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Harvesting Methuselah's clams-
Is the geoduck fishery sustainable, or just apparently so?

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Abstract

Geoducks (*Panopea abrupta*) are very large and very long-lived bivalves, with potential life-spans well beyond 100 years. Such long life-spans should be expected to confer great stability to these populations. We re-examine information about the ecology and dynamics of geoduck populations in Washington State and British Columbia, and explore the implications for stock assessment and management. We identify strengths and shortcomings of the two management systems, and highlight urgently needed information. Our analyses suggest a long-term trend of declining recruitment over a large spatial scale, so that recent recruitment could be 40-50% of that during the 1930's. Recommendations are provided to further investigate this apparent phenomenon and the potential role played by fishing activities.

Résumé

La panope (*Panopea abrupta*) est un très gros bivalve; de très longue durée de vie, elle peut atteindre plus de 100 ans. Une telle longue durée de vie devrait en principe accorder une très grande stabilité aux populations. Le présent document passe en revue des données sur l'écologie et la dynamique des populations de panope de l'État de Washington et de la Colombie-Britannique et explore les répercussions de la durée de vie sur l'évaluation et la gestion des stocks. Les forces et les faiblesses des deux régimes de gestion sont identifiées, ainsi que les besoins urgents en données sont mis en lumière. Les analyses semblent indiquer une tendance à la baisse du recrutement à long terme sur une grande échelle spatiale, de sorte que le recrutement récent pourrait n'atteindre que de 40 à 50 % du niveau observé dans les années 30. Les auteurs recommandent que ce phénomène apparent et le rôle potentiel joué par les activités de pêche soient davantage étudiés.

Outline

0. INTRODUCTION

Geoducks (*Panopea abrupta*), the largest infaunal bivalves in the World[1], sustain one of the most significant fisheries in the northeastern Pacific, from Southeast Alaska to the Puget Sound (Fig. 1). They are harvested by commercial divers in shallow subtidal grounds.

Adult geoducks are found aggregated in dense beds, and have tremendous reproductive potential: millions of larvae are produced *per capita* during each reproductive season. Intuitively, such populations are regulated through over-compensatory post-dispersal density-dependence; a virtually unlimited supply of prospective settlers would be regularly available to fill-in gaps created by mortality of residents in crowded beds. Using close-population stock-recruitment relations as a metaphor, these are situations in which the slope of the ascending branch is typically very steep (*i.e.*, the parameter capturing the density-independent phase tends to be high): few breeders can quickly saturate a population decimated by mortality (*e.g.* by fishing). Geoducks are among the longest-lived animal species: maximum age recorded is above 140 years (Shaul and Goodwin, 1982). Extreme longevity should confer great stability to such populations.

Factually, however, the dynamics of geoduck populations remain little known, particularly regarding responses to fishing. The following are major sources of concern:

- Longevity could convey a misleading sense of stability or resiliency. Trends in recruitment rate, for example, could be obscured. In fact, several studies (discussed below) suggest very low recruitment levels in recent decades, too low to compensate losses to natural mortality.
- Depensatory mechanisms[2], that might dominate the dynamics at low density levels (*e.g.* after fishing), are poorly understood. These include the density-dependence of fertilization rate and preferential settlement of larvae in the vicinity of adults.
- Some depensatory mechanisms could be exacerbated by the allocation of fishing effort to the densest beds, or confounded with deleterious environmental effects of fishing operations.
- As is the case in other benthic fisheries, serial spatial allocation of fishing effort could result in hyperstable depletion, trends in *CPUE* underestimating the real rate of decline of total abundance.
- Poaching and, more significantly, highgrading are difficult to control, this resulting in an underestimation of effective harvest rates.

The exploitation of long-lived species poses difficult problems to management. Sustainable harvest levels are forcefully very small, and responses to management actions, and consequent learning, take place at a very slow pace. These problems were recognized early on in the development of geoduck fisheries, and a series of tight regulations were imposed to prevent overfishing. Low nominal harvest rates (1% to 3%), commensurate with estimated natural mortality, are a centerpiece in the management of the Washington and British Columbia fisheries. Geoducks, however, are in one sense unusual among longevous organisms: unlike trees and many deep-water fishes, they grow fast during their early 7-10 years, and afterwards their size remains virtually unchanged. On average, geoducks of 15 and 100 years of age do not differ significantly in weight (Breen and Shields, 1983; Harbo et al., 1983). Given this, and assuming strong post-dispersal overcompensation, sustainable harvest rate could be possibly higher than dictated by intuition or popular rules of thumb. The question of whether current levels of harvesting are unsustainable or over-conservative remains open.

Geoduck fisheries have been managed in British Columbia (Canada) and Washington (U.S.A.), the main producing areas, in radically different ways. In British Columbia the harvest level is controlled

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[1] Maximum weight recorded formally is close to 4 kg, although there is reference to geoducks as heavy as 5 kg having been harvested (Anderson, 1971), and anecdotal talk of 8-kg individuals (Skog, 1996). Mean weight of marketed individuals is ca. 1 kg. Maximum size (shell length) recorded in surveys is 206 mm (Goodwin, 1976).

[2] Under *depensatory* density-dependence the per-capita reproductive contribution of an individual decreases with density. The typical example is fertilization rate, which decreases with the availability of potential partners. Depensatory mechanisms are significant when population size is low.

through individual quotas and limited entry, while in Washington fishing rights over small "tracts" are auctioned every year. Summing up the contrasts, Freeman (1984) wrote that "*British Columbia manages the geoduck like a fish, Washington like a tree. Both methods are controversial*". Implications of the two strategies were clearly outlined by Fyfe (1984):

> "*In Washington State, with a smaller area to manage, the harvest concentrates within well-defined boundaries", while "in British Columbia the fishery is spread over the whole coast" […] "The relative merits of an intensive harvest in discrete patches vs. a moderate harvest over large areas are presently unknown*."[3]

After 25 years of the systems being in place their relative merits remain arguable, and have not been rigorously assessed, although a few studies have contributed important insights (Fyfe, 1984; Goodwin and Shaul, 1984; Campbell et al., 1998). At stake is the sustainability of a fishery whose absolute and relative significance has increased over the last 20 years, a time during which many traditional fisheries have declined or collapsed in the region.

Here we re-examine information about the ecology and dynamics of geoduck populations publicly available in Washington and British Columbia, and explore its implications for stock assessment and management. We point strengths and shortcomings of the two management systems, and highlight key pieces of information that are urgently needed to understand the status of the resource and its responses to fishing. The one risk being faced is that geoduck's extraordinary longevity, hyperstable depletion, "invisible" depensatory mechanisms and underestimation of the catch may be concealing the unsustainability of current harvest levels, at least in some regions.

1. BACKGROUND

1.1. Geoduck Biology

1.1.1. Distribution. The geoduck, *Panopea abrupta* (Conrad, 1849) is distributed from SE Alaska to Central California. Most significant fisheries operate in the Puget Sound region (Washington State) and along the coasts of British Columbia. There is an incipient but promising fishery developing in Alaska, and the prospects are being considered for one in Oregon. The known depth range extends from the low intertidal zone to 110+ m (Jamison et al 1984). Density increases gradually with depth down to 25 m, at least in some locations (Campbell et al., 1996b). Burrowing depth within the sediment increases with size, to a maximum of *ca.* 0.9 m (Andersen, 1971, his. Fig. 33).

1.1.2. Age and growth. Initial attempts to estimate geoduck age from external shell rings were unsuccessful (Andersen, 1971; Goodwin, 1976). Studies addressing growth by means of mark-recapture methods or modal displacements (Andersen, 1971; Goodwin, 1976) concluded that growth is fast during the early years of life (20-30 mm/year), but insignificant in larger geoducks. A successful technique to read internal rings in the hinge of the shells was first developed by Shaul and Goodwin (1982), and soon after utilized in several studies (Table 1). Geoducks were convincingly shown to be extremely longevous: with a maximum recorded age of more than 140 years they are among the oldest-lived animal species. Mortality and recruitment rates must therefore be very low. Growth parameters for the von Bertalanffy model have been estimated in a few studies (Bradbury et al., 1998; Hoffmann et al., 2000; Noakes and Campbell, 1992). Growth rate shows strong spatial gradients. In Puget Sound average size decreases from south to north, and from shallow to deep (WDF & DNR, 1985, p. 11; Goodwin and Pease, 1991). Hoffman et al. (2000) discussed the management implications of spatial variation in growth rate.

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[3] It should be obvious that the sentence "*In British Columbia the fishery is spread over the whole coast*" in Fyfe (1984) does not imply that effort is either *evenly* or *randomly* distributed across space. It implies that fishers have more freedom to spread effort over the larger areas opened in Canada.

1.1.3. Reproduction and early development. Sexes are separate (Andersen, 1971; Goodwin, 1976); males appear to mature one year earlier than females (Andersen, 1971). The spawning season in Puget Sound runs between spring (March or April) and early summer, peaking in June (Goodwin, 1976). It is commonly held that geoducks are "dribble" (partial) spawners; a single female may release millions of eggs during a spawning season. Spawning has been observed in the field (Goodwin, 1976, p. 52): "*sex products flowed from the excurrent siphon continuously over a period of several minutes*". The dynamics of fertilization (which is external) has not been investigated.

The pelagic larval stage lasts 25 days under hatchery conditions, at 17º C (Beattie and Goodwin, 1993), but might extend longer in nature (up to 40-50 days). Larval behavior and advection/retention mechanisms have not been investigated. Settlement may be facilitated or even induced by chaetopterid tube-worms (Cooper and Pease, 1988), the most conspicuous infaunal element in geoduck beds. Facilitation of larval settlement in the vicinity of adult siphons (whether due to chemical attraction or hydrodynamically-mediated mechanisms) has been often invoked but never investigated experimentally. After settlement, post-larvae move at the sediment surface for several weeks (King, 1986; Cole, 1991), feeding on surface deposits until metamorphosis. Then siphons develop and juveniles start burying into the sediment. Suspension feeding begins at that stage.

1.1.4. Natural mortality. Predation risk is very high during early benthic life (Goodwin and Shaul, 1984), but decreases quickly after the age of one year (Sloan and Robinson, 1984). Predation on adult geoducks seems to be rare, but some cases have been reported involving the starfish *Pisaster brevispinus* (Fyfe, 1984, p. 91). One event in which a single geoduck was eaten by a starfish lasted one week. Natural phenomena creating anoxic conditions at the sediment-water interface can also affect geoducks, either through physiological stress or increased exposure to predators. Such conditions can be induced by massive squid spawning (Fyfe, 1984, p. 92) and drifting masses of marine vegetation (Andersen, 1971). Exposure of distressed geoducks to predation by the starfish *Pycnopodia helianthoides* was well documented by Fyfe (1984, p.92). In these few cases of observed predation by starfish the empty shells layed at the sediment surface.

The natural mortality rate of adult geoducks can be estimated directly by tracking the fate of individuals whose location has been mapped in experimental plots. This constitutes an exceptional opportunity to observe an often elusive process as it unfolds. Such an experiment was conducted by Fyfe (1984), who recorded the fate of all the residents in a 10-m^2 plot during one year; over that period 18 individuals died out of an of initial population of 70. After one year the size of the plot was extended to 15 m^2 and followed by an additional 10 months, over which 9 geoducks died out of an initial population of 52. Most of the individuals seemed to have died *in situ*, leaving the shells in live position within the sediment: "*location where a geoduck was known to have existed was covered with a patch of white film, similar to patches (bacteria or fungus) typically associated with decay in a moist environment"; "observation [of sediment underneath those patches] strongly support the assumption that these geoducks died and were not merely retracted*". This study, though small in scale and restricted to a single location, is valuable in two senses: it demonstrated the possibility of tracking mapped patterns over time, and showed rates of natural mortality far higher than the average rates currently accepted, which would be inconsistent with the longevity reported for these animals[4].

All published estimates of the rate of natural mortality of geoducks are based on "catch curve" analysis of age frequency distributions (AFDs) of live animals, collected between 1979 and 1982 (Table 1). In all cases, a constant coefficient of natural mortality (M) was estimated by fitting the exponential model to a range of ages selected *ad-hoc* (Table 2). Analyzed AFDs show remarkable scarcity of individuals younger than 20-50 years. This pattern has been discussed in relation to gear selectivity (Breen and Shields, 1983; Noakes, 1992) and trends in year-class strength (Sloan and Robinson, 1984). Given empirical

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[4] WDFW is currently conducting a larger scale study of natural mortality by means of in-situ tagging. Preliminary unpublished results indicate mortality rates much lower than those currently accepted, in the order of 0.016-0.018 yr^{-1} (Bradbury, pers.comm.)

knowledge of the fishing process, age-selectivity is unlikely for geoducks older than 4-10 years; the pattern is likely to reflect low recruitment before the 1980's.

1.1.5. Recruitment[5]. The term "recruitment" is used here with reference to vulnerability to commercial gear or "showing" ("countability" of siphons during surveys), which are taken as equivalent. This follows explicit assumptions made by diving biologists familiar with this resource.

Direct observations of geoduck pre-recruit abundance have been rare (Table 3). Studies were probably discouraged by the generalized perception of very low and spatially variable recruitment rate. Goodwin (1976) followed two year classes, apparently settled in 1969-1970. Consistently, AFDs from the Hood Canal region indicate that two discernible year-classes settled around 1970. Sampling with an unselective suction dredge (the Venturi dredge) conducted all over Puget Sound and Hood Canal indicated that the density of pre-recruits was extremely low.

Evidence of very weak year-classes during the 1970s across a broad geographic region is consistent with the pattern found in AFDs during the early 1980s (studies listed in Table 1): under the assumption of constant recruitment, age classes 50+ and younger seem to be underrepresented in the samples, both in Washington and British Columbia. Further, there seems to be indication of a gradually declining trend in year-class strength beginning decades before. The emphasis in those studies was on the estimation of growth and mortality parameters; the apparent trend in recruitment received little attention, although it was noticed by some authors:

> "*The relatively low proportion of 11- to 20-yr-old geoducks may indicate poor recruitment during at least the previous 10 yr. A similar decline in geoduck recruitment has occurred in other British Columbia localities*" (Sloan and Robinson, 1984, p. 136)
>
> "*Recruitment rate has declined during the past 30 years for unknown reasons not related to harvest. Because of this, the current harvest rate may have to be adjusted in the future*" WDFW & WDNR (1985, p.13)
>
> *"The relatively low proportion of 10-25 yr-old geoducks may indicate poor recruitment during the 15-yr period prior to sampling in 1978-1981. This suggests that poor recruitment occurred during the period 1955-1970, and perhaps more recently."* (Bradbury et al., 1998, p. 51)

Others interpreted the (apparent?) pattern as the result of a highly variable and patchy process:

> "*Recruitment is highly variable from area to area and year to year; however, in some locations, some recruitment occurs every year*" (Goodwin and Shaul, 1984, p. 20).
>
> "*The age frequencies support the contention of Shaul & Goodwin (pers. comm.) that recruitment in geoducs is constant and low*" (Breen and Shields, 1983, p.8)
>
> "*These data might suggest that settlement of juvenile geoducks has periodic peaks with a low amplitude and long period"* (*Ibid*.)

1.1.6. Spatial structure of populations. Geoduck stocks are structured as metapopulations, collections of populations of sedentary adults connected with each other by means of the dispersal of meroplanktonic larvae. Relatively small, open segments of populations (not necessarily discrete, typically with an area of 20-50 ha) are defined as "tracts" in Washington , or "beds" in British Columbia (*e.g.* Harbo

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[5] According to Hand et al. (1998, p. 17), "*research projects are nearing completion that were designed to examine recruitment characteristics of geoduck populations and evaluate the sustainability of the harvest rate […] These studies are in their fifth to sixth years and results should be available for use in stock assessment within a couple of years.*"

et al., 1995)[6]. No serious effort has been made to group beds into metapopulation units, although some stocks (*e.g.* Hood Canal or southern Puget Sound) could possibly correspond to metapopulation-level units. In such systems it is most important to characterize the spatial scales of interest, e.g: *large* (metapopulations), *intermediate* (a bed within a metapopulation), or *small* (the neighborhoods of resident individuals within a bed). Large-, intermediate- and small-scale processes are exemplified, respectively, by larval dispersal, short-term fishers behavior, and fertilization.

Any segment of such benthic metapopulations is open to recruitment by larvae from other beds. Availability of new settlers depends on local conditions prevalent in other regions, as well as larger-scale environmental conditions affecting spawning, and advection and survival of larvae. In general (and in geoducks in particular) there is virtually no connection between the reproductive contribution of a given site and recruitment to that site. Pre- and post-dispersal phenomena are decoupled at relevant spatial scales, with the result that key processes in the dynamics may be completely blurred if analyzed at the wrong spatial scale. Close stock-recruitment relations, *e.g.* the Ricker or Beverton-Holt models usual in fisheries, can be misleading in this context.

1.1.7. Density-dependence. As is the case with most benthic sedentary organisms, density-dependence in geoduck metapopulations is likely to be significant only during benthic stages (larval settlement through fertilization). Duration of the pelagic larval stage is relatively short, and larvae are diluted in a large volume of water. Density-dependent interactions have small operational scales, as individuals are influenced only by their neighbors (Orensanz et al., 1998), even if neighborhoods may be widened by water flow, *e.g.* in trophic interactions among suspension feeders. The effects of localized (small-scale) density-dependence on the dynamics of the metapopulation are mediated by larval dispersal. Thus, it is convenient to distinguish between pre- and post-dispersal density-dependent mechanisms (Botsford and Hobbs, 1995), whether these are compensatory or depensatory ("Allee effects"). Pre-dispersal density-dependent processes are those that affect the reproductive output either directly (e.g. fertilization success), or indirectly (e.g. density-dependent growth). They depend on the concentration profile of the populations, which summarize the density conditions experienced by individuals. Post-dispersal processes affect the rate of recruitment through the effect of resident densities on larval settlement and survival of pre-recruits. Figure 2 and Table 4 summarize the types of density-dependence most frequently presumed and/or investigated for benthic sedentary invertebrates with broadcast spawning, external fertilization, and pelagic larvae. Several of these hypotheses were early identified by Fyfe (1984, pp. 3-5) as significant for geoduck population dynamics. Below we review presumable mechanisms of density-dependence and evidence of their significance in the case of geoducks (Table 5).

Pre-dispersal, compensatory. Although density-dependent growth has been occasionally invoked in relation to geoducks (*e.g.* WDFW and WDNR, 1985, p. 127) it has never been demonstrated. Fyfe (1984, p. iv) found that *"geoduck shell size was not correlated with observed population density"* for a moderate range of densities (4.0-7.7 geoducks/m^2) in Clayquout Sound (west Vancouver I.), although he observed (*op. cit.*, pp. 95, 98 and 104) that the size of eleven 4-year-old recruits was positively correlated with the distance to their nearest adult neighbor. Besides this, there is no evidence of post-dispersal compensatory growth in geoducks. Goodwin and Pease (1991) analyzed extensive survey samples covering the entire Puget Sound, but found no significant relation between length or weight and density (*op. cit.*, p.71).

Breen and Shields (1983) examined the spatial pattern of distribution at small scales. Geoducks were counted in 3-4 plots at each of five locations in British Columbia. Each plot, 5m x 6m, was partitioned into 30 1-m^2 quadrats. The variance/mean ratio of the counts indicated that geoducks were evenly distributed at the small scale of the plots, suggesting spacing-out and perhaps saturation of the sites.

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[6] The terms "bed" and "tract", as used respectively in British Columbia and Washington, have analogous meaning. Throughout the text we use the term "bed" (widely used in the shellfish literature) as a general ecological or spatial category. The term "tract" is used only in the context of management policy in Washington.

Intriguingly, the pattern was also found in plots whose density had been reduced by fishing. The meaning of this observation is unclear.

Pre-dispersal, depensatory. Density-dependent fertilization rate remains undocumented in the case of wild bivalve populations, geoducks included.

Post-dispersal, compensatory. In the case of geoducks there is no evidence of residents inhibiting settlement rate or the growth rate of post-larvae and juveniles, nor of them increasing the mortality rate of the latter.

Post-dispersal, depensatory. The occurrence of enhanced settlement or survival of juveniles in the vicinity of adults is suggested by the results of *Experiment 4* of Goodwin and Shaul (1984), although possible mechanisms involved are unclear. They seeded hatchery-reared juveniles on a 100-m^2 experimental plot, half of which had been previously harvested using commercial gear. The plot was sampled 5-6 months later with a Venturi dredge (considered unselective), and all geoducks (adults and juveniles) were counted. Density of surviving juveniles was 2.4 times higher in the unharvested than in the harvested half. Decreased recruitment rate following the harvest may result from processes other than depensation. During operations with commercial gear juveniles neighboring harvested adults are blasted out of the sediment and die. Sediment disturbance could have an effect on settlement. Goodwin and Shaul (1984, their *Experiment 6*) tried to separate experimentally the effects of disturbance and depensation. Plots, 153-m^2 each, were marked at two different locations; each was divided into 15-m^2 subplots. Three treatments were applied: resident adults removed with commercial gear, identical level of disturbance without removal of any adults, and control. The experiment run through one reproductive/settlement season. Their results were inconclusive due to very low number of new settlers during the single season when the experiment was conducted.

Clustering of juveniles in the neighborhood of adult geoduck siphons (e.g. Goodwin and Shaul, 1984, their *Experiment 5*) has been interpreted by some as evidence of some kind of Allee effect. Fyfe (1984) observed that the nearest neighbor of 15 recent recruits (age 4+-5+ years) was a much older adult. This result is of little significance as most of the individuals in his study plot were older geoducks. Small-scale aggregated (non-uniform) pattern of geoduck spatial distribution has been sometimes discussed in relation with density-dependent processes. Two studies (Andersen, 1971, his fig. 35, and Fyfe, 1984) mapped the location of individual geoducks in experimental plots, but the analyses were inappropriate; these data sets should be re-analyzed using techniques adequate to mapped patterns (*e.g.* Orensanz *et al.*, 1998). Fyfe (*op. cit.*) investigated pattern for different age intervals in three 16-m^2 plots. Contagion appears to be higher for the strong year-classes that had settled about 40 years before the experiment was conducted. The pattern is difficult to interpret.

Summing up, the few data available tend to be more supportive of some combination of [environmental deterioration + incidental juvenile mortality + depensation] than of compensation (Table 5). This, and its implications for management, has been long acknowledged by scientists at WDFW:

> “*The decreased number of juveniles in the fished beds is probably due to an adverse effect of fishing on recruitment […] The low number of juveniles 1-3 years age group was probably due to lower post-harvest recruitment, again suggesting that commercial geoduck fishing has an adverse effect on recruitment*” (Goodwin and Shaul, 1984, p.14).

Hand et al. (1998, p. 17), on the other hand, suggest the existence of evidence to the opposite:

> *“There have been recent reports from commercial fishers of high proportions of juveniles in some beds that have been heavily fished in the past. This is substantiated by some aged biological samples taken during surveys (unpublished data).”*

If ever demonstrated, low levels of compensation could be attributable to currently reduced density levels, which are suggested by the analysis of AFDs.

1.2. Origins and Development of the Fishery

Intertidal geoducks have been harvested for centuries, first by native Americans and more recently by recreational fishers. The commercial fishery started in Washington State in 1970, and has been always restricted to subtidal stocks. After 1974 a major market was established in Japan, which created the opportunity for an explosive development of the fishery. During the late 1980s the market shifted from exports of processed meats to Japan, to live exports to China, with Hong Kong becoming the main distribution center.

Two State agencies, the Washington Department of Fish and Wildlife (WDFW) and the Department of Natural Resources (DNR), participate in management in Washington State. WDFW is in charge of surveys and assessment, selection of tracts to be harvested each year, establishing harvest rate, and monitoring the ecological effects of fishing activities. WDFW also has enforcement powers (the NMFS is involved to a lesser degree); "sting" operations are conducted by undercover detectives with the Special Investigations Unit (SIU). DNR marks the tracts, appraises the value of the resource, and conducts public auctions. Other federal and state agencies, as well as local governments, constrain geoduck harvests for various reasons (*e.g*. water quality standards, navigation lanes, conflicts in the use of the coastal zone, etc.) Tracts are leased to private individuals or companies through a public auction system; the State contracts to the highest *responsible* bidder. In addition, a contract price/lb is evaluated by a state economist's appraisal of the clams in a given tract. The amount collected by the State is generally above 50% of the landed value. The total revenue to the State from "*Aquatic Resource Activities*" (originating to a large extent from the geoduck fishery) was ca. US$ 13.5 million in 1998 (DNR, 1998). Part of the State's revenue is transferred to WDFW, mostly to fund a geoduck hatchery program. Enforcement has been very tight since the last 1980s, when an illegal fishing scheme (popularly known as "Clam Scam") was exposed (Summers, 1994).

On December 20, 1994, a federal court ruling known as the Rafeedie shellfish decision upheld the rights of several Native American tribes to collect shellfish in Puget Sound (Fangman et al., 1996). This drastically changed the management of geoduck and other shellfish stocks in the region. Since then, half of the annual quota (in the form of tracts) is allocated to the tribes and is co-managed between the later and the State. State/Tribal Geoduck Harvest Plans are agreed upon for each management region, every year, in compliance with an Interim Management Agreement. Tracts assigned to the tribes are not part of the auction process. Openings and closures of the tracts allocated to the tribes are regulated by the tribes themselves.

The British Columbia fishery started in the Inside Waters of Vancouver Island in 1976, and by 1980 had expanded to other regions. Entry was not limited during the beginnings of the fishery; the number of licenses grew fast to a maximum of 101 in 1979, when a moratorium was introduced and licenses were made non-transferable. Between 1980 and 1981 the moratorium evolved into a formal limited entry program, with the number of licenses reduced to 55. Licenses, held by vessel owners, were made transferable between vessels but not between persons. Each vessel operates with up to 3-4 divers; the number of the latter is not limited. The fishery is currently managed through a combination of limited entry and individual quotas (see Section 1.5.2); since 1989 the TAC has been split in equal parts among license owners, as requested by the Underwater Harvesters Association (UHA)[7]. For a detailed account of the development of this fishery and its management see Muse (1998) and Heizer (2000). The management system now in place has been credited for reducing effort while increasing rent through improved product quality and access to new markets. The uneven distribution of the rent between license-holders and crews (mostly divers) continues to be an issue that could generate political uncertainty. In recent years the fishery grew to become the major invertebrate fishery in the province, with landings valued at Can$ 33,698 million in 1997; the all-time record was Can$ 42.5 M in 1995 (Hand et al., 1998).

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[7] For more information see UHA's homepage at http://www.geoduck.org, which also contains much information about geoducks and their fishery.

Main features of the management systems in place in British Columbia and Washington are outlined in Table 6.

By 1978 there was already interest in the geoduck resource from Southeast Alaska, which has supported a small fishery since the late 1980s. Main known beds are located near Ketchikan and Sitka. A management system is still evolving; State managers have studied the British Columbia case in search of a possible model for Alaska. Currently there are 65 active permits (56 of them "resident") in the fishery[8]. The GHL (Guideline Harvest Level) for the Ketchikan area during the 1998-99 fishing season is *ca*. 50 tons.

The nominal catch is an underestimate of real catch in both fisheries, due to two components whose magnitude is difficult to guess: *highgrading* and *poaching*. The first motivation to highgrade is the great difference in price between high quality (white) and low quality (brown) meats, because individual quotas in British Columbia and taxes on landings in Washington do not contemplate grade of the product. According to WDNR's geoduck managers (Steve Jennison and Doug Williams, pers. comm.), highgrading in the non-Indian fishery was drastically reduced after 1995, when "spotchecks" (which may involve State divers) begun. They estimate that highgrading adds 1% or less to the catch in this sector of the fishery, while it might run as high as 30%-40% in the tribal fishery where (always according to their opinion) controls are looser. The same sources indicated that poaching has increased in recent years to ca. 15%-20% of the nominal catch, mostly because of complications with enforcement following implementation of the Rafeedie Decision. Adding up, the non-reported catch could be as high as 30%-40% of the nominal catch. According to other well-informed sources these figures are grossly inflated; the combined rate of poaching and highgrading in the fishery at large is likely to be closer to 10%. An undercover investigation conducted in 2000 by WDFW, including dive surveys, indicates discard rates between 2% and 28% (average of six surveyed sites was 12%) (Bradbury, pers. comm.)[9]

Currently there is substantial interest in aquaculture and enhancement using hatchery-reared juveniles. Captive reproduction was first accomplished at WDFW's Point Whitney Laboratory (Goodwin, 1973; Goodwin et al., 1979; Beattie and Goodwin, 1993). In 1982 WDFW and DNR decided to implement an enhancement program to accelerate recovery of harvested beds (Beattie and Goodwin, 1993). Although "seed" production was successful, the survival of seed planted by broadcasting juveniles from boats was extremely low, presumably due to predation (Beattie, 1992). The program was discontinued in 1991. Intertidal planting experiments were conducted during the early 1990s. Juveniles were protected within perforated segments of PVC pipe. The technical results were encouraging, but the cost is prohibitively high for the technique to be used in the enhancement of subtidal stocks. In British Columbia the UHA, in conjunction with Island Scallops (an aquaculture firm), have been reseeding sections of the Strait of Georgia since 1994, when "seed" was first produced in hatchery conditions. With financial assistance from the provincial government the firm has developed a planting machine, a development which could possibly make enhancement viable.

Experimental aquaculture on a commercial scale was initiated during the early 1990s by private entrepreneurs in Washington State, most notably Taylor Fishing Farms of Shelton, a firm with a solid experience in clam and oyster farming; the first harvests were expected to take place in the late 1990s. Aquaculturists are currently experimenting with devices to reduce predation, and with optimum planting density. There has been some concern about the mixing of separate gene pools in hatchery operations. Currently there are projects under way at the School of Fisheries, University of Washington, to determine the genetic structure of the Puget Sound stocks, and on the possibility of using triploids in aquaculture.

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[8] For updated information on permits see http://www.cfec.state.ak.us/PSTATUS/PSJ11A.HTM, and for GHLs http://www.cf.adfg.state.ak.us/region1/k%5Ffishry.htm#geoduck.

[9] The issue of highgrading in the Washington fishery caught the attention of the public on February 25, 2001, after information originating from WDFW led to a journalistic investigation published by The News Tribune, of Tacoma, Washington (Bob Mottram: "Geoduck fishery in crisis Dumping, killing of lower-grade, undesirable clams depletes beds, pushes industry to brink of collapse").

1.3. The Fishing Process

While fishing area restrictions by regulation exist in both Washington and British Columbia, their role is most important in Washington, where specific beds ("tracts") are selected for auction each year. Understanding the dynamics of the fishing process is comparatively more important in the Canadian system, because here much of the spatial allocation of fishing effort is controlled by fisher's behavior. The fishing process in British Columbia has been well described by Campbell et al. (1998); there is not an equivalent description for the Washington system, although valuable insights have been provided by WDFW and WDNR (1985).

1.3.1. The elementary fishing operation. Commercial divers with hookas use hand-held water-jets (nozzles) to dig the clams, one at a time (for description see WDFW and WDNR, 1985). The number of geoducks gathered by an individual commercial diver per unit of time is a function of prey density, a relationship known in ecology as the *functional response* (Holling, 1966). The functional form of the response is presumably asymptotic, the reason being that there is an upper limit to the number of geoducks that a diver can catch per unit of time. Lets denote as T_h (*handling time*) the time required by a diver to capture and handle an individual geoduck. Total handling time per diving time unit (T) should be reasonably well approximated by T_hC, where C is the number of geoducks caught. Total diving time can be split into search time (T_s) and handling time, so that $T = T_s + T_h C.$ Assuming that catch per search time is proportional to density (D),

$$\frac{C}{T - T_h C} = pD\,,$$

and rearranging,

$$\frac{C}{T} = \frac{pD}{1 + T_h pD}$$

Notice that when $T_h p \to 0$ the model collapses to simple proportionality between C/T (*i.e. CPUE*) and D. The best known application of the functional response in shellfisheries is the assessment of fishing power in the commercial diving abalone fishery of Victoria (Australia) by Beinssen (1979). In this and other similar studies, however, the functional response is inextricably confounded in the data with the effects of non-random effort allocation. Campbell et al. (1998) collected an exceptional data set for the geoduck fishery (his Fig. 4:A). A 2440-m^2 plot was depleted over three consecutive fishing seasons; density was estimated concurrently. Commercial divers were made to fish systematically along a fixed transect grid, thus removing from the data the confounding effect of density-dependent effort allocation. To our knowledge this is the only data set allowing the use of the functional response model for the experimental estimation of handling time in a commercial diving fishery. We fitted the model to data made available by Campbell; estimated parameter values were $T_h = .31$ minutes/geoduck, and p = 3.6. The estimate of T_h falls within the range of .25 to .5 minutes/geoduck indicated by WDFW and WDNR (1985, p. 12).

1.3.2. Catchability. As in other benthic fisheries, vulnerability to the fishery is governed by a number of factors and varies greatly across space and over time; main factors are summarized in Table 7

1.3.3. Selectivity. . Entries in Table 7 corresponding to size and meat quality (dark-light, the lighter the better) refer to "gear" selectivity, defined in this case as the ability of the diver to select from a mixture of classes. From the viewpoint of the fishing process, selection associated with the spatial allocation of effort is probably more significant. Quality standards, including meat color and size, vary among markets; large geoducks are favored in exports to China, while relatively small geoducks have become increasingly popular in the domestic US market (Bradbury, pers. comm.). Geographic gradients in size and meat color are well documented and known to fishers, and so market preferences translate into patterns of spatial effort allocation

Regarding the “gear” selection component, Campbell et al. (1998, their Fig. 4:B) showed implicit evidence of size-selection. In the depletion experiment cited above, mean weight of geoducks in the catch declined after the density threshold for commercial fishing was reached. When divers were forced to fish beyond that threshold they started to gather smaller individuals, indicating that these were selected against when density was above the threshold. This experiment, in which divers were forced to fish systematically, does not reflect the dynamics of the fishing process. Yet, for that very reason, “gear” selection can be isolated from the effect of uneven spatial effort allocation. The two are confounded in observations in which divers are allowed to behave “normally”.

Age-selection, an important consideration in modelling, is correlated with size-selection, at least in the case of young/small geoducks. There is general consensus about geoducks becoming available to commercial divers between the ages of 4 and 12 years (Harbo et al., 1983), although it is well accepted that for practical purposes it can be assumed that geoducks are fully recruited by an age of 8 to 10 yr (Harbo et al., 1983; Bradbury et al., 1998). In Washington geoducks first enter the fishery at 300 g, a weight that is usually attained at the age of 5-7 years. WDFW biologists conducted surveys between 1973 and 1985 in which they mimicked the selectivity of commercial divers; out of ca. 12,000 geoducks sampled, only 2% weighted less than 300 g (Bradbury et al., 1998).

1.3.4. Depletion. Understanding the depletion process of benthic resources requires consideration of fishers’ behavior in relation to spatial stock structure, including not only abundance but also the various other factors affecting vulnerability (Table 7), and consequently *CPUE*. As suggested earlier, the significance of those factors is likely to differ between the Washington and British Columbia management regimes. Important questions include:

- Is there a density threshold below which divers stop fishing?
- Are there departures from proportionality between density and CPUE, and if so what is their sign?
- To what extent do presumable departures from proportionality relate to the spatial pattern of distribution of the stock, and how is the latter itself affected by the fishing process?
- What is the spatial scale perceived by fishers while they make decisions on effort allocation?
- Is that scale commensurate with the observational scale of scientific surveys?

Although the fishing process has not been fully assessed, some important insights are contained (albeit often implicitly) in the existing literature, briefly reviewed below.

If divers are not 100% efficient the harvest of a patch stops when a certain threshold density level is reached. Change in visibility caused by fishing itself is just one possible source of inefficiency. A show factor less that 100% is another. If fishing is not 100% efficient, a diver returning to a harvested patch will likely decide that fishing is no longer rewarding. Under such a scenario the fishing process will tend to uniformize density across the bed, down to or below the threshold level. Some authors have suggested threshold density levels in the range of 0.2 to 0.6 geoducks/m^2 (Breen and Shields, 1983; Fyfe, 1984, p.8). Campbell et al. (1998) observed that CPUE, weight of geoducks in the catch, and the fraction of missed stings declined rapidly after the threshold level of 0.5 geoducks/m^2 was reached.

1.3.5. Highgrading. Once removed from the sediment geoducks cannot rebury themselves. Mortality of discarded geoducks is 100%. Since size and quality of a geoduck cannot be exactly determined by the diver before pulling it from the sediment, size limits are not a viable management measure. Quality of geoducks is related to the color of the meats: white meats have a much better market than dark ones. Highgrading occurs largely under water, as geoducks of poor quality are discarded *in situ*, creating serious problems for the assessment of the stock and the management of the fishery.

1.3.6. Incidental fishing mortality. Negative effects of fishing on post-harvest recruitment have been the matter of concern by scientists and managers. Incidental mortality of juveniles is a fact well known to field biologists:

> "*Small geoducks […] are blown out of the substrate and end up on the surface next to or in the hole created by the water jet where the adult was harvested*" (Goodwin and Shaul, 1984, p. 3)

Other ecological side-effects of geoduck fishing are generally regarded as minor (Goodwin, 1978; Breen and Shields, 1983). The main visible disturbance of the removal of individual geoducks is the relatively short-term effect on the substrate. Thus, the absolute number of geoducks removed from a given plot is a reasonable index of disturbance. WDFW found no evidence of significant long-term ecological effects after 24 years of study, even though several of those possible effects have been scrutinized repeatedly in the environmentally sensitive atmosphere prevailing in the Puget Sound region.

1.4. Stock Assessment

***1.4.1. Washington*:** Stock assessment is described in detail in Bradbury et al. (1998). For purposes of stock assessment and management fishing grounds are partitioned into six *Management Regions* (North, Central and South Puget Sound, Hood Canal, Strait of Juan de Fuca, and San Juan Islands), each comprising a variable number of "*tracts*", more or less arbitrarily defined beds. The 1998 geoduck atlas (Sizemore et al., 1998) lists 267 tracts, with a total of ca. 11,940 ha (average tract area ~ 45 ha).

The biomass of each tract is assessed by the Washington Department of Fish and Wildflife (WDFW)[10] through direct transect surveys conducted by the biologists of the agency, following a quasi-systematic design. It is estimated as the product of average density, mean weight and area of the tract. Average density is estimated from siphon counts along 6x150 ft stripes, corrected by a "*show factor*" (estimated fraction of the siphons that are visible, or "*showing*"; Goodwin 1973, 1977). The biomass of a Region is the sum of the biomasses of all its known harvestable tracts. Direct diving surveys have been conducted uninterruptedly since 1967, when the basic technique was developed.

Only a limited number of tracts can be surveyed each year. The most recent estimate is used for the others, with catches subtracted when fishing has occurred after the last survey. No adjustments are made to account for natural mortality or recruitment, either separately or pooled as a recovery rate factor. Biomass estimates for all the surveyed tracts are published annually by WDFW and DNR (*e.g.* Sizemore et al., 1998).

1.4.2. British Columbia: Stock assessment is described in detail in Hand et al. (1998). For purposes of stock assessment and management the geoduck fishing grounds are partitioned as follows:

- Waters of the entire province are divided in three "*Regions*" (North Coast, West Coast, Inside Waters).
- Each Region is subdivided in three subregions with roughly equal geoduck fishing areas.
- Each subregion is partitioned into *Geoduck Management Areas (GMAs)*, of which currently there is a total of 243.
- Each GMA comprises a variable number of "*beds*". The estimated total bed area is ca. 25,200 ha (Hand et al., 1998, their Table 12), with an approximate mean bed area of 22 ha.

Catch and effort data were initially collected through a mandatory logbook program implemented in 1977, but inconsistencies were found with port validation. This led, after 1996, to a program (funded by the industry) in which port monitors collect harvest information from fishers at the time of landing[11]. Highgrading, due to dark-meat geoducks being discarded underwater, results in an underestimate of fishing mortality, but its magnitude has not been assessed. Since CPUE is not accepted as a reliable index of abundance, catch-effort data are not used in stock assessment.

Quotas (see Section 1.5.2) are based on virgin biomass, which is calculated on a bed-by-bed basis as the product of three factors:

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[10] The agency has a long experience in direct diving surveys, which started in 1967 and were never interrupted.

[11] The observer program is contracted by the UHA to Archipelago Marine Research, a private firm.

- ***Area of known geoduck-bearing habitat***, based on harvest logs and charts provided by fishers. Estimates are revised annually to incorporated newly found beds. The information is compiled and analyzed using geo-spatial software; bed areas are calculated from polygonal approximations, and in some cases "scaled" down using catch data and an *ad-hoc* protocol (Hand et al., 1998, p. 11). It is acknowledged that estimated bed area is affected by significant mapping errors (Hand et al., 1998, p.10).
- ***Virgin geoduck density***. Pre-harvest mean density has been estimated in a number of beds from a number of direct surveys. Surveys of some mapped beds have been conducted in collaboration between DFO and the industry since 1995, following a standardized protocol (Campbell et al., 1998). Since only a handful of beds have been surveyed, "virgin" biomass of beds and GMAs are generally based on *ad-hoc* extrapolations and adjustments (Hand et al., 1998, pp.13-16).
- ***Mean geoduck weight***. Analogous ad-hoc procedures are used to calculate mean weight for beds, GMAs and Regions.

1.5. Harvest Strategies

1.5.1. Washington. The harvest strategy has changed recently from constant catch to constant harvest rate. In the old strategy (before 1998) the nominal catch was determined as 2% of virgin biomass; it varied from year to year due to adjustments of the estimated virgin biomass. A constant harvest rate strategy has been introduced recently (2.7% of present biomass), based on the $F_{40\%}$ reference level.

A key element in the harvest strategy is that a tract is not opened to the harvest until a survey indicates that it has recovered to pre-harvest conditions. We refer to this, for brevity, as the "recovery provision".

Tracts considered non-harvestable do not enter the quota calculations. Areas inhabited by geoducks can be non-commercial because of pollution, low density, small extension, substrate, land-use conflicts, navigation, depth (too deep or too shallow), proximity to shore, conflicts with conservation priorities (*e.g*. eelgrass beds or proximity of bald eagle nests), etc. All these areas beyond reach of the commercial fishery constitute substantial reproductive refugia.

1.5.2. British Columbia. The harvest strategy currently in place in British Columbia, planned for a 50-year horizon, consists of three elements:

- ***Constant catch***. Hand et al. (1998, p. 17) discuss rationales supporting constant harvests that range between 0.5% and 2% of virgin biomass (B_0) per year, calculated for each bed as

  $$B_0 = AD_0\overline{W}$$

  where A is the area of the bed, D_0 is estimated virgin density, and $\overline{W}$ is mean individual weight (*op.cit.*, p.18). The current goal is 1% of virgin biomass per year. Thus, the long-term goal is to harvest 50% of the virgin biomass over a 50-year horizon.
- ***Three-year rotation time***, introduced in 1989. Within each region, subregions are harvested every three years. The quota for that year is three times the calculated annual quota[12]. The rationales for the 3-year rotation are purely logistic: easy monitoring, reduced number of landing ports, concentration of the assessment effort.
- ***Even distribution over time of the catch***, known as the "amortization program" (in place since 1995), motivated by the desire to compensate for high quotas in some areas that result from various factors (estimation errors among them). Annual quotas are adjusted (down) to evenly spread the reminder of $.5B_0$ over time, through the end of the 50-year horizon.

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[12] The sole exception is Clayoquot Sound, which is harvested every year.

Hand et al. (1998, p.2) characterize this strategy as a "*fixed sustainable harvest rate*", contradicting the explicit description in the same document of a *de facto constant catch* harvest strategy (see above). The recommended quota (a fraction of the virgin biomass) fluctuated in the past from year to year not because of updates of the estimated current abundance in combination with a constant harvest rate, but rather due to (1) adjustments made to the estimated virgin biomass, and (2) virgin biomass not being exactly the same among the subregions rotationally harvested in subsequent years. The catch has stabilized at 1797 tons since 1997.

2. SOURCES OF INFORMATION AND DATA ANALYSIS

2.1. Sources of information.

This report is based on publicly available information from Washington and British Columbia. These sources include the refereed literature, non-refereed technical reports (including annual and statistical reports) from the Washington Department of Fisheries and Wildlife (WDFW, formerly WDF) and Department of Natural Resources (DNR), and Canada's Department of Fish and Oceans (DFO, previously Fisheries Research Board of Canada), and management plans and other documents produced by WDFW, DNR and DFO. Data were digitized from the original figures when not available from the source agencies. Some older documents (including correspondence) were obtained from Washington State's Archives (Olympia), the Special Collections of the University of Washington's library, and screening of microfilmed journals. Valuable data, in all cases supporting publicly available documents, was provided by scientists and managers of all the agencies listed above. Several persons involved with the geoduck fishery (see the Acknowledgement section) shared with us valuable opinion and insight.

2.2. Natural mortality.

We assessed natural mortality with a data-set documented by Goodwin and Shaul (1984, their Fig. 6), but never before analyzed. Live geoducks and dead shells were collected from one-m^2 quadrats at three locations (Figure 3) with a Venturi dredge (reputed to be non-size selective). Only paired shells of dead animals found in the upright position within the sediment were retained to prevent the possible bias introduced by shell transport. The authors claimed that "*geoduck shells remain in the substrate many years after the death of the clam*". Thus,

$$N_i = \sum_{a=i}^{A} n_a \ ,$$

where i indexes age, A is maximum age, n_i is the number of shells of age i in the sample, and N_i is the number of shells of individuals that died at age i or older (*i.e.* that reached at least age i), should provide a schedule of average survival more reasonable than the AFD of live animals. Situations that might bias the pattern are non-stationarity in the survival schedule, or an overwhelming contribution to the dead-shell pool by one or a few year classes that have not still vanished completely. The later is unlikely in the case of geoducks, due to high longevity and low recruitment rate.

There are, in addition, two main possible sources of bias due to the *post-mortem* dynamics of the shell population:

1. *Taphonomic bias*. This would occur if the rate of diagenesis of empty buried shells varied with the age of the individual at the time of death. Fyfe (1984) showed that shell thickness increases with age, but diagenesis rates are unknown.
2. *Age-specificity in the rates of mortality due to sources that result in empty shells left at the sediment surface after death*. Goodwin and Shaul (1984) argued that most adult shells remain within the sediment. This is consistent with direct observation of natural mortality by Fyfe (1984), described earlier. While stressed individuals may be preyed upon by starfish, their shells ending up at the sediment surface, this seems to be a comparatively rare phenomenon. Removal of whole animals (shells included) by predators has been well documented for juvenile (small) geoducks, whose burrows are comparatively short, but seems to be rare in adults.

A low cut-off point of 5-10 years should be utilized to minimize these potential biases.

2.3. Historical series of year-class strength.

Published studies of age-structure of populations from Washington and British Columbia, six in total, are summarized in Table 1. In total, 7251 geoducks were aged in the combined studies, most of them sampled during the five-year period 1979-1983. Only one age-frequency distribution has been published from samples collected during the last 16 years (Noakes, 1992; n=394; see Table 1). The data from Washington were made available by Alex Bradbury (Washington Department of Fisheries and Wildlife); sampling locations are shown in Figure 3. Data from British Columbia were reconstructed by digitizing published figures (see Table 1 for references). One of the samples was taken from the commercial catch (Harbo et al., 1983); all the others were obtained during surveys of harvested and unharvested beds, mostly with commercial gear. Data were first scrutinized at the maximum scale of geographic aggregation *used by the authors* (generally that covered by the entire sample). Analyses were then conducted at scales smaller (single locations, harvested vs. unharvested sites, etc).

2.4. Experimental recovery.

During the early 1980's Lynn Goodwin (Washington Department of Fish and Wildlife) started one of the most interesting research projects dealing with geoduck harvests, which is now continued by Alex Bradbury and his co-workers. Fifteen tracts (Fig. 4) due to be fished were selected and sampled before the harvest, most of them between 1979 and 1985 (one was sampled in 1972). Within each tract, a variable number of fixed stations (between 8 and 36) were defined, each consisting of a 83.6-m^2 (900 squared feet) stripe, whose geographic location was specified as best as possible. The total number of stations that was visited on the three occasions (all tracts pooled) was 324 (see Table 8 for a summary, and Goodwin, 1996, for complete information). Adult geoducks were surveyed visually on each occasion. Each station was revisited after the harvest (1.45 to 9.1 yr after the pre-harvest survey), and again several years later (7 to 20 years after the first post-harvest survey). Data were not corrected with a "show factor", and for that reason this set is not comparable (in absolute terms) to corrected data from surveys.

3. RESULTS

3.1. Natural Mortality

The AFD of the dead-shell sample (n=459), and the cumulative frequency distribution and its log, are shown in Figure 5. Notice that the latter departs from linearity, expected under the exponential model. Mortality seems to increase with age, which is to be expected under most biologically reasonable models. Age-dependent survival has been modeled with the Weibull function (Miller and Freund, 1965),

$$N(t) = N_0 e^{-\alpha t^{\beta}}$$

where α and β are parameters and t is age of a cohort. The exponential model is a particular case of the Weibull model for β=1. We fitted the Weibull model to the observed cumulative distributions (Fig. 5, left). Estimated parameters are

$$\hat{\alpha} = 0.00174 \text{ yr}^{-1}$$

$$\hat{\beta} = 1.64$$

The Weibull model provides a very good fit over the entire age range. The exponential model seems to be a reasonable approximation to average survival for the age range 20-90 years (Fig. 5, right). The estimated value of M (0.036 yr^{-1}) is within the narrow range estimated by Noakes (1992; Table 2).

3.2. Recruitment and Year-Class Strength

The six existing AFDs (Table 1), illustrated in Figure 6, share a consistent pattern: age classes younger than (at least) 30 years appear underrepresented in the samples from both Washington and British Columbia. Given what is known about gear selectivity (Section 1.3.3), the latter cannot account for the trend. Consistently, the samples from harvested and unharvested sites in British Columbia (data from Breen and Shields, 1983) show closely similar patterns.

Time series of relative year-class strength were computed by back-calculating relative abundance at age 5+ for all the age groups represented in each sample. In these backwards projections we used the parameters estimated for the Weibull distribution (Section 3.1). Back-calculation with the exponential function ($M=.035\ yr^{-1}$) tends to exaggerate recruitment declining trends in pre-1980 decades, as shown in Figure 7 (top) with 65 year-classes (1915-1980) represented in the Washington AFD (Goodwin and Shaul, 1984).

Comparison of year-class strength time-series back-calculated (1915-1980) for the largest samples from Washington (Goodwin and Shaul, 1984) and British Columbia (Breen and Shields, 1983), show intriguingly coincident patterns (Fig. 7, bottom). The rate of decline in year-class strength is comparable across these two large geographic domains. The trends seem to be coincident even at smaller frequencies, although cross-correlation between the two series could be more apparent than real.

All but one of the AFDs were obtained around 1980, and are thus indicative of a declining trend in annual recruitment rate during at least 6 decades (1915-1980), and at a large geographical scale. A sample collected in 1990 near Gabriola Island (Noakes, 1992, his figs. 1-2; see Table 1) shows scarcity of individuals younger than 50 years, suggesting that recruitment continued declining during the 1980s.

3.3. Post-Harvest Recovery

At the time of the first post-harvest survey, density (D_{post}) was 5% to 56% of the pre-harvest level (D_{pre}) (Table 9). After a few years of recovery, density observed during the second post-harvest visit (D_{rec}) had increased in all the beds (Fig. 8), reaching from 13% to 117% of the pre-harvest level (Table 9). Close examination of Figure 8 reveals the existence of two clusters of trajectories (see Table 8 for details):

- *Fast recovery cluster*, including Mahnckes, Trebble Point, Fern Cove, Dolphin Point, Vashon East 1, Indian Island and Agate Pass. Average annual recovery rate in this group ranged between 5.1 and 11.2 geoducks/plot.
- *Slow recovery cluster*, including Big Hunter, Dougall Point 1 and 2, Fudge Point, Henderson, Kala Point, Walan Point and Anderson Cove. Average annual recovery rate in this cluster was in the range of 1.0 to 2.6 geoducks/plot.

Recovery rate results from the balance between recruitment and mortality. The recovery process was analyzed under the assumption that natural mortality is invariant across space, which is justified if (as is most likely the case) geographic variation in recovery reflects largely variation in recruitment. Four different models of the recovery process are discussed below, each of them based on a specific hypothesis about density-dependence of recruitment. Mortality was modeled with the exponential and the Weibull functions in the case of constant recruitment; since difference from the application of the two were biologically insignificant, only the exponential model was used in subsequent analyses. This is convenient, besides, because the age composition of the individuals surviving the harvest is not known.

The four hypotheses, and the corresponding models are introduced below. The scope of these models is restricted in three ways:

- They deal exclusively with post-dispersal events, the only segment of the recruitment process than can be appropriately examined with the data available.

- Post-dispersal density-dependent phenomena that affect recruitment are spread over the early years of the life-history of a year-class, from adult-larval interactions at the time of settlement through competitive interactions during the first 5 years of life, at least. These components cannot be discriminated with data from WDFW's post-harvest recovery experiments, since the time that lapsed between post-harvest and post-recovery surveys ranged from 7 to 20 years.
- The models contain no time lags, although eventual adult-larval interactions would affect recruitment with a 5+-year lag.
- It is assumed that the supply of settling larvae is site-specific and independent of local resident abundance. Trends in settlement rate cannot be assessed with these data.

Hypothesis 1: Constant recovery rate. A form of this hypothesis has been proposed by WDF biologists (Goodwin, 1996; Bradbury et al., 1998):

1. Post-harvest recovery is linear (*i.e*. recovery rate is constant) until pre-harvest density, D_{pre}, is reached. Intuitively, recruitment rate has to increase given that recovery is positive, since recruitment has to sustain population growth and offset mortality rate, which is proportional to abundance.
2. After density recovers back to D_{pre} recovery rate drops abruptly to 0. Notice that this implies that pre-harvest abundance was at equilibrium, with deaths balanced (on average) by recruitment (*i.e.*, $R = D_{pre}(1 - \mathrm{e}^{-M})$).

Lets denote recovery rate as $\Delta D = D_{i+1} - D_i$. Writing

$$D_i = D_{i-1}\mathrm{e}^{-M} + R_i$$

$$D_{i+1} = D_i\mathrm{e}^{-M} + R_{i+1},$$

substracting the second equation from the first, and rearranging,

$$R_{i+1} - R_i = \Delta D - \Delta D\mathrm{e}^{-M} \quad ,$$

which is a constant, lets call it *K*. Then

$$R_{i+1} = R_i + K \quad ,$$

and more generally

$$R_i = R_1 + (i-1)K \quad \text{, where}$$

$$R_1 = \Delta D + D_{post}(1 - \mathrm{e}^{-M})$$

Given that recovery rate was positive in all 14 stations, the assumption of linear recovery implies linearly increasing recruitment. An increasing trend in recruitment following the harvest is consistent with post-dispersal depensation (facilitation by resident adults) and recovery from environmental disturbance by the fishing process. Goodwin (1996, p.2) incorrectly contrasted linear recovery with density-dependence, probably because of mistaking constant recovery for constant recruitment.

Hypothesis 2: Constant recruitment rate. Under this hypothesis the recovery trajectory is nonlinear,

$$D_t = D_{post}\mathrm{e}^{-Mt} + R\sum_{\mathrm{i=1}}^{\mathrm{t}}\mathrm{e}^{-M(i-1)}$$

There is no post-dispersal density-dependence, *i.e*. no inhibition or facilitation of recruitment by the resident population. Abundance increases asymptotically towards equilibrium, at which deaths are balanced by recruitment.

Hypothesis 3: Compensation. In the simplest case recruitment rate declines linearly with the abundance of residents,

$$R = \alpha - \beta D$$

$$D_{t+1} = D_t e^{-M} + \alpha - \beta D_t$$

When density reaches equilibrium (at D_{eq}) recruitment is balanced by mortality,

$$D_{eq}(1-\mathrm{e}^{-M}) = \alpha - \beta D_{eq}$$

$$\beta = \frac{\alpha}{D_{eq}} - (1-\mathrm{e}^{-M})$$

Replacing above and rearranging,

$$D_{t+1} = \alpha + D_t(1-\frac{\alpha}{D_{eq}})$$

Hypothesis 4: Depensatory and compensatory phases. The logistic equation constitutes a very simple model of a recovery process that goes through a sequence of depensatory and compensatory phases, with recruitment first increasing with density until a maximum is attained, and decreasing thereafter:

$$R = D\phi\left(\frac{D^* - D}{D^*}\right)$$

Density is projected as

$$D_{t+1} = D_t\mathrm{e}^{-M} + D_t\phi(1-\frac{D_t}{D^*}),$$

which, if reparameterized in terms of equilibrium density,:

$$D_{eq} = D^*\left(1-\frac{1-\mathbf{e}^{-M}}{\phi}\right),$$

has the familiar (discrete) logistic form

$$D_{t+1} = D_t + (\phi + \mathbf{e}^{-M} - 1)D_t\left(1-\frac{D_t}{D_{eq}}\right), \qquad \phi > 1-\mathbf{e}^{-M}$$

Under hypotheses 1, 3 and 4, density is assumed to be at equilibrium prior to harvest, and to recover back to that level after harvest. Under model 2, density also approaches equilibrium, but this is different from the pre-harvest level. Figure 9 illustrates recovery trajectories under the four hypotheses for the Mahnckes tract. In each case, parameters were estimated by forcing the density trajectory to pass through D_{post} and D_{rec}. For models 1,3 and 4, $\hat{D}_{eq}$ was set equal to D_{pre}. Estimated parameters are used in Section 3.5 to explore rotational harvest strategies.

Positive post-harvest recovery, as observed in WDFW's recovery experiment, is not inconsistent with any of the hypotheses listed in Table 5. Besides, some effects are inextricable from each other with the information currently available. Under the hypothesis of constant recovery rate (*i.e.* gradually increasing recruitment rate), in particular, possible effects of environmental impact of the gear, incidental mortality of pre-recruit residents and depensation are likely to be confounded.

Results from the recovery experiment weakly support the combined [depensation + incidental juvenile mortality] hypotheses: post-harvest recovery rate is significantly and positively correlated with the number of clams left by the harvest (P = 0.03, N=14). The relation is significant even if the data point for Treble Point (highest D_{post}, Table 8) is excluded from the analysis. Under the environmental disturbance hypothesis, alternatively, disturbance of a plot should be proportional to the number of geoducks removed by the harvest. Post harvest recovery, however, is not significantly correlated with the estimated number of clams removed, ($D_{pre} - D_{post.}$). This is consistent with empirical evidence indicating that habitat disturbance by the commercial harvest is limited and short-lasting.

3.4. Depletion and Concentration Profiles.

Consistently with WDFW's assertion (Section 1.3.4), the data are not suggestive of a fix threshold, but of uniform harvest rate. Positive correlation between pre- and post-harvest density (Fig. 10, top) is statistically significant whether the data are pooled by site (left), or the plots are taken separately (right), and whether the data from Treble Point (highest density, see figures) is included or not. The distribution of the fraction left after the harvest is shown in Fig. 10 (bottom left; the Agate Pass tract, which was revisited long after the pre-harvest survey, was excluded); the mean, 0.28 (SE = 0.016, N = 264), is well within the range guessed by WDFW (0.25-0.30; Section 1.3.4). There is no comparable information available for the Canadian fishery, in which fishers' behavior is likely to be different.

The largest data set on the spatial distribution of density was compiled by Goodwin and Pease (1987, 1991) between 1967 and 1985. They presented a pooled quadrat frequency distribution covering that 18-yr period and the entire Puget Sound (Table 10; Figure 11, data digitized from fig. 6 in Goodwin and Pease, 1991). The surveys covered beds and marginal areas, as reflected in the fair number of 0-values (Fig. 11, top); density ranged between 0 and 12 geoducks/m^2, with an average of 1.66 geoducks/m^2 (including marginal areas). While the distribution of density is strongly affected by the inclusion of marginal areas, the distribution of concentration (informative about the second order properties of the spatial process) is rather robust. The size of the quadrats used in the survey (41.6 m^2; Table 10) is probably commensurate with the spatial scale of the fishing process (*i.e.*, the scale at which fishers make decisions about "staying or moving on"), but may be larger than the scale appropriate for the specification of some density-dependent processes (*e.g.* fertilization rate). The concentration profile (Fig. 11, middle) is intermediate between Types C (at low to middle density) and B (at middle to high density) in Orensanz et al. (1998, comparable to Types III and II, respectively, in Prince and Hilborn, 1998). In the population at large, ca. 95% of the individuals occurred at densities above the commercial threshold (0.3-0.5 geoducks/m^2; Section 1.3.4); 50% of the organisms experienced a concentration higher than 3.6 geoducks/m^2 (Figure 11., bottom). This profile is probably a reasonable characterization of the average conditions prevailing in the un-harvested beds during the early years of the fishery.

The best existing information about changes in concentration profiles induced by the fishery was produced by WDFW's recovery experiment (Sections 2.4 and 3.3). Changes in the profile between the pre- and post-harvest surveys, and between post-harvest and post-recovery surveys, are shown in Figure 12. This is a very broad depiction, as pre-harvest density and time between post-harvest surveys varied among beds; adjusting the profiles for those differences would be a futile exercise. The pre-harvest profile corresponds to the Type C of Orensanz et al. (1998, equivalent to Type III of Prince and Hilborn, 1998); the post-harvest profile corresponds to, respectively, Types A (Type I in Prince and Hilborn, 1998). From a biological perspective, the important point is that the fishery does not only removed a substantial quantity of geoducks, but that those which survived the harvest were very "diluted" (Figure 12, top to middle). After a few years of recovery the profile began converging back to Type C; as abundance increased the absolute number of isolated individuals decreased (Figure 12, middle to bottom). The three cumulative profiles are compared in Figure 13. The percentage of geoducks above the commercial threshold (as perceived at the spatial scale defined by quadrat size, which is not necessarily that of the divers) was 95% in the pre-harvest condition, then dropped to 65% after the harvest and rebound to *ca.* 80% after some years of recovery (the last figure may have varied among beds for the reasons indicated above).

Campbell et al. (1996a,b) presented density data for two beds that had been heavily fished in the southern interior waters of British Columbia (Comox and Marina). The two profiles (reconstructed from tables in the original documents) are strikingly similar to each other (Fig. 14, middle), but different in shape from the post-harvest concentration profile from Puget Sound recovery beds. The meaning of that difference is difficult to ascertain as the size of the quadrats used in the two surveys was very different (5 vs. 80+ m^2). The ranges of density are, however comparable, as most of the individuals occurred at concentrations below 2.5 geoducks/m^2; dilution, though, was higher in the two beds from British Columbia.

Density was estimated in the Puget Sound survey (Figure 11; Goodwin and Pease, 1991) and the recovery beds (Figure 12; Goodwin, 1996) with differing protocols (Goodwin, 1996, p.3; Bradbury, pers. comm.): quadrat size in the experiment was twice that used in the surveys, and a "show factor" correction was used only in the latter. The two profiles are not comparable for that reason. Geoducks are concentrated at *estimated densities* below 12 m^{-2} in the survey sample, while density of *show counts* in the pre-harvest component of the recovery experiment are concentrated at half that level (6 m^{-2}).

3.5. Optimal Rotation Strategy

Spatial rotation is a practicable harvest strategy provided that the resident population is sedentary, and that the harvested region can be partitioned into subregions separately manageable. Such strategies have two rationales (Botsford et al., 1993):

- A *pulse fishing* rationale: each plot or subregion can be realistically harvested every once in a while. Virtually the entire economically harvestable stock is taken on each occasion. The stock recovers between successive harvests.
- A *metapopulation* rationale: settling larvae originate in the regional reproductive pool (the sum of plots or subregions).

The two main management controls that can be applied under such scenarios include the number of partitions and the time between successive harvests.

Following a complete harvest, biomass starts to grow from 0 (at t=0) and keeps growing with the recruitment of new cohorts. Eventually, as recruitment and growth are balanced by mortality, an equilibrium is reached. In a rotational fishery a new harvest occurs much earlier. The longer the harvest is delayed, the longer it takes to acquire revenues from future harvests (Clark, 1976). Although the general presentation of the rotation problem is more easily introduced for the case of 100% harvest pulses, the rationale can be expanded to the case in which a remnant is left by the harvest. In the latter case, however, a comparison of rotational and non-rotational strategies (*e.g.* given a global target harvest rate) may be difficult.

If costs of fishing are negligible (or at least are independent of the size of the stock), the optimal harvest strategy consists of a sequence of harvest events at specific times $t = T_1, T_2, T_3, \ldots$, with the entire stock being harvested at each time. The optimal spacing of harvests must be determined from the Faustmann's equation (Clark, 1976),

$$\frac{V_1^{\#}(T)}{V_1(T)} = \frac{\delta}{1 - e^{-\delta T}}$$

$$V_1(T) = \sum_{k=1}^{T} e^{-kM}\, w(k)$$

where $V^{\#}(t)$ is the rate of increase in net biovalue in the absence of fishing (*i.e.* the potential or natural rate of increase in biovalue), k indexes cohorts, $w(k)$ is the average weight of individuals of cohort k, and it is assumed that the k^{th} cohort is recruited at time k. $V_1(T)$ denotes the value of the stock T years after a complete harvest (notice that T is an integer in this formulation). Optimal rotation period can be found graphically by plotting the curve $\Delta B(T) / B(T)$, where B is biomass, onto a chart with a family of curves of the form

$$\frac{\delta}{1 - \mathbf{e}^{-\delta T}} ,$$

each of them corresponding to a value of annual discount rate, $i = (\mathbf{e}^{\delta} - 1)$. This is equivalent to calculating the difference between leaving the geoducks in the ground, and harvesting them and putting the proceeds of the sale in the bank, at different interest rates (one per curve). Geoduck recruits quickly approach asymptotic size;

age of maximum biomass of a cohort is around 22 years (Figure 17, top). Optimal rotation (under the hypothesis of constant recruitment) is shown in Figure 17 (bottom, left), constructed with realistic growth and natural mortality parameters. The optimal rotation time is the same for all the grounds, 28 years, the reason being that growth and mortality rates were assumed spatially invariant in the analyses. This corresponds to an annual harvest rate of 3.6%.

Rotation strategies were investigated graphically for the four hypotheses about post-dispersal recruitment introduced in Section 3.3. We consider individuals instead of biomass, for two reasons: recovery rates are generally expressed in terms of density, and omitting growth facilitates centering the discussion on recruitment alone. Density-dependent growth and survival were not considered, as their significance has not been demonstrated. Pre-dispersal density-dependence (e.g. reproductive rate per capita) is beyond the frame of the analysis; larval supply is assumed constant in all the scenarios. Results are illustrated in Figure 15 for one of WDFW experimental tracts (Mahnckes). Under *constant recruitment* there is no rationale (other than bioeconomic considerations) for delaying the harvest; notice that this is not the case when biomass is considered instead, which was discussed above. Under the *constant recovery hypothesis* (Figure 15:B) the only reason not to harvest every year would be related to the cost of fishing. Otherwise, *T* has no effect until the equilibrium level is reached, but money is lost if the harvest is delayed beyond that time. Under the *compensation hypothesis* it never pays off to have the harvest delayed (Figure 15:C), because recruitment declines constantly as biomass is accrued. Under *logistic recovery* (Hypothesis 4) the harvest should be delayed at least until a certain threshold is reached (below which depensation prevails). Beyond that threshold it pays-off to delay the harvest until a certain optimal T (Figure 15:D), which in this case (contrary to the constant recruitment hypothesis) varies from plot to plot. The reason is that in the analysis it is assumed that density was at the equilibrium level before the harvest, so equilibrium level varies from plot to plot. Although the higher and lower rotation times yield the same long-term returns, the upper level should be preferred in view of considerations of pre-dispersal depensatory dynamics (lower reproductive output *per-capita* at low density levels).

Model 4 (logistic recovery) can be seen as a somewhat more realistic, smoothed-out version of Model 1 (constant recovery rate). As expected, maximum rotation time for the constant recovery model and long rotation time under logistic recovery are comparable (Table 11; Fig. 16). If all the geoducks in the plot are harvested, the upper level under Model 4 tends to be longer than maximum rotation time under Model 1, but the pattern is reverted under a more realistic harvest rate (e.g. 80%, Figure 16, bottom). Neither under Models 1 or 4 are rotation times clearly split by the slow/fast recovery dichotomy, because (i) optimal rotation time is governed by both recovery rate and pre-harvest density (assumed at equilibrium), and (ii) there seems to be no correlation between pre-harvest density and observed recovery rate. Optimum rotation time (ORT, defined as longest time under Model 4 and D_{post}=0) is longest for the four recovery beds in southern Puget Sound, ranging from 57 to 130 years (corresponding range of harvest rates is 0.8% to 1.8%). The two beds from the Port Townsend area and the one from Hood Canal fall in the slow-recovery cluster, but ORTs are relatively short (31-38 years and 16 years, respectively) because pre-harvest density was lowest in those three beds. In most of the beds from the fast-recovery beds ORT was in the range 18-31 years; the exceptions were Dolphin Pt. (which had fully recovered during the post-recovery survey) and Treble Pt. (66 years), because pre-harvest density was highest there.

4. DISCUSSION

The limited information available suggests serious reasons for concern: long-term declining trends in population size, depensatory dynamics, and geographic variation in recruitment. These, together with their implications, are discussed below.

4.1. Harvest Strategies

The nominal harvest rates implemented in British Columbia and Washington (Section 1.5) have been justified by a few exploratory analyses:

- In British Columbia, under a constant catch strategy, the nominal catch is set at $0.01B_0$. (B_0 is the virgin biomass). Constant catch and rotation strategies were examined in two projection exercises, using realistic growth and mortality parameters. Campbell and Dorociez (1992) investigated the effects of uncertainty in the estimation of B_0. Recruitment was assumed constant, at a level of $0.016B_0$. Notice that this proportionality is comparable to that observed in Puget Sound since 1920 for the relation between R_t and B_t (Figure 21, top), but low compared to constant recruitment rate estimated from the recovery experiments ($0.048D_0$ on average; see below in this same section). Breen (1992) incorporated a stock-recruitment relation (not specified in his published report); he concluded that the harvest strategy in place in British Columbia is conservative.

- In Washington, recommendations were recently made to (i) move from a constant catch ($0.02\ B_0$) to a constant harvest rate strategy, and (ii) set the target harvest rate at 2.7% of the current biomass. The rational for the harvest rate is a calculation of $F_{40\%}$ (Bradbury et al., 1998; Bradbury and Tagart, 2000).

In the case of British Columbia, using a reasonable level of natural mortality ($M=0.035\ yr^{-1}$, see Section 2.2) and Campbell and Dorociez's assumption about recruitment, population size would drop to 32% of virgin biomass by the end of the 50-year horizon over which the current policy is to be implemented. In Campbell and Dorociez's projection population declines (with or without harvest) until the declining number of deaths (proportional to population size) is balanced by constant recruitment. Obviously, harvest rate (based on a constant catch strategy) increases as population declines, to 3.1% by the 50th year in our example.

Results of our calculations of yield and reproductive output per recruit[13] for different harvest levels are comparable to those of Bradbury et al. (1998, their Table 7) (Figure 17), but a 2.7% harvest rate corresponds to an $F_{50\%}$ rather than to an $F_{40\%}$ harvest strategy. At equilibrium the $F_{40\%}$ strategy reduces population size to 40% of virgin biomass. So, in the long run, the nominal policy recently implemented in Washington may be more conservative than the policy implemented in British Columbia (at least for the recruitment rate considered by Campbell and Dorociez).

Based on a ballpark calculation Bradbury et al. (1998, p. 51) roughly estimated that the abundance of geoducks in Washington's harvestable beds in 1997 was 80% of "virgin" biomass in 1970, at the onset of the fishery. We computed simple projections using 1970 as the base year, "virgin" biomass (taken as 100) estimated by WDFW (136 million pounds), an average weight of 2.24 pounds/geoduck (calculated with data from the recovery beds), a natural mortality rate of $0.035\ yr^{-1}$, reported annual catches (WDFW and WDNR, 1995; Bradbury, pers. comm., for 1996-1997). Constant recruitment was assumed. The ratio of estimated constant annual recruitment (R, Section 3.3) to pre-harvest density (D_{pre}) was calculated for each recovery bed. Average R/D_{pre} ratios [14] were computed for the pool of all beds (reflecting conditions during the 1980s), and for the fast- and slow-recovery clusters. A range of constant recruitment figures for the entire sound was calculated as the product between "virgin" abundance (N_0) and the average R/D_{pre} ratios. The value of the calculated ratios were: 0.048 (or 4.8%) for the pool of all beds, 0.025 for the slow-recovery cluster, and 0.075 for the fast-recovery cluster. Projections of abundance are shown in Figure 18. Using the calculated average ratio, abundance in 1997 was almost exactly 80% of N_0 (1970), consistently with the guesstimate by WDFW. If anything, these trends are overly optimistic. Given that (i) all evidence points to very low recruitment during (at least) the 1960s and 1970s, and (ii) catch figures are underestimates, it is likely that abundance in 1997 was well below the level suggested both by WDFW guess and by our crude projection.

With these optimistic projections the nominal harvest rate for 1997 was 3%. Using the fast- and

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[13] We use the Weibull survival model and knife-edge recruitment. Results of the calculation vary depending on the growth, mortality and recruitment parameters utilized, but do not change the general form of the yield and reproductive output per recruit curves.

[14] Use of data from the recovery experiment in the calculation of the ratio assumes that the "show factor" error was comparable in the pre-harvest, post-harvest and post-recovery counts.

slow-recovery scenarios as extreme conditions for the entire stock, the harvest rates projected for that year were, respectively, 2% and 6.5%. Even assuming that all the catch was reported before 1994, but incorporating the upper bound of highgrading and poaching levels suggested by DNR managers for the post-Rafeedie years in 1994-1997 (Section 1.2), projected 1997 harvest rates would be 4% (average), 2.5% (fast-recovery scenario), and 9.5% (slow-recovery scenario). Assessment of highgrading, and to a lesser extent poaching, should be a major subject of concern in both Washington and British Columbia.

The notion of rotation has been always present in discussions of geoduck management, for different reasons. The 3-year rotation policy in place for each management region in British Columbia has purely operational motivations (easy monitoring, reduced number of landing ports, concentration of the assessment effort). Under the Washington management system rotation allows directing the harvests and balancing the quality of the catch, makes it feasible to comply with health-related closures (PSP, colliform bacteriae), and facilitates enforcement. Pulse fishing and rotation have been often discussed in relation to harvest rates in both management systems (WDFW and DNR, 1985; Breen, 1992, Campbell & Dorociez, 1992; Bradbury et al., 1998). Constant harvest rate and constant catch policies have corresponding pulse/rotation alternatives.

Under the $F_{40\%}$ policy, the 2.7% harvest rate recently implemented in Washington corresponds to a rotation time of 37 years, once the population has reached equilibrium at $0.4B_0$. The optimal rotation time calculated by us under the constant recruitment rate assumption (also built into yield-per-recruit analysis) was shorter (28 years), but as in the case of yield-per-recruit analysis this value depends on the growth and mortality parameters utilized in the calculations. Generally, rotation times in the range of 30-35 years appear to be conservative and close to optimal assuming constant recruitment and realistic growth and mortality parameters.

Models of the recovery process other than constant recruitment imply specific statements about recruitment rate, which in our case were based on the results of WDFW's recovery plots (Sections 3.3 and 3.5). Under the constant recovery model and an optimal rotation strategy, biomass reaches equilibrium at $0.5B_0$ by the end of the first rotation cycle, while harvest rate increases from $1/T$ to $2/T$ (T being time between successive harvests). Optimal rotation time (ORT) varies spatially within the Puget Sound region and undoubtedly throughout the entire geographic range of the species, as convincingly shown by results from the recovery experiments. The latter give a depiction of the dynamics of harvested geoduck stocks which is more proximate than yield-per-recruit or optimal rotation analyses under the assumption of constant recruitment. ORTs estimated from actual recovery trajectories were longest in southern Puget Sound (four recovery beds): ca. 85 years on average. The southern Puget Sound includes some of the best beds in Washington, and has been harvested longer and more intensively than other regions in Puget Sound (Bradbury, pers. comm.). As discussed below, it appears that harvest strategies should be tuned regionally to reflect perceived geographic variation in recruitment and recovery rates.

4.2. Declining Trend in Recruitment

AFDs assembled around 1980 are indicative of a declining trend in recruitment during at least three decades before 1975, and perhaps longer. This is a most disturbing result, since under such a scenario the fishery would be unsustainable, no matter how low the harvest rate. Alternatively, the declining trend in recruitment rate could be an artifact due to systematic under-estimation of age (mostly for older individuals), with a consequent overestimation of natural mortality. In that case the turnover of the population would be even slower than currently accepted. There is some preliminary indication that this could be the case, at least to some extent (Are Strom, pers. comm.).

Besides AFDs and beyond 1980, other data are informative about trends in abundance: the results from the recovery experiments in Washington, and trends in CPUE in British Columbia. These are discussed below.

In order to compare the absolute recruitment rates estimated from the experimental recovery plots with the trends in relative recruitment rate back-calculated from the composite AFD from Puget Sound, we re-scaled the back-calculated trends using the pre-harvest densities observed in the experimental recovery plots. This is justified by the fact that the two data sets were obtained during the same years, and that the two sets of sampling locations were widespread over the Puget Sound Basin. Levels of recruitment back-calculated for pre-1975 decades are commensurate with recruitment rates estimated for the recovery plots during the 1980s (Figure 19). Estimated recruitment rate was in the range of 0.013-0.049 recruits/m^2 in the slow-recovery cluster of plots, and 0.071-0.150 recruits/m^2 in the fast-recovery cluster[15]. On average, the recruitment rate estimated for the slow-rate cluster is within the bounds expected from AFDs for pre-1980 decades, while the rates estimated for the fast-recovery plots is comparable to the upper boundary level during the 1930s and the 1940s. This suggests that the low levels of recruitment calculated from AFDs for pre-1980s decades persisted during the 1980s in the slow-recovery cluster, while recruitment may have rebound to pre-decline levels in the fast-recovery cluster. The same pattern is captured in different ways in the various analyses described in this report. Under the constant recruitment hypothesis (Model 2), for example, fast- and slow-recovery plots are converging to density levels that are, respectively, higher and lower than pre-harvest density.

Because of differences in management strategy, interpreting CPUE data is more meaningful in the British Columbia fishery than in Washington, since here fishing effort is serially re-allocated in space by regulation. In the case of sedentary organisms, CPUE is a poor index of abundance for a number of reasons, hyperstable depletion being perhaps the most prevalent. Under hyperstability abundance declines faster than CPUE. This is problematic if CPUE is used in stock assessment as an index of abundance and, even worse, because the trend lends fishers and managers an intuitive but false feeling of “stability”. In the geoduck fishery hyperstability can have two main origins: “saturation” due to handling time, and sequential shifts in the spatial allocation of fishing effort as harvested sites are serially depleted. The experiment conducted by Campbell et al. (1998) indicates that handling time, alone, can generate hyperstability (Section 1.3.1).

Depletion at the large of scale of sub-regions was illustrated by Campbell et al. (1998, their Figs. 7 and 8). Their data show two phases in the development of the fishery, illustrated in Figure 20 for the south inside waters (SIW) subregion. Before 1990, as new beds became available to the fishery, CPUE showed an increasing trend. After 1990, when virtually all geoduck beds had been harvested at least once, CPUE declined steadily. By 1995 CPUE had declined to ca. 80% of the 1990 level. If CPUE were an index of abundance, and provided that harvest rate was effectively 1% and natural mortality was .035 yr^{-1}, the decline requires 0-recruitment rate. In that scenario, a recruitment rate above 0 would imply that CPUE declined faster than abundance (hyperdepletion), while the opposite is expected under hyperstability. While hyperdepletion (CPUE declining faster than abundance) may appear unlikely at first sight, it may be the result of fishers’ behavior, as suggested by Austin (quoted by Orensanz and Jamieson, 1998, p. 447):

> “*Market conditions greatly affect CPUE. In some fisheries, commercial diving being a good example, there is a hands-on approach to harvesting, and market price often makes fishers work slower and more carefully to make sure that a better quality product is delivered to the market. Average catch/day of geoduck divers [in British Columbia] is less now than five years ago, because fishers want to maintain their market price. This reduces their CPUE, but it does not mean the industry is in decline*”.

This interpretation, however, does not explain why CPUE continued to increase during the 1990-1995 period in the north coast region, while it declined at unison in the other two regions (west coast of Vancouver Island and south inside waters), which have been more heavily harvested. Whichever the case, it is clear that CPUE data from the British Columbia fishery deserve closer scrutiny. The depletion process has not been assessed for the commercial fishery; while the needed data may exist, they are not readily accessible at the present time (Claudia Hand, personal comm.).

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[15] Notice that here, as in other cases involving results from the recovery experiments, figures correspond to show counts, not to densities estimated with a “show factor” correction.

4.3. Depensation

As a bed or tract is depleted there is, besides the obvious change in total abundance, a less apparent effect on the spatial pattern of distribution, in particular of its second order properties (*i.e.* concentration, or distribution of organisms relative to each other; Orensanz et al., 1998). The most significant aspects of spatial pattern are captured by concentration profiles at a scale relevant to the process under study (Orensanz et al., 1998; Prince and Hilborn, 1998). Change of concentration profiles due to fishing can have pre-dispersal depensatory effects. In the case of benthic organisms with broadcast spawning and external fertilization, pre-dispersal depensation is due to the concentration-dependency of fertilization rate (Levitan and Sewell, 1998; Orensanz and Jamieson, 1998). This phenomenon has been best documented for sea urchins, but is likely to occur in all sedentary broadcast spawners. The effects of this mechanism on population dynamics are almost impossible to detect because of the different operational scales of fertilization and dispersal.

Change in the concentration profile by fishing was documented by Campbell et al. (1998) through an experiment discussed earlier in relation to handling time (Section 1.3.1). Their profiles, however, are not informative about the effects of the commercial fishery, because divers were made to fish along a systematic path. Data generated by WDFW's experimental recovery plots are most informative (Section 3.4). These are among the best data-sets available in the fisheries literature, clearly showing the change in the concentration profile as a result of commercial fishing.

The implications of depensation for management are different under the Washington and British Columbia harvest strategies. The British Columbia strategy, in which relatively large regions are lightly harvested every year should be preferred if density-dependence were predominantly depensatory. Differences between the two systems, however, may be more apparent than real. In British Columbia effort may be concentrated in small areas, albeit due to fishers behavior rather than regulation. The spatial dynamics of the fishing process remain little investigated in British Columbia (the subject is far less relevant in Washington).

Evidence of post-dispersal depensation in geoducks is weak but consistent (Section 1.1.7; Table 5), and is supported by recovery rate in the experimental plots. While the levels at which pre- and post-dispersal depensation occur are uncertain in the case of geoduck stocks, the long-term decline in density suggested by the analysis of AFDs reinforces the need for caution. The impending risk is that harvests could compound the effects of natural causes, accelerating an existing trend and creating everywhere the scenario required for depensation to occur.

4.4. Geographic Pattern in Recruitment

Evidence of highly variable recovery rate in WDFW's experimental plots (Section 3.3 and 4.4) prompts the question of whether there is some identifiable distinction between slow- and fast-recovery clusters. Goodwin (1990, p.29) offered a clue:

> *" In general, recruitment is higher in tracts where water currents are of medium velocity, such as the northern end of Hood Canal, Wyckoff Shoal, and the east side of Bainbridge Island, and very low in areas with little water current like the upper ends of Carr and Case Inlets."*

Beds in the *fast-recovery cluster* tend to coincide with moderate to fast water currents:

- Indian Point, located at an exposed location at the south of Admiralty Inlet.
- Agate Pass, well known for its rather fast currents.
- Dolphin Point and Vachon East, located along the west coast of Vashon Island.
- Information is ambiguous in the case of Fern Cove, on the NE of Vashon Island, but currents are presumably in the moderate category.
- Mahnckes, located in Pitt Passage.
- Treble Point (Anderson Island, south of Mahnckes), where currents are "moderate" according to

Bradbury (pers. comm.).

Beds in the *slow-recovery cluster* tend to coincide with “slow” water currents:

- Kala Point and Walan Point are located between Marrowstone Island and the mainland, an area characterized by eddy circulation, little current action (Bradbury, pers. comm.), and predominantly fine sediments.
- Dougall Point and Fudge Point are located in Case Inlet, a region with very weak currents.
- Of the other two locations in the South Puget Sound region, currents are “significant” in Big Hunter but “moderate to weak” in Henderson.
- Anderson Cove, located in Hood Canal, has very little current action (Bradbury, pers. comm.)

There are few contradictions, mostly Big Hunter which falls in the slow-recovery cluster in spite of significant currents. It must be stressed, however, that “flow” categories are subjective. Bradbury (pers. comm.), assuming that the current regime is correlated with sediment texture, calculated an “index” based on the latter. No correlation was found between the index and recovery rate.

The dynamics of recruitment could be affected by other environmental factors. Slow-recovery beds tend to be located in confined waters: the southern end of Puget Sound, the embayment south of Port Townsend, and Hood Canal; locations in the fast-recovery cluster, by contrast, are located along main Puget Sound and parallel waterways west of Vashon and Bainbridge Islands. If this pattern were real, its hypothetical causes could relate to connectivity in geoduck metapopulations: beds exposed to relatively intense flushing might receive settling larvae from a larger set of sources.

Post-hoc speculation about geographic patterns in the dynamics of recovery would be insufficient to specify spatially variable harvest rates, but should be the basis to advance hypotheses that could be addressed through an expanded network of monitored plots. The implications for management are serious. The dynamics of geoduck beds vary so much over the Puget Sound basin (and presumably also in British Columbia) that a single harvest strategy may prove unsustainable in some subregions. The possibility of spatial variation in the harvest rate was advanced by Campbell and Dorociez (1992), but never explored further. Yet, both fisheries are managed with implicit (albeit radically different) goals regarding spatial variability in harvest rate:

- In British Columbia the implicit goal is to make the distribution of the harvest rate as even as possible (primarily over time, but consequently also in space). The management component implemented to that end is the so called “amortization program”.
- In Washington there is a global harvest rate, but the “recovery provision” (Section 1.5.1) effectively leads to spatial tracking of recovery rate, as fast-recovery tracts are visited more often than slow-recovery ones.

In both systems there are other sources of spatial variation in harvest rate. Conflict with other users of the sea bed (primarily in Washington), accessibility (*e.g.* depth), and fishers’s (primarily in British Columbia), sequester large segments of the population to the harvest, creating significant *de facto* reproductive refugia. This, more than any fishery regulation, may be the ultimate guarantee for the sustainability of these fisheries.

Spatial patterns of harvest are hard to reconstruct from WDFW or DFO documents. In Washington the largest portion of the harvest tended to concentrate in the South Region of Puget Sound before 1994 (Bradbury, pers. comm.), for different reasons. First, those areas are closest to management agencies and traditional processing sites, and more accessible to stock assessment crews; second they harbor good geoduck beds in terms of size, density and quality. After the Rafeedie Decision was implemented the harvest had to be spread out over all the management regions. Historically, then, harvest rates have been much higher in the South Region, which happens to be within the slow-recovery cluster.

Under the “recovery provision” the Washington system provides for a sustainable fishery if the management region contains a mixture of fast and slow recovery tracts (or beds); the combined recovery of the mixture is such that the target harvest rate can be sustained. If this were not the case, the harvest could turn into a mining operation: after all beds have been harvested once the fishery should be closed until some beds start reaching the pre-harvest level. Some parts of Puget Sound (e.g. Case Inlet) may fit this depiction.

4.5. Summary

Adult geoducks are found aggregated in dense beds, and have tremendous reproductive potential: millions of larvae are produced *per capita* during each reproductive season. Intuitively, such populations are regulated through over-compensatory post-dispersal density-dependence; a virtually unlimited supply of prospective settlers would be regularly available to fill-in gaps created by mortality of residents in crowded beds. Using close-population stock-recruitment relations as a metaphor, these are situations in which the slope of the ascending branch is typically very steep (*i.e.*, the parameter capturing the density-independent phase tends to be high): few breeders can quickly replenish a population decimated by mortality (*e.g.* by fishing). Geoducks are among the longest-lived animal species: maximum age recorded is above 140 years (Shaul and Goodwin, 1982). Extreme longevity should confer great stability to such populations.

However, as discussed above, AFDs compiled around 1980, combined with existing estimates of natural mortality, suggest that by that time recruitment rate had been declining over decades at a large geographic scale. The reasons remain unknown. Evidence of low settlement/recruitment rate in locations where the resident population was removed (experimentally or by fishing) is consistent with this depiction. Abundance presumably declined monotonically, trailing the downward trend in year-class strength (Figure 21). Our backcalculations suggest that abundance in recent years could be as low as 40-50% of its level during the 1930s, at least in Puget Sound. If this were the case, abundance would be (on average) well below the level at which widespread compensation may be expected to occur, assuming that carrying capacity has not changed.

Recovery-rate data from harvested beds in Washington point to broad geographic patterns of post-harvest dynamics; in some regions recruitment rate does not appear to have rebound during the 1980s. Under the constant recruitment hypothesis, several beds are not recovering to the pre-harvest density level; under the constant recovery rate or depensation-compensation models recovery time would be in the order of 85 years in southern Puget Sound. In the worst case, abundance could be declining in low-recruitment regions to levels at which depensatory mechanisms start to operate. Post-harvest concentration profiles indicate that, as expected in a diving fishery, reduction in abundance is accompanied by dilution of the stock. If, as suggested by AFDs, the stock is at an historical low level, the possibility of widespread pre-dispersal depensation is perhaps the most troublesome of all concerns, even if the most difficult to gage.

The Washington system has two significant safeguards against overfishing: extensive *de facto* reproductive refugia and the “recovery provision”. Both have potential limitations. The main refugium is in deep water beds, whose abundance has been guessed but never assessed. Also, it is unknown to what degree deep beds contribute to recruitment in shallow regions.

Nominal harvest rates are relatively low in both systems: $0.01B_0$ (constant catch) in British Columbia, $.027B_t$ (constant harvest rate) in Washington. The first has been justified through intuition and simple projection exercises, the second by the $F_{40\%}$ criterion. Data from the recovery experiment point to a far more proximate alternative, one rarely encountered in fisheries management. Most significantly, the recovery data incorporate the effects of trends in recruitment, poaching and highgrading. A well designed monitoring program, based on the WDFW’s recovery experiment as a precedent (see below), could reveal geographic patterns and temporal trends, permit testing significant hypotheses on geoduck dynamics, and point to eventual reasons for concern.

Sustainability of this fishery may be more problematic than we anticipated at the onset of this inquiry. Only a catastrophic event could impede harvests from taking place over the next decade. But geoducks are unusual animals. While extreme longevity must confer high stability to this system, perceived stability may be exaggerated as a result of short-term observation scale.

Recommendations on most urgently needed research

We perceive the following as the most urgently needed research components to reduce serious risks and uncertainties in the management of this resource:

[1] AFDs have not been collected in Washington or published in British Columbia since the early 1980s. An extensive ageing program (or communication of existing results), with broad geographic coverage, is urgently needed in both areas. In the past AFDs were collected mostly to assess growth and mortality parameters, but the reconstruction of historical time series of year-class strength should be the focus in the future.

[2] Washington's recovery experiment is the most significant source of knowledge about the dynamics of harvested geoduck populations, yet it remains largely unutilized. An expanded program along these lines could provide consistent and proximate rationales for sound management. Recommendations to that end follow:

- The recovery experiment conducted by WDFW should be expanded, and if possible coordinated with a similar effort in British Columbia.
- The expanded network should be designed to investigate habitat-related and location-related effects on recovery rate.
- Habitat variables (*e.g*. sediment type, currents) should be assessed objectively in the plots (*e.g*. through the deployment of current meters).
- Geographic coherence in recovery should receive special attention, as it is possibly a major consideration in the identification of metapopulations and the bounding of management units.
- Plots in beds that have been never open to the fishery should be included in the network to serve as controls.
- Plots in harvested beds should be inconspicuously marked, so that recovery incorporates the effects of poaching.
- Plots should be revisited frequently (ideally on an annual basis). Emphasis should not be in testing the statistical significance of differences in abundance between successive sampling dates, but on tracking trends at multiple locations.

[3] Catch and effort data from the British Columbia fishery should be carefully scrutinized. Even if limited as an index of abundance, experimental data (*e.g*. as presented by Campbell et al., 1998, and re-analyzed here in Section 1.3.1) should make it possible to investigate trends in CPUE. Besides CPUE, the spatial dynamics of effort allocation should be a significant component in the assessment of this fishery.

[4] A GIS component should be added to the stock assessment, both in Washington and British Columbia. This seems an obvious requirement when, as seems to be the case in British Columbia, the spatial allocation of harvest effort needs to be fine-tuned if the fisheries are to be sustainable. The GIS system should incorporate environmental information (*e.g*. current patterns), and ideally should have a good interface with spatial statistics software (*e.g*. as between ARCVIEW and S++ Spatial). Use of geo-spatial software by DFO is a significant step in that direction.

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[16] A revision of the EIS is in the making, but is not expected to be available to the public until sometime during year 2000.

TABLES

Table 1. Published age frequency distributions of live geoduck samples from Washington and British Columbia, with indication of maximum recorded ages.

Site	**Years**	**Type of sample**	**Sample size**	**Maximum age (years)**	**Study**
Puget Sound and Hood Canal (Washington), 2	1979-1982	11 unharvested sites; commercial gear	1736	131	Goodwin & Shaul, 1984
		3 unharvested sites, venturi dredge	421		
Clayoquot Sound, west coast of Vancouver I.	1980	Unharvested site; commercial gear	260	101	Fyfe, 1984
Both coasts of Vancouver I. (BC), 5 sites	1981	Harvested and unharvested sites; depletion of plots with commercial gear	2276	126	Breen & Shields, 1983
British Columbia (mostly west coast of Vancouver I.), eight landing sites	1981-1982	Commercial catch	1396	146	Harbo et al., 1983
Hammond Bay, near Nanaimo (BC)	1982-1983	Commercial gear	365	107	Sloan & Robinson, 1984
Ladysmith Hbr., near Nanaimo (BC)	Nov-Dec, 1980	Previously unharvested site; presumably commercial gear	403	102	Noakes & Campbell, 1992
Near Gabriola Island (BC)	1990	Presumably commercial gear	394	105	Noakes, 1992[1]

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[1] Noakes (1992) also reports the AFD of samples from Bamfield (his Fig.3:A, n=993) and Ladysmith (his Fig. 3:B, n=847). It is not clear if the sample from Ladysmith used in the study by Noakes and Campbell (1992, n=403) is a subset of that reported by Noakes (1992)

Table 2 . Published estimates of the exponential coefficient of natural mortality (M). In all cases they are based on catch-curve analysis.

Study[1]	Low cutoff	High cutoff	Age interval for grouping the data	Range of estimated *M* values (yr^{-1})
Breen & Shields (1983)[2]	10	None	2?	.014 - .019
Sloan & Robinson (1984)	0 21	None	5	.035 .054
Noakes (1992)[3]	20-50	None	5	.034 - .038
Bradbury et al. (1998); Bradbury and Tagart (2000)[4]	28	98	1	.0226

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[1] Details of each study in Table 1.
[2] The sample from one location, deemed uninterpretable, was excluded from the analysis.
[3] Based on data published by Breen and Shields (1983), Harbo et al. (1983) and Noakes and Campbell (1992).
[4] Based on data published by Goodwin and Shaul (1984).

Table 3. Published information on pre-recruits abundance and recruitment rate for various sampling devices, and associated size or life-history stages

Region	Site	Type of study	Sampling techniques	Years	Life-history stage	Observation	Study
Dabob Bay, Hood Canal (WA)	Fisherman Pt.	Tracking SFDs over irregularly spaced dates	Purportedly unselective samples collected by divers	1969-1972	Juvenile pre-recruits (ages 1+ to 2+)	1969-1970 YCs tracked; 1968 and 1971-1972 Ycs apparently insignificant	Goodwin (1976)
“”	Dosewallips River	“”	Catch from sport diggers	1968 and 1972	“”	1968 and 1969-1970 YCs observed in the SFDs	“”
West coast of Vancouver I. (BC)	Clayoquot Sound	Follow-up of mapped individual location in a 10-15 m^2 stripe.	Monthly visual checks.	1980-1982 (22 months)	Siphons visible to divers.	No recruitment observed.	Fyfe (1984)
		Three 16-m^2 plots dug-out, all geoducks aged; one plot revisited 2 years after sampling.	Commercial gear		Vulnerable to commercial gear	No geoducks younger than 4 years; no recruitment in one of the plots 2 years after sampling	
Puget Sound	Four widespread sites	10- to 12-m^2 plots (one per site) excavated; excavated plots and adjacent undisturbed controls sampled 11 years later	Venturi dredge	Plots excavated in 1970, resampled in 1981	0-4 years old	No juveniles (0-4 yr) found in 6 out of 8 plots in 1981, and only one in each of the other two (one disturbed, one control)	Goodwin & Shaul (1984), their Experiment # 1
North end of Hood Canal (WA)	Port Gamble	One-m^2 quadrats sampled annually.	“”	1977-1981	Young of the yearc	0.4-1.6 juveniles per m^2	“” Their Experiment # 2
Puget Sound and Hood Canal	Six widespread sites; harvested and undisturbed beds	Mostly one-m^2 quadrats (some were larger), one-time sampling	“”	Not stated; presumably late 1970s or early 1980s	0-4 years old	Average per m^2 (n): Fished: 0.54 (62) Undisturbed: .78 (79)	“” Their Experiment # 3

Table 4. Basic hypotheses about density-dependent processes in populations of benthic, sedentary suspension feeders with broadcast spawning, external fertilization, and pelagic larval development. "Density", as used here, corresponds to the first order properties of the spatial process; "concentration" corresponds to the second order properties (Orensanz et al., 1998)

	Compensatory	Depensatory	Interaction
Pre-dispersal, Concentration-dependent: Concentration profile of residents affecting reproductive output	Growth rate and (consequently) reproductive output (*e.g.* number of eggs spwned *per* reproductive season, *per capita*) reduced at high concentration[1].	Fertilization rate declines at low density, a phenomenon that has received considerable attention in recent years (Levitan and Sewell, 1998); well documented for sea urchins.	Due to balance at the local scale, the reproductive contribution **per site** may be relatively invariant over a wide range of density of resident adults
Post-dispersal, Density-dependent: Density profile of residents affecting settlement/recruitment rate	Settlement/recruitment inhibited at high density of adult residents, due either to filtration of settling larvae, or to over-competition of pre-recruits by resident adults.	Preferential settlement and/or survival of juveniles in the vicinity of resident adults. Facilitation of settlement may relate to attraction of settling larvae to adult conspecifics, or to hydrodynamics around siphons at the benthic boundary layer (*e.g.* Jumars et al., …).	When both operate, recruitment to a given site could be highest at an intermediate level of density of adult residents

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[1] The effects of competition on growth rate are likely to be effective only above some density threshold (*T1* in Fig. 2). Per-capita reproductive contribution rarely drops to 0 at carrying capacity, although this has been shown to happen in some sea urchins.

Table 5. Hypotheses proposed to explain the local effects of the harvest on post-harvest trends in recruitment rate, and supporting evidence. Only hypotheses involving local-scale processes are listed. "Recruits" include pre-harvest resident juveniles and post-harvest new settlers.

Hypothesis	**Recruitmen trends expected under hypothesis**	**Existing evidence**
No effect	Same recruitment trends in harvested and unharvested plots	Negated by the repeated direct observation of juveniles being dislodged from the sediment by harvesting operations[1]. Inconsistent with observation of higher density of pre-recruits in unharvested plots than in harvested ones of the same tracts (Goodwin and Shaul, 1984; their Experiment # 3).
Post-dispersal over-compensation	Recruitment rate high immediately after harvesting, then gradually decreasing.	No experimental evidence of post-dispersal compensation. If observed, declining recruitment rate after the harvest could be confounded with global declining trends.
Post-dispersal depensation	Negative effect of removal of resident adults; settlement/recruitment improves as the adult resident population builds up.	Consistent with positive correlation between number of adults left by the harvest and recovery rate in the recovery experiment. Suggested by recurrently observed aggregation of juveniles in the vicinity of adults. Enhanced survival consistent with experimental results on survival of planted juveniles (Goodwin & Shaul, their Experiment # 4).
Incidental mortality	Recruitment drops after the harvest due to the incidental mortality of juveniles, then recovers as post-harvest settlers start reaching harvestable size	Indicated by the repeated direct observation of juveniles being dislodged from the sediment by the harvest. Presumably exacerbated by the tendency of juveniles to occur in the vicinity of adults (*e.g.* Goodwin & Shaul, 1984, their Experiment # 5). For that reason, consistent with positive correlation between number of adults left by the harvest and recovery rate in the recovery experiment.
Environmental impact	Gradual increase in recruitment rate after "healing" of the substrate from disturbance caused by the harvest	Inconsistent with lack of correlation between number of clams harvested (an index of disturbance) and recovery rate in the recovery experiment. Inconsistent with repeated documentation of moderate ecological effects of harvesting. Experimental results inconclusive (Goodwin & Shaul, their Experiment # 6).

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[1] Notice that, due to incidental juvenile mortality, recruitment rate will tend to increase over time following the harvest, even if settlement rate is constant and not affected.

Table 6. Comparison of Washington and British Columbia management systems.

		Washington	British Columbia
	Commercial fishery started	1970	1976
	Administrative level at which the fishery is assessed and managed	State	Federal
	Agencies involved in assessment and management	Washington State Departments of Fish and Game (WDFG) and Natural Resources (WDNR) Sampling conducted by the agency	Department of Fisheries and Oceans (DFO) Sampling contracted with a private company (Archipelago)
Assessment	Mapping of beds or tracts based on:	Direct diving surveys; visual census of abundance	Information from log-book program
Harvest strategy	Nominal strategy	Constant harvest rate (2.7% of standing stock)	Constant catch (1% of virgin biomass)
	Rationale	Reference points ($F_{40\%}$)	Conservative policy; no formal rationale
	Effort allocation	Pulse fishing with rotation.	Effort spread over the entire region
Management	Management system	State agencies auction chunks of quota, by tract	IVQs
	Participation of fishers in assessment/management	Not significant	High, mostly through UHA involvement; fishers provide information to observers
	Funding of stock assessment/management	Directly by the State, but indirectly through heavy taxation of the fishers	Significant direct contribution from the industry
Management issues	Quality selectivity	Highgrading, discards in situ (on the bottom) Encouraged by taxing system and market demand, combined	Selection by spatial allocation of effort Encouraged by market demand
	Poaching	Discouraged through enforcement	Nominally discouraged through user rights (IVQ system)
	Allocation	Very complex after the Rafeedie decisions, which granted 50% of the quota to the tribes	Simple; quota divided in equal parts among license holders
	Conflict with other users of the coastal zone	High, mostly with beach-owners, recreational users, environmental or conservation concerns, etc	Comparatively low; much of the fishing grounds in low populated regions

Table 7. Factors influencing vulnerability in the geoduck fishery.

Factor	**Comments**	**Documentation**
Exposure, accessibility and proximity to port	These factors are well illustrated by the Canadian fishery, which has gradually expanded over the years into more remote beds of the North Coast.	Campbell et al. (1998)
Depth	Areas deep are beyond the reach of commercial divers, at least with the diving technology currently in use.	
Type of substrate	Sediment quality affects the ease of digging: softer sediments (silt or sand) are more easily harvested than comparatively harder ones containing shell or rocks.	Campbell et al. (1998)
Visibility	Silting created by fishing itself interferes with visibility making it difficult for fishers to work close to each other; also forces development of non-visual skills for geoduck search (e.g. tactile recognition and spatial memory).	
Seasonal level of activity	Fishers locate a geoduck by the opening of its siphons at the sediment surface, called a "show". Assessment of the "show factor" (fraction of adults "showing") has been an early and concern in the estimation of abundance from visual census data. Showing has a strong seasonal component, being minimal in winter (down to 5% in January; Goodwin, *op.cit.*) and maximal in summer (above 95% in Fyfe's study, *op.cit.*). WDFW uses a 0.75 show factor to correct visual surveys of abundance.	Goodwin (1973, 1977) Fyfe (1984)
Size[1]	Sizes of the animal and the show are correlated only in the case of smaller individuals. Size-selectivity is implicit in Figure 4:B of Campbell et al. (1998). As depletion proceeded below a density of 1 geoduck m^{-2}, mean weight in the catch declined consistently during the second year of the experiment. This is indicative of larger geoducks having been removed first. In the commercial fishery divers may select smaller or larger sizes depending on the market.	Campbell et al. (1998)
Age[1]	Gear age-selectivity reflects correlation between size and age; no selection is likely for geoducks older than 10 years. "*The detection of a 4 year old geoduck appears to be no less efficient than that of an older one*" (Fyfe, *op.cit.* p. 6). A size at recruitment of 300 g, originally suggested by Goodwin (unpubl.) corresponds (on average) to ages of 5 to 7 years, depending on the ground. Harbo et al. (1983) claimed (but did not substantiate) that recruitment to the fishery may take place between the ages of 4 and 12 years.	Fyfe (1984) Goodwin (unpubl., cited by Bradbury et al., 1998) Harbo et al. (1983)
Quality[1]	Besides size, quality is associated with meat color (the lighter the better), which is not predictable from the show. High-grading, a major and generally acknowledged problem in geoduck fisheries, is associated with meat color. Quality may vary with age (the older the darker).	
Location as related to size and/or quality	Color and size vary geographically. In the absence of regulations fishers tend to harvest high quality beds first, a major concern in the Canadian fishery.	
Density	Discussed in the text in relation with the functional response and the depletion process.	
Areas unavailable due to various regulations	Fishing in Washington is restricted by regulation to depths in the range 5.5-21 m. Other restrictions (enforced in the two countries) are related to pollution, military use, navigation lanes, the recreational use of the coastal zone, environmental impact, trespassing of private tideland boundaries (in Washington only), etc.	

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[1] This refers to "gear" selection, not to indirect selection through the spatial allocation of effort.

Table 8. Summary of data from WDFW Recovery Study (mostly from Goodwin, 1996; some data from WDFW, 1998 Atlas). Densities are averages for all the plots from each bed.

Bed name (bed name and number as in Atlas, WDFW, 1998)	Bed number	Area of bed (ha)[1]	Number of plots	Date of pre-harvest survey	Pre-harvest density (average per plot)	Period of the harvest	Harvest (number of geoducks)[2]	Harvest rate[3]	Date of post-harvest survey	Time between pre- and post-harvest surveys (yr)	Post-harvest density (per plot)	Date of post-recovery survey	Time between post-harvest and post-recovery surveys (yr)	Post-recovery density (per plot)
Kala Pt.	4250	26.3	20	Apr. 1985	68.3	1985/86	270000	0.94	Oct. 1987	2.5	3.3	June 1993	5.6	9.2
Walan Pt.	4350	61.5	24	June 1985	45.3	1986/87	353000	0.79	Sep. 1988	3.3	6.4	Sep. 1993	5.0	11.4
Indian I	4700	30.8	22	May 1985	94.4	1985/86	361000	0.78	Oct. 1987	2.4	14.2	June 1995	5.7	61.5
Agate Pass	6800	63.1	21	Apr. 1972	91.5	1970/80	3625000	*	May 1981	9.1	22.9	May 1992	11.0	78.8
Dolphin Pt.	9000	14.6	24	May 1983	104.1	1984	441000	*	July 1985	2.2	57.8	June 1993	7.9	121.8
Fern Cove	9400	46.9	36	May 1983	123.4	1984	472000	0.51	July 1985	2.2	55.4	June 1992	6.9	118.6
Vashon E 1	9750	21.4	26	Apr. 1983	159.2	1984	395000	0.73	July 1985	2.3	23.6	Sep. 1993	8.2	83.4
Mahnckes	12950	29.5	28	June 1983	160.6	1984	201000	0.27	July 1985	2.1	39.3	May 1993	7.8	126.8
Treble Pt	13300	6.1	14	June 1983	294.3		259000	0.91	July 1985	2.1	124.0	May 1993	7.8	193.5
Dougall Pt. 2	15550	8.1	8	May 1982	142.1		349000	*	June 1984	2.1	25.9	Jul. 1994	10.1	45.4
Dougall Pt. 1A	15600	10.5	14	Apr. 1984	118.5		351000	*	July 1986	2.3	13.9	Jul. 1994	8.0	28.7
Fudge Pt	15650	28.3	22	May 1982	108.0		574000	1.18	June 1984	2.1	26.0	Jul. 1994	10.1	37.1
Henderson	16250	23.9	33	May 1984	175.3		714000	1.07	July 1986	2.2	54.5	Jul. 1992	6.0	69.0
Big Hunter	16900	37.6	16	Feb. 1981	154.7		951000	1.02	Aug. 1982	1.5	13.8	May 1993	10.8	42.3
Anderson Cv.	22550	26.3	13	May 1985	47.3		96000	0.48	Oct. 1988	3.4	3.9	June 1992	3.7	13.0

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[1] The size of three beds (Agate Pass, Mahnckes, Treble Pt.) reported by Goodwin (1996, transcribed here) and WDFW (Atlas, 1998) are inconsistent.

[2] There are some inconsistencies between the catch reported by Gooodwin (1996, in numbers) and in the WDFW Atlas (WDFW, 1998, in pounds). For Dougall Pt. 1A and 2, and Fudge Pt., the number of pounds and geoducks is the same. For Mahnckes, the Atlas reports too many pounds, and for Dolphin Pt. too few, for the numbers reported by Goodwin (1996).

[3] Entries marked as "*" correspond to incongruously high apparent harvest rates.

Table 9. Summary of exploratory analysis of data from WDFW Recovery Study (Table 8).

					Model 1: Constant recovery rate		Model 2: Constant recruitment rate			Model 3: pure compensation $R = \alpha-\beta D$		Model 4: depensatory and compensatory phases
Bed name (bed name and number as in Atlas, WDFW, 1998)	Bed number	Post-harvest as a fraction of pre-harvest density	Post-recovery as a fraction of pre-harvest density	Pre-harvest R if population at equilibrium	Average recovery rate (geoducks/yr)	Time to recover to pre-harvest condition, constant recovery rate	Recruitment rate	Equilibrium density under constant recruitment	Time to recover to pre-harvest condition, constant R[1] (yr)	α	β	ϕ
Kala Pt.	4250	0.05	0.13	2.3	1.05	65	1.1	32.7	N/A	1.08	0.016	0.240
Walan Pt.	4350	0.14	0.25	1.6	1.01	45	1.2	35.9	N/A	1.23	0.027	0.184
Indian I	4700	0.15	0.65	3.2	8.32	11	8.6	249.3	11	13.02	0.138	0.449
Agate Pass	6800	0.25	0.86	3.1	5.10	18	6.1	178.0	16	13.00	0.142	0.295
Dolphin Pt.	9000	0.56	1.17	3.6	8.10	11	10.2	296.0	5	N/A[2]	N/A	N/A
Fern Cove	9400	0.45	0.96	4.2	9.12	14	11.1	323.9	7	38.83	0.315	0.463
Vashon E1	9750	0.15	0.52	5.5	7.33	22	8.6	249.3	26	11.16	0.070	0.275
Mahnckes	12950	0.24	0.79	5.5	11.19	14	12.7	367.8	12	23.69	0.148	0.339
Treble Pt	13300	0.42	0.66	10.1	8.87	33	13.0	377.1	31	18.69	0.063	0.155
Dougall Pt. 2	15550	0.18	0.32	4.9	1.93	73	2.9	83.7	N/A	2.59	0.018	0.110
Dougall Pt. 1A	15600	0.12	0.24	4.1	1.86	64	2.4	69.3	N/A	2.25	0.019	0.149
Fudge Pt	15650	0.24	0.34	3.7	1.10	98	2.0	58.0	N/A	1.56	0.014	0.085
Henderson	16250	0.31	0.39	6.0	2.43	72	4.3	124.0	N/A	3.70	0.021	0.096
Big Hunter	16900	0.09	0.27	5.3	2.65	58	3.2	92.7	N/A	3.15	0.020	0.162
Anderson Cv.	22550	0.08	0.27	1.6	2.45	19	2.4	70.9	29	2.70	0.057	0.441

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[1] N/A: equilibrium density calculated for constant recruitment is below pre-harvest level.

[2] Dolphin Point recovered to a density higher than D_{pre}

Table 10. Density of geoducks estimated during diving surveys. The estimates were based on show counts (adjusted with a “show factor”) in all cases. Estimates for small experimental plots are not included.

Region	**Period**	**Status**	**Quadrat size**	**Mean density (geoducks per m^2)**	**SD**	**N (quadrats)**	**Source**
South Puget Sound	Cumulative sample; presumably from 1967 through mid 1980s[1]	Presumably unharvested beds	41.6 m^2	2.0	2.5	2966	Goodwin & Pease (1987, 1991)
Central Puget Sound	“”	“”	“”	1.7	2.2	3014	“”
Hood Canal	“”	“”	“”	1.9	2.4	1408	“”
Strait of Juan de Fuca	“”	“”	“”	0.6	0.9	1094	“”
North Puget Sound	“”	“”	“”	0.2	0.4	196	“”
Puget Sound (recovery beds)	1979-1985[2]	Pre-harvest	83.6 m^2	1.44	1.01	300[3]	Goodwin (1996)
“”	Beds revisited 1.5 to 3.4 years later	Post-harvest	“”	0.49	0.69	“”	“”
“”	Beds revisited for a second time 3.7 to 10.8 years later	Post-recovery	“”	0.89	1.04	“”	“”
Marina (British Columbia, South Inside Waters)	1992	Heavily fished	5 m^2	0.23	-	3843	Campbell et al. (1996b)
Comox (Ibid.)	1993	“”	5 m^2	0.30 (0.68-0.80 at 12-16 m depth)	-	3238	Campbell et al. (1996a)

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[1] Average density for the entire Puget Sound was 1.66 geoducks m^{-2}

[2] The Agate Passage bed, what first sampled in 1972 and revisited 9 years later, was not included in the analysis.

[3] A group of 24 plots with anomaloues data were excluded from the analysis. Anomalies include post-harvest grwater than pre-harvest density, and obvious outlaying figures.

Table 11. Rotation times and associated harvest rates for Models 1 and 4. No discount rate was considered.

Model:	Constant Recovery Rate			Depensation/Compensation Phases			
	Maximum rotation time	Harvest rate corresponding to maximum rotation time (as %)	Years to recover to 20% of pre-harvest density	Minimum rotation time	Maximum rotation time	Harvest rate corresponding to optimal rotation time (as %)	Years to recover to 20% of pre-harvest density
Big Hunter	58	1.7	11	9	57	1.8	30
Dougall Pt 2	73	1.4	14	15	92	1.1	48
Fudge Pt	98	1.0	19	22	130	0.8	66
Mahnckes	14	7.0	4	5	26	3.8	14
Treble Pt	33	3.0	7	10	66	1.5	38
Fern Cove	14	7.4	3	4	18	5.6	9.5
Henderson	72	1.4	14	18	117	0.9	63
Dolphin Pt	11	9.0	3	N/A	N/A	N/A	N/A
Vashon E 1	22	4.6	4	6	31	3.2	17
Dougall Pt 1A	64	1.6	12	10	60	1.7	30
Indian I	11	8.8	2	4	18	5.6	10
Kala Pt	65	1.5	13	7	31	3.2	15
Walan Pt	45	2.2	9	9	38	2.6	17
Anderson Cove	19	5.2	4	4	16	6.3	7
Agate Pass	18	5.6	4	5	27	3.7	13

FIGURES

Figure 1 Historical catch (metric tons) in Washington and British Columbia.

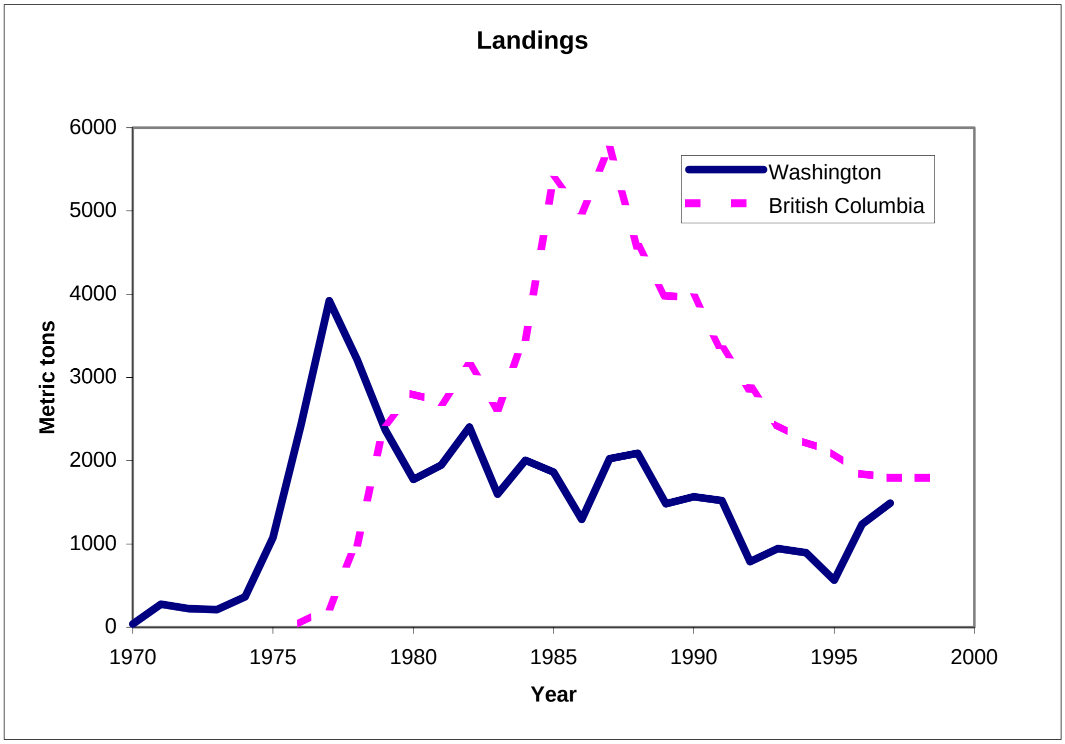


Figure 2 Basic forms of density-dependence documented or hypothesized for sedentary benthic invertebrates with broadcast spawning and pelagic larvae. Relations are depicted as linear for graphical simplicity, but can be non-linear depending upon scales of choice and nature of the process. Important thresholds in the density of local residents are indicated. *K*: carrying capacity, *T1*: density above which the reproductive output (*e.g.* number of eggs spawned per spawning event) starts to decline. *T2*: density below which there is no significant fertilization. *T3*: Density above which residents interfere with settlement or recruitment. *T4:* Density below which new settlers are not attracted to site, or settlers do not survive. *T5*: density above which there is no further facilitation of settlement or settlers' survival.

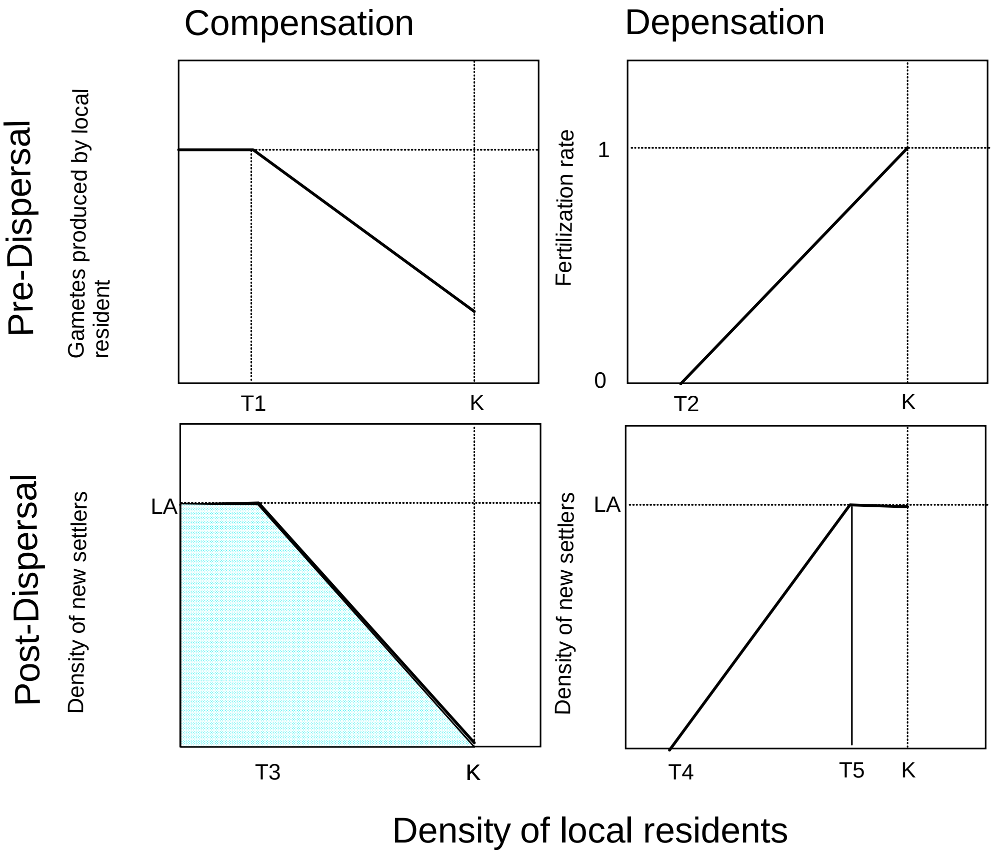


Figure 3 Puget Sound: sites from where age frequency distributions were reported by Goodwin and Shaul (1984). Sample size between parentheses. Arrows: sites at which samples were obtained with a Venturi dredge, allowing the collection of juveniles and cluckers (paired empty shells buried in live position).

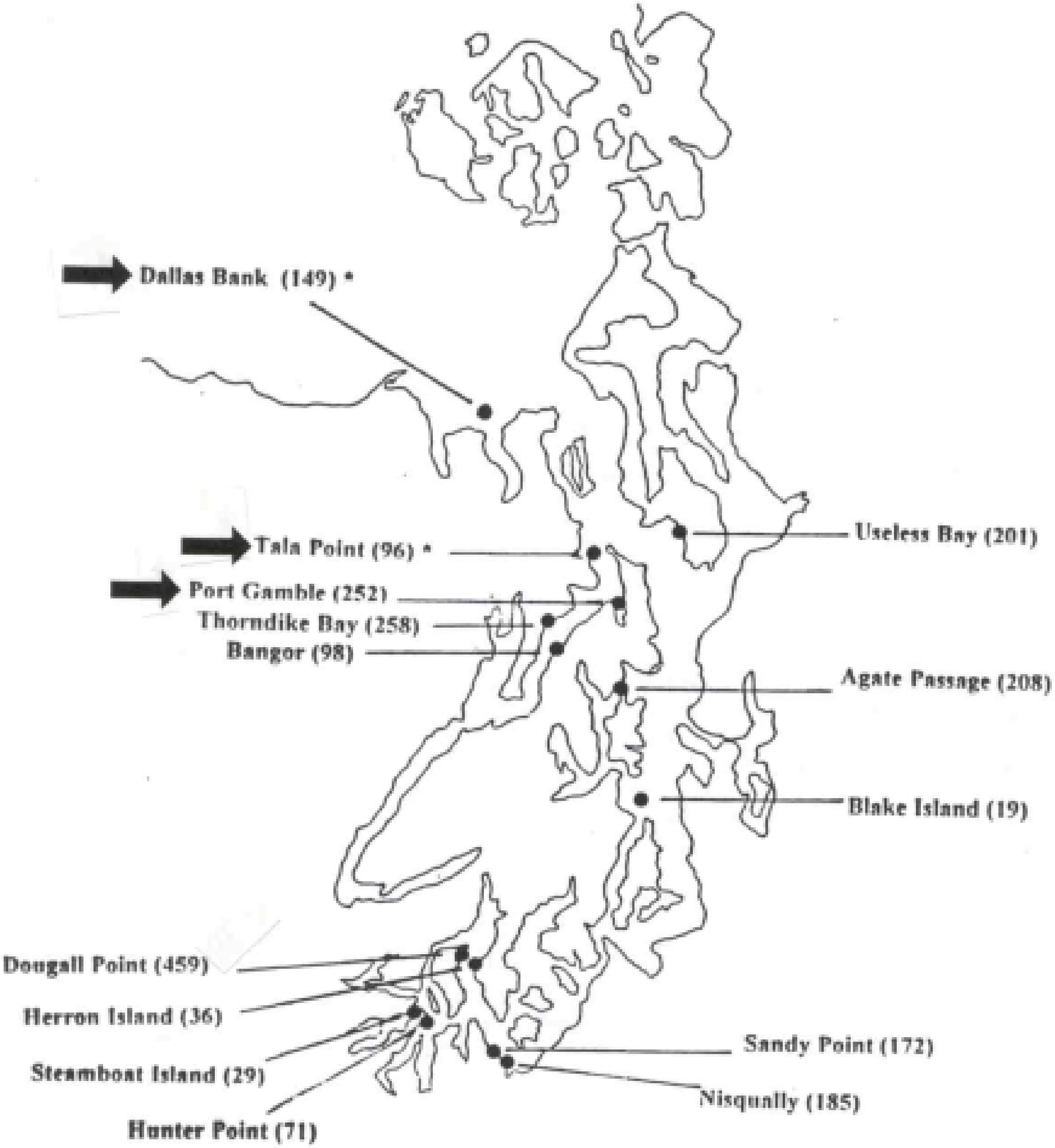


Figure 4 Puget Sound: sites of WDFW recovery experiment. Labeled on the right: fast-recovery cluster; labeled on the left: slow-recruitment cluster

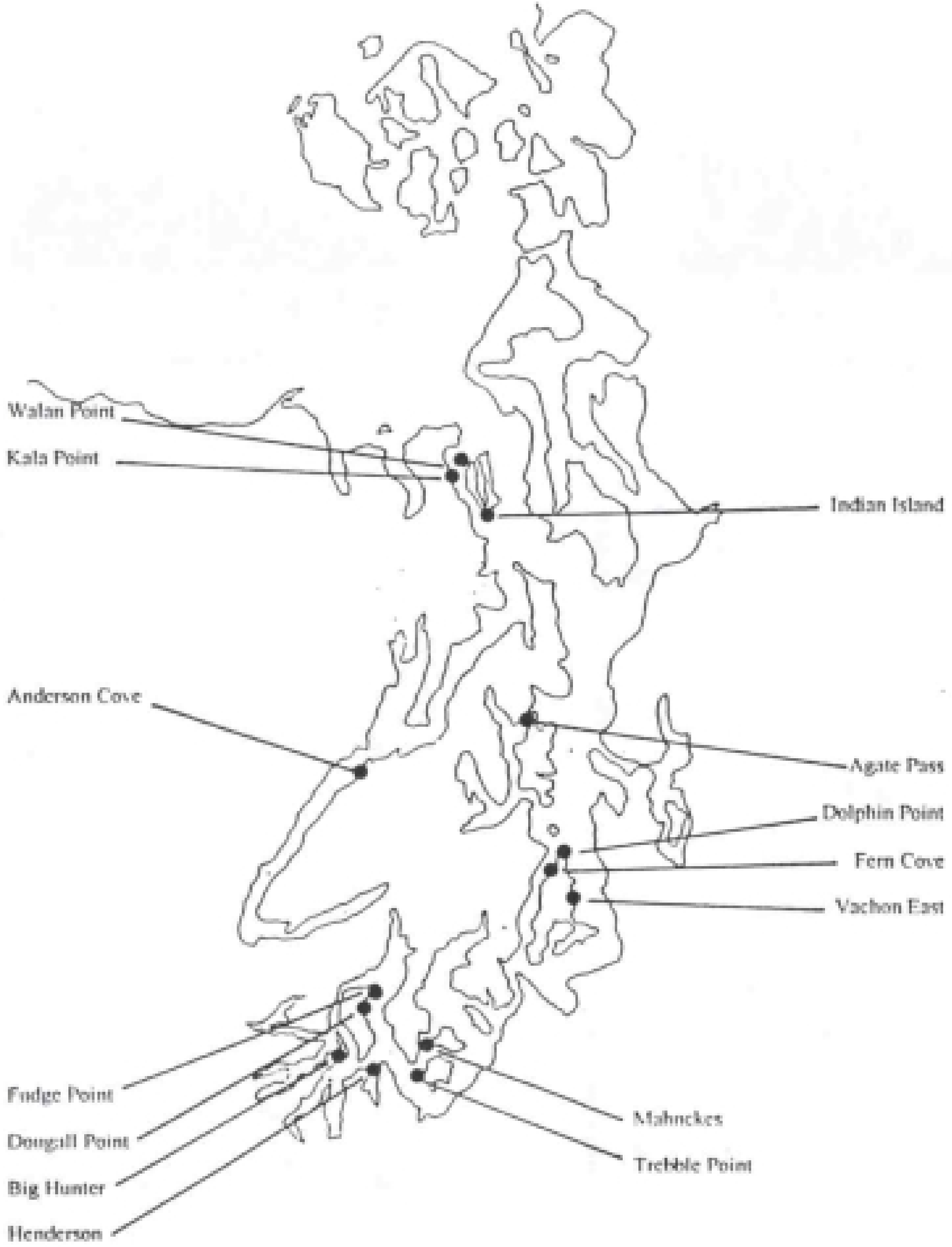


Figure 5 Natural Mortality. Left: Weibull distribution, right: exponential function. Top: AFDs and model fit; middle: fit of the cumulative AFD by the two models; bottom: ibid., log scale

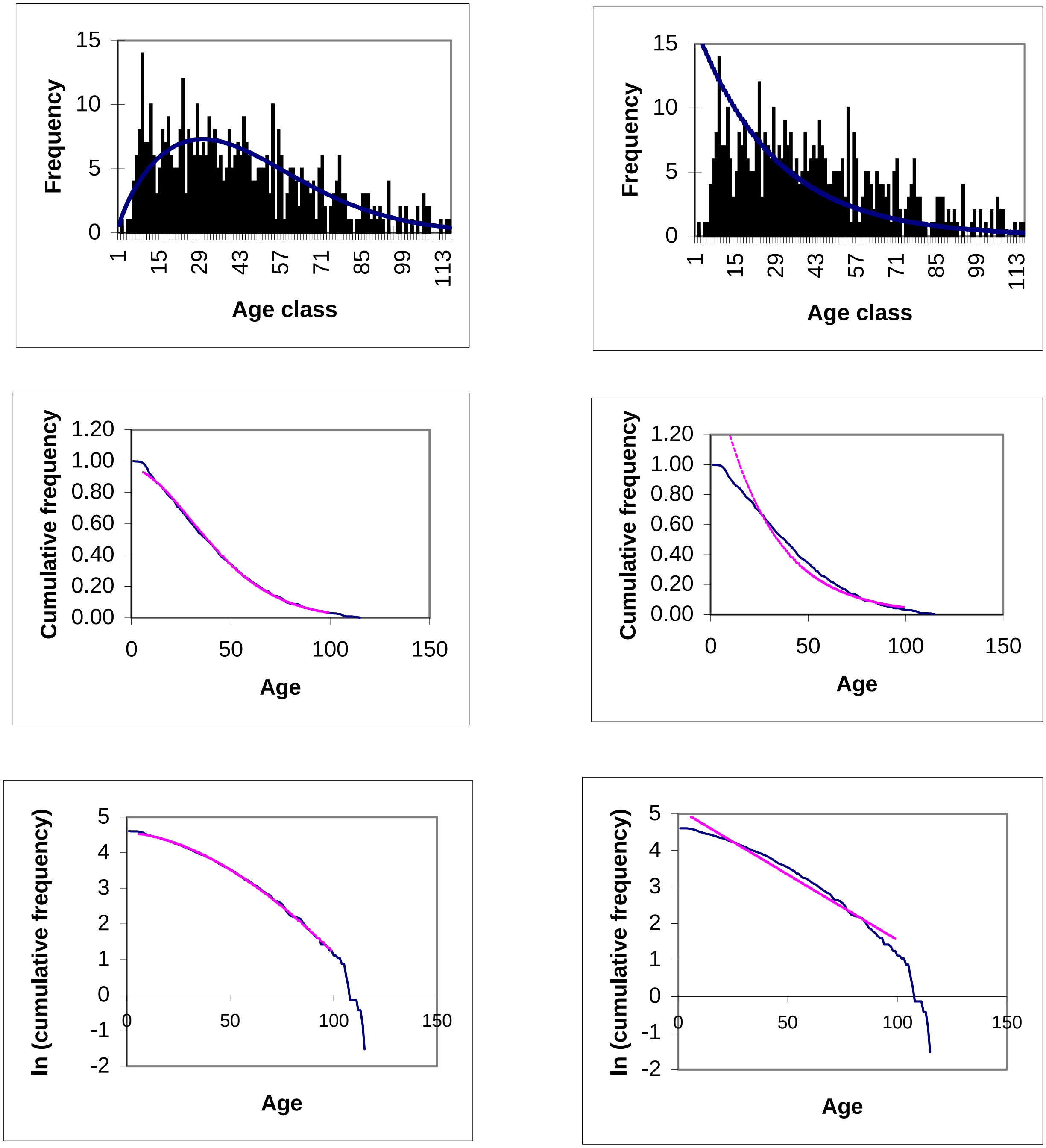


Figure 6 Age frequency distributions published for Washington and British Columbia. Geographical levels of aggregation is the highest used by the original authors. Width of intervals same as in original figures.

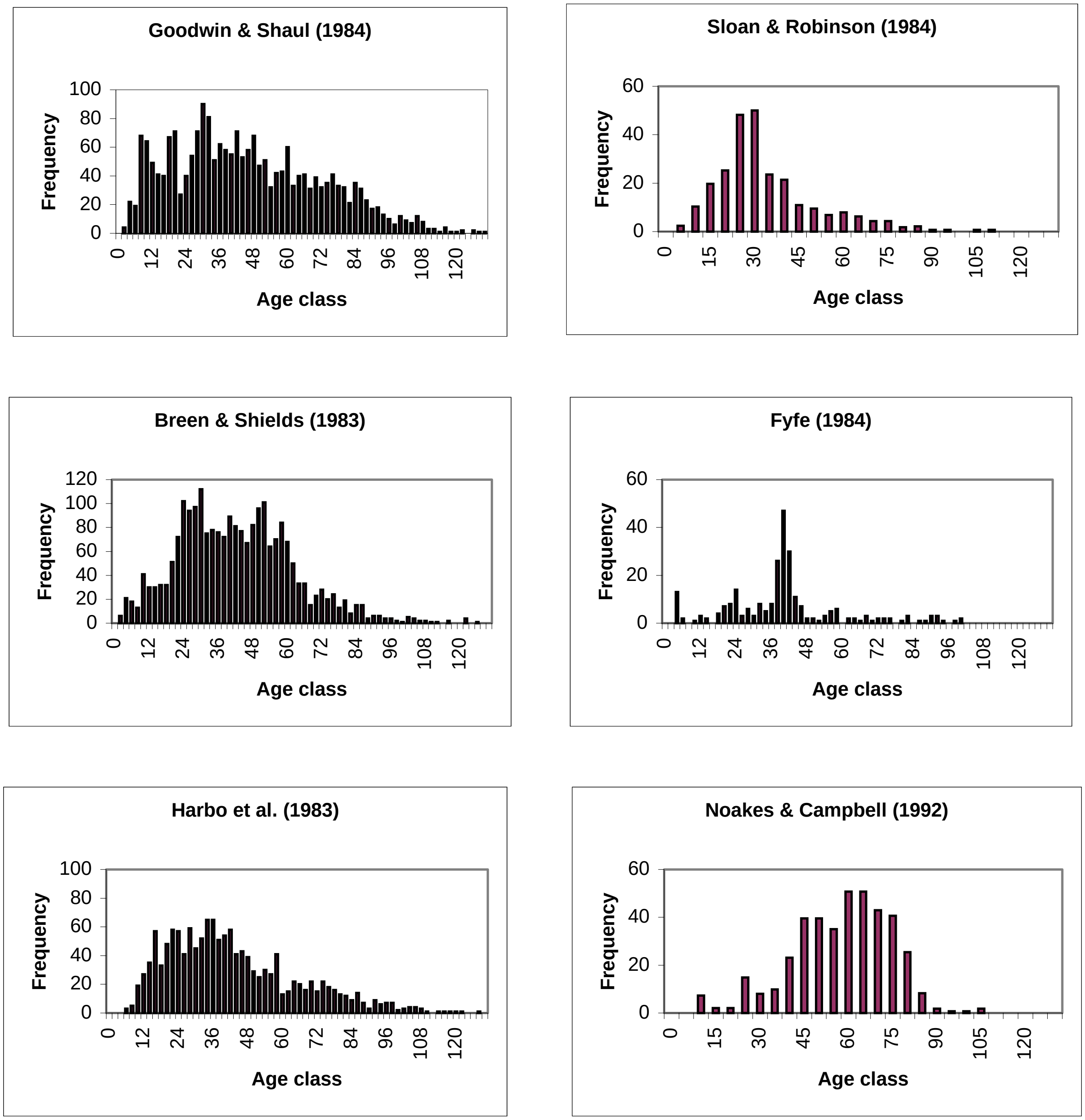
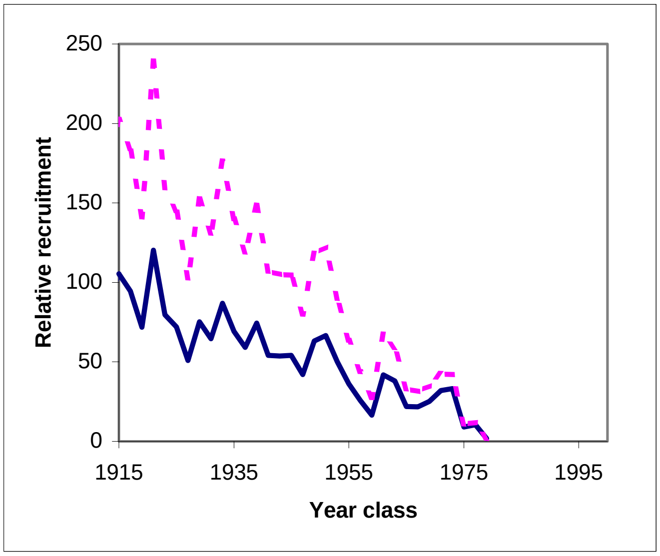


Figure 7 Trends in year class strength (1915-1975) back-calculated from age frequency distributions. Top: Puget Sound (data from Goodwin and Shaul, 1984), back-calculation with the exponential (dashed line) and the Weibul (solid line) functions. Bottom: Back-calculation of series from British Columbia (top; data from Breen and Shields, 1983) and Washington (bottom; data from Goodwin and Shaul, 1984) compared (Weibul function).



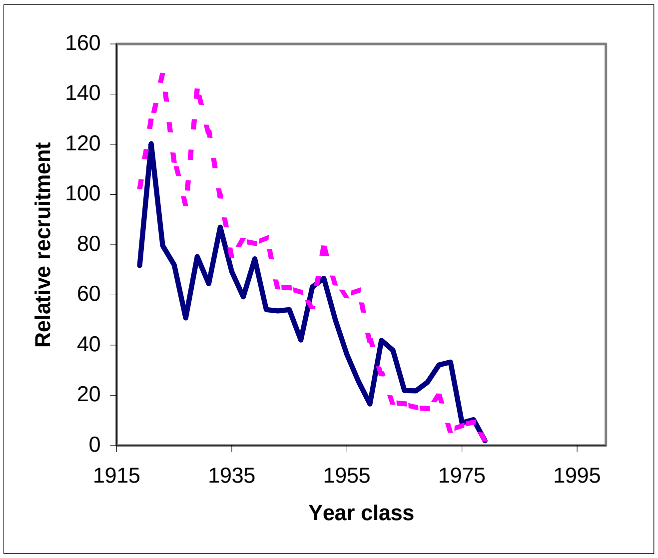


Figure 8 Top: recovery of harvested plots. Bottom: relation between pre-harvest density and annual recovery rate. Notice the existence of two clusters. The intermediate point corresponds to Agate Pass, in which timing of the samples was rather different from the other sites. The high-density point corresponds to Treble Point.

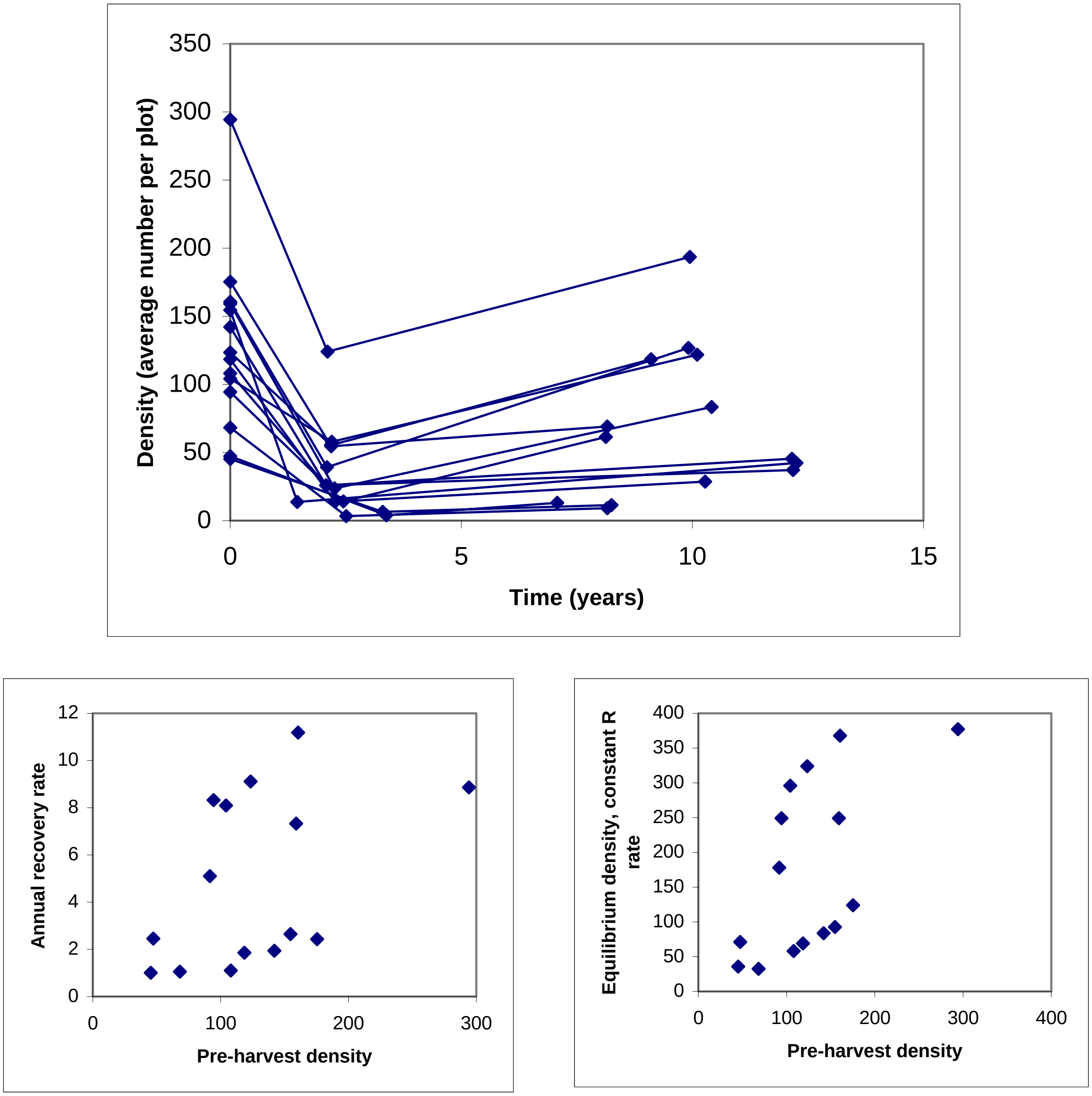


Figure 9 Post-harvest recovery under 4 different models, as exemplified by the Mahnckes tract. 1: constant recruitment, 2: constant recovery, 3: logistic recovery, 4: pure compensation.

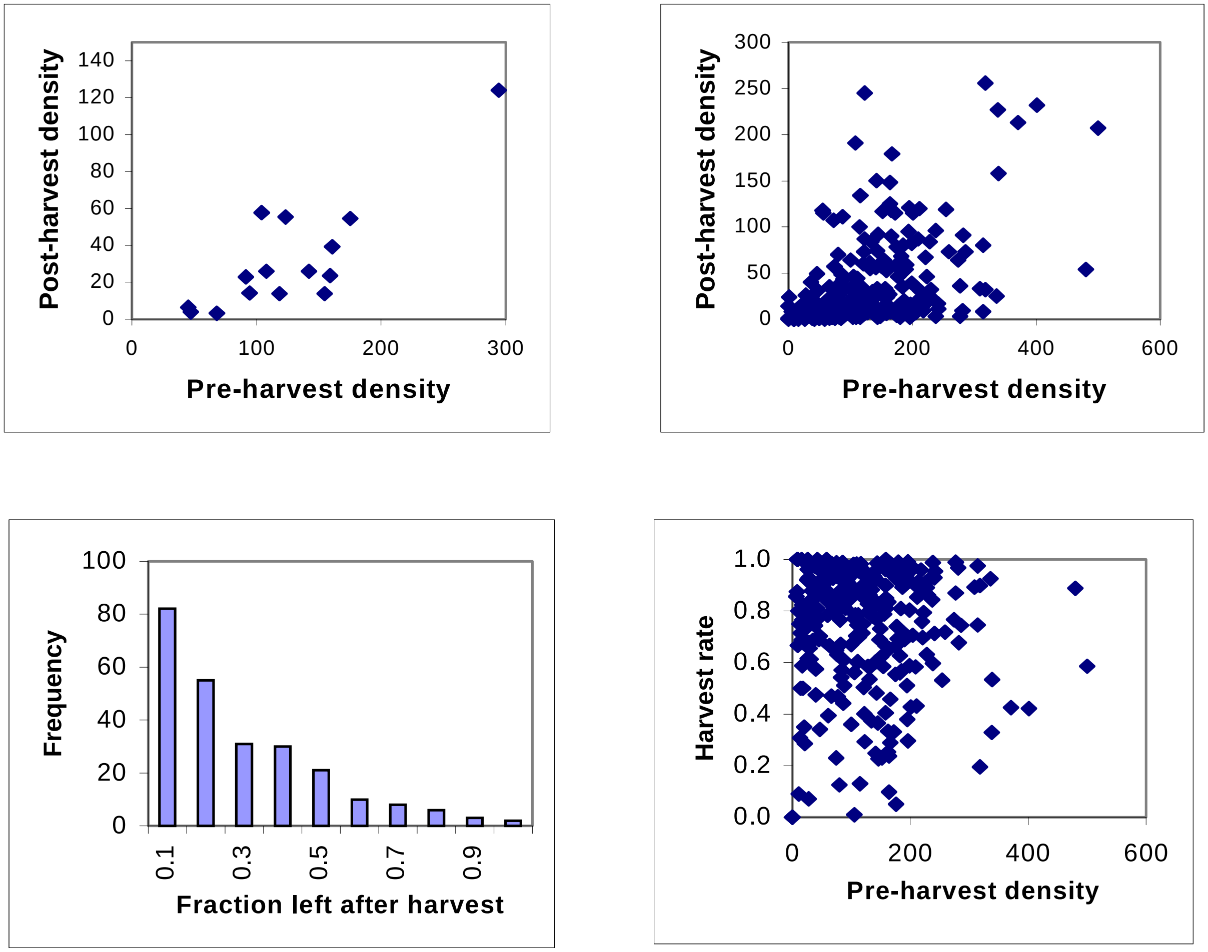


Figure 10 Harvest rate in recovery plots. Top: relationship between pre- and post-harvest density; left: averages for the 15 recovery beds, right: values of the individual plots. Bottom left: frequency distribution of the fraction left by the harvest (individual plots). Bottom right: relationship between pre-harvest density and harvest rate (individual plots).

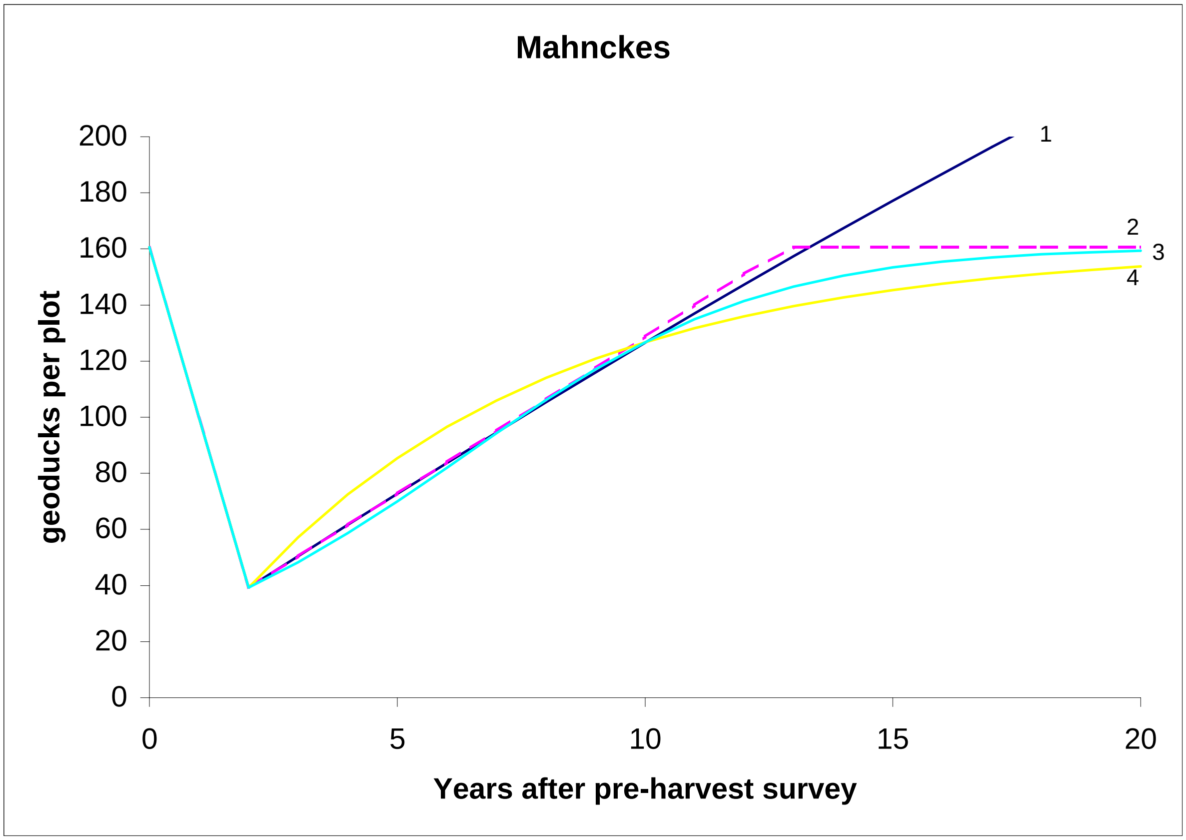


Figure 11 Survey samples collected by WDFW between 1967 and 1985 (from Goodwin and Pease, 1991, Fig. 6. Top: density frequency distribution. Middle: concentration profile. Bottom: accumulated concentration profile: percent of individuals concentrated above x-level.

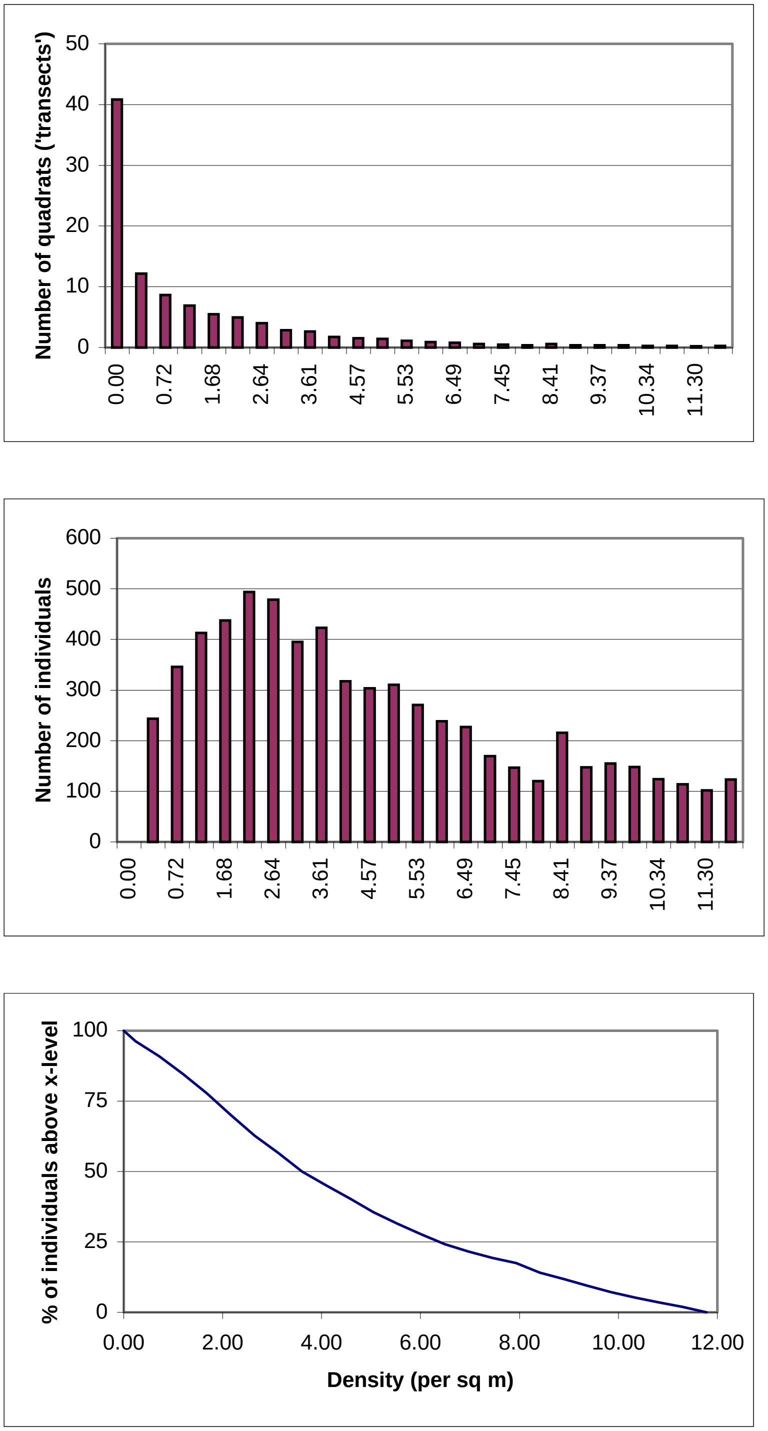


Figure 12 Recovery beds (individual plots pooled). Left: density frequency distributions; right: concentration profiles. Top: pre-harvest; middle: post-harvest; bottom: post-recovery.

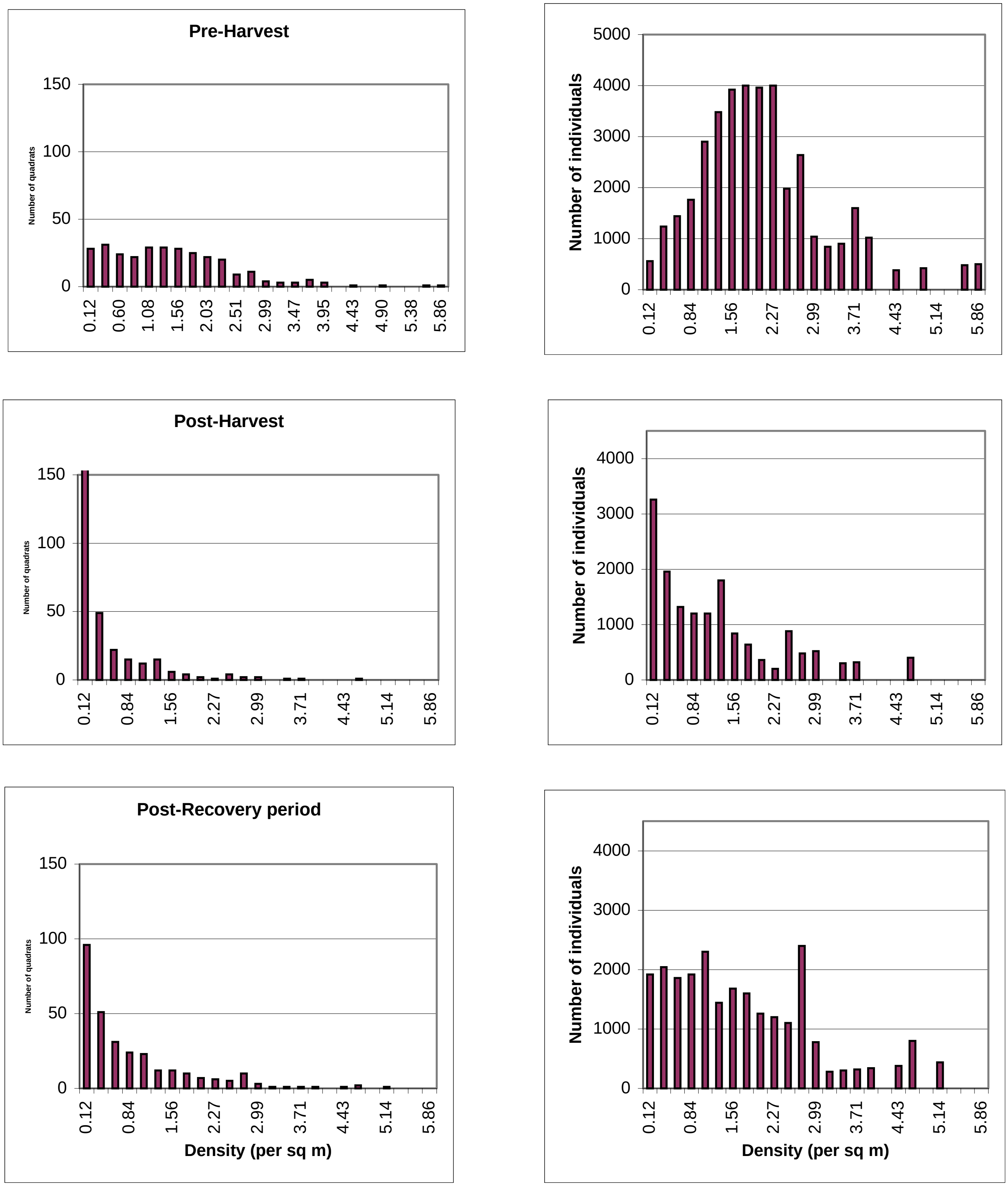


Figure 13 Recovery beds (individual plots pooled). Accumulated concentration profile (percent of individuals concentrated above x-level), pre- and post-harvest and post-recovery samples.

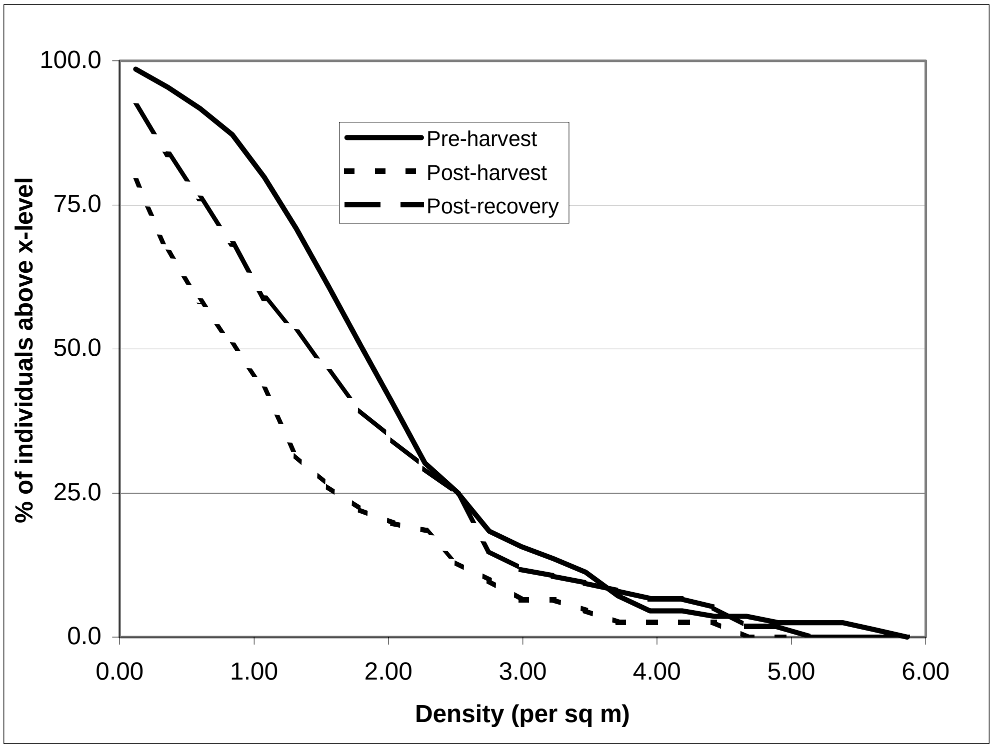


Figure 14 Surveys of the Comox (left) and Marina (right) beds (inner waters of southern British Columbia), which had experienced heavy harvest (data reconstructed from tables in Campbell et al., 1996a,b). Top: density frequency distributions; middle: concentration profiles; bottom: accumulated concentration profiles (percent of individuals concentrated above x-level). See Table 10 for details.

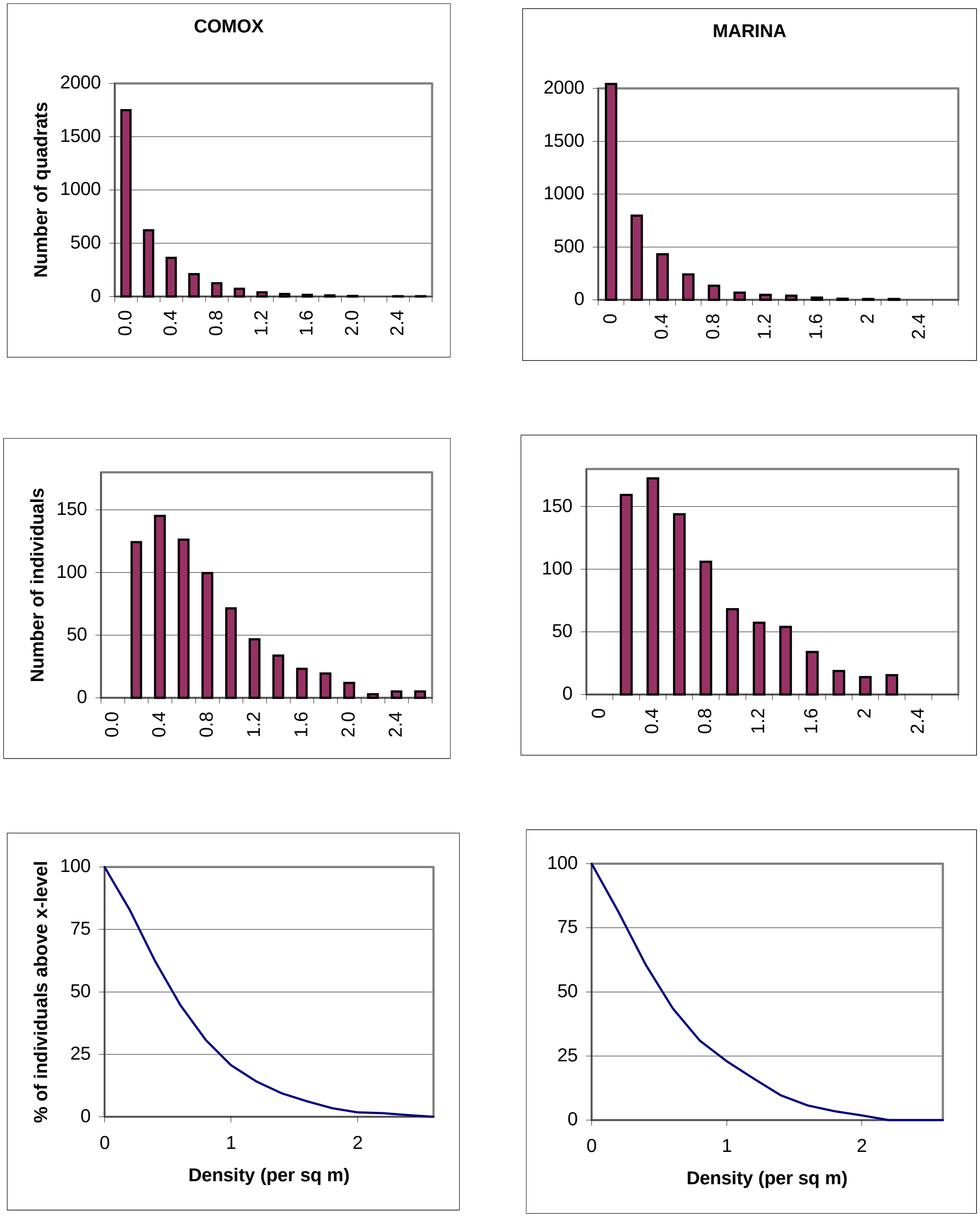


Figure 15 Optimal rotation under four hypotheses on recruitment, illustrated with the Mahnckes bed. All the analysis were made on the basis of numbers, not biomass.

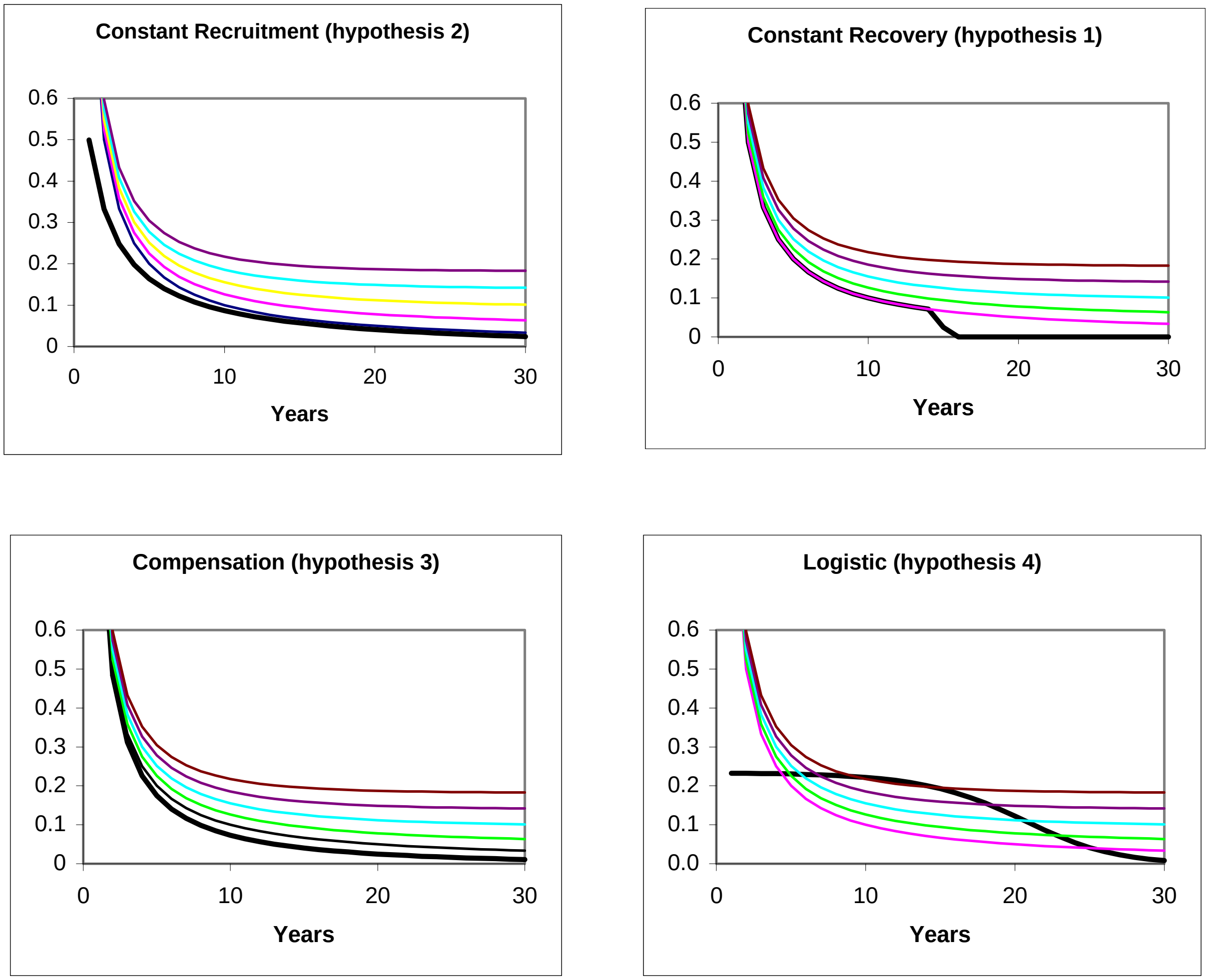
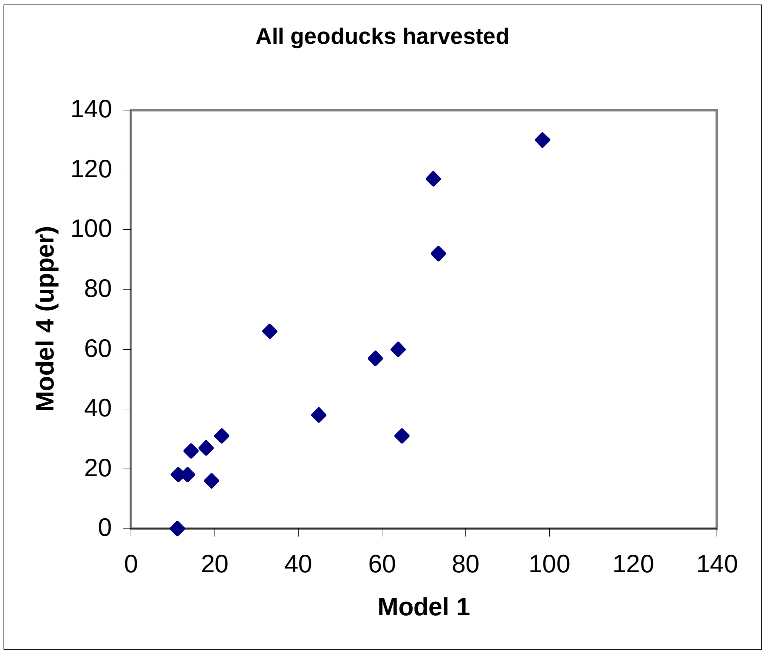


Figure 16 . Rotation. Maximum rotation time (Model 1, constant recovery rate) compared to optimal rotation time (Model 4). Top: complete pulse fishing (all geoducks removed by each harvest. Bottom: 80% harvest rate.



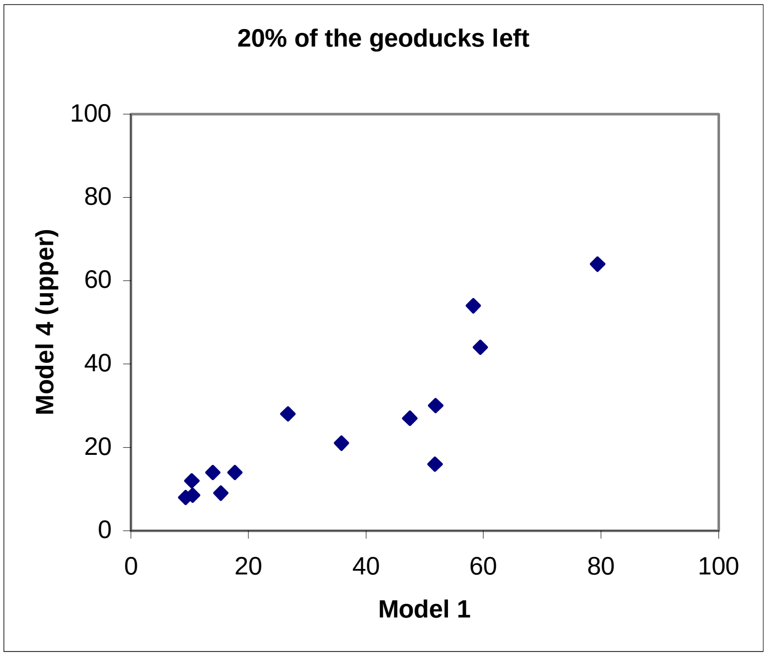


Figure 17 Balance between growth and mortality under constant recruitment, using realistic parameters. Top: biomass trajectory of a cohort (maximum at *ca*. 22 years). Bottom left: optimal rotation (optimal rotation time *ca*. 28 years). Bottom right: yield and reproductive output per recruit for different harvest rate levels (an $F_{50\%}$ strategy corresponds to a 2.7% harvest rate).

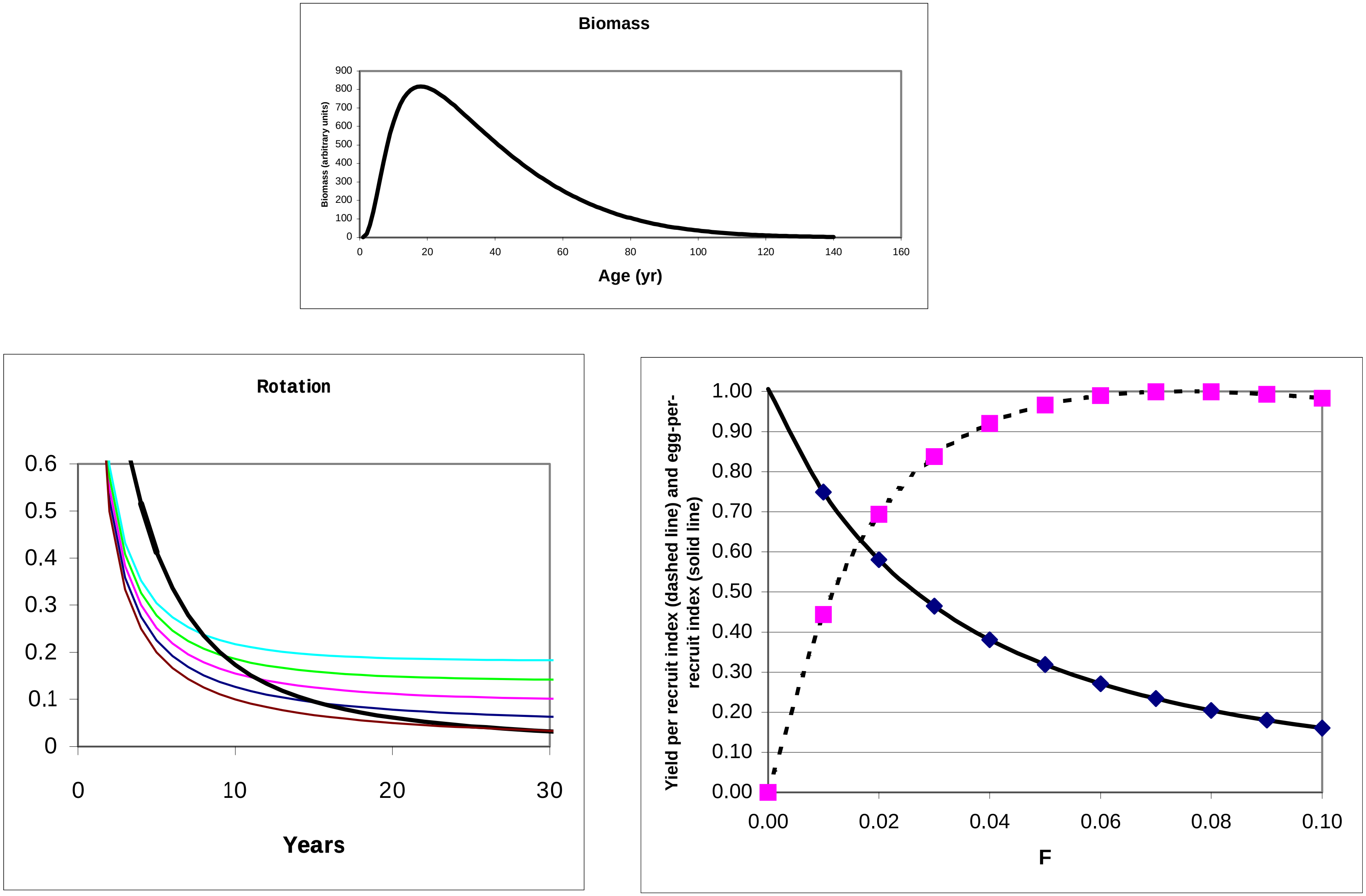
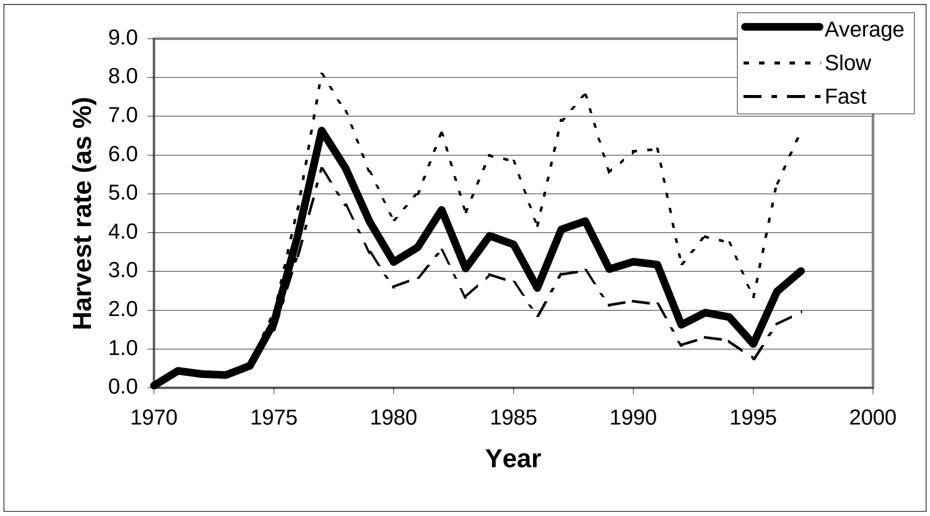


Figure 18 Puget Sound. Projections of abundance and harvest rate under three different scenarios (fast- average and slow-recovery), from 1970 (beginning of the fishery) to 1997 (last year for which catch data are available. See text for explanation.



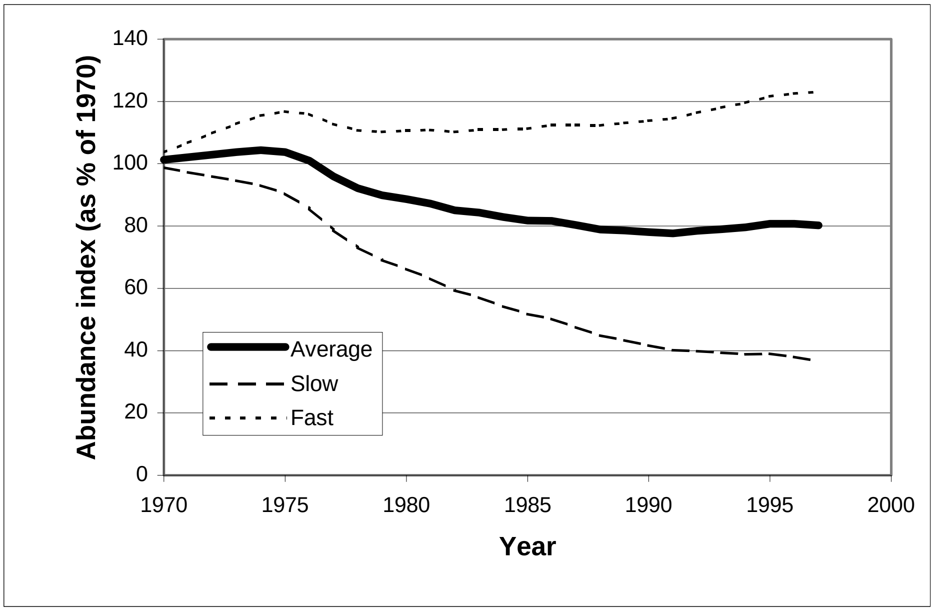
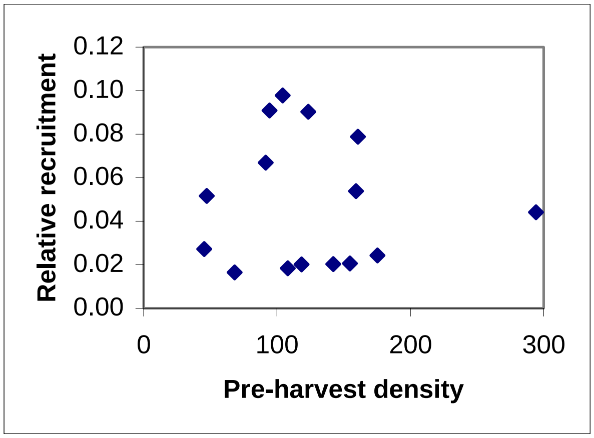


Figure 19 Top: relative recruitment vs. pre-harvest density (geoducks/plot); relative recruitment is defined as annual recruitment rate, calculated under the constant recruitment model, as a fraction of pre-harvest density. Bottom: historical trend in YCS; the two curves have been scaled to maximum and minimum density (per m^2) in the experimental recovery plots; horizontal bars to the right are annual recruitment rates (per m^2) in the experimental recovery plots, calculated for the constant recruitment rate model.



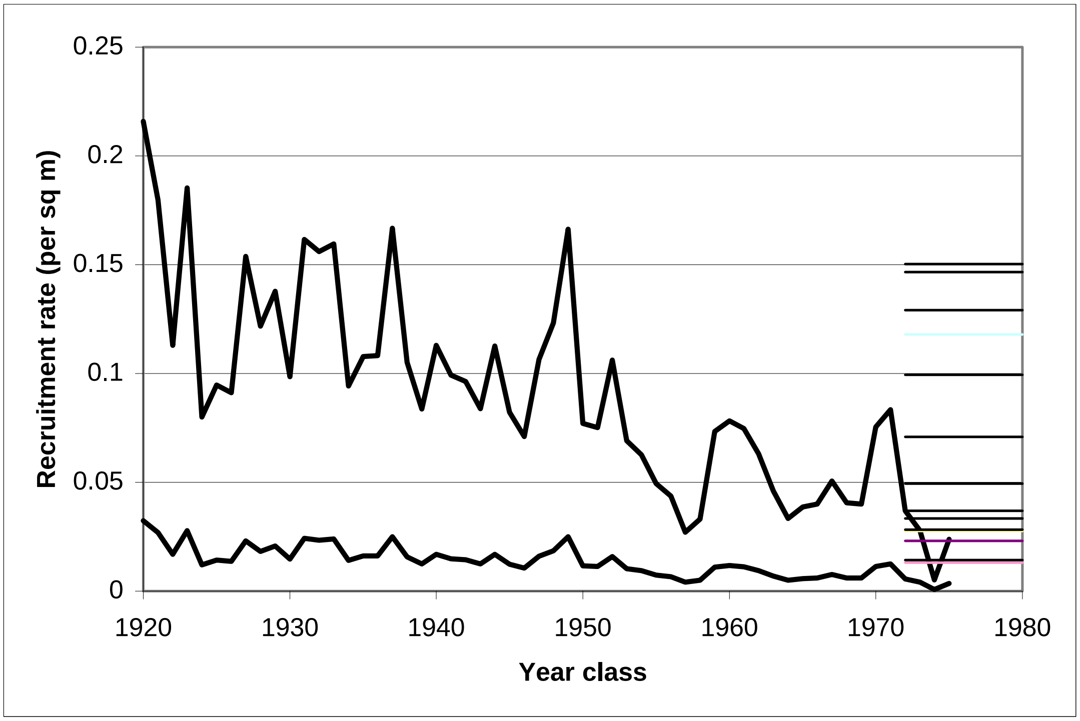


Figure 20 Trends in CPUE (kg/minute) and percentage of geoduck bed area harvested at least once, South Inside Waters region of British Columbia (from Campbell et al., 1998, Figs. 7 and 8).

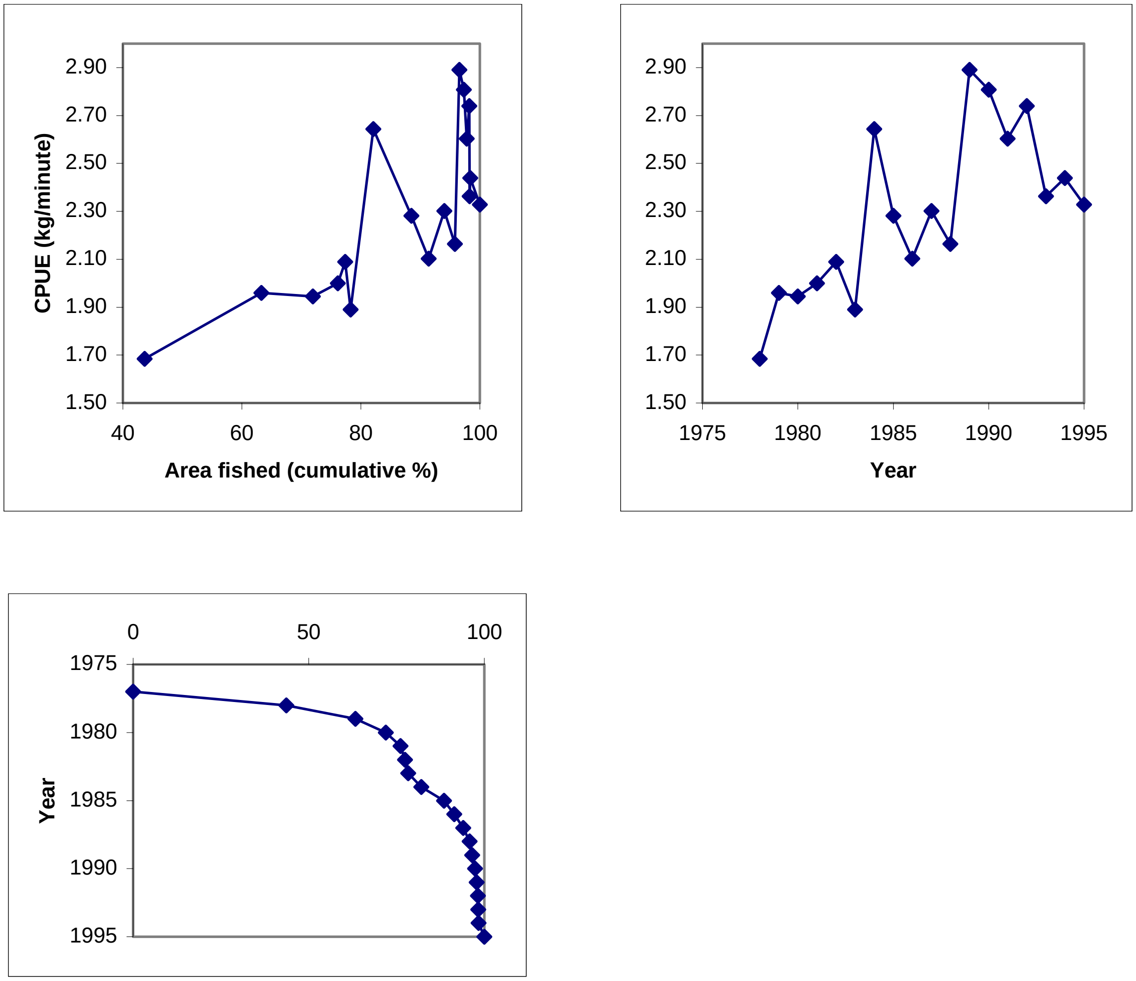


Figure 21 Puget Sound, historical trends of abundance (relative index) and relative recruitment (as a % of stock abundance) reconstructed from age frequency distributions for the period 1920-1975 (compare to Figure 7; data from Goodwin and Shaul, 1984).