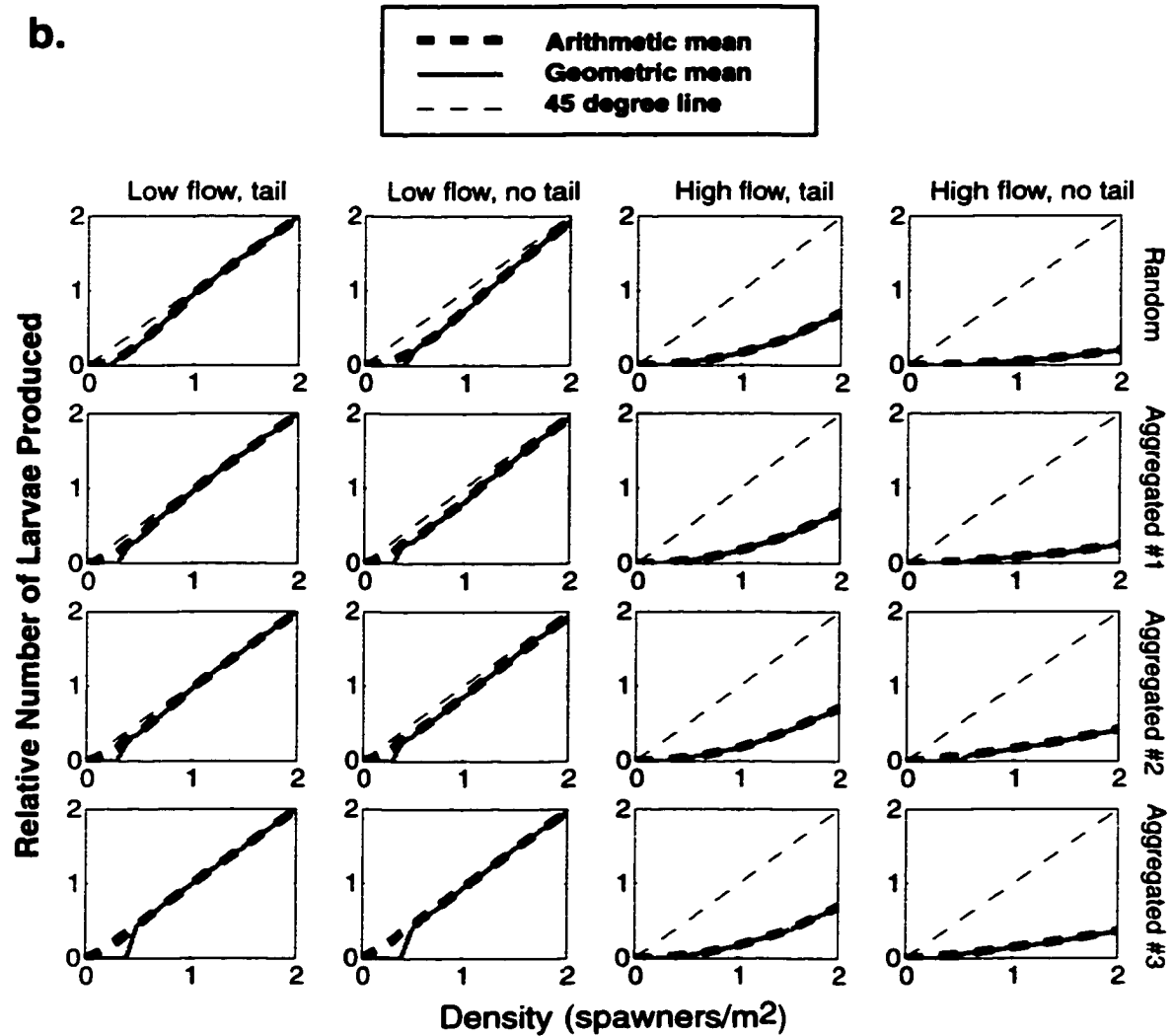
Figure 12b.   Relationship between density and the relative larval production (density
* average percent of eggs fertilized) for simulations with varying
gamete dispersal distributions and adult spatial distribution patterns.
The dotted line represents the geometric mean, the thin line represents
the arithmetic mean, and the thick line (45 degree line) is shown to
emphasize the decrease in the production of larvae relative to a model
assuming 100% fertilization..

Effects of fishing on local spatial distribution and reproduction of a broadcast spawner: the red sea urchin in northern California

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Abstract

As catch of the red sea urchin *Strongylocentrotus franciscanus* in northern California has declined to less than 10% of its maximum level, there is concern that the stock is recruitment overfished. Red sea urchins are broadcast spawners and exhibit an Allee effect in recruitment: a decline in the fraction of eggs fertilized at low density because of increased distance between spawners. To assess the effects of this fishery on recruitment in northern California, we sampled local spatial distributions and used this information to estimate larval production. Density was quite variable (0.1-2.0 urchins/m^2), but showed no systematic patterns within or between fished sites. Indices of aggregation were highest at low densities. To describe the reproductive success implied by each distribution, we used an individually-based model that simulated the fertilization process of broadcast spawners based on spawner locations. Because the dynamics of this process are uncertain, we used a range of gamete dispersion functions corresponding to varying flow regimes. Computed fertilization success was higher for sites with higher densities and higher levels of adult aggregation. Computed fertilization for observed distributions was higher than for simulated random distributions of spawners at the same densities, indicating the positive effect of aggregation on reproduction. An estimate of total larval production for all sites in 1996-1998 was approximately 1/3 of the estimated total larval production in the early years of the fishery (1988-1989). Approximately 75% of the realized decline can be attributed a decline in mean density, with the remaining 25% attributed to the fertilization Allee effect. Although the fishery has reduced the fraction of high density locations, the remaining high density areas provide most of the larval production for the population. This result underscores the need to base projections

of the impact of fishing on the distribution of densities throughout the stock rather than the average density.

Introduction

Reduced density due to fishing can impact the population biology of fished species in many ways. Fishery models describing stock-recruitment relationships often assume that while density-dependence may be compensatory at high density, it is linear at low density. However, it is clear that many harvested populations reach a limit in their ability to tolerate harvest when fished to very low levels, and instead collapse or remain at low levels of population abundance (e.g. right whale (Fowler and Baker 1991); white abalone (Tegner et al. 1996)). For some species, there may be an Allee effect at low levels of abundance, such that recruitment decreases to zero below a threshold level of abundance or is severely reduced to levels below that which a linear decline would predict (Allee 1931). Many mechanistic explanations have been suggested for Allee effects, including decreased mating success due to inability to find mates (Errington 1940, Dobson and Lyles 1989, Lamberson et al. 1992), decreased reproductive efficiency due to processes which require high densities of individuals (e.g. pollen limitation: Lamont et al. 1993, Kunin 1997; broadcast spawning: reviewed in Levitan 1995, Levitan and Sewell 1998), and decreased survival due to predator defense being correlated with density (Leopold 1933).

The red sea urchin *Strongylocentrotus franciscanus* fishery in California targets a species that is hypothesized to have Allee effects at low density. This fishery began in the 1970's in southern California and expanded to northern California in the early 1980's. Landings peaked in northern California in 1988 at a level of 30 million pounds, and have drastically declined to the current level of approximately 10% of the maximum harvest (Figure 1). Fishery managers have observed a concurrent decline in density from an

average of 1.7 total sea urchins per m^2 in 1989 to 0.6 per m^2 in 1994 (Kalvass and Hendrix 1997). As densities are less than half of the pre-fished level, there is concern that fishing has decreased reproductive success and the red sea urchin is recruitment overfished (Kalvass and Hendrix 1997).

Red sea urchins are hypothesized to exhibit two different Allee effects. In the first, juvenile urchins reside beneath the spine canopy of the adults, receiving protection from predators and possibly gaining increased food supply (Tegner and Dayton 1977, Breen et al. 1985). The Allee effect addressed here is reduced fertilization success at low density, resulting from increased gamete dilution as distance between spawners is increased at lower densities (Levitan et al. 1992, Levitan et al. 1991).

Some aspects of the Allee effect of decreased fertilization success at reduced density in benthic marine invertebrates have been studied. Researchers have shown that fertilization declines as density decreases (Yund and McCartney 1994, Downing et al. 1993, Yund 1995, Brazeau and Lasker 1992, Levitan and Young 1995, Levitan 1991), as wave action increases (Denny and Shibata 1989, Pennington 1985, Mead and Denny 1995, Epel 1991), and as distance between spawners decreases (Pennington 1985, Yund 1990, Grosberg 1987, Yund 1995, Brazeau and Lasker 1992, Levitan et al. 1992). However, studies of fertilization have generally been in laboratory environments or at very small scales (very few numbers of individuals spawning) in field studies (Pennington 1985, Levitan et al. 1992).

Fishery management models for the red sea urchin have included Allee effects, with some models assuming a threshold density below which no fertilization occurs (Botsford et al. 1993, Quinn et al. 1993). Botsford et al. (1993) chose a critical threshold

of 0.7 urchins/meter^2 of spawner density for fertilization success in their model of a rotating harvest scenario for this fished invertebrate. Pfister and Bradbury (1996) also modeled a rotating harvest strategy for *S. franciscanus*, examining two mathematical representions of an Allee effect: 1) a non-linear Type II functional response when the population dropped below 50% of pre-harvest levels and 2) a more extreme linearly decreasing function with decreasing density. Quinn et al. (1993) used a log-linear relationship between fertilization success and average nearest neighbor distance to represent an Allee effect in *S. franciscanus* populations. Each of these models chose density-dependent relationships somewhat arbitrarily, based on limited field and laboratory studies of the fertilization Allee effect (Pennington 1985, Levitan et al. 1992, Levitan et al. 1991). None of these models accounted for the effects of variability in density between sites and the effect of aggregation. If the local spatial distribution affects reproductive dynamics, this simplification may be inappropriate.

In a previous study we developed a model of fertilization dynamics of benthic marine invertebrates, and used it to describe the effects of adult density, adult aggregation, and varying distribution of spawned gametes on the stock-recruitment relationship (Lundquist and Botsford 2000). The model was based on sperm dispersal data under varying flow conditions for the green sea urchin *Strongylocentrotus droebachiensis* (Lundquist and Botsford 2000, Pennington 1985). Our results indicated decreasing fertilization efficiency and increasing variability in fertilization success as density decreased. Increasing aggregation of adult spawners resulted in increased fertilization success, as expected. However, the stock-recruitment relationship varied and depended on the shape of the gamete dispersal distribution. Increasing width of the

gamete dispersal distribution (representing decreased water flow) and a longer tail on the gamete distribution (representing gamete physiological qualities that increase the distance over which gametes are viable) both increased fertilization success. Some combinations of width and tail of the gamete dispersal distribution indicated non-linear behavior at low densities (e.g. 'low flow, tail' and 'low flow, no tail'), while others displayed reduced larval production at all densities (e.g. 'high flow, tail' and 'high flow, no tail').

Particularly interesting was the lack of direct threshold below which fertilization dropped to zero, as is postulated in many models of Allee effects (Begon et al. 1986, Quinn et al. 1993, Botsford et al. 1993). Instead, the model predicted a large increase in variability in fertilization success between different simulations and an increasing chance of zero fertilization as density decreased. This stochasticity was due to the spatial distribution of adults. Essentially, the variability in nearest neighbor distances becomes larger as density decreases, thus increasing the range of possible values of fertilization success.

Here we sample spatial distributions and determine the effect of local spatial distribution on a population's contribution to the supply of planktonic larvae, as well as the effect of the fishery on the total larval production from all locations. We use our fertilization model (Lundquist and Botsford 2000), driven by observed distributions of adult spawners of the red sea urchin *Strongylocentrotus franciscanus* at various locations in northern California to determine the larval production implied by these distributions. Our specific goals are 1) to sample spatial variation in density and the degree of aggregation, 2) to estimate larval production implied by these spatial distributions, and 3) to compare current with pre-fishery density distributions and larval production.

Methods

Sampling Sites

Our sites were selected to include one sampling location approximately every 10 minutes of latitude over the range of the northern California fishery between Bodega Bay (38°19.2 N) and Caspar (just south of Fort Bragg) (39°21.5 N) (Figure 2). Red sea urchins are fished from 4 major ports in northern California (Bodega Bay, Point Arena, Albion and Fort Bragg). The sites included two adjacent reserve and fished locations (Caspar and Bodega Bay), and one location (Salt Point State Reserve) that is not fully protected due to its unclear status in state regulations as a marine reserve (McArdle 1997) and evidence of fishing from size frequency distributions (Morgan et al. 2000a). General habitat characteristics of most sites included a relatively exposed coastline, rocky substrate, and a surface kelp canopy of the bull kelp *Nereocystis leutkeana*. Bodega Bay lacks both a surface canopy of *N. luetkeana* and an extensive understory canopy of *Pterygophora californica*, though periodic accumulations of drift algae from northern sites does occur. The primary predators observed at our study sites are the seastars *Pycnopodia helianthoides* and *Pisaster* spp. (Moitoza and Phillips 1979, Mauzey et al. 1968, Lundquist, pers. obs.). Other northern California predators include rock crabs (*Cancer* spp.) and leather stars (*Dermasterias* spp.), both present at low abundances and determined through field observations to have little effect on red sea urchin abundance compared to the effect of *P. helianthoides* (Lundquist, pers. obs.). Sites exhibit some local heterogeneity of substrate, including kelp cover, substrate type (rock or sand), and landscape rugosity.

Field collection

Red sea urchin populations were surveyed using 5 m by 30 m transects. Over

7000 m^2 of sea urchin habitat was sampled, primarily in the summer of 1996, with

additional collections in summer, 1997, and spring and fall of 1998. Transect lines were

dropped from the surface in order to minimize bias in selecting areas to be sampled.

We compared methods of transect data collection to determine the survey method

which minimized the time required per amount of area surveyed while estimating density

at a fine enough spatial resolution to capture the effects of aggregation on reproductive

dynamics for the fertilization model. We tested three different sampling procedures: 1)

labor intensive mapping of individual sea urchin locations within the transect area, 2) sea

urchin counts within 1/2 m by 1/2 m quadrats (600 counts per transect), and 3) sea urchin

counts within 1/2 m by 1 m quadrats (300 counts per transect). Comparable simulations

with the two quadrat sampling methods differed by less than 5% in average fertilization

percentage in all but one case (Appendix 1). Mapped transect methods usually gave

slightly higher values than both quadrat sampling methods, though the maximum

difference in fertilization between mapping methods and quadrat sampling methods was

less than 12% (Appendix 1). We concluded that the sampling strategy of 1/2 m by 1 m

quadrats, which required the least effort, was the most efficient method for describing the

local spatial distribution.

For each 5m by 30m transect, SCUBA divers recorded the number of urchins

within each 1/2 m by 1 m quadrat. 42 transects were completed in 1996 at 11 locations, 7

transects in 1997 at 2 locations, and 4 transects in 1998 at 3 locations. Urchins within

and alongside the transects were collected and measured to determine the size frequency distribution and percentage of adult urchins at each site. Destructive substrate sampling was not performed; thus, the proportion of individuals under 15 mm was likely underestimated. Size distributions were used to calculate the percentage of juvenile (0-60 mm), pre-legal adults (61-89 mm) and legal adults (90 mm+) at each site.

Data Analysis

Average transect density was calculated as the total number of individuals divided by the total area sampled. Transects varied in size from 12.5 m^2 to 150 m^2, with most transects being 150 m^2. Data were combined for 1996, 1997 and 1998 to calculate an average site density. Density estimates for each site were calculated from the mean of all quadrat counts from all transects completed at a site. Four of the 51 randomly dropped transects contained no sea urchins. As these areas were of similar habitat and topographic relief of transects that included sea urchins (often located within 100 m of a transect with sea urchins), these zero transects were included in calculations of density and fertilization.

We estimated the precision of our estimates by treating them as abundance estimates using standard quadrat sampling techniques (Seber 1982). These estimates were not straightforward because we did not know the total area of sea urchin habitat within each site. We therefore calculated the coefficient of variation, assuming our sample (total area of one transect = 300 quadrats = 150 m^2) was one of three proportions of the total area (S_i) at a site: 1) 1/10 of the total area sampled (S_i = 300 quadrats times 10 = 3000 total quadrats = 1500 m^2), 2) 1/20 of the total area sampled (S_i = 6000 quadrats =

3000 m^2), and 3) 1/50 of the total area sampled ($S_i = 15,000$ quadrats $= 7500 \text{ m}^2$). The variance estimate was calculated according to the quadrat sampling methods outlined in Seber (1982), where

$$\hat{\sigma}_i^2 = \frac{S_i^2}{s_i} v_i \left(1 - \frac{s_i}{S_i}\right)$$

(1)

$\hat{\sigma}_i^2$ is the variance estimate of population abundance at site i

s_i is the number of quadrats sampled at site i

v_i is the variance estimate from quadrat counts for site i

We calculated the expected percentage error (coefficient of variation) in the estimate of total population abundance at a site as the $\hat{\sigma}_i / \hat{N}_i$, where the estimate of total population abundance, $\hat{N}_i = d_i S_i$ and d_i is the average density per m^2 from site i. Note from equation (1) that the coefficient of variation goes to a constant as S_i goes to infinity.

To determine whether populations were aggregated, we calculated various indices of aggregation for each transect. All aggregation indices were calculated using counts of 1/2 m by 1 m quadrats. Variance to mean ratios were calculated and tested for aggregation using a chi-square test (Krebs 1989). We also calculated the Morisita index of dispersion (I_δ) and corresponding chi-square and p-values. As the variance to mean ratio and I_δ are known to vary with both the mean and sample size, we also calculated Morisita's standardized index of dispersion (MSID), which is standardized for density and sample size (Krebs 1989). This index ranges from -1.0 to $+1.0$. An index of 0.0 indicates a random pattern of spatial dispersion, positive indices indicate aggregated patterns, and negative indices indicate uniform or regular patterns of dispersion. The

index has 95% confidence limits at +0.5 and –0.5, signifying that a transect with a MSID of greater than 0.5 is significantly more aggregated than a randomly distributed population. The average MSID at each site was calculated using all quadrat data from all transects at that site.

Fertilization Model

To estimate the reproductive success implied by the observed densities of urchins at each site, we used the individually-based simulation model of fertilization presented in Lundquist and Botsford (2000). For each distribution, we created a mapped spatial distribution of individual urchins based on observed transect data and estimated fertilization success based on theoretical distributions of egg fertilization rates with distance from male spawners. Empirical data (number of urchins per 1/2 m by 1 m quadrat) were converted to mapped spatial distributions by generating uniform random x and y coordinates to place each sea urchin within each quadrat. The gender of each sea urchin was determined randomly, assuming an equal sex ratio. We used a uniform random number generator to determine if a sea urchin was a reproductive adult (> 60 mm) based on the percentage of adults found in size frequency distributions at each site (Morgan et al. 2000b).

As we did not know the actual water flow conditions and sperm dispersal distributions during spawning of the red sea urchin in northern California, we created four different distributions of gametes to assess a range of possible conditions. Theoretical distributions of egg fertilization rate with distance from male spawners were estimated based on empirical fertilization data from Pennington (1985). Pennington

performed an *in situ* fertilization experiment for *S. droebachiensis*, a congener of *S. franciscanus* with similar gamete properties (Levitan 1993), measuring the fertilization of stationary egg masses at increasing distances from the release of a sperm solution. Pennington's observations of fertilization included low current trials with velocities of less than 0.2 m/s and a high current trials with velocities greater than 0.2 m/s. We converted these empirical results to negative exponential distributions of fertilization rate (via dilution of sperm from a spawning male) with distance, which we termed 'low flow, no tail' (LFNT) and 'high flow, no tail' (HFNT). As the negative exponential decline did not accurately represent the non-negligible tail of the empirical fertilization data at relatively large distances from spawning individuals (Pennington 1985), we modified the LFNT and HFNT distributions by adding a tail to each distribution, representing an extended distance over which viable gametes are available for fertilization. The two modified distributions are termed 'low flow with tail' (LFT) and 'high flow with tail' (HFT). Sperm dispersal distributions with tails were normalized to the corresponding distributions without tails to maintain a constant sperm supply.

To estimate the variability in fertilization at each site, we performed 100 simulations for each transect for each of the four sperm dispersal distributions, varying the random placement and gender of spawners within each quadrat. The variability in these simulations represented both uncertainty in measurement, as we did not know the exact location of sea urchins within each quadrat, and interannual variability in sea urchin distributions as sea urchins likely reform spatial distributions during each spawning season. The percentage of eggs fertilized for each adult female was calculated as the cumulative percentage of sperm reaching each adult female from all adult males within

the grid, based on the sperm dispersal distribution. Average fertilization was calculated for each simulation as the average fertilization percentage of all females in a given simulation.

To test whether aggregation of adults in observed distributions increases fertilization success, we compared the fertilization results based on observed spatial distributions to simulation runs based on populations with the same density as observed transects, but with sea urchin locations within the 5 m x 30 m quadrats generated from a uniform random distribution.

Larval Production

To determine the current stock-recruitment relationship at low densities, we used results from the fertilization model to estimate larval production. Larval production for each transect was calculated as the adult density (sea urchins > 60 mm) times average fertilization success for both the observed simulations and the random simulations. We determined the mathematical relationship between adult density and larval production by fitting a polynomial to plots of computed larval production versus density from the simulated distributions. Total larval production for 1996-1998 fished observed transects and 1996-1998 randomly distributed transects was calculated as the sum of larval production for individual transect, normalized to the total area sampled. To assess the effects of the Allee effect on current larval production, the maximum possible total larval production was calculated for 1996-1998 transects as the total larval production assuming no Allee effect (i.e., 100% fertilization success).

In addition to the samples we collected, we obtained data from California Department of Fish and Game (CDFG) (Peter Kalvass, pers. comm.) from transects collected in Sonoma and Mendocino Counties in 1988 (n=105) and 1989 (n=76). We used 1988-1989 CDFG data as a proxy for pre-harvest conditions, as these were the first years that sea urchin data were collected in northern California. CDFG transects sampled the number of sea urchins per 1 m by 5 m quadrat along a 30 m transect line. We used size frequencies collected at Point Cabrillo Marine Reserve in Mendocino County, California, in 1989 (Morgan 1997) to estimate the percentage of adults in order to compute adult density for the CDFG transects.

We wished to compare total larval production between years, as well as the relative contribution of declines in density, the fertilization Allee effect, and the effect of aggregation to declines in larval production. To estimate total larval production from the CDFG data, we calculated larval production for each 1988-1989 CDFG transect using the estimated relationship between larval production and adult density generated from observed transect simulations. Total larval production for 1988-1989 transects was calculated as the sum of larval production for all individual transects, normalized to the total area sampled. The maximum possible total larval production was calculated for both 1988-1989 as the total larval production assuming no Allee effect (i.e., 100% fertilization success).

Results

Density

Average density in 1996 varied with site between 0.1 and 2.0 sea urchins/m^2 (Figure 3a, Table 1). Some sites (Albion, Saunders) had much higher average densities than neighboring sites (Figure 3a). Juvenile density was higher at some sites north of Point Arena (Elk, Albion, and Caspar Reserve), with all other sites having low densities of juveniles in 1996. In general, total density and adult density showed no discernable pattern over space.

Comparison of adjacent fished and reserve locations showed that reserves had higher average densities than fished sites (reserves: 1.079 sea urchins/m^2; fished site: 0.803 sea urchins/m^2) (Figure 3a,b). However, because of the high variance in density between transects at both fished and reserve locations (see Appendix 2), this difference is not significant (t=-0.901, p=0.19). Density differences between reserve and fished locations appeared constant through time, as the differences were also present in 1997 and 1998 collections (Figure 3b). One location, Caspar Reserve, had much higher numbers of juveniles compared to its adjacent fished site (Figure 3a). Both reserve locations showed higher densities of legal-sized adults than adjacent fished sites.

Coefficients of variation for most sites indicated between 5 and 15% error in estimates of total abundance, based on the quadrat count estimates (Table 1). Larger percentage error in estimation of abundance occurred for sites with lower sampling effort. Some sites showed high variability in sea urchin density when comparing multiple transects performed at a single site (see Appendix 2). Patchiness of sea urchin spatial distributions is the likely explanation, as these sites often had both low and high density transects, which in turn increased the variance of the stratified estimate of abundance.

Aggregation

All transects exhibited significant aggregation using the variance to mean ratio,

Morisita's I_δ and the Morisita's standardized index of dispersion (MSID) (Appendix 2).

We can compare the level of aggregation at different densities using the MSID, as the

MSID is independent of both sample size and density (Krebs 1989). Average MSID

indices for each site showed no discernable pattern across space (Figure 4a).

Aggregation (MSID) was significantly negatively correlated with both adult density (sea

urchins >60mm) ($r=-0.631$, $p<0.05$) and with total density ($r=-0.574$, $p<0.05$). Transect

data from low density areas (less than 0.5 sea urchins/m^2) had higher levels of

aggregation using the MSID (Figure 4b). In these low density transects, most sea urchins

were located within a small area of the transect, resulting in these high indices of

aggregation.

Fertilization Success

All of our variations of the fertilization model produced a pattern of increasing

fertilization success with increasing transect density. For the low flow gamete dispersal

distributions (LFT and LFNT), the percent of eggs fertilized was high (90-100%) for sea

urchin densities above approximately 1 sea urchin/m^2 (Figure 5a,b). However, as density

decreased below 1 sea urchin/m^2, average fertilization declined and the variance of

fertilization success increased. The high flow simulations (HFT and HFNT) produced

low fertilization rates for all transect densities, rarely higher than 40% even at high

densities (Figure 5c,d). High flow simulations also showed a pattern of increasing

variance in fertilization success as density decreased.

Patterns of average transect fertilization at each site showed relatively low variability in fertilization across sites (Figure 6). 'Low flow' (LFT and LFNT) simulations showed high rates of fertilization for all sites, with small decreases in fertilization noted at some sites (Figure 6a,b). Two of these outlying sites (Caspar fished and Gunderson) were two of the lowest density sites. Salt Point Reserve and Albion each included transects with no sea urchins and zero fertilization success, resulting in the low values of average fertilization success at these sites. The site with the lowest average density (Stewarts Point) was surprisingly successful in the fertilization model in both of the low flow simulations. This could easily be explained, as Stewarts Point had the highest aggregation (MSID = 0.6536) of all sites, resulting in high fertilization success (Lundquist and Botsford 2000). Coefficients of variation (CV) between average site values were relatively low at 18.5% and 20.7% for the LFT and LFNT simulations. Results from high flow (HFT and HFNT) simulations showed consistent low fertilization success (< 40%) for all sites (Figure 6c,d), with no distinct pattern in terms of adult density as was seen in the low flow simulations. The CV's for the HFT and HFNT simulations were roughly 1.5 to 2 times larger than those of the low flow simulations, at 42.7% and 30.7%, respectively, reflecting greater variability in average site values of fertilization success than was seen in the low flow simulations. Correlations between adult density and fertilization success at each site were significantly positive only for the HFT simulations ($r=0.665$, $p<0.05$).

To determine the effect of aggregation on fertilization success, we compared fertilization success from observed transect simulations with results expected if sea urchins were distributed across the entire transect according to a uniform random

distribution (Figure 7a,b,c,d). Fertilization based on observed transects was higher than fertilization based on hypothetical transects for all four types of sperm dispersal distribution, implying that the aggregative behavior of red sea urchins is beneficial to their reproductive success over a broad range of possible fertilization dynamics. Average site values of fertilization success based on randomly generated distributions resulted in much higher CV's (LFT: 40.6%, LFNT: 47.5%, HFT: 58.2%, HFNT: 63.9%), reflecting a larger range of values of fertilization success when spawners were distributed randomly.

Larval Production

The effect of local density appeared to be as important as fertilization success in determining larval production at a site, as plots of larval production (Figure 8a,b,c,d) showed similar patterns across sites to that of sea urchin density (Figure 3a). Correlations between adult density and average larval production at a site were significantly positive for all four gamete dispersal distributions (LFT: $r=0.810$, $p<0.01$; LFNT: $r=0.825$, $p<0.005$; HFT: $r=0.828$, $p<0.005$; HFNT: $r=0.712$, $p<0.05$). While low density sites may have high values of fertilization success due to high levels of aggregation (i.e., Stewarts Point), the few individuals and thus small number of fertile gametes produced relative to high density sites implies that these low density sites are less likely source populations for larval export.

To determine the effect of density and fertilization on the stock-recruitment relationship for red sea urchins in northern California, we examined the relationship between adult density (stock) and larval production (recruitment). For the low flow

gamete distributions, plots of larval production versus adult density indicated only a slight deviation from the linear relationship expected if there was no effect of fertilization on larval production at densities above 0.5 urchins/m^2 (Figure 9a,b). At lower densities (< 0.5 sea urchins/m^2), the relationship between larval production and adult density demonstrates a gradual non-linear Allee effect. As noted in Lundquist and Botsford (2000), this Allee effect does not appear in the form of a strict decline to zero at a threshold, but rather as a slight nonlinear decrease in larval production as density decreases. As expected from the low levels of fertilization success at high flow (Figure 5c,d), larval production for high flow simulations showed reduced larval production at all densities and an approximately linear relationship between larval production and adult density (Figure 9c,d).

Comparison of larval production from observed transect data with larval production expected from a randomly distributed pattern showed higher values of larval production for the observed simulations as compared to the randomly generated simulations (Figures 9a,b,c,d). The random simulations exhibit a more pronounced decline in larval production at low density, implying that the observed highly aggregated sea urchins are less subject to Allee effects at low density than if they were randomly distributed.

Comparisons to pre-harvest years

Estimates of density calculated for 1988 (n=105) and 1989 (n=76) CDFG transect data showed a wider range of densities than is present in data collected in 1996-1998 for both fished and reserve locations (Figure 10a,b,c). Less than half of all 1988-1989

transects had total densities of less than 0.5 sea urchins/m^2, with some transects including

values of up to 20 sea urchins/m^2 (Figure 10a). In contrast, half of the 1996-1998 fished

transect data (n=40) had density values less than 0.5 sea urchins/m^2 and the distribution

of density values ranged between 0 and 5 sea urchins/m^2 (Figure 10b). Reserve transects

in 1996-1998 had a more uniform distribution than the fished transect data, with less than

half of the transects at densities less than 0.5 sea urchins/m^2 (Figure 10c), though our

analysis is limited due to small sample size (n=13).

To determine the relative effect of the fishery on larval production, we compared

estimated total larval production computed for 1988-1989 with larval production

computed for 1996-1998 (Table 2a). Total larval production in 1996-1998 was

approximately one third of the estimated 1988-1989 larval production values. This

decline in larval production is similar across the four possible gamete dispersal

distributions.

The decline in larval production would have been between 3 and 23% more

severe, relative to 1988-1989 CDFG values, if sea urchins had been distributed randomly

(Table 2a). The estimates based on 1996-1998 random transects represent declines in

larval production of 9-69% compared to 1996-1998 observed transects. The HFNT

simulations had noticeably larger declines due to the limited distance of effective

fertilization of this gamete dispersal distribution.

To obtain a general idea of the relative contributions of the decline in density and

the fertilization Allee effect to larval production, we compared the estimates of larval

production from our fertilization model with the maximum possible larval production

(which assumes 100% fertilization success). Total declines in larval production in 1988-

1989 relative to maximum possible larval production in 1988-1989 ranged from less than 10% for the two low flow simulations to 58% and 79% for the HFT and HFNT simulations (Table 2b). Observed 1996-1998 estimates showed similar declines relative to maximum possible larval production in 1996-1998 with low flow simulations producing mild decreases in larval production of less than 10%, and high flow simulations producing severe decreases of 60-80% (Table 2b).

We examined the decline expected due to density alone, comparing average adult sea urchin density from 1988-1989 CDFG transects versus average density from this study. Average adult density in our study was 43% of the 1988-1989 average adult density (Table 2c), while we estimated a decline to 32-36% of 1988-1989 larval production (Table 2a). Thus, approximately 75% of the realized decline in larval production can be explained by declines in average density, with the remaining 25% of the realized decline due to shortening of the density distribution and the fertilization Allee effect.

Discussion

These results demonstrate that while fishing can decrease the larval production of a population, as decreased fertilization efficiency at low density results in low levels of larval production, the majority of the decline in larval production can be explained simply by a decrease in mean density. In the northern California red sea urchin fishery, the spatial variation in larval production was determined primarily by variation in density between sites. What is surprising is that the additional decline in larval production attributed to the fertilization Allee effect is small, accounting for only 5-15% of the total

decline in larval production, relative to 1988-1989 data (though this is approximately 25% of the expected larval production relative to the decline in density).

One possible explanation for the less severe Allee effect is that average transect density (average 1996-1998 density = 0.611 adult sea urchins/m^2) has not declined below levels of 0.5 sea urchins/m^2, a level at which declines in recruitment due to the fertilization Allee effect are particularly severe. This implies that roughly half of the individuals in the population are experiencing density levels sufficient for fertilization success. Large proportions of low densities occur in both 1988-1989 and 1996-1998. Thus, the primary difference between 1988-1989 and 1996-1998 lies in the lack of high density (>5 sea urchins/m^2) transects in 1996-1998.

This result is in part due to a lack of a direct threshold Allee effect, as assumed in many fishery models (Pfister and Bradbury 1996, Quinn et al 1993, Botsford et al 1993). An analytical model of fertilization has shown that strict threshold declines occur only if spawners are located in a regular equi-distant pattern with a sharply declining sperm dispersal distribution (Lundquist and Botsford 2000). A gradually decaying sperm dispersal distribution or a randomly distribution of individuals both change the dynamics and lessen the effect of this critical threshold. This implies that it is the stochastic nature of the spatial distribution of individuals that is responsible for the lack of strict threshold Allee effect.

A major concern in the 'fishing down' of this sea urchin population is that denser patches of benthic invertebrates are serially depleted, with catch and CPUE remaining relatively high until these dense populations no longer remain (Jamieson 1993, Parker et al. 1992, Orensanz et al. 1998, Prince and Hilborn 1998, Keesing and Baker 1998). The

range of density has clearly declined since 1988-1989 CDFG surveys, as no sites were observed with densities greater than 5.0 sea urchins/m^2. The current highest density sites (e.g. Albion) were also comprised primarily of juveniles. A large proportion (approximately 1/3) of the 1996-1998 larval production could be attributed to the adult densities present in the five most dense sites, compared to the five most dense sites in 1988-1989 accounting for only 18% of the larval production. This concentration of larval production in fewer locations than in earlier years should cause concern, as we are relying on fewer areas to provide the majority of larvae to the population. In addition, the average density of the five most dense transects has declined from approximately 12 sea urchins/m^2 in 1988-1989 to approximately 2 sea urchins/m^2 in 1996-1998, a six-fold decline in density for these highest density areas.

We use larval supply as an estimate of recruitment, setting aside the complex relationship between larval supply and juvenile settlement. Erratic recruitment of sea urchins in northern California has been noted by many researchers (Ebert et al. 1994, Ebert and Russell 1988, Wing et al. 1995a,b). However, the exact coupling between fertilized eggs through planktonic larval stages, settlement to the benthos and survival to reproductive adults is not known. In general, while juvenile and adult survival has been studied, actual field fertilization rates, survival through the planktonic life stages, and the physical oceanographic and behavioral processes resulting in settlement are unknown.

Another factor ignored here is spatial variability in actual recruitment. Some researchers have demonstrated correlations between headland structures and larval recruitment (Ebert and Russell 1988, Wing et al. 1995a,b, Morgan et al. 2000b). One mechanism for the difference in recruitment is the hypothesized retention of larvae near

major headlands, which move onshore and northward during relaxation of upwelling winds, resulting in greater settlement to the north of headlands (Wing et al. 1995a,b, 1998, Morgan et al. 2000b).

Another factor, juvenile mortality, may also differ between sites due to Allee effects of decreased protective spine canopy habitat for juveniles (Tegner and Dayton 1977, 1981). While laboratory and field experiments have documented decreased mortality for juvenile sea urchins that utilize the adult spine canopy habitat (Breen et al. 1985), recent exploration of size distributions over space in northern California indicate this spine canopy Allee effect does not produce the observed spatial distribution of juvenile abundance (Morgan et al. 2000b).

Our average site estimates of density may have been affected by sampling error or insufficient sampling effort. Red sea urchins exhibit a patchy distribution due to their aggregative behavior, as well as their tendency to reside in patchily distributed rocky reef habitat. Proper techniques for sampling highly aggregated species have been the subject of management and monitoring programs (McShane 1994, 1998). Other researchers have found variation in density and other population parameters to occur over smaller spatial scales than that over which populations are managed (McShane et al. 1994). However, it is clear that our limited sampling effort was more efficient in describing the range of densities within the entire northern California population rather than density within individual sites, as shown by the high variance in density among transects within a site.

Additional marine reserves may be useful in protecting areas with high adult density. Not only is the average density higher in reserves than in fished areas, but the density distribution of all reserve sites contains a larger proportion of high density

transects than the fished density distribution. Reserve sites also contained a larger range of adult sea urchins sizes, as adults greater than the legal size limit of 89mm are a larger proportion of the population in reserve locations (Figure 3a, Morgan et al. 2000b). As gonad size increases volumetrically with sea urchin test diameter, the larger sizes of sea urchins in reserve locations imply that more fertile gametes are produced in these locations compared to sites lacking large sea urchins (i.e. Albion, Elk which have high total sea urchin densities, but have few large adults). On the other hand, density-dependent growth in reserve areas might limit per capita reproductive output (Parrish 1999).

The lack of inclusion of sea urchin size as an additional factor affecting fertilization in our models to determine larval production implies that our model gives a conservative underestimate of the actual decline in larval production due to fishing. Other models of fertilization Allee effects have predicted much larger declines in egg production, with reductions of density by half resulting in order of magnitude declines in egg production (Claereboudt 1999). The assumption of synchronous spawning in our model is also conservative, and violation of this assumption would result in further decreases in larval production (Levitan and Sewell 1998). This is not likely a realistic assumption, as sea urchin populations in nature are rarely observed to spawn synchronously (Pennington 1985, Levitan 1988). There is also little evidence for increased aggregative behavior during spawning for red sea urchins (Levitan 1988, Pennington 1985, Pearse et al. 1988). Other species form aggregations for spawning, such as those found in sea cucumbers and starfish populations (Run et al. 1988, Hamel et al. 1993, McEuen 1988).

A final comment on the assumptions of the fertilization model lies in our description of the flow regime. While we considered only two types of flow for which there was empirical data on sea urchin fertilization (Pennington 1985), actual conditions in northern California during red sea urchin spawning are unknown. Some researchers hypothesize that sea urchins will spawn during low flow conditions, an optimal behavior that has been observed in other intertidal and subtidal invertebrates and vertebrates (Petersen 1991, Serrao et al. 1996, Breen and Adkins 1980, Stekoll and Shirley 1993). Other species have been observed spawning during turbulent conditions (Grange 1976, Desrosiers and Dube 1993). The predicted spawning period of red sea urchins is during the upwelling season in northern California (Wing et al. 1995a), implying that the sea urchins are spawning during high flow conditions (Strathmann 1987, Bennett and Giese 1955, Bernard 1977, Pearse 1980). Thus, the less conservative, high flow dynamics may more accurately represent the conditions experienced by these organisms during spawning.

In summary, we determined that the fishery has caused a reduction in larval production. However, the spatial variation in density, both within and between sites, was large, and the influence of local densities is greater than the influence of the Allee effect on this decrease in larval production. In recent years, the fishery has modified the local density distribution, as there are now more extremely low density sites subject to Allee effects, and no high density sites. The result is a decline in larval production due to the fishery to levels of approximately one-third of pre-harvest larval production. A continuing trend of fishing out high density areas will only increase the likelihood of reproductive failure as average density of all areas approaches levels where fertilization is

reduced due to Allee effects. Protection of some areas as reserves may be a means of increasing recruitment.

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Table 1. Average red sea urchin density and aggregation at northern California sites. Aggregation indices and coefficients of variation as explained in text.

site	# transects***	area sampled (m²)	# urchins	average density (urchins/m²)	st. dev.	Variance	Variance:Mean	MSID****	CV (1/10th) (area=1500m²)	CV (1/20th) (area=3000m²)	CV (1/50th) (area=7500m²)
Casper fished	2	300	30	0.100	0.962	0.925	9.250*	0.5592***	35.12	37.25	38.47
Casper reserve	3	450	491	1.091	2.461	6.056	5.551*	0.5031***	6.29	6.83	7.29
Albion	5	675	1051	1.557	3.455	11.934	7.665*	0.5017***	4.48	5.32	5.76
Elk	4	550	327	0.595	2.965	8.793	14.778*	0.5113***	11.97	13.59	14.46
Gunderson	4	600	218	0.363	2.044	4.178	11.510*	0.5132***	12.58	14.53	15.58
Point Arena	6	825	424	0.514	2.098	4.403	8.566*	0.5051***	6.74	8.56	9.48
Saunders	2	300	286	0.953	2.399	5.754	6.038*	0.5053***	9.19	9.74	10.06
Gualala	2	300	118	0.393	1.928	3.718	9.461*	0.5200***	17.90	18.99	19.61
Stewarts	1	150	19	0.127	1.297	1.683	13.250*	0.6536***	56.12	57.66	58.56
Salt Point	7	837.5	587	0.701	2.541	6.455	9.208*	0.5038***	5.89	7.52	8.35
Ocean Cove	4	525	305	0.581	2.598	6.751	11.620*	0.5095***	11.13	12.54	13.31
Fort Ross	1	150	122	0.813	2.017	4.069	5.005*	0.5055***	13.58	13.96	14.17
Bodega fished	2	300	188	0.627	1.587	2.518	4.016*	0.5053**	10.38	11.01	11.37
Bodega reserve	10	1275	1277	1.001	2.602	6.769	6.763*	0.5013**	1.99	3.90	4.69

*Significant at p<0.01
**Significant at p<0.05
***MSID (aggregation) calculations do not include zero transects

Table 2: Comparison of larval production" between 1988-1989 CDFG data and expected larval production from current transect data.

Table 2a. Larval production relative to 1988-1989 larval production

	Gamete Dispersal Distribution			
	Low flow, tail	Low flow, no tail	High flow, tail	High flow, no tail
1988-1989 CDFG data	1.000	1.000	1.000	1.000
1996-1998 observed transects	0.356	0.350	0.317	0.331
1996-1998 random transects	0.321	0.278	0.244	0.104

Table 2b. Larval production relative to maximum possible larval production (maximum possible larval production refers to larval production assuming no Allee effect and 100% fertilization success)

	Gamete Dispersal Distribution			
	Low flow, tail	Low flow, no tail	High flow, tail	High flow, no tail
1988-1989 CDFG data	0.984	0.954	0.419	0.207
1996-1998 observed transects	0.945	0.902	0.359	0.185

Table 2c. Relative declines in density

	Adult Density (sea urchins/m²)	Relative Decline in Adult Density
1988-1989 CDFG data	1.415	1
1996-1998 transect data	0.611	0.432

"We used two regression relationships, based on larval production from observed transect data, to determine the relative larval production for each of the four gamete dispersal distributions. For transects with densities less than 0.5 urchins/m², we used a best fit polynomial regression to account for nonlinear decreases in larval production at low densities ('low flow, tail (LFT)': $y=-0.0517x^3+0.1992x^2+0.8175x$, $R^2=0.9990$; 'low flow, no tail (LFNT)': $y=-0.0539x^3+0.2386x^2+0.7256x$, $R^2=0.9977$; 'high flow, tail (HFT)': $y=-0.1579x^3+0.5907x^2-0.0551x$, $R^2=0.8833$; 'high flow, no tail (HFNT)': $y=0.0276x^3-0.0320x^2+0.1645x$, $R^2=0.8787$). For transects with densities greater than 0.5 urchins/m² we used a linear regression through the origin to determine relative larval production (LFT: $y=0.9867x$, $R^2=0.9974$; LFNT: $y=0.9586x$, $R^2=0.9933$; HFT: $=0.4306x$, $R^2=0.8370$; HFNT: $y=0.2093x$, $R^2=0.8347$).

Appendix 1: Fertilization percentage comparing three sampling methods.

site	date	sampling method	fertilization percentage - LFT		fertilization percentage - LFNT		fertilization percentage - HFT		fertilization percentage - HFNT	
			mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.
Bodega Reserve	9/17/1997	map	0.583	0.208	0.636	0.206	0.077	0.056	0.121	0.106
Bodega Reserve	9/17/1997	1/2 m x 1/2 m	0.503	0.175	0.619	0.210	0.060	0.022	0.068	0.041
Bodega Reserve	9/17/1997	1/2 m x 1 m	0.544	0.166	0.520	0.214	0.058	0.019	0.045	0.034
Bodega Reserve	10/20/1997	map	0.954	0.049	0.909	0.057	0.210	0.036	0.249	0.058
Bodega Reserve	10/20/1997	1/2 m x 1/2 m	0.954	0.049	0.918	0.061	0.178	0.029	0.162	0.037
Bodega Reserve	10/20/1997	1/2 m x 1 m	0.952	0.043	0.901	0.057	0.192	0.035	0.135	0.035
Albion	10/19/1998	1/2 m x 1/2 m	1	0	0.988	0.008	0.634	0.043	0.177	0.015
Albion	10/19/1998	1/2 m x 1 m	1	0	0.987	0.008	0.635	0.036	0.170	0.015
Salt Point	10/20/1998	1/2 m x 1/2 m	1	0.001	0.976	0.014	0.546	0.032	0.155	0.013
Salt Point	10/20/1998	1/2 m x 1 m	1	0.002	0.973	0.015	0.544	0.036	0.147	0.013

**LFT=low flow, tail; HFT=high flow, tail; LFNT=low flow, no tail; HFNT=high flow, no tail

Appendix 2: Values of density and aggregation for individual transects. Aggregation indices as explained in text.

site	transect#	date	area sampled (m²)	# of urchins	mean density (M)	variance (V)	V:M ratio	Chi-Square	Morisita Index	Chi-Square	MSD
Albion	deep1	8/29/1996	150	9	0.06	0.41	3.43	1024.08*	91.67	1024.30*	0.6442**
Albion	deep2	8/29/1996	150	0	0.00	0.00	na	na	na	na	na
Albion	deep3	8/29/1996	75	0	0.00	0.00	na	na	na	na	na
Albion	deep4	8/29/1996	75	338	4.51	29.33	3.25	484.82*	2.00	484.78*	0.5030*
Albion	deep1	8/29/1996	150	306	2.04	14.82	3.63	1086.07*	3.58	1086.20*	0.5040**
Albion	deep4	10/19/1998	150	306	2.04	13.51	2.55	761.31*	2.16	759.52*	0.5017*
Bodega Fished	deep1	9/27/1996	150	124	0.83	3.09	1.87	558.05*	3.11	558.26*	0.5029*
Bodega Fished	deep1	10/21/1997	150	64	0.43	1.88	2.20	657.52*	6.70	657.88*	0.5082*
Bodega Fished	deep1	9/10/1996	150	84	0.56	1.53	1.37	408.99*	2.32	408.86*	0.5012*
Bodega Reserve	deep2	9/10/1996	75	32	0.43	1.86	2.17	323.10*	6.65	324.25*	0.5152*
Bodega Reserve	deep1	9/1/1998	150	20	0.13	0.43	2.93	1663.61*	72.63	1660.00*	0.6164**
Bodega Reserve	deep2	9/24/1996	150	395	2.63	15.42	5.56	875.54*	2.46	875.63*	0.5022**
Bodega Reserve	shallow#2	9/17/1997	150	21	0.14	0.53	3.11	565.96*	14.29	564.71*	0.5182**
Bodega Reserve	map#1	10/20/1997	50	89	1.78	11.06	6.39	152.23*	3.37	307.63*	0.5103**
Bodega Reserve	map#2	10/20/1997	150	130	0.87	6.39	2.11	1101.65*	7.23	1102.30*	0.5098**
Bodega Reserve	shallow#1	10/20/1997	100	252	2.52	10.63	3.00	419.72*	3.58	945.62*	0.5040**
Bodega Reserve	shallow#2	5/4/1998	150	25	0.17	1.00	3.69	897.00*	26.00	899.00*	0.5386*
Bodega Reserve	shallow#1	5/4/1998	150	229	1.53	11.27	4.56	1103.36*	4.53	1103.30*	0.5055**
Bodega Reserve	shallow#2	9/19/1996	150	30	0.20	1.83	na	1370.17*	37.93	1370.00*	0.5592**
Caspar Fished	deep1	10/23/1997	150	0	0.00	0.00	na	na	na	na	na
Caspar Fished	deep1	9/19/1996	150	309	2.06	5.95	1.44	431.81*	1.43	431.78*	0.5005*
Caspar Reserve	deep1	9/18/1996	150	20	0.13	0.70	2.65	781.34*	26.84	790.00*	0.5392**
Caspar Reserve	shallow#1	9/18/1996	150	162	1.08	9.69	4.49	1341.62*	7.48	1341.70*	0.5103**
Caspar Reserve	shallow#1	10/23/1997	150	39	0.26	5.38	10.34	3091.78*	40.62	1189.40*	0.5871**
Elk	shallow#1	8/27/1996	150	229	1.53	21.76	7.13	2132.36*	74.49	3091.80*	0.6212**
Elk	deep1	9/5/1996	150	26	0.26	3.11	5.98	1189.41*	9.04	2133.00*	0.5131**
Elk	deep2	9/5/1996	150	33	0.22	1.89	4.30	1285.02*	31.82	1285.20*	0.5492**
Elk	shallow#2	10/1/1996	150	122	0.81	4.07	2.50	748.24*	4.67	743.57*	0.5055*
Fort Ross	deep1	9/4/1996	150	72	0.48	3.17	3.30	986.39*	10.68	986.33*	0.5151**
Gualala	deep1	9/4/1996	150	46	0.31	4.27	6.95	2077.90*	40.58	2080.10*	0.5646**
Gualala	shallow#1	9/11/1996	150	20	0.13	0.44	1.64	491.21*	23.72	1389.80*	0.5364**
Gunderson	shallow#1	9/11/1996	150	49	0.33	3.04	4.64	1388.46*	8.56	548.35*	0.5102**
Gunderson	shallow#2	9/11/1996	150	34	0.23	0.83	1.83	547.29*	19.27	2381.50*	0.5299**
Gunderson	shallow#3	9/12/1996	150	115	0.77	12.21	7.96	2379.92*	11.05	490.00*	0.5125**
Gunderson	deep1	7/25/1996	75	140	1.87	21.78	5.83	869.10*	6.18	869.29*	0.5166**
Ocean Cove	deep1	8/20/1996	150	71	0.47	8.26	6.62	1978.85*	24.99	1978.30*	0.5390**
Ocean Cove	deep2	8/16/1996	150	11	0.07	0.86	5.92	1769.42*	147.27	1761.70*	0.7403**
Ocean Cove	deep3	8/20/1996	150	83	0.55	4.60	4.16	1244.12*	12.52	1243.50*	0.5183**
Ocean Cove	deep4	9/3/1996	150	0	0.00	0.00	na	na	na	na	na
Salt Point	deep1	7/24/1996	150	0	0.00	0.00	na	na	na	na	na
Salt Point	deep1	7/25/1996	12.5	33	2.64	35.57	6.74	161.68*	6.30	161.70*	0.5813**
Salt Point	deep2	8/20/1996	150	0	0.00	0.00	na	na	na	na	na
Salt Point	deep3	8/20/1996	150	23	0.15	1.14	3.73	1113.92*	37.94	1111.80*	0.5584**
Salt Point	deep4	8/21/1996	75	187	2.49	30.60	6.14	914.44*	5.11	914.34*	0.5132**
Salt Point	deep5	8/21/1996	75	74	0.49	4.66	4.75	1418.89*	16.33	1417.90*	0.5245**
Salt Point	shallow#1	10/20/1998	150	270	1.80	7.75	2.15	643.35*	2.28	643.32*	0.5018*
Point Arena	deep1	8/21/1996	160	74	0.49	5.32	5.40	1613.57*	18.99	1612.50*	0.5290**
Point Arena	deep1	8/21/1996	150	44	0.29	2.30	3.92	1171.00*	21.25	1169.60*	0.5320**
Point Arena	deep2	8/22/1996	75	102	1.36	7.21	2.65	395.07*	395.06	3.44*	0.5070**
Point Arena	deep3	8/22/1996	150	69	0.46	3.52	3.83	1144.00*	13.43	1144.00*	0.5196**
Point Arena	shallow#1	8/23/1996	150	33	0.22	1.06	2.41	721.68*	14.20	721.55*	0.5196**
Point Arena	shallow#2	9/4/1996	150	102	0.68	7.98	5.86	1750.91*	15.38	1750.90*	0.5233**
Point Arena	shallow#3	8/28/1996	150	185	1.23	7.34	2.98	890.33*	4.21	890.14*	0.5049**
Saunders Reef	deep1	8/28/1996	150	101	0.67	4.03	2.99	894.56*	6.95	894.05*	0.5091**
Saunders Reef	deep2	10/2/1996	150	19	0.13	1.68	6.63	1981.17*	94.74	1986.30*	0.6535**
Stewarts Point	deep1										

*Significant at p<0.001
**Significant at p<0.05

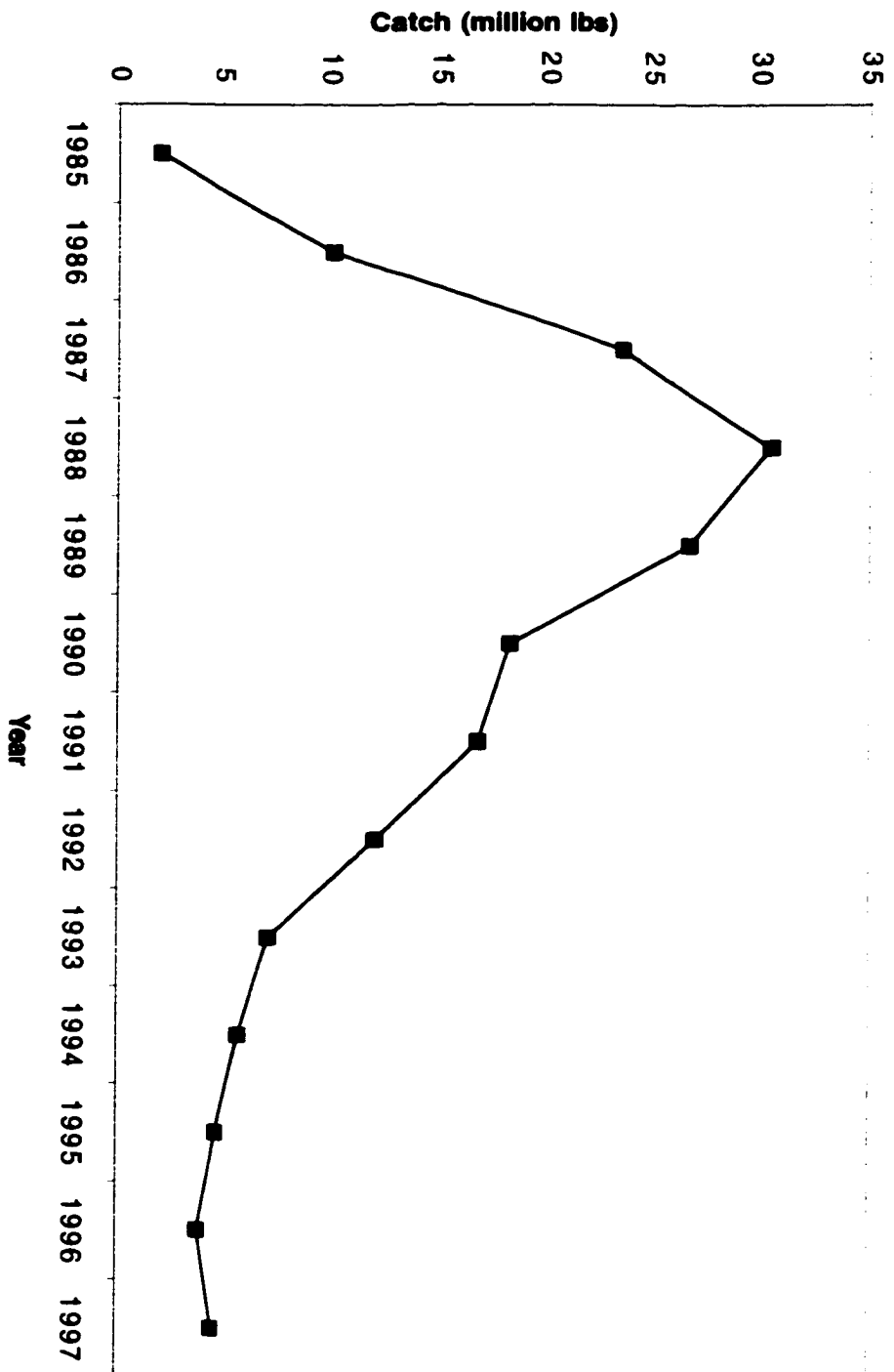**Northern California Red Sea Urchin Landings**

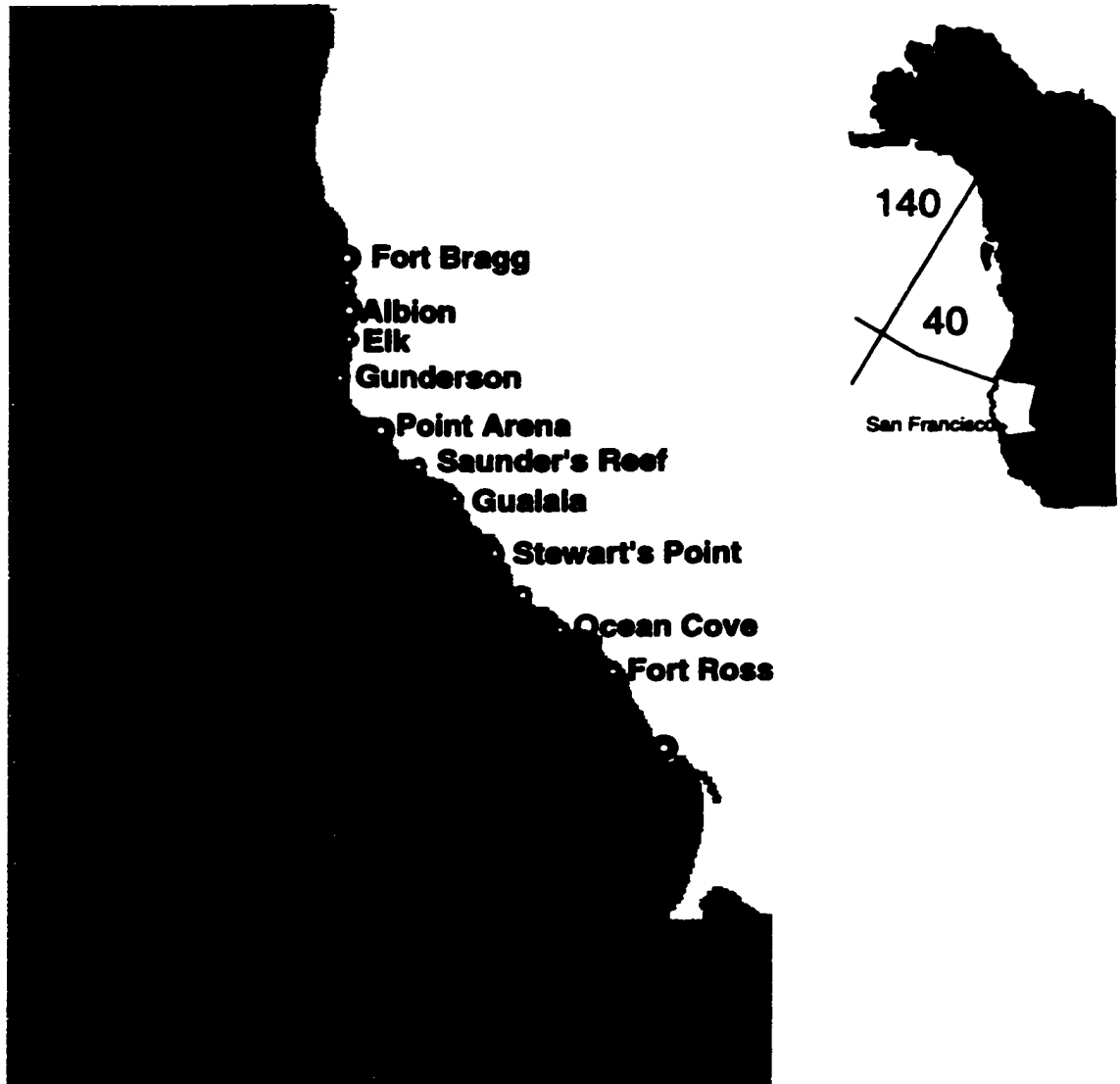Figure 1. Catch (million pounds) for the northern California red sea urchin fishery.

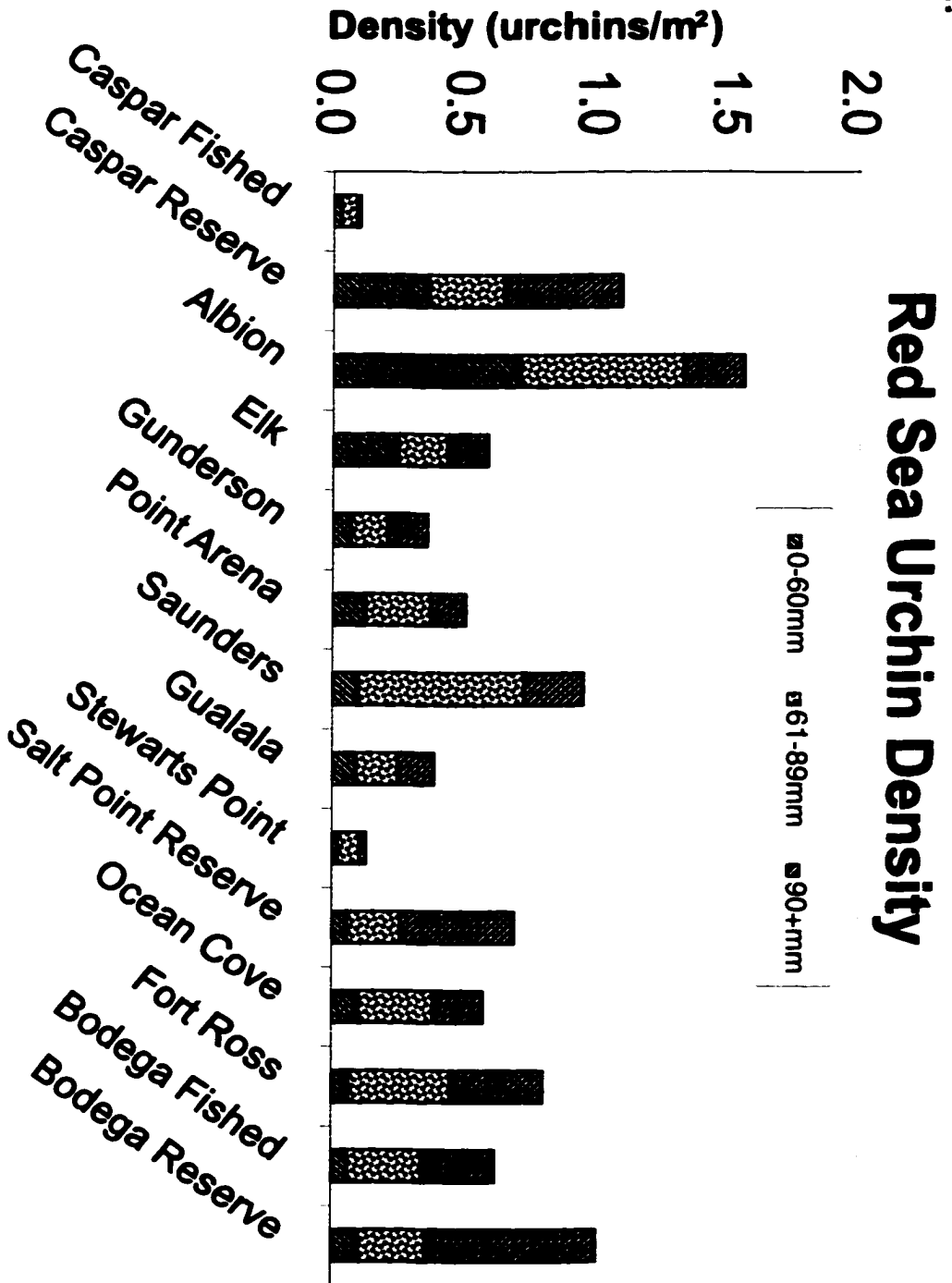Figure 2. Field sites in Sonoma and Mendocino Counties, northern California.

a.

Red Sea Urchin Density

Legend: 0-60mm, 61-89mm, 90+mm

Density (urchins/m²): 0.0, 0.5, 1.0, 1.5, 2.0

Sites: Caspar Fished, Caspar Reserve, Albion, Elk, Gunderson, Point Arena, Saunders, Gualala, Stewarts Point, Salt Point Reserve, Ocean Cove, Fort Ross, Bodega Fished, Bodega Reserve

Figure 3. a) Observed red sea urchin densities (1/m²) from transect data for field sites in northern California. Densities are separated into juveniles (0-60 mm), pre-legal adults (61-89 mm), and legal adults (90+ mm). Headland features are located at Point Arena and Point Reyes, south of the Bodega Marine Reserve.
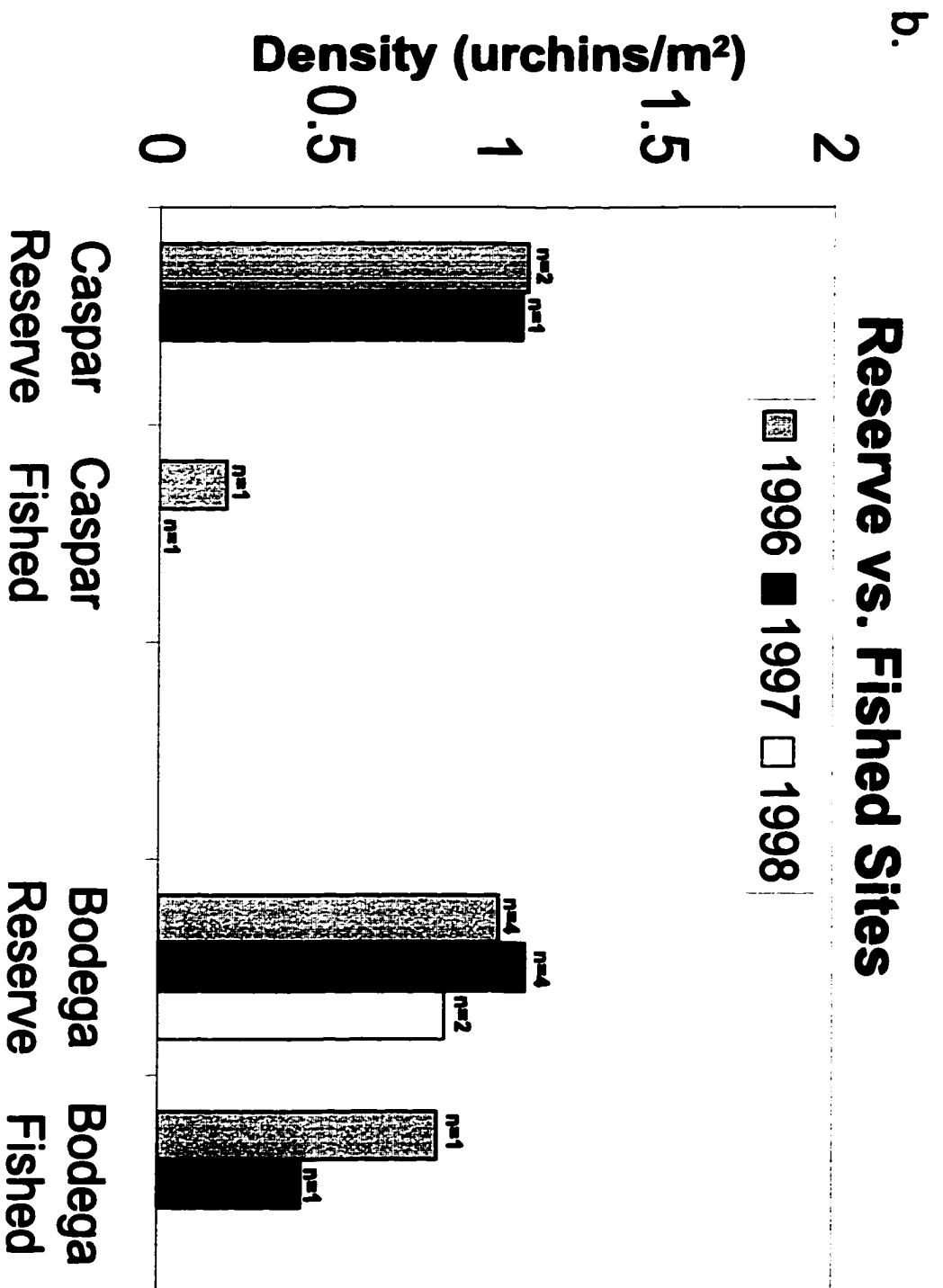
Figure 3. b) Observed red sea urchin densities from transect data for field sites in northern California. Density at adjacent fished and reserve locations in 1996-1998. (n = number of transects of 300 1/2 m by 1 m quadrats).

a.

Aggregation by Site
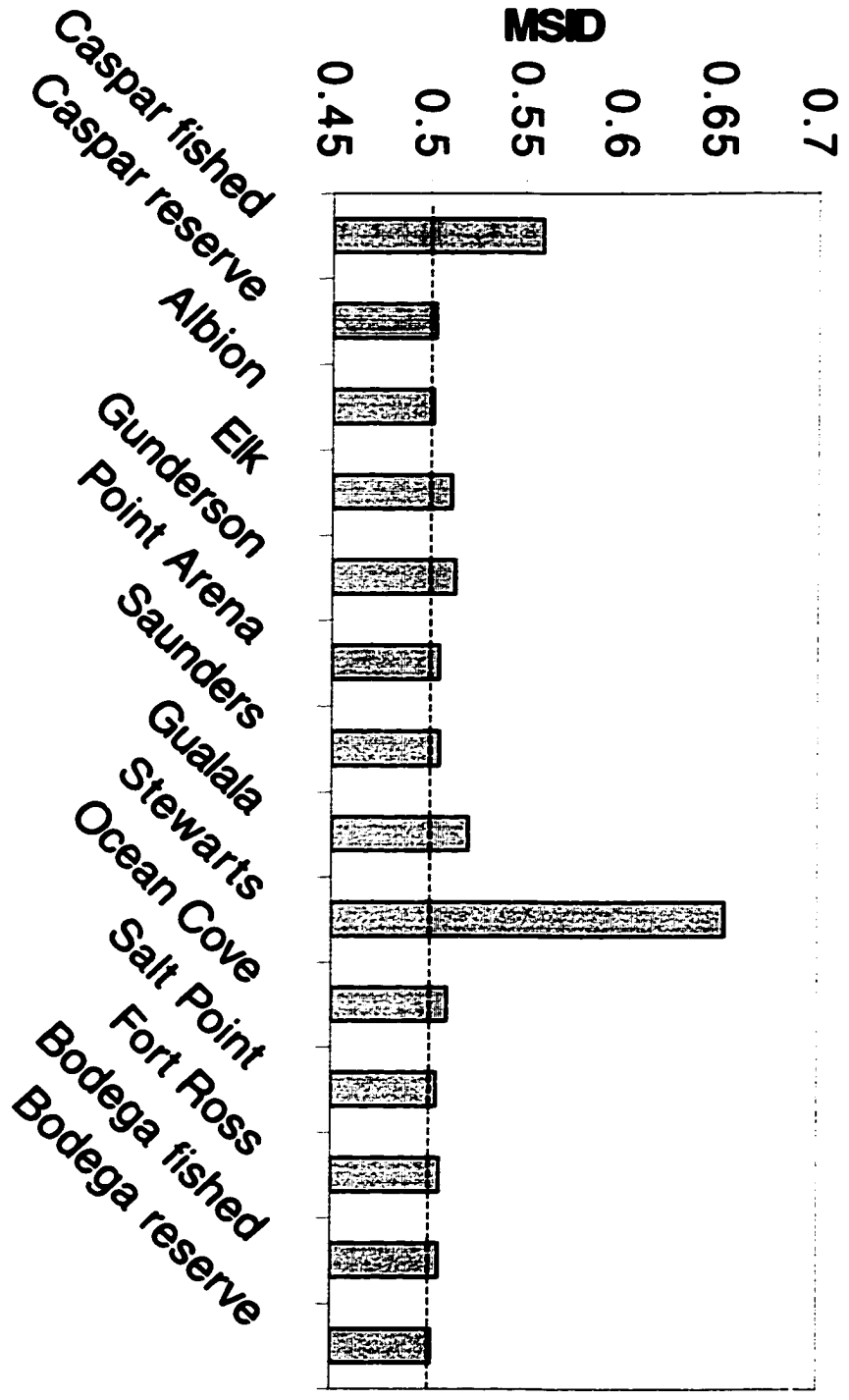
Figure 4. a) Standardized Morisita index of dispersion (MSID) versus site, from north to south. Dashed line represents significant aggregation at p<0.05.

b.

Aggregation versus Density
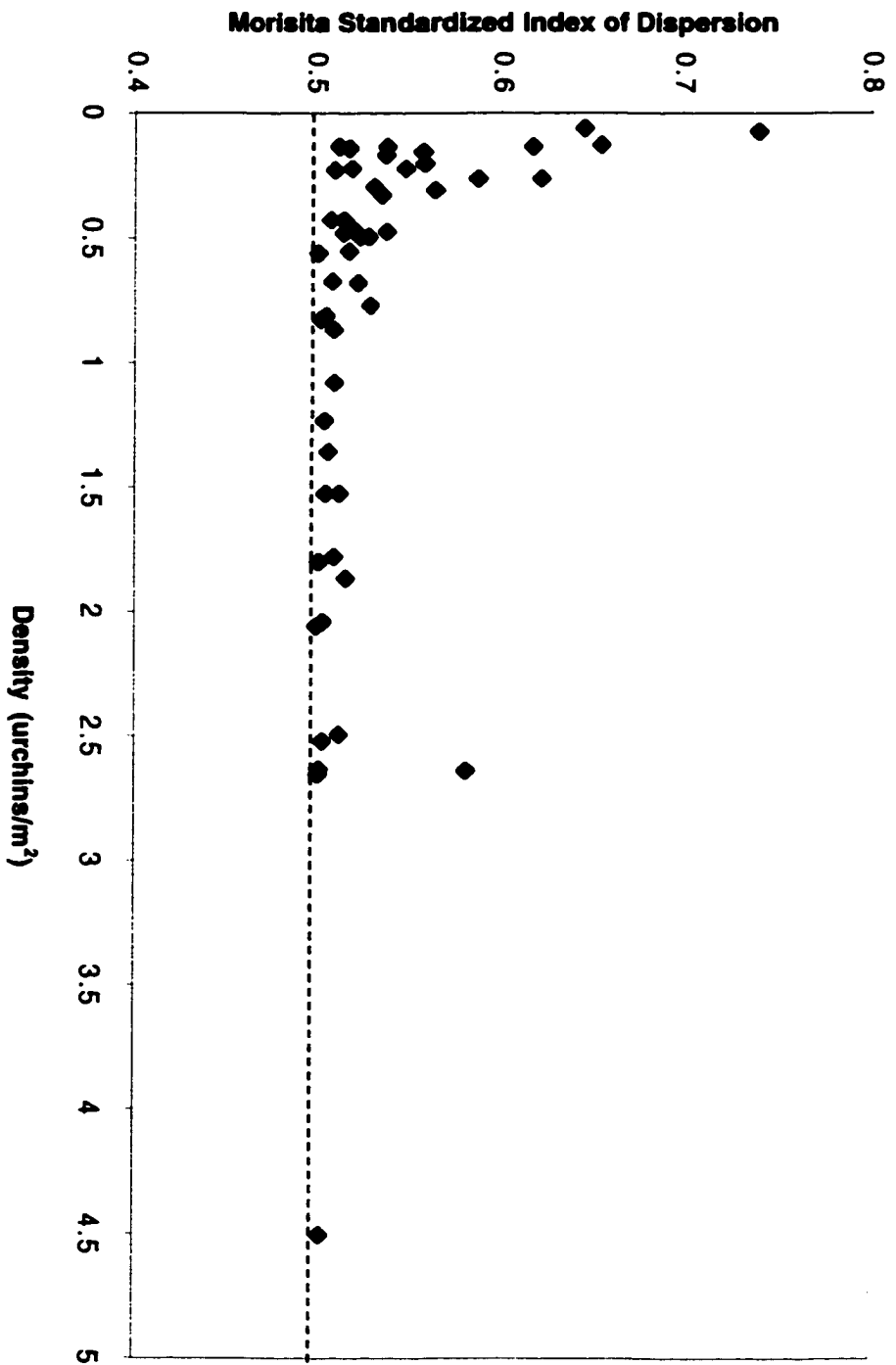
Figure 4. b) Standardized Morisita index of dispersion (MSID) versus density (sea urchins per m²). Dashed line represents significant aggregation at p<0.05.
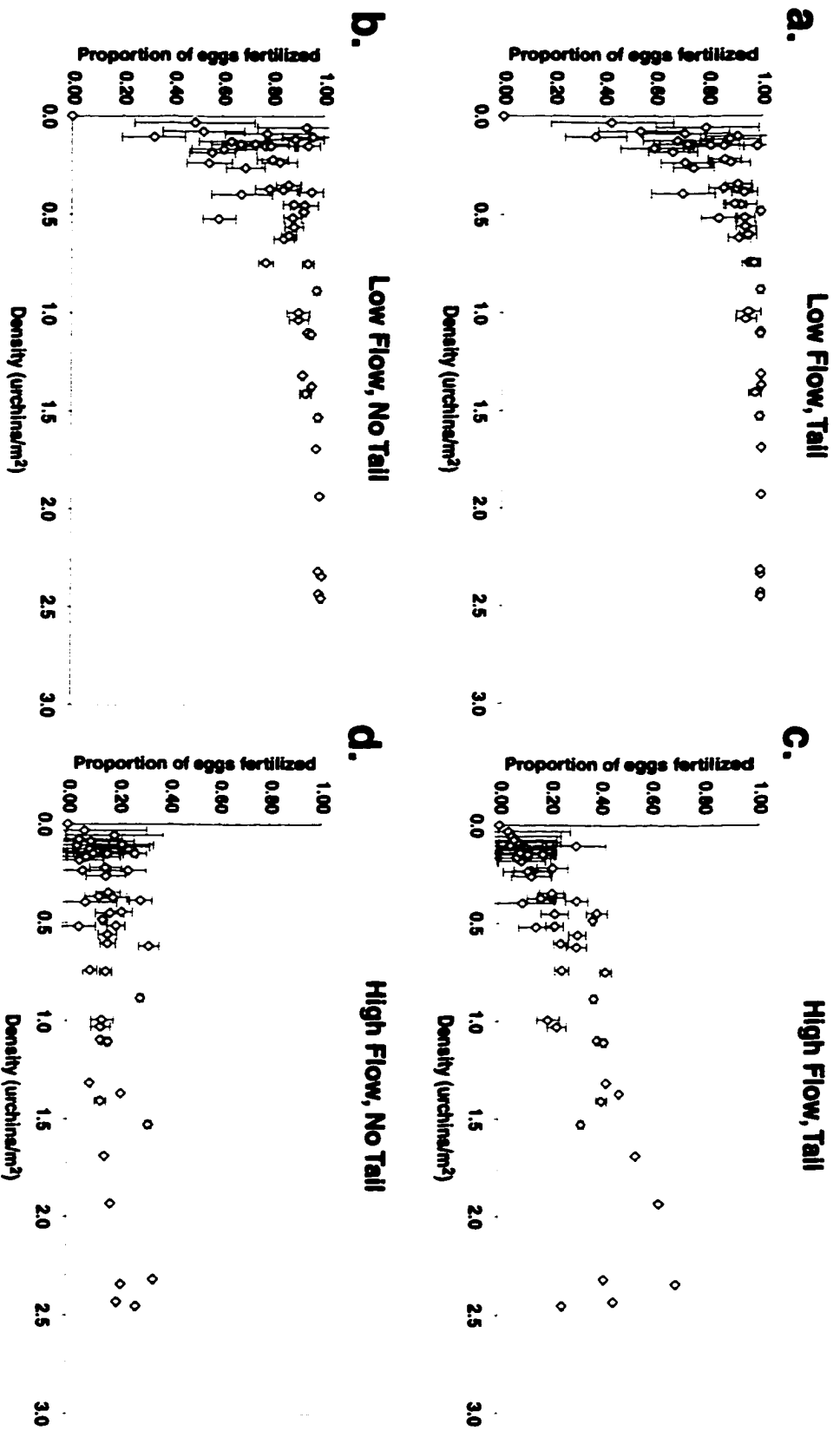
Figure 5. Proportion of eggs fertilized versus adult density (sea urchins/m²) using a fertilization model with a) a low flow sperm dispersal distribution with an extended tail; b) a low flow sperm dispersal distribution with no tail; c) a high flow sperm dispersal distribution with an extended tail; and d) a high flow sperm dispersal distribution with no tail. Each box represents one transect data point with corresponding one s.d. bars.
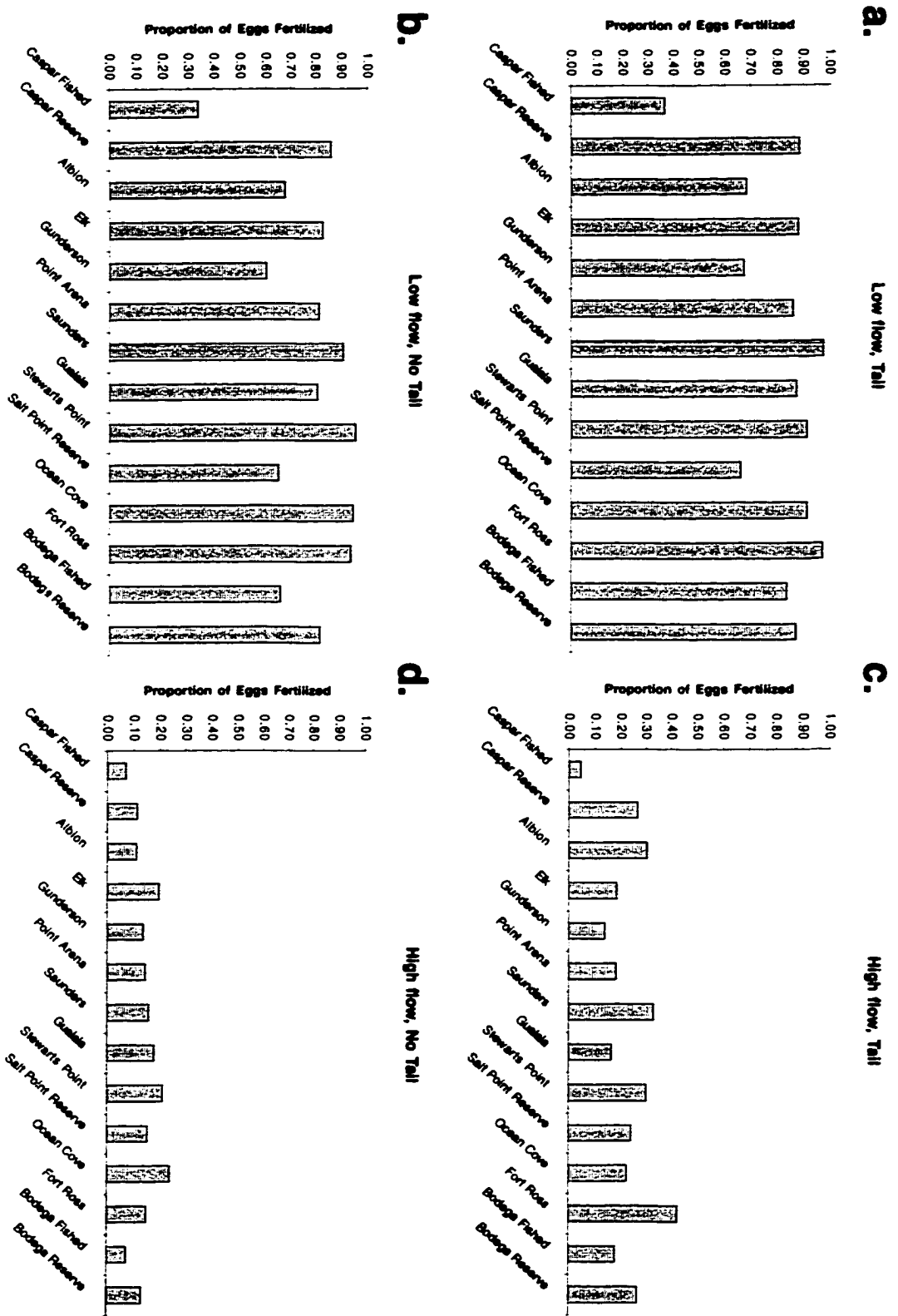
Figure 6. Proportion of eggs fertilized versus site (north to south) using a fertilization model with a) a low flow sperm dispersal distribution with an extended tail; b) a low flow sperm dispersal distribution with no tail; c) a high flow sperm dispersal distribution with an extended tail; and d) a high flow sperm dispersal distribution with no tail.
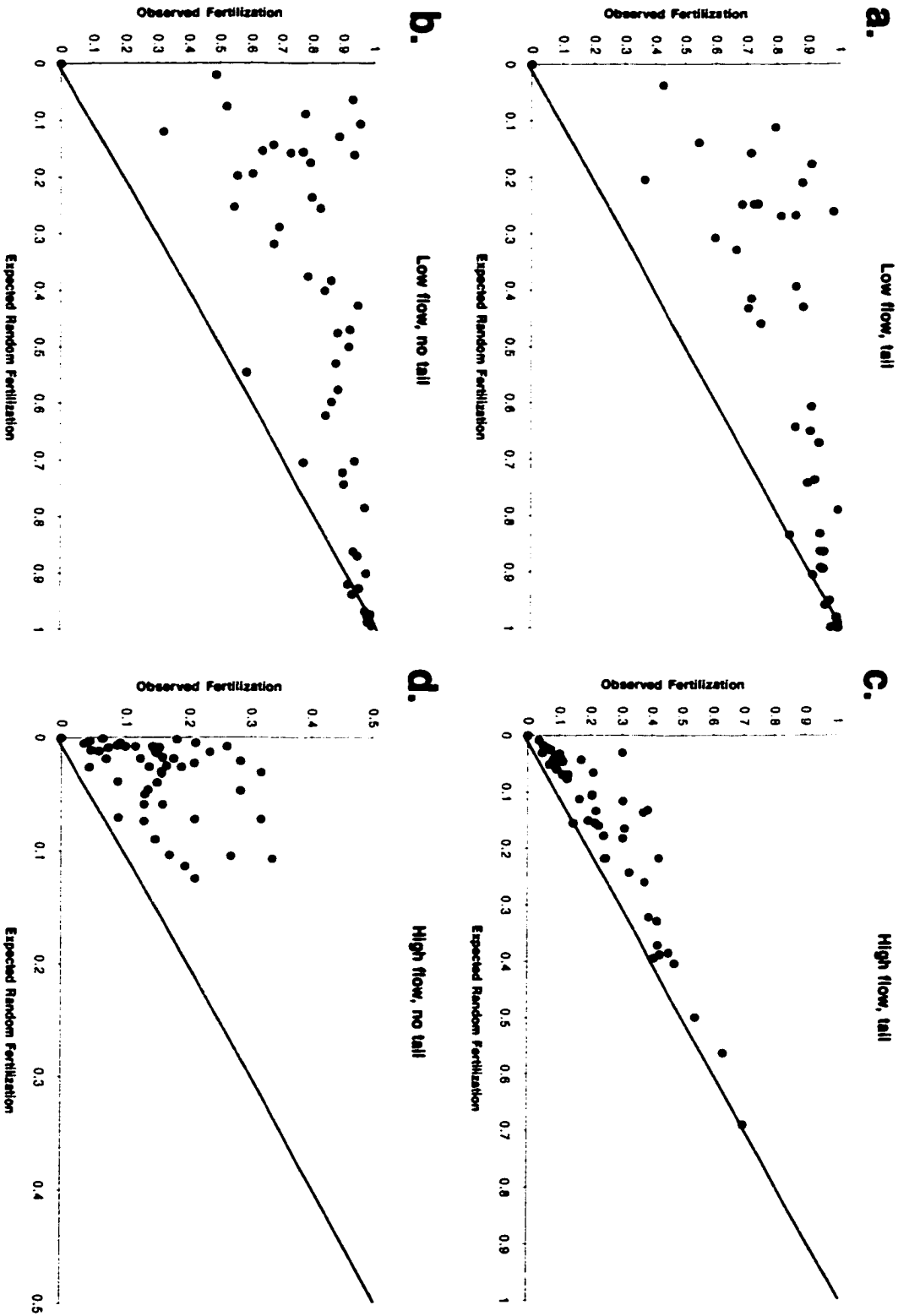
Figure 7. Proportion of eggs fertilized using a fertilization model based on observed transect data compared to proportion of eggs fertilized using a fertilization model with a uniform randomly generated spatial pattern at the same density as the observed transect data, for a) a low flow sperm dispersal distribution with an extended tail; b) a low flow sperm dispersal distribution with no tail; c) a high flow sperm dispersal distribution with an extended tail; and d) a high flow sperm dispersal distribution with no tail.
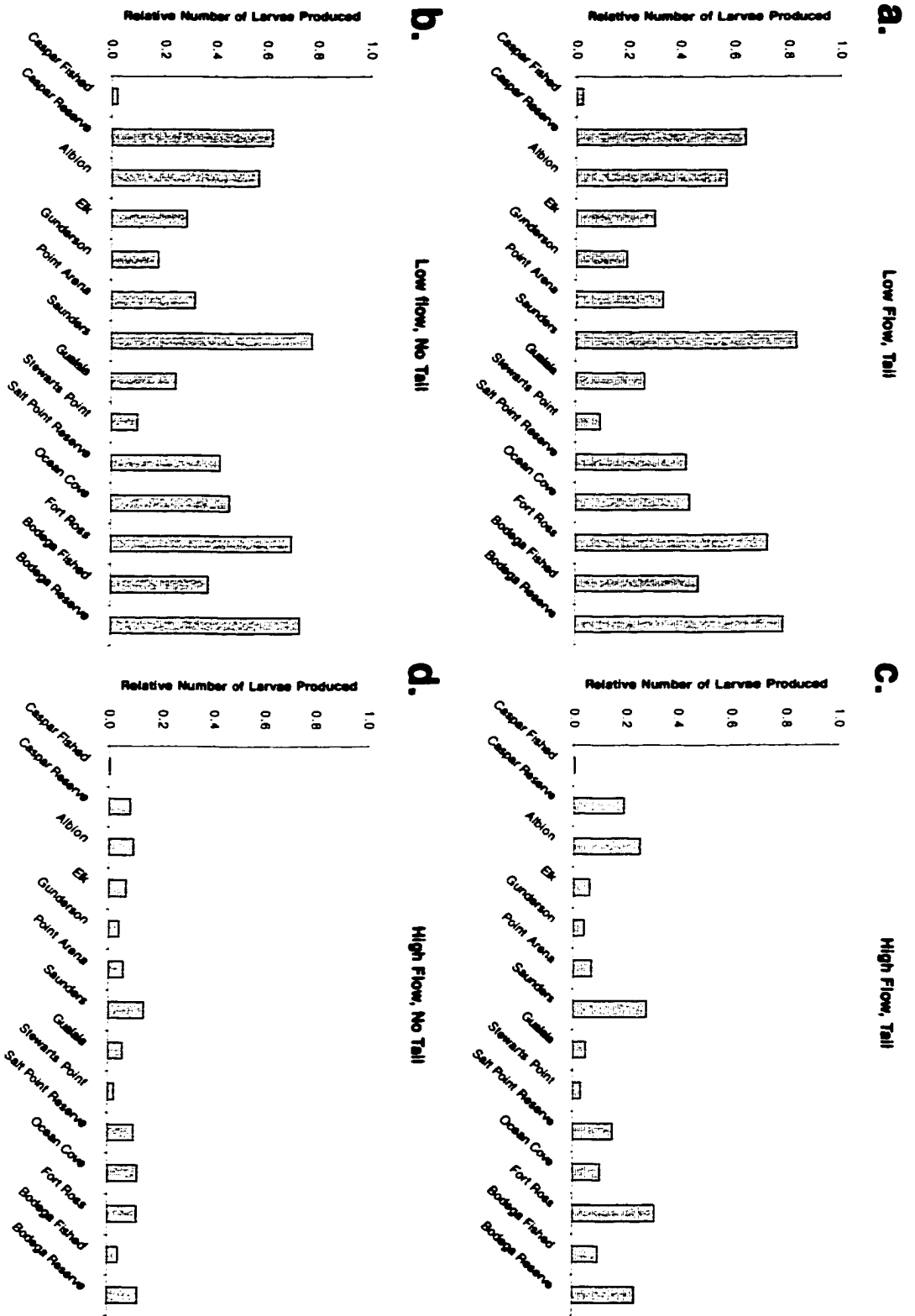
Figure 8. Larval production (adult density times average fertilization percentage) versus site (north to south) for a) a low flow sperm dispersal distribution with an extended tail; b) a low flow sperm dispersal distribution with no tail; c) a high flow sperm dispersal distribution with an extended tail; and d) a high flow sperm dispersal distribution with no tail.
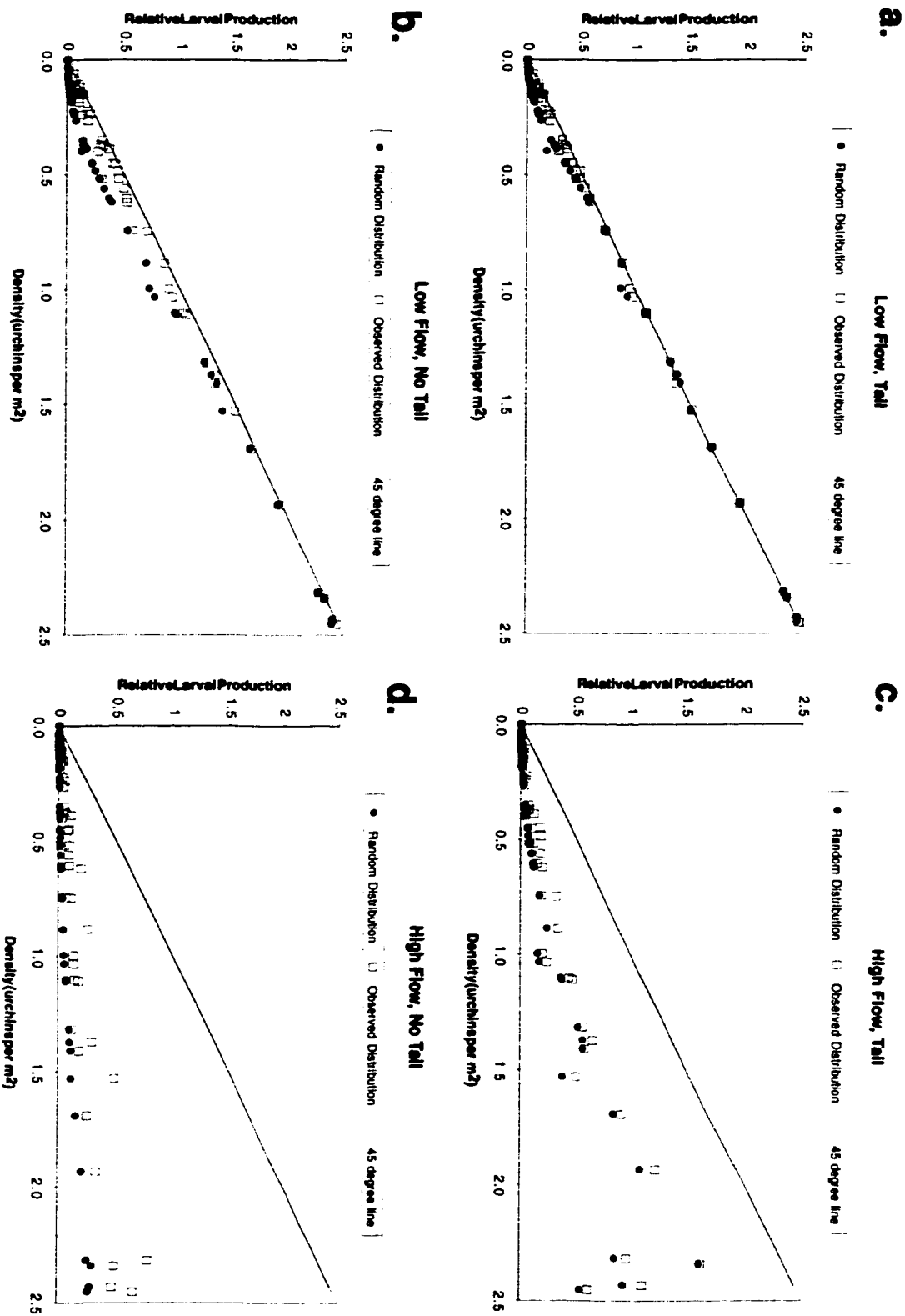
Figure 9. Larval production (adult density times average fertilization percentage) versus adult density for simulations run with observed transect data and simulations run with randomly generated spatial distributions for a) a low flow sperm dispersal distribution with an extended tail; b) a low flow sperm dispersal distribution with no tail; c) a high flow sperm dispersal distribution with an extended tail; and d) a high flow sperm dispersal distribution with no tail. A 45 degree line is presented to show expected larval production given 100% fertilization success.
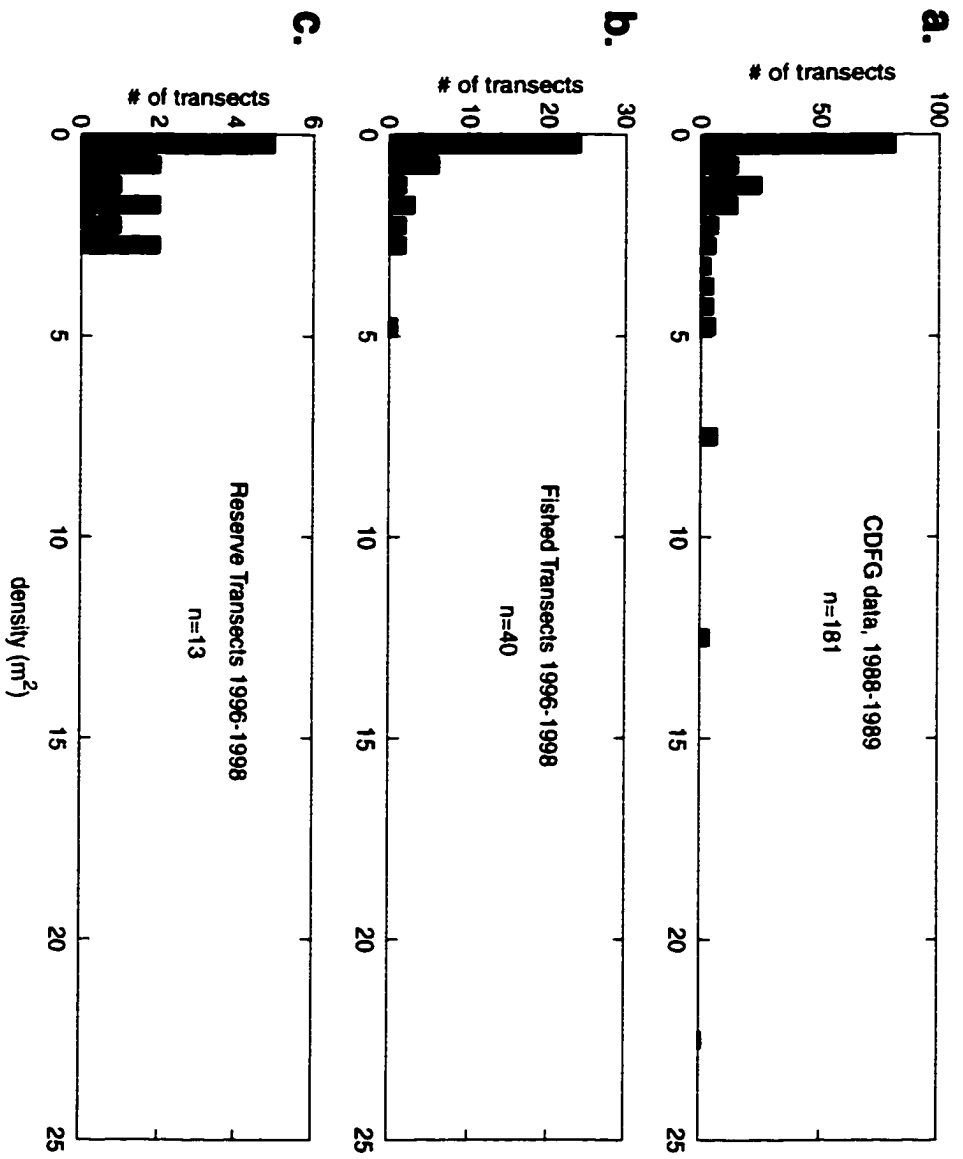
Figure 10. Distribution of transect density values for a) CDFG 1988-1989 data (n=181 transects of six 1 m by 5 m quadrats); b) transect data for this study (1996-1998) at fished locations (n=40 transects of 300 1/2 m by 1 m quadrats); and c) transect data for this study (1996-1998) at reserve locations (n=13 transects of 300 1/2 m by 1 m quadrats).

Running head: Invertebrate settlement during ENSO events

Effects of El Niño and La Niña on local invertebrate settlement in northern California

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A bstract

During the spring and summer upwelling season (April through August) of the years 1997 through 1999, we monitored settlement of juvenile crabs and sea urchins in northern California. Oceanographic conditions during these three years included an El Niño in 1997-1998, and a La Niña in 1999. Prior settlement data had shown strong annual settlement in years during which an intra-annual upwelling/relaxation mechanism was dominant. During active upwelling, invertebrate and fish larvae were retained south of Point Reyes. When winds relaxed, larvae could be transported northward and onshore in warm, saline water, and settle on our collectors at the Bodega Marine Laboratory. During years in which this upwelling/relaxation mechanism was dominant and salinity was inversely correlated with temperature, cancrid crab settlement could be predicted by higher temperatures which represented relaxation flow. The settlement response in 1997 and 1998 was similar to earlier years, but 1999 was definitely unusual. In 1997, the lack of an inverse correlation between temperature and salinity indicated wind-driven upwelling/relaxation was not dominant and cancrid crab settlement was not correlated with temperature. In 1998, temperature and salinity were inversely correlated, but wind and temperature were not as highly correlated as in previous years. Settlement appeared to be driven by relaxation, but the relationship was not as strong as in previous years. Although they appeared to settle during relaxation events, neither sea urchin nor non-cancrid crab settlement was correlated with temperature. In 1999, strong, constant upwelling winds resulted in no relaxation events and settlement was an order of magnitude lower than any previous year. On interannual scales, results from these three years were consistent with previous results for cancrid crabs, showing a negative

correlation with windstress, but 1999 was not consistent with previous findings for non-cancrid crabs of a negative correlation between temperature and settlement.

Introduction

The dramatic changes in physical oceanographic conditions and biological productivity in the California Current System (CCS) during El Niño events are well documented (Chelton et al. 1982, Glynn 1988, Tegner and Dayton 1987). The general biological effect of El Niño-Southern Oscillation (ENSO) events on marine animals in the CCS is reduced productivity at all trophic levels. Reduced chlorophyll levels (Lenarz et al. 1995) indicate lower primary productivity. A negative correlation between zooplankton biomass in California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys (Chelton et al. 1982) and lower abundance in more northern waters (Brodeur et al. 1992) indicate lower secondary productivity. Effects at higher trophic levels include smaller size and lower catches of salmon (Johnson 1988, Kope and Botsford 1992, Pearcy 1992), reduced survival of Pacific mackerel (Sinclair et al. 1985), reduced recruitment in rockfish species (Yoklavich et al. 1996, Ralston and Howard 1995), and decreased reproductive success of seabird colonies (Ainley et al. 1995).

While ENSO related effects on productivity have received much attention, the effect of ENSO events (both anomalously warm El Niño and cold La Niña events) on settlement of planktonic larvae has rarely been documented. A few relatively short time series for settlement of benthic invertebrates in the CCS provide some insight into individual species responses to oceanographic conditions, including ENSO events. Sea urchins exhibit patchy and episodic settlement (Pearse and Hines 1987, Ebert et al. 1994, Sloan et al. 1987). During El Niño years, sea urchins have settled at lower levels in southern California (Tegner and Dayton 1987, Ebert et al. 1994), but at higher levels in

northern California (Ebert et al. 1994). Larval rockfish have shown low abundances during both strong El Niño and La Niña events, and appear to have highest survival in years of intermediate temperature (Ralston and Howard 1995, Yoklavich et al. 1996).

Upwelling winds in the CCS are generally higher during non-ENSO years. Moreover, the time series of upwelling index, ocean temperature and sea level in central California can be represented by a single time series of its first principle component (empirical orthogonal function), which represents ENSO/non-ENSO conditions (equal loading of temperature, upwelling and sea level) (Kope and Botsford 1992). However, a relationship between the intra-annual, weekly time scale wind patterns of interest here, and ENSO conditions has not been identified. On annual time scales, successful nearshore settlement of larvae of benthic and intertidal invertebrates is generally greater during periods of lower upwelling winds (Roughgarden et al. 1988, Ebert et al. 1994, Connolly and Roughgarden 1999). However, the sampling in these studies is over short time periods.

Here we compare settlement of marine invertebrates at Bodega Marine Laboratory during the 1997-1999 period with results from previous sampling from 1992-1996, described in Wing et al. (2000). This comparison can be naturally phrased in terms of the influence of ENSO events on settlement at this location because a strong El Niño occurred during 1997 and 1998, and there was a strong La Niña in 1999. In the earlier sampling of invertebrate settlement, we identified a mechanism by which larvae were retained in the lee of Point Reyes (Figure 1) during active upwelling (Wing, et al. 1998)

and were transported poleward and settled onshore during occasional relaxations or reversals of upwelling winds (Send et al. 1987, Wing et al. 1995a,b). Examination of inter-annual variability in this mechanism during the years 1992-96 revealed that this mechanism did not operate consistently each year (Wing et al. 2000). While intra-annual patterns in upwelling winds were not the same each year, daily temperature at BML covaried significantly with daily wind stress in each year. However, covariability between local temperature and salinity did not always indicate an upwelling/relaxation pattern; correlations were significantly negative only in 1992, 1993, 1995 and 1996. During these years that indicated an upwelling/relaxation pattern, settlement of cancrid crabs could be predicted by higher BML temperature, which reflected the relaxation flow. There was a significant correlation between cancrid crab settlement and temperature, except in 1995, in which samples may not have been frequent enough to identify this relationship (Wing et al. 2000). Weekly settlement of non-cancrid crabs and sea urchins were not correlated with fluctuations in local temperature, in part because their settlement seasons are much shorter, and there were fewer opportunities to observe settlement. Interannual variability in total annual settlement of non-cancrid crabs as positively correlated with La Niña conditions. Of these years, 1992 through 1994 were moderate ENSO years, and 1995 through early 1997 were moderate La Niña years.

Here we present settlement observations of crab and sea urchin species during the anomalous 1997-1999 period and examine: 1) intra-annual variability in settlement due to local wind forcing and the wind relaxation mechanism as proposed by Wing et al.

(1995a,b, 1998, 2000), and 2) interannual variability and the effect of anomalous oceanic conditions during these three years on invertebrate settlement.

Materials and Methods

<u>Oceanographic Data</u>

Oceanographic data used in this study were collected from multiple sources. Time series of wind velocities, temperature and salinity were obtained from Bodega Marine Laboratory's (BML) Meteorological and Oceanographic Monitoring Station (MOMS), located offshore of BML (38°19'N, 123°04'W). Data from MOMS are collected as 20 minute averages for sea surface temperature and conductivity sensors, and as 10 minute averages for wind velocity data. Temperature time series for 1999 was obtained from NOAA buoy NDBC 46013 (38°14'N, 123°18'W), as temperature data were not continuously available from MOMS over the 1999 sampling period. MOMS temperatures and buoy temperatures were highly correlated over periods when both data sources were available (r=0.899). No salinity data were available near Bodega Bay in 1999. For each settlement season (April 30-August 13, day 120-day 225), we calculated daily averages of wind velocities, temperature, and salinity. Alongshore windstress (317°) was calculated from wind velocities (Pond and Pickard 1983), according to

$$\tau = \rho_a C_N V^2$$

where τ = magnitude of wind stress at 317°

ρ_a = density of air = 1.3 kg/m^3

C_N = drag coefficient

V = magnitude of wind velocity at 317° (m/s)

C_N was calculated per Trenberth et al. (1990) as a step function where

$$10^3 C_N = 0.49 + 0.065V \qquad \text{for } V > 10 \text{ m/s}$$

$$= 1.14 \qquad \text{for } 3 \leq V \leq 10 \text{ m/s}$$

$$= 0.62 + 1.56/V \qquad \text{for } V \leq 3 \text{ m/s}$$

To reflect the variability in wind that is associated with wind relaxation events, we also present an index of relaxation strength using a nonlinear transformation of the alongshore windstress values. Relaxations occur when winds cease or reverse direction from the typical alongshore (317°) direction during upwelling periods, and these events are recognizable in the windstress time series as periods of low or negative values. Researchers have postulated that several days of wind relaxation are necessary for larvae to be transported from upwelling retention zones south of Point Reyes to the sampling location at Bodega Head (Figure 1, Send et al. 1987, Wing et al. 1995a,b, Wing et al. 2000). To reflect this multi-day relaxation period, we calculated a four day running average of $\log_{10}$ (windstress+1) as an indicator of relaxation flow reaching the BML site as in Wing et al. (2000). We calculated correlations among all oceanographic variables using a standardized linear correlation statistic (Zar 1984). 95% confidence limits were calculated based on sample size during the primary settlement period (April 30-August 13, day 120-225) (n=106).

To put the influence of local oceanographic conditions on settlement in the context of anomalous ENSO events, we compared annual settlement to ocean basin scale and other large scale indices of ENSO and upwelling. Daily Bakun upwelling indices were obtained from the National Oceanic and Atmospheric Adminstration (NOAA) for

latitude 36° N. Monthly standardized Southern Oscillation Indices (SOI) were obtained

from the NOAA Climate Prediction Center. The SOI is the standardized monthly mean

pressure difference between Darwin, Australia and Tahiti, French Polynesia. Negative

values correspond to warm El Niño events, while positive value correspond to cold La

Niña events. An extratropical analog to the SOI has recently been created to more

accurately describe the strength of ENSO events in the mid-latitude Northern Hemisphere

regions (Schwing et al. 2000). Data for this alternative index, the Northern Oscillation

Index (NOIx) were obtained from the NOAA Pacific Fisheries Environmental

Laboratory. The NOIx is the standardized monthly mean pressure difference between the

North Pacific High (35° N, 135° W) and Darwin, Australia (Schwing et al. 2000).

Invertebrate Settlement Data

We sampled settlement of crabs and sea urchins on an approximate weekly time

scale during the spring and summer of 1997 through 1999 at the Bodega Marine

Laboratory (38.19° N, 123.04° W) (Figure 1). The general characteristics of our

collection site include an exposed coastline and a rocky substrate. During each year, we

placed an array of three collector moorings at 10-12 m depth separated by approximately

100 m. While collections generally occurred weekly, several were delayed due to

inclement weather, and sampling periods varied from one week to one month. Because

of this, some important variability occurring at weekly (or shorter) time scales may have

been left unresolved for some time periods.

We sampled juvenile invertebrates with two types of settlement collectors. The 'brush' collectors consisted of four, seven inch long, wood-backed scrub brushes with polypropylene bristles, based on methods of Ebert and colleagues (Ebert and Russell 1988, Ebert et al. 1994). The 'bag' collectors were constructed from 1/2 inch Nytex plastic mesh, forming a 75 cm long bag with a 30 cm wide opening that contained a 1 m by 5 m section of #30 3/4 inch nylon mesh trawl netting, based on methods of Wing et al. (2000). Each settlement collector mooring consisted a polypropylene line with net floats for buoyancy, anchored to the bottom with a 25 kg cement anchor. One 'brush' and one 'bag' collector were attached to each mooring line such that the settlement collectors floated approximately 0.5 to 1 m above the bottom. After weekly exchange, collectors were rinsed in fresh water, and the resulting material fixed in ethanol for later enumeration and identification of newly settled crabs and sea urchins.

We identified crab and sea urchin species to genus using a dissecting microscope. Sea urchin species included the red sea urchin *Strongylocentrotus franciscanus* and the purple sea urchin *S. purpuratus*. Cancrid crab species included larval and juvenile crabs of primarily *Cancer antennarius* and *C. productus*, but also some individuals of *C. magister* and *C. gracilis*. Other crab species included primarily porcellanid crab megalopae and juveniles (*Petrolisthes* spp.), and also various majid (*Pugettia producta*, *Loxorhynchus crispatus*), pagarid (*Pagarus* spp.), and grapsid (*Hemigrapsus nudus*) species. To analyze settlement patterns, we consider settlement of all sea urchin species combined, and settlement of cancrid crabs and settlement of non-cancrid crabs separately.

Settlement rates were calculated as the average number of settlers per brush collector per day of the collection period for each taxon. Bag collector data were not used in the average calculation in order to be able to make comparisons to prior years of settlement data at BML (Wing et al. 1995a,b, Wing et al. 2000). Average daily settlement rates were calculated for each collection period from April 30 to August 13 (day 120-225) each year.

Intra-annual correlations of settlement with physical variables

To determine correlations between oceanographic variables and invertebrate settlement, we calculated average values of temperature, salinity, alongshore windstress, $\log_{10}$ (windstress+1), and upwelling over each sampling period. Correlations between these oceanographic values and average settlement on brush collectors of sea urchins, cancrid crabs, and non-cancrid crabs during each sampling period at Bodega Head were calculated using a standard linear correlation statistic (Zar 1984). 95% confidence intervals were calculated based on sample size (number of sampling periods) for each year.

Interannual correlations of settlement with physical variables

Annual settlement rates for cancrid crabs, non-cancrid crabs, and sea urchins were calculated for each year (1997-1999) of settlement collection. These were calculated as the average settlement rate over the period of April 30 to August 13 (day 120 to day 225) of each year. Annual values of oceanographic variables (temperature, salinity, windstress, $\log_{10}$(windstress+1), and upwelling index) were calculated as the mean value

of daily time series over the day 120 to day 225 period. Annual values of the Northern

Oscillation Index (NOIx) and Southern Oscillation Index (SOI) were calculated as the

mean value of the monthly time series over the April to August period.

Results

Intra-annual variability in settlement and oceanographic conditions

The years 1997-1999 included more extreme values of basin scale indicators of

ENSO conditions. Time series of NOIx and SOI indicate these are anomalous years with

extremely low values in late 1997 and early 1998, representing strong El Niño conditions,

and extremely high values in 1999 representing strong La Niña conditions (Figure 2).

During years of previous settlement monitoring at BML, 1992 and 1993 appear as mild

El Niño years in both indices, while 1994 represents a transitional year of moderate

conditions for both indices. The NOIx shows early 1995 to be an El Niño event of

similar magnitude to 1992-1993, but the SOI gives no implication of anomalous

conditions. 1996 through early 1997 appear as mild La Niña events in both indices.

1997

During the early settlement period of 1997 (day 120 to approximately day 150),

covariability among oceanographic variables (temperature, salinity, alongshore

windstress, and $\log_{10}(windstress+1)$) showed conditions typical of the

upwelling/relaxation season at this location (Figure 3a,b). High windstress values were

associated with low temperatures and high salinities, due to Ekman transport of warm

surface water layers offshore, and replacement by cold, upwelled water. When the winds

relaxed, however, e.g. day 135 to 140, oceanographic conditions reversed, resulting in a rapid rise in temperature and decrease in salinity that has been associated with alongshore transport during wind relaxation periods (Send et al. 1987, Wing et al., 1995a,b). Water to the south of Point Reyes is fresher and warmer than upwelled water (Schwing et al. 1991, Wing et al. 1998).

At approximately day 150, there appears to be a shift from a system dominated by upwelling and relaxation to one in which wind relaxation events resulted in temperature increases but temperature showed no inverse correlation with salinity. The remainder of the settlement period of 1997 was marked by increasing temperature and salinity, and decreasing alongshore windstress, atypical of conditions in the upwelling season in northern California, but more common of late summer and early fall in this region (i.e. the relaxation season of Largier et al. (1993)).

Windstress was negatively correlated with temperature, as is expected in this system, where upwelling conditions are generated by strong wind forcing (Table 1a). A stronger correlation was seen between temperature and the smoothed log of windstress, which is also expected as this index reflects the degree of relaxation (Table 1a). Salinity, however, was not correlated with temperature, indicating that wind-forced upwelling/relaxation variability was not occurring during the 1997 season, particularly in the later part of the season (Table 1a).

In 1997, there were no significant correlations between any one of the three taxa (cancrid crabs, non-cancrid crabs, and sea urchins) and temperature during the settlement period (Table 1b), as was the case in some earlier years (e.g. 1994) when the upwelling/relaxation mechanism was not dominant. Cancrid crabs settled after a

prolonged relaxation event early in the season (approximately day 140) and once during a relaxation late in the season (day 205) (Figure 3c). Non-cancrid crabs settled during the early prolonged relaxation event and once later in the season (Figure 3d). Sea urchins showed a brief, but small pulse of settlement during the relaxation event at approximately day 195 (Figure 3d).

1998

While 1998 began under El Niño conditions, basin scale indicators show a return to non-ENSO conditions near the beginning of our sampling period (Figure 2). Local oceanographic conditions superficially resembled those typically observed during the upwelling/relaxation pattern. Although temperatures were 2-3°C above normal, the typical pattern of upwelling periods punctuated by wind relaxation events occurred in 1998 (Figure 4a). All events in 1998 were associated with a temperature increase and salinity decrease, though the magnitude of the change in temperature and salinity was usually related to the length of the wind relaxation period (Figure 4b). Temperature was significantly negatively correlated with both windstress and $\log_{10}(\text{windstress}+1)$ in 1998 (Table 1a), though the low correlations (lowest of the 1992-1999 time series) indicated that local wind-forcing was not a strong driver of local relaxation. Temperature and salinity were significantly inversely correlated (Table 1a).

Settlement of cancrid crabs appeared to occur during relaxations (Figure 4c), but this response is not reliable enough to produce a significant negative correlation between temperature and settlement (Table 1b). Three periods of low settlement at high temperature (days 120-127, 155-161, and 210-217) actually drive the correlation between

settlement and temperature negative. Though it could be argued that in each of these periods, temperature is high while settlement is low because the sampling period covers the end of a relaxation event, the temperature/settlement relationship is not as strong as in previous years. Note, however, that this is in part due to the limitation of weather and other factors on our ability to sample frequently enough. At several times in the sampling season, sample collection was delayed, and the period between samples was two weeks, diminishing our ability to detect responses to rapid changes in temperature. The extended settlement collection periods which encompassed both warm and cold periods likely confounded any correlation between settlement and oceanographic variables; however, it appears that the deviation from the upwelling/relaxation mechanism during 1998 cannot be completely explained solely by the lack of sampling resolution. Instead, it appeared that the intrusion of remote forcing changed the dynamics of the local upwelling/relaxation pattern.

Non-cancrid crabs showed highest settlement during wind relaxation periods at approximately day 135 and day 150 early in the season, and during a later relaxation at about day 215 (Figure 4d). Sea urchins settled unusually early in the season at high levels, overlapping a wind relaxation event at day 135, and continuing to settle the following week (Figure 4d). A smaller settlement pulse of sea urchins was observed later in the season following the day 175 and day 195 relaxation events. Sea urchin settlement rates were an order of magnitude higher in 1998 than in 1997.

1999

Basin scale indicators show strong evidence of La Niña conditions at the beginning of our sampling period; however, these conditions declined to moderate levels by the end of our sampling period (Figure 2). The early part of the settlement season was dominated by strong alongshore upwelling winds, resulting in prolonged periods of lower temperatures than usual (Figure 5a,b). The lack of variability in temperature, combined with the strong alongshore winds, resulted in no clear evidence of relaxation in the temperature time series (Figure 5b). Two atypical wind relaxation events did occur during the season, at day 145 and day 190, but neither event was associated with a substantial increase in temperature of the magnitude observed during similar events in 1997 and 1998 (Figure 5b). The second relaxation event occurred near the beginning of a general increase in temperature that continued through the remainder of the settlement season (Figure 5b). However, the lack of decrease in temperature as winds commenced after this event make it unlikely that the temperature increase was related to wind relaxation events (Figure 5a). Correlations between daily values of temperature and windstress and temperature and $log_{10}(windstress+1)$ were significant, showing evidence of wind-forced upwelling (Table 1a).

In 1999, settlement of all taxa was very low, with background levels at least an order of magnitude less than those seen in 1998 (Figure 5c,d). Settlement of cancrid crabs showed a significant negative correlation with temperature (Table 1a), likely spurious and due to the low rate of crab settlement observed occurring only during the early, colder portion of the settlement season, rather than reflecting settlement in relation to any upwelling/relaxation pattern. Settlement of non-cancrid crabs and sea urchins showed no significant correlations with temperature (Table 1b).

<u>Interannual variability in settlement and oceanographic conditions</u>

Cancrid crabs had lower settlement in years with high seasonal alongshore windstress, $\log_{10}$(windstress+1), and upwelling values (Figure 6, Table 2). Apparently, high winds do not allow sufficient periods of relaxation for planktonic cancrid crabs from south of Point Reyes to reach this point (BML) on the coast. Settlement of non-cancrid crabs had earlier been shown to depend on La Niña conditions, in that higher settlement was seen in years with low temperatures, high upwelling indices, and high salinity (Wing et al. 2000). These relationships were upset by the anomalously high upwelling winds in 1999 (Table 2). While the previously observed negative correlation between non-cancrid crab settlement and temperature is evident, the addition of 1999 to the time series resulted in a dome-shaped relationship between settlement and temperature (Figure 7). A similar dome-shaped relationship is observed between non-cancrid settlement and upwelling. Sea urchin settlement was not significantly correlated with any oceanographic variables, though the analysis showed relatively high negative correlations with windstress, $\log_{10}$(windstress+1), and upwelling (Table 2). Sporadic settlement of sea urchins, with five of the eight years having little or no settlement, provides few data points for study, though sea urchins appear to follow the trends predicted for settlement in response to the upwelling/relaxation mechanism.

Discussion

In general, settlement behavior in 1997 and 1998 was similar to previous years, but 1999 was unusual due to the extremely strong upwelling winds. In 1997, the lack of

inverse correlation between temperature and salinity indicated wind-driven upwelling/relaxation was not dominant and cancrid crab settlement was not correlated with temperature. In 1998, temperature and salinity were inversely correlated, and settlement appeared to be driven by relaxation. In 1999, strong, constant upwelling winds resulted in no relaxation events and settlement an order of magnitude lower than any previous year.

It is somewhat surprising that our 1998 data did not result in the expected positive correlations between temperature and settlement of cancrid crab and sea urchin species. However, the lack of data resolution, as many collections occurred at a biweekly to monthly scale, likely contributed to this lack of correlation. Examination of the oceanographic and settlement data on a fine scale (Figure 4) does show visual evidence of settlement occurring following wind relaxation events; however, as collection periods generally averaged over both upwelling and relaxation conditions, we are unable to document the correlation between settlement and relaxation normally evident in good settlement years. Instead, our 1998 (and 1999) data emphasize the necessity of examining settlement processes at the relevant temporal scale. As settlement seems to occur over the first few days of a relaxation event, weekly or even daily settlement monitoring is much more useful in evaluating the settlement responses to local oceanographic conditions.

The 1999 settlement was very unusual. High upwelling conditions and only a few weak, ineffective relaxation events led to a lack of noticeable levels of settlement of any taxa. It may be that the constant, extreme upwelling winds of the early part of the season had resulted in stronger alongshore and offshore transport of the warm surface layer, such

that a longer relaxation event was required for nearshore temperatures to show an increase due to this relaxation event. Another equally likely hypothesis for the lack of settlement is that larvae were transported out of the retention zone area into the stronger than normal alongshore flow of the coastal jet (Hayward et al. 1999), and were thus lost from the local system.

Non-cancrid crabs exhibited intra-annual settlement in response to wind relaxation events, though correlations in oceanographic variables over the season do not show the same pattern of strong negative correlations between wind values and settlement. The short settlement period of porcellanid crabs, with large pulses primarily occurring early in the settlement season, makes it difficult to elucidate direct associations of settlement with oceanographic variables over the entire settlement season, as noted in Wing et al. (2000). Previous observations had shown that non-cancrid crabs exhibited highest settlement in years with low temperatures, strong upwelling, and low salinity (Wing et al. 2000). The highest two years of settlement were 1994 and 1996, those years with the highest non-ENSO index values for the NOIx. Our 1999 results modified this simple linear response between La Niña type conditions and non-cancrid crab settlement to a non-linear, dome-shaped response of settlement to both temperature and upwelling conditions. This implied that non-cancrid crabs generally settle strongest in years of high upwelling (and presumably high CCS productivity); however, extremely high upwelling is detrimental to settlement of these crabs. It has also been suggested that the lack of settlement in April through August of 1999 could be explained by temperature-related disruptions in reproductive timing, as gravid porcellanid crabs were not observed until late summer (Robert Toonen, *pers. comm*).

Sea urchin settlement continued to be sporadic in these years, and reasons for the exact timing and magnitude of settlement are still unknown. Other researchers have documented similar episodic settlement of sea urchin species (Pearse and Hines 1987, Tegner and Dayton 1981, Tegner and Dayton 1987, Ebert and Russell 1988), as well as settlement of sea urchins in response to wind relaxation events (Miller and Emlet 1997). In spite of the sporadic temporal nature of sea urchin settlement, the spatial pattern of recruitment provides evidence that sea urchins respond to the alongshore transport in the upwelling/relaxation mechanism near headlands (Wing et al. 1995b). The pattern of recent recruitment in size distributions of the red sea urchin indicate higher settlement just to the north of Point Reyes and Point Arena than elsewhere (Morgan et al. 2000; cf. Ebert and Russell 1988).

The results presented here represent local settlement at BML, a single point on the coast, which does not necessarily reflect the coast-wide strength of settlement of the species described here. Settlement at BML could be under the influence of two individual mechanisms, one which determines general annual strength of the year class in the plankton all along the coast in that year, and another that determines how much of that year class settles at this specific location as determined by local winds and associated circulation.

Our ability to make any of these generalizations about ENSO related settlement effects is entirely related to the long term monitoring program in place at the BML site. Though this long term data set is, in itself, rather short (only eight years), it is clear that any shorter time series would not allow for any conclusions on the effect of relatively rare ENSO (of at least the 1997-1998 magnitude) events. Many settlement studies lack

the background context of average settlement and there is a dire need for more long time series such that these anomalous events can be put in context. While we will never know what past settlement data was like, long term monitoring projects will allow us to document the effects of future anomalous events, including ENSOs and global warming on invertebrate settlement.

Acknowledgements

a)	Windstress vs. Temperature	Log₁₀(windstress+1) vs. Temperature	Temperature vs. Salinity
1997	**-0.354**	**-0.733**	0.087
1998	-0.217	**-0.334**	**-0.737**
1999	**-0.377**	**-0.584**	NA

Significant correlations (p<0.05) are in bold.

b)	Taxon	Temperature	
1997	Cancrid crab	-0.178	(n=12)
	Non-cancrid crab	0.151	
	Sea urchin	0.431	
1998	Cancrid crab	-0.302	(n=12)
	Non-cancrid crab	-0.084	
	Sea urchin	-0.298	
1999	Cancrid crab	**-0.586**	(n=12)
	Non-cancrid crab	-0.229	
	Sea urchin	-0.261	

Significant correlations (p<0.05) are in bold.

Table 1. Intra-annual correlations between a) daily values for oceanographic variables (April 30-August 13), and b) between invertebrate settlement rates and temperature averaged over each settlement collection period, 1997-1999.

	Cancrid crabs	Non-cancrid crabs	Sea urchins	
Salinity	0.277	0.591	0.018	(1992-1998 only)
Temperature	0.476	0.044	0.395	
Windstress	**-0.777**	-0.140	-0.339	
Log_{10}(windstress+1)	**-0.900**	-0.217	-0.539	
Upwelling	-0.645	-0.120	-0.423	
NOIx	-0.027	0.028	0.256	
SOI	0.199	-0.318	0.128	

All variables are based on the years 1992-1999, except for salinity which is based on 1992-1998. All values are calculated as the average during the settlement period of day 120 to day 225 (April 30 to August 13). Significant correlations ($p < 0.05$) are in bold.

Table 2. Interannual correlations between settlement and oceanographic variables.

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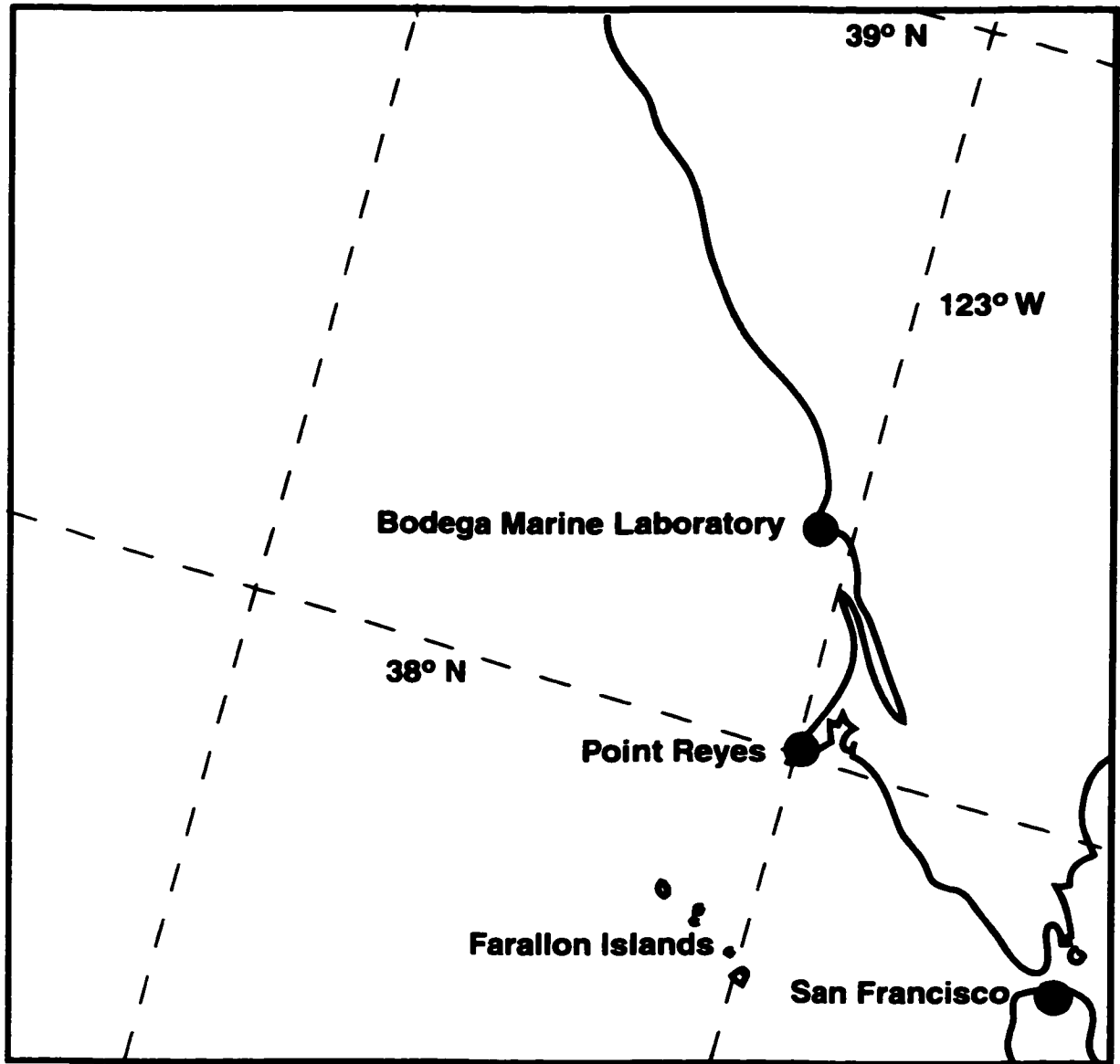
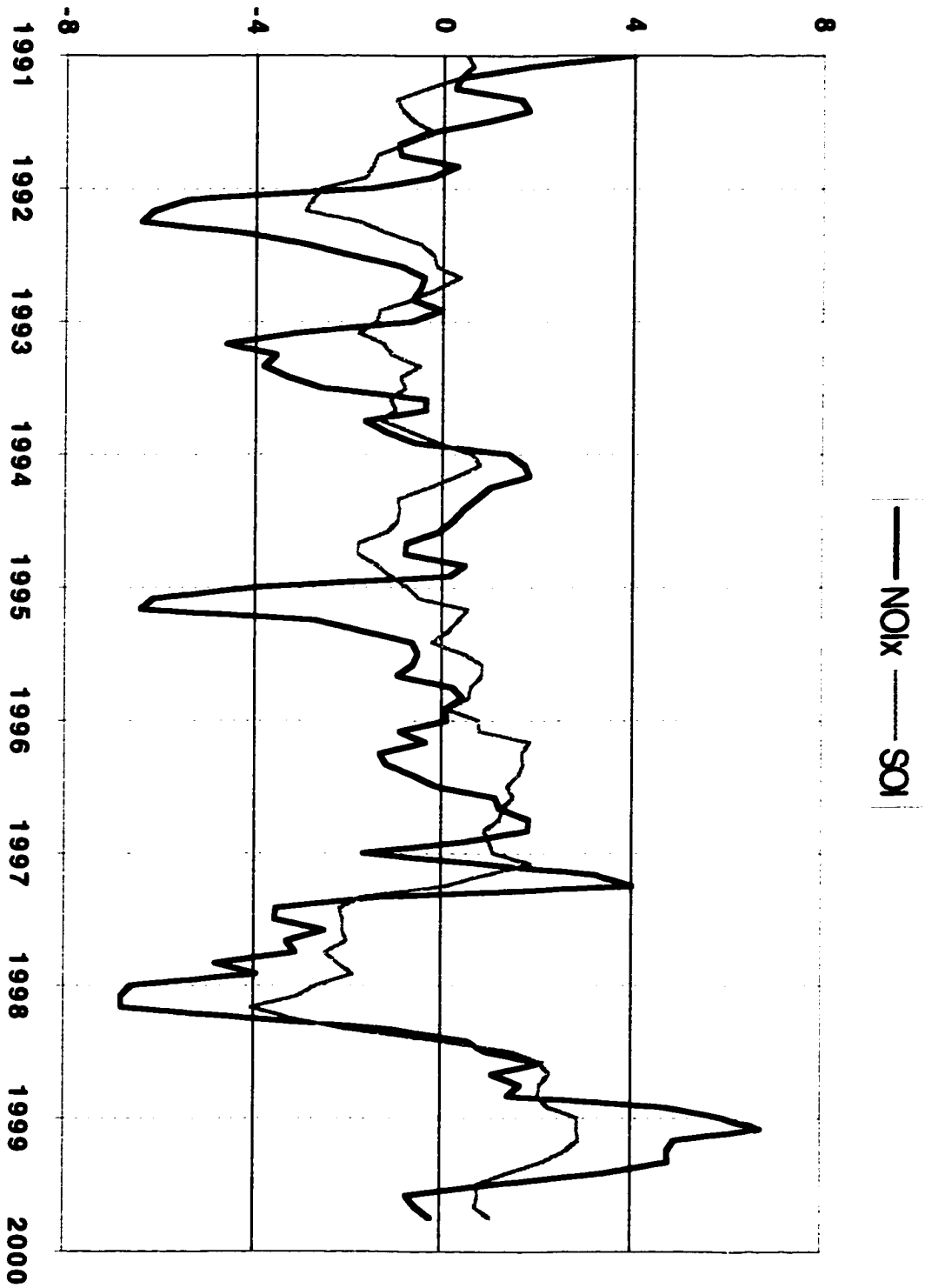Figure 1. Map detailing location of study site at Bodega Bay, California.

Figure 2. Time series of monthly extratropical Northern (NOIx) and Southern (SOI) Oscillation Indices. Positive values indicate La Niña conditions and negative values indicate El Niño conditions. Time series are presented as 3 month running averages.
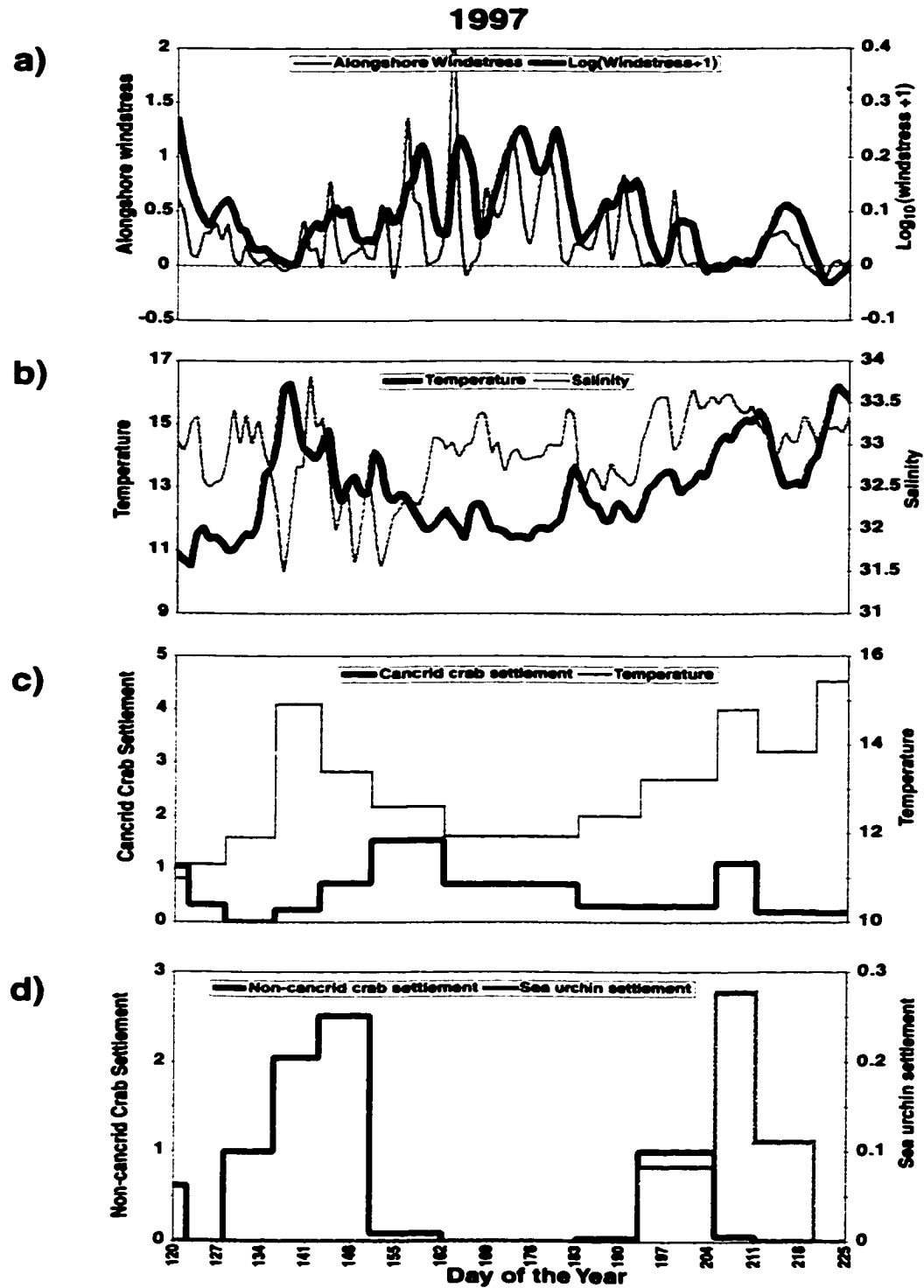
1997

a)

Alongshore windstress · Log₁₀(windstress+1)

Alongshore Windstress — Log(Windstress+1)

b)

Temperature · Salinity

Temperature — Salinity

c)

Cancrid Crab Settlement · Temperature

Cancrid crab settlement — Temperature

d)

Non-cancrid Crab Settlement · Sea urchin settlement

Non-cancrid crab settlement — Sea urchin settlement

Day of the Year

Figure 3. 1997 time series at Bodega Head of (a) alongshore windstress (dynes/cm², dashed line) and $\log_{10}$ (windstress+1) (bold line), (b) temperature (°C, solid line) and salinity (ppt, dashed line), (c) settlement per brush collector day of cancrid crabs (bold line) and average temperature per sampling period (dashed line), and (d) settlement per brush collector day of non-cancrid crabs (bold line) and sea urchins (dashed line). Note that in (c) and (d), settlement lines are extended over the entire settlement period, though this does not imply constant settlement over this period.
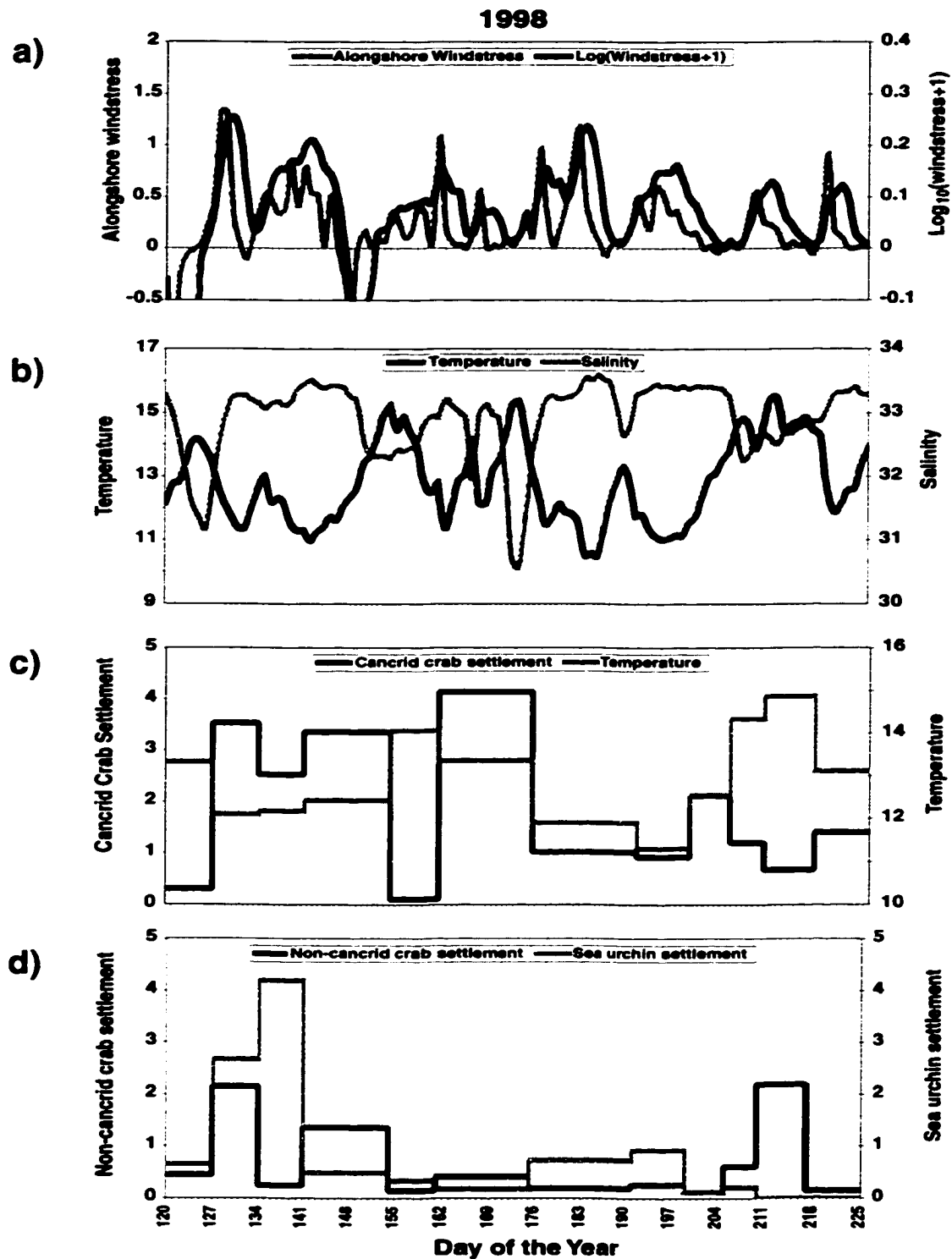
1998

Figure 4. 1998 time series at Bodega Head of (a) alongshore windstress (dynes/cm^2, dashed line) and $\log_{10}$ (windstress+1) (bold line), (b) temperature ($^{\circ}$C, solid line) and salinity (ppt, dashed line), (c) settlement per brush collector day of cancrid crabs (bold line) and average temperature per sampling period (dashed line), and (d) settlement per brush collector day of non-cancrid crabs (bold line) and sea urchins (dashed line). Note that in (c) and (d), settlement lines are extended over the entire settlement period, though this does not imply constant settlement over this period.
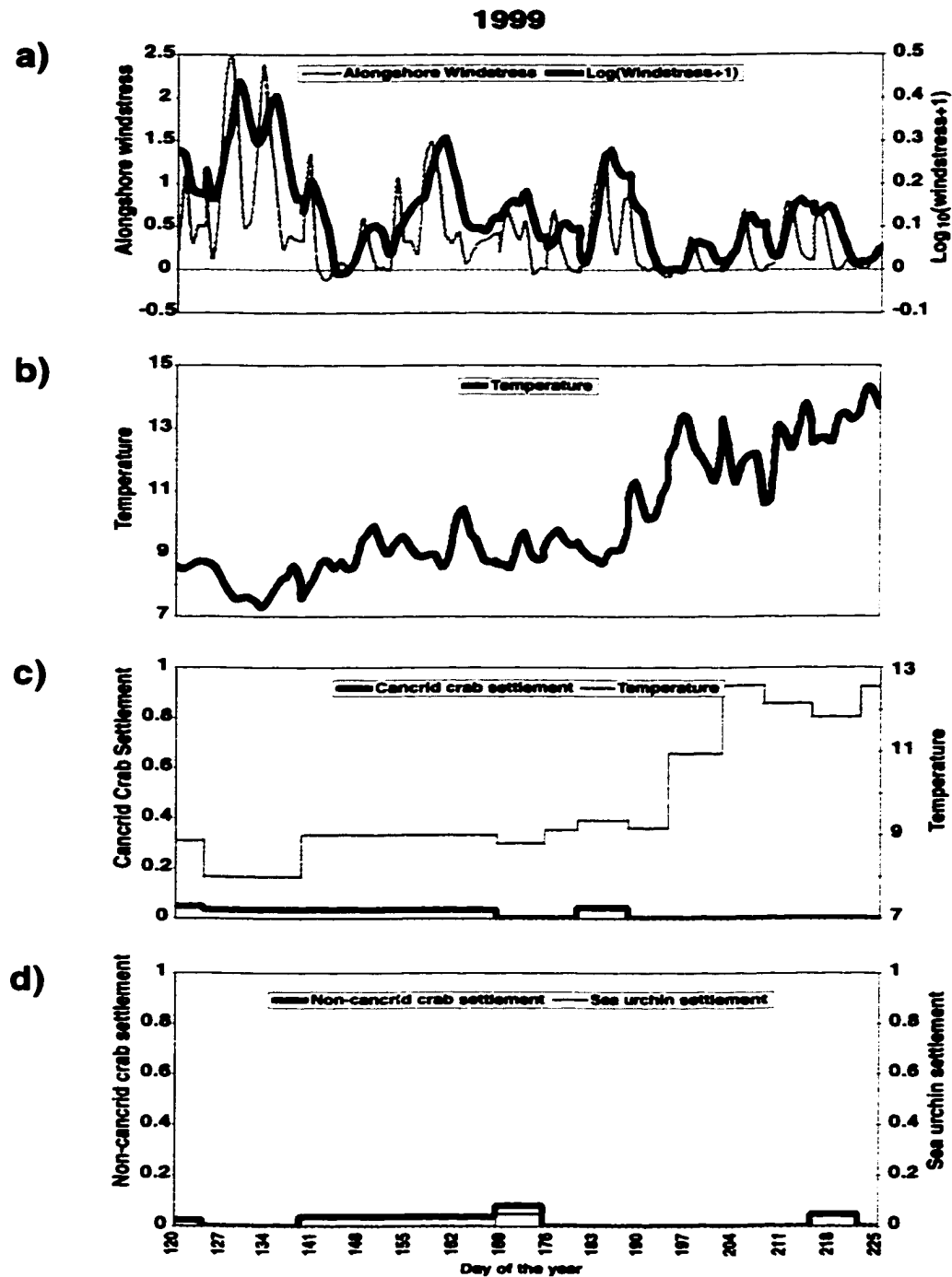
1999

a)

b)

c)

d)

Figure 5. 1999 time series at Bodega Head of (a) alongshore windstress (dynes/cm², dashed line) and $\log_{10}$ (windstress+1) (bold line), (b) temperature (°C, solid line) and salinity (ppt, dashed line), (c) settlement per brush collector day of cancrid crabs (bold line) and average temperature per sampling period (dashed line), and (d) settlement per brush collector day of non-cancrid crabs (bold line) and sea urchins (dashed line). Note that in (c) and (d), settlement lines are extended over the entire settlement period, though this does not imply constant settlement over this period.
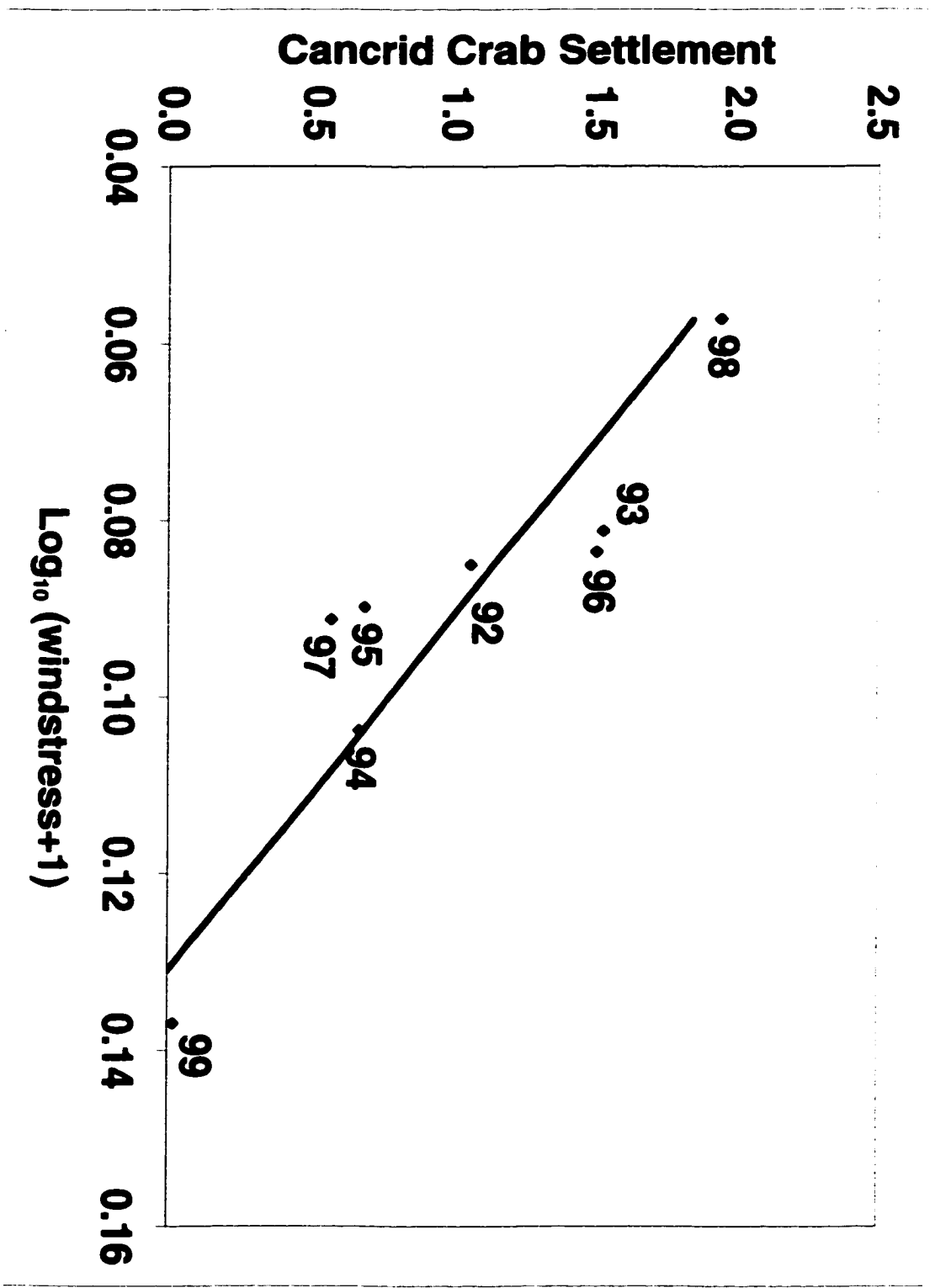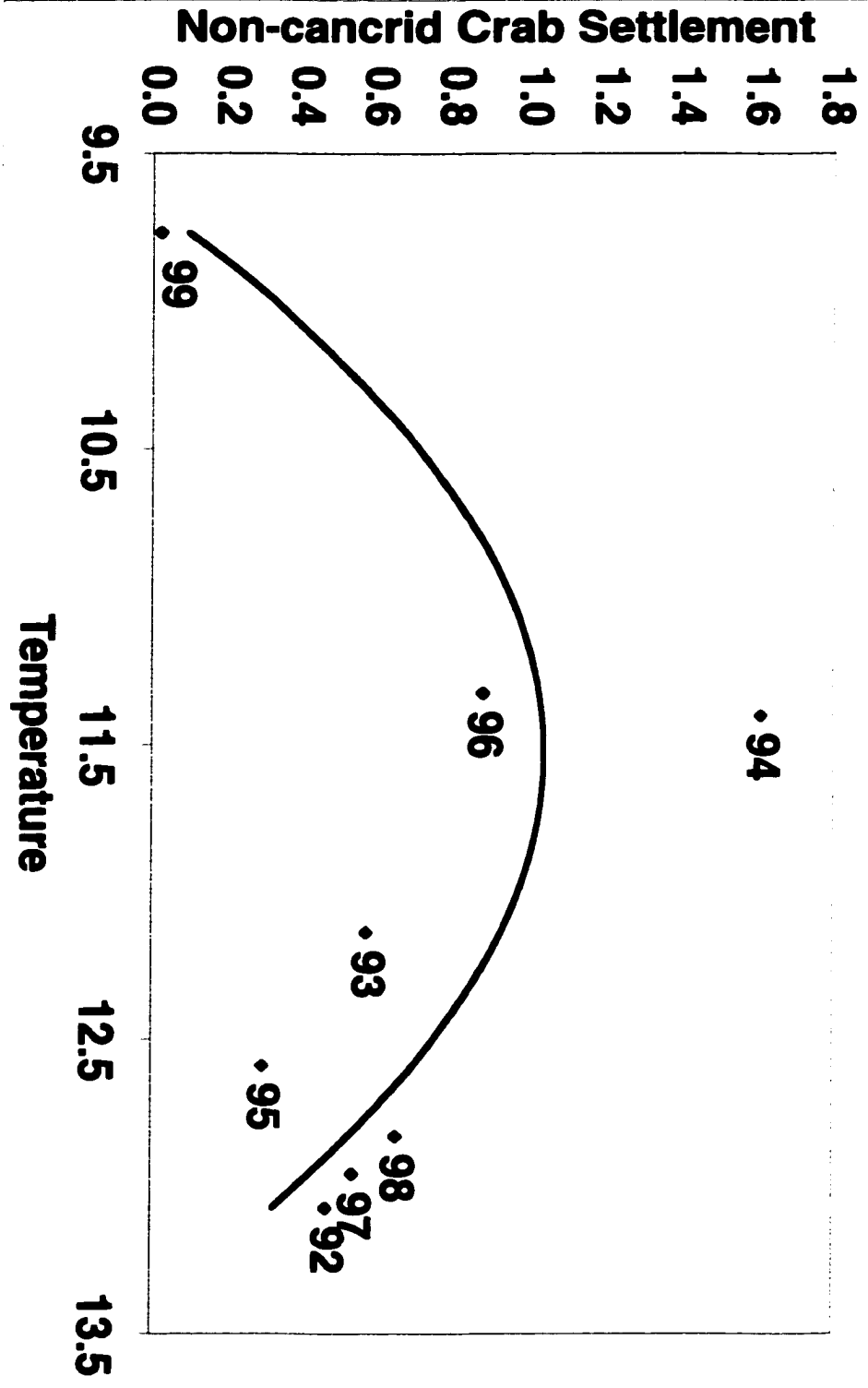
Figure 6. Linear regression of seasonal (April 30 – August 13) cancrid crab settlement on brush collectors during 1992-1999 at Bodega Head with seasonal average of $\log_{10}$ (windstress+1) (y = -24.37x + 3.18, R^2 = 0.8376) collected at BML MOMS.

Figure 7. Non-linear regression of seasonal (April 30 – August 13) non-cancrid (porcellanid, grapsid, pagurid, and majid) crab settlement on brush collectors during 1992-1999 at Bodega Head with seasonal average of the temperature ($y = -0.3824x^2 + 8.7761x - 49.116$, $R^2 = 0.6483$) collected at BML MOMS.