MANIPULATIONS OF ADULT DENSITY AND JUVENILE HABITAT QUALITY IN NORTHERN ABALONE STOCK RESTORATION

by

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B.Sc., Simon Fraser University, 1998

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

in the
Department of Biological Sciences

SIMON FRASER UNIVERSITY
Spring 2005

APPROVAL

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Degree: Master of Science

Title of Thesis:

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Abstract

Wild abalone populations throughout the world have declined dramatically over the past 40 years due primarily to market demands for the mollusc's edible foot. Northern abalone (*Haliotis kamtschatkana*), the only abalone species occurring in British Columbia (B.C.), is widely thought to be threatened by potential population collapse as a result of low adult densities that impair reproductive potential. This study examined the hypothesis that the abundance of wild northern abalone populations are below a critical density required for successful reproduction and assessed two techniques that may aid the 'recovery' of northern abalone in B.C.

In the first study, I created dense aggregations of mature abalone during the reproductive period to test whether abalone preferred high density spawning aggregations that theoretically enhance reproductive potential. Twelve weeks following the manipulations, transplanted abalone had dispersed from enhanced densities at different rates and one year later, abalone densities had returned to pre-treatment levels. Slower rates of transplanted abalone dispersal at specific locations indicated that artificially aggregated abalone may have an enhanced theoretical reproductive potential. However, transplanted abalone dispersing to pre-treatment densities indicated that wild populations do not necessarily suffer from impaired reproductive potential.

In the second study, I installed artificial habitats that provided standardized surrogate habitat for juvenile abalone and surveyed surrounding natural habitats to determine an index of juvenile abalone abundance. Juvenile abalone used artificial structures at greater mean densities than nearby natural habitat and juvenile abalone abundance was significantly different between sites but not within sites, suggesting artificial structures showed promise in their ability to detect area specific differences in recruitment and to easily measure juvenile abalone abundance. Benefits of these studies in relation to abalone stock restoration are discussed.

Acknowledgements

I would like to thank my senior supervisor, Ron Ydenberg, for his willingness to welcome a full-time employed MSc candidate and his extremely patient support throughout my long-distance student life. To Leah Bendell-Young, thank you for being a member of my supervisor committee and for your constructive comments that helped to clarify my thoughts.

I am grateful to Alan Campbell for originally introducing me to the world of northern abalone, participating in my supervisory committee, and providing extensive logistical support in the form of divers and an office at the 11th hour.

I especially owe thanks to my employers in Haida Gwaii, the Haida Fisheries Program, for understanding and supporting my pursuit of further education, adapting to my absence during the fall and winter months, and welcoming me back each spring. In particular, I thank my supervisor, Pat Fairweather, for responding well to my never ending list of needs and Russ Jones, for prioritizing abalone research among the Haida Nation and providing technical feedback on research findings.

Many skilled divers have assisted with underwater data collection during this project. For their professionalism, calmness and attention to detail in thick kelp forests along remote coasts, I thank Vanessa Bellis, Doug Brouwer, Dominique Bureau, Robert Gurr, Peter Katinic, Joanne Lessard, Barbara Lucas, James Patterson, James Pegg, Pauline Ridings, Robert Russ, Brad Setso, Dimitri Tzotzos and George Wesley.

Thanks to the crew of the Canadian Coast Guard Ship *Vector* who have provided critical logistical assistance each year, including the delivery of several thousand concrete bricks and providing accommodations to otherwise cramped divers. Additional vessels with crew that provided logistical assistance include the MV *Haida Provider* with Wylie Brillion and Kevin Mearns and the MV *Haida Guardian* with Robert Russ.

This work was financially supported by the Haida Tribal Society, Fisheries and Oceans Canada's Subvention Grants Research Program, Environment Canada's Habitat Stewardship Program for Species at Risk and the Centre for Wildlife Ecology at Simon Fraser University.

Finally, I owe my current state of sanity to my wife, Carolyn terBorg, for simply being there for me while I tried to juggle far too many things at the same time. Your encouragement and support made this thesis less a burden and more a journey.

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Chapter 1
General Introduction

Northern abalone, *Haliotis kamtschatkana* (Jonas), were the target of ancient First Nation fisheries and recent recreational and commercial dive fisheries in British Columbia (B.C.) due to the high value of the mollusc's large edible foot (Sloan and Breen 1988). Dramatic increases in Asian market demand and harvesting technology during the 1970s led to a greatly expanded fishery in both scale and efficiency (Fedorenko and Sprout 1982). In 1977, Fisheries and Oceans Canada (DFO) responded to concerns from resource users and the threat of severe overfishing by implementing management actions that reduced annual fishery landings but were unable to halt the decline of known northern abalone populations (Fedorenko and Sprout 1982). After abalone abundance surveys indicated populations had declined more than 75% during 1978-1984 (Winther et al. 1995), a coast-wide ban on First Nation, recreational and commercial fisheries was implemented in 1990 to stop the population decline and allow northern abalone stocks to rebuild naturally (Campbell 2000). Additional abalone population surveys at long-term index sites during 1987-1998 (Carolsfeld et al. 1988; Thomas et al. 1990; Farlinger et al. 1991; Winther et al. 1995; Thomas and Campbell 1996; Campbell et al. 1998, 2000) were unable to detect any significant population increases and were the basis for northern abalone's classification as 'threaten' by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in April 1999. Dominant factors that are thought to contribute to the continued low abundance of northern abalone populations include illegal harvesting and low recruitment due to impaired reproductive ability (Campbell 2000, Toole et al. 2002, Atkins et al. 2004).

In this thesis, I investigated the hypothesis that the current density of wild northern abalone are below a critical level required for successful reproduction. To test this hypothesis, I artificially increased the density of mature abalone to determine if abalone remained in enhanced densities for the duration of the spawning season. To determine if abalone were reproducing successfully, I measured juvenile abalone recruitment within artificial concrete-block structures that provided surrogate habitat to cryptic juvenile abalone. The relationship between these investigations, abalone ecology and abalone stock restoration is discussed.

Northern Abalone Ecology

Distribution

Northern abalone have a coastal distribution from Sitka Island, Alaska (Paul and Paul 1981) to Baja California (McLean 1966) and are the only abalone species found in B.C. Among the 95 or so described abalone species that live on the coasts of temperate and tropical continents, 'northern' abalone have the distinction of being the most northerly distributed (Mottet 1978). They are usually found in patchy distribution on exposed and semi-exposed portions of the coast, from the lower intertidal zone to a depth of 20 m (Thompson 1914, McLean 1966). Within their rocky subtidal habitat, northern abalone may be distributed differently according to their life stage (Sloan and Breen 1988).

Reproductive biology

Maturity, sexuality and fecundity

In B.C., northern abalone become reproductively mature between 44 and 64 mm SL (shell length), depending on factors such as day length, temperature and food quality and availability (Quayle 1971, Mottet 1978, Paul and Paul 1981, Campbell et al. 1992, 2003). This size at maturity corresponds to an age of ~3 years based on the analysis of annual growth rings deposited in the spire portion of the shell (Shepherd et al. 2000).

At maturity, identification of the separate sexes is relatively easy to determine based on the color of ripe gonads (Quayle 1971). The dark green (female) or pink/beige (male) gonads are visible by forcing down the epipodium on the abalone's right side. Northern abalone in B.C. may have ripe gonads year round, with a seasonal peak from April to June (Quayle 1971, Campbell et al. 2003).

Northern abalone are highly fecund, with the number of eggs produced being directly proportional to shell size and body weight (Campbell et al. 1992, 2003). In examination of histological sections of female gonads collected in Barkley Sound and southeast Haida Gwaii (Queen Charlotte Islands), Campbell et al. (1992, 2003) estimated that a 40 mm SL female had 90,594 eggs, a 125 mm SL female had 3.0 million eggs and a 144 mm SL female had 11.3 million eggs. This high fecundity is thought to compensate for the constant hydrodynamic mixing on wave-swept rocky shores that rapidly dilutes gametes released into the surf zone (Denny and Shibata 1989).

Spawning and fertilization

Similar to other haliotids (Webber 1977), northern abalone are broadcast spawners, they form aggregations to simultaneously release their gametes in the shallow water where fertilization occurs (Breen and Adkins 1980). In the only described natural northern abalone spawning event, Breen and Adkins (1980) observed mature individuals stacked on one another in piles of up to six; the tendency for spawners to be located high up on boulders or stipes of kelp; and the raising up of their shells while gametes are released. Females released eggs with irregular strong puffs while males released sperm more continuously.

The primary benefit of aggregative behaviour before and during spawning is the allowance of non-sedentary mature abalone to promote the synchronous release of gametes and enhance the rates of successful egg fertilization (Quayle 1971, Shepherd 1986*a*, McShane 1992). Aggregations of high fecundity free-spawning abalone influence reproductive success by concentrating gametes in a potentially turbulent environment (Giese and Pearse 1974, Shepherd 1986*a*, Denny and Shibata 1989). Decreases in the abundance or density of spawning aggregations and the removal of large individuals as a result of fishing may therefore reduce rates of reproduction by significantly lowering the amount of eggs and sperm able to make contact. The importance of spawner aggregations or adult densities in relation to the successful fertilization of eggs is gaining greater attention in recent studies and will be the focus of Chapter 2 in this thesis.

The periodicity and duration of spawning for northern abalone is not known (Sloan and Breen 1988). Studies on other haliotids suggest that it varies widely between localities and years (Shepherd 1986*a*), and may depend on the local variability in environmental conditions such as temperature and storms (Sasaki and Shepherd 1995). The findings by Quayle (1971) and Campbell et al. (2003) that mature northern abalone may have ripe gonads year round, with a seasonal peak from April to June, implies that this species more commonly spawns during the spring months and is capable of spawning during other times of the year if environmental conditionals are favourable. Additional factors that may influence spawning include the presence of gametes from conspecifics in the surrounding water, availability of food, hormonal factors and degree of gonad maturation (Shepherd and Laws 1974, Morse et al. 1977).

Larval and early benthic phases

Our knowledge of northern abalone larval development, larval settlement and metamorphosis into the early benthic phase is derived from studies in hatcheries and comparisons with other *Haliotis* species (Beaudry 1983, Olsen 1984, Calderwood 1985, McShane 1992, Pearce et al. 2003).

Successfully fertilized eggs are negatively buoyant and hatch within 48 hours (Pearce et al. 2003) into a phototropic, non-feeding planktonic larval stage of short duration (Olsen 1984) and limited dispersal (Prince et al. 1987). The rate of planktonic larval development and resulting duration of larval life is primarily temperature dependant (Leighton 1972), with a period of about 10 days at 12°C for northern abalone (Pearce et al. 2003). Feeding on stored nutrients, the spherical shaped trochophore larvae initially attempt to swim upward by cilial beating, a behaviour that provides little directional movement but nevertheless is thought to aid in dispersal and avoid benthic filter feeders (Mileikovsky 1971). As a result of this difficultly orienting in the water and the extensive vertical water mixing of the wave-swept shores where abalone inhabit, abalone larvae may be assumed to disperse as passively transported particles (Butman 1989). This passive transport of abalone larvae implies their dispersion across large distances but the relatively short duration of planktonic life (10 to 12 days) and the complex hydrodynamics in near shore environments, particularly those coastal environments with an abundance of large macroalgae, may facilitate larval retention and settlement within kilometres of their natal habitat (Tegner and Butler 1985, McShane et al. 1988*a*). To further limit planktonic larvae dispersal away from potentially suitable habitat, Prince et al. (1987) suggests that spawning occurs at times of low water movement so the negatively buoyant eggs hatch in nearby natal habitats and remain in cryptic areas after settlement.

Abalone larvae must settle on suitable substrata before the stored yolk reserves are exhausted (Leighton 1972). Suggested mechanisms of selective larval settlement include chemical attraction, substratum topography and presence of conspecifics or predators (McShane 1992). Within their natural environment, abalone larvae generally settle on coralline red algae (i.e., *Lithothamnium* spp. and *Lithophyllum* spp.) that provide shelter and food for larvae as they metamorphose into the benthic life stage (Morse and Morse 1984, Shepherd and Turner 1985). Within mariculture facilities, abalone larvae readily settle on diatom films or artificial substrata and settlement is

improved if the diatom films have been previously grazed by conspecifics (Ebert and Houk 1984).

The association between newly settled abalone larvae and coralline red algae is well documented (McShane 1992). In summary, the surface of coralline algae is prone to excessive growth by foliose algae or colonizing animals if not kept clean (Steneck 1986). The grazing of epiphytes on coralline algae by red sea urchins (Paine and Vadas 1969), adult abalone (Morse and Morse 1984), and other herbivorous gastropods such as chitons and limpets (Fletcher 1987) helps maintain a clean surface. In return for their constant cleaning efforts, the coralline algae provides grazers with chemical cues for larval settlement, a source of diatoms and micro-algal food, and pigmentation that helps small abalone appear cryptic (Morse and Morse 1984).

Once abalone larvae have settled, they begin feeding on benthic micro-algae and diatoms, metamorphous into a light sensitive juvenile phase and seek habitats in cracks and undersides of rocks (Olsen 1984, McShane 1992).

Juvenile and adult phases

Distribution

Northern abalone juveniles and adults may be distributed differentially within their rocky subtidal habitat (Sloan and Breen 1988). Newly settled juvenile northern abalone (<10 mm SL) are difficult to find (DeFreitas 2003), but as stated previously, they are associated with encrusting coralline algae that commonly cover exposed bedrock or boulders located seaward of macroalgae beds (Breen 1980). Juvenile northern abalone measuring 10-70 mm SL generally occupy cryptic habitats before emerging once again to exposed surfaces as adults (≥70 mm SL) (Breen and Adkins 1979, 1981; Boutillier et al. 1985). Breen (1980) suggested these habitat shifts result from changes in diet with size and the effects of predation as very small juveniles graze microalgae and benthic diatoms found primarily on exposed rocks; larger juveniles switch to feeding on drift macroalgae at night and seek shelter during the day to avoid predation; and adult abalone experience less predation and can therefore remain exposed continuously.

Locomotion

Northern abalone utilize their large muscular foot for locomotion across firm substrates and to move their shells for specific activities. They are generally slow moving or stationary during the day but are capable of rapid movements when avoiding

predators (B. DeFreitas personal observation) or crossing sand and mud substrates in search of food. Specialized northern abalone movements include quick shell-twisting and running when confronted by the sunflower seastar (*Pycnopodia helianthoides*); re-righting themselves if placed upside down on their shell; capturing drift algae by 'standing' on the posterior portion of the foot while facing into the current and then 'stomping' down once contact with algal food is made; climbing up and down stalks of large brown algae to feed; and raising their shells during spawning (Sloan and Breen 1988). In general, northern abalone movements may vary according to the amount of available crevice space and drift algae (Breen 1980, Mottet 1978).

Predation

Predators of northern abalone include *Enteroctopus dofleini* (Hartwick et al. 1981); sunflower seastar (*P. helianthoides*); rock crabs (*Cancer productus*); wolf eel (*Anarrhichthys ocellatus*); rock fish (*Sebastes* spp.) sculpin fish (family Cottidae); river otter (*Lutra canadensis*); mink (*Mustela vison*); and sea otters (*Enhydra lutris*) where they occur (Sloan and Breen 1988, Watson 2000). To dislodge abalone that are firmly attached to rock substrate and avoid damage to the abalone's delicate foot, a *P. helianthoides* arm can be used to induce a natural escape response (Emmett and Jamieson 1988).

Study Area

Geographic area

This study was conducted within a community created abalone research area located on the southeast coast of Haida Gwaii (Queen Charlotte Islands), B.C. (Fig. 1.1). The abalone research area encompasses portions of Lyell and Ramsay Islands, all of Faraday and Murchison Islands and is surrounded by the Gwaii Haanas National Park Reserve / Haida Heritage Site. The abalone research area is the western portion of the Juan Perez Sound commercial abalone fishery area closure that was implemented in 1973 by DFO to protect First Nations and recreational fishing opportunities (Fedorenko and Sprout 1982). A total of 10 subtidal study sites were distributed within the abalone research area (Fig. 1.2).

Fishery history

The southeast coast of Haida Gwaii (Pacific Fishery Management Area 2E) was one of several areas in the north coast of B.C. where the majority of commercial abalone

fishery landings occurred between 1961 and 1986 (Sloan and Breen 1988). From 1977 to 1990, over 30% (543,049 kg) of all recorded commercial landings in B.C. were from the southeast Haida Gwaii region (Winther et al. 1995), a reflection of the area's historically high abundance of northern abalone.

Survey history

Due to the high abundance of northern abalone and resulting concentration of commercial fishing effort, the southeast coast of Haida Gwaii was one of two areas in B.C. surveyed by DFO every 3-5 years during 1978-2002 (Breen and Adkins 1979; Boutillier et al. 1985; Carolsfeld et al. 1988; Thomas et al. 1990; Winther et al. 1995; Campbell et al. 2000; Atkins et al. 2004). These fishery-independent surveys collected a time series of northern abalone densities and size frequencies that continue to be used as an index to determine population abundance. The general survey method at each index site within the survey area involves divers searching for and measuring all visible abalone found within a 1 m^2 quadrat that is placed 16 times within a 7 m by 17 m area (Breen and Adkins 1979). Divers do not generally search for cryptic or juvenile abalone because attempting to find them by searching under rocks is time consuming, the abundance estimates are unreliable and the majority (>90%) of fully mature abalone are exposed (Campbell 1996). Atkins et al. (2004) reported average abalone densities of 0.32/m^2 for total emergent (all sizes), 0.11/m^2 for emergent mature (≥70 mm SL) and 0.21/m^2 emergent juvenile and youth (<70 mm SL) for the 2002 survey in the research area.

The Council of the Haida Nation Fisheries Program (HFP) has conducted annual ecological assessments, abalone population surveys and mark-recapture monitoring within the abalone research area during 1998-2003 (Jones et al. 2003). Preliminary surveys of the abalone research area during February 2001 indicated average abalone densities of 0.32/m^2 total emergent (all sizes), 0.23/m^2 emergent mature (≥70 mm SL) and 0.09/m^2 emergent juvenile and youth (<70 mm SL) (DeFreitas, unpublished).

Objective and Outline

The goals of the national recovery strategy for the northern abalone in B.C. (Toole et al. 2002) are to initially halt the decline of existing wild populations and eventually increase the number and density of abalone to levels where populations become self-sustainable. The recovery strategy highlights several biologically limiting factors that

make this species vulnerable to overexploitation and contribute to the lack of population recovery. These factors include: low or sporadic recruitment; short larval period; slow growing; long-lived; patchy distribution; and the aggregation of mature individuals in shallow water that makes them easily accessible to harvesters. Additionally, the recovery strategy states that low abalone abundance may be impairing the reproductive ability of abalone populations and that our knowledge of abalone recruitment is poor due to the cryptic behaviour of the juvenile life stage. In view of these national efforts to restore northern abalone populations in B.C. and better understand the factors that contribute to the lack of population recovery, the overall aim of this study is to investigate the hypothesis that wild abalone population densities are below a critical threshold required for successful reproduction and test possible stock restoration methods.

The first objective of this study was to investigate the effects of artificially increasing the density of mature northern abalone in the wild to determine if and how long northern abalone maintained these dense spawning groups. I predicted that if the current density of mature abalone are below a critical threshold required for successful reproduction, transplanted abalone will remain in enhanced densities for the duration of the reproductive season (until ~July). Alternatively, if the current density of mature abalone are sufficient for successful reproduction, I predicted that transplanted abalone will disperse across the available habitat during the reproductive season. To achieve this first objective, I measured the initial density of mature northern abalone at 8 replicate sites, increased the density of spawners by collecting and marking mature abalone from neighbouring areas and transplanting them to experimental plots, and measured the resulting changes in abalone density over time.

The second objective of this study was to measure juvenile northern abalone density within standardized concrete-block habitats and within natural rocky substrate habitats. I predicted that if the current density of mature abalone are below a critical threshold required for successful reproduction, there would be an overall low abundance of juvenile abalone and no significant difference in juvenile abalone densities measured in artificial and natural habitats. Alternatively, if the current density of mature abalone are sufficient for successful reproduction, I predicted there would be an overall high abundance of juvenile abalone and a significant difference in juvenile abalone densities measured in artificial and natural habitats. To achieve this second objective, I installed 24 artificial habitats at 6 sites and measured juvenile abalone densities within both artificial and natural habitats during the same time periods.

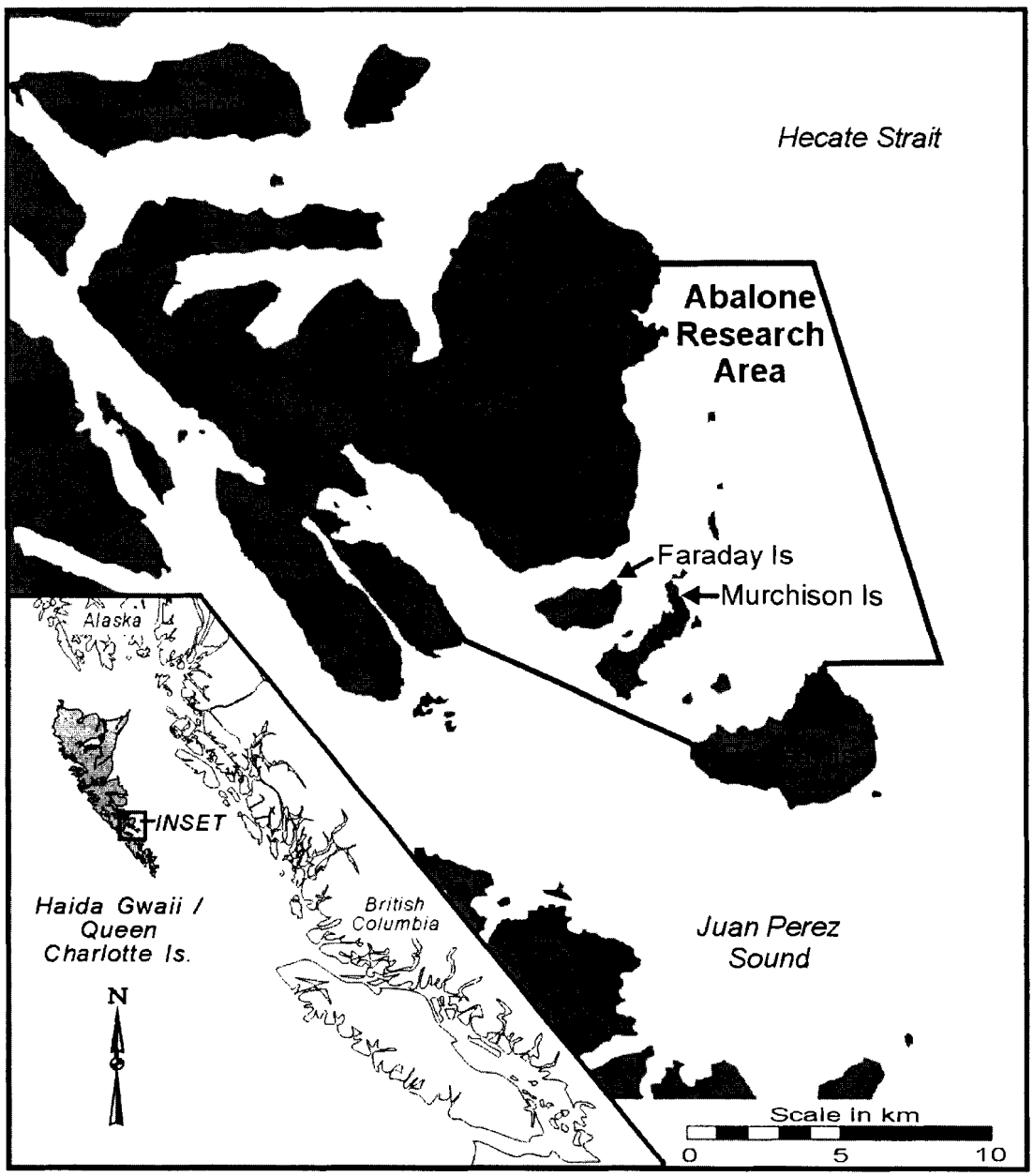

Figure 1.1. Location of abalone research area along southeast coast of Haida Gwaii (Queen Charlotte Islands), B.C.

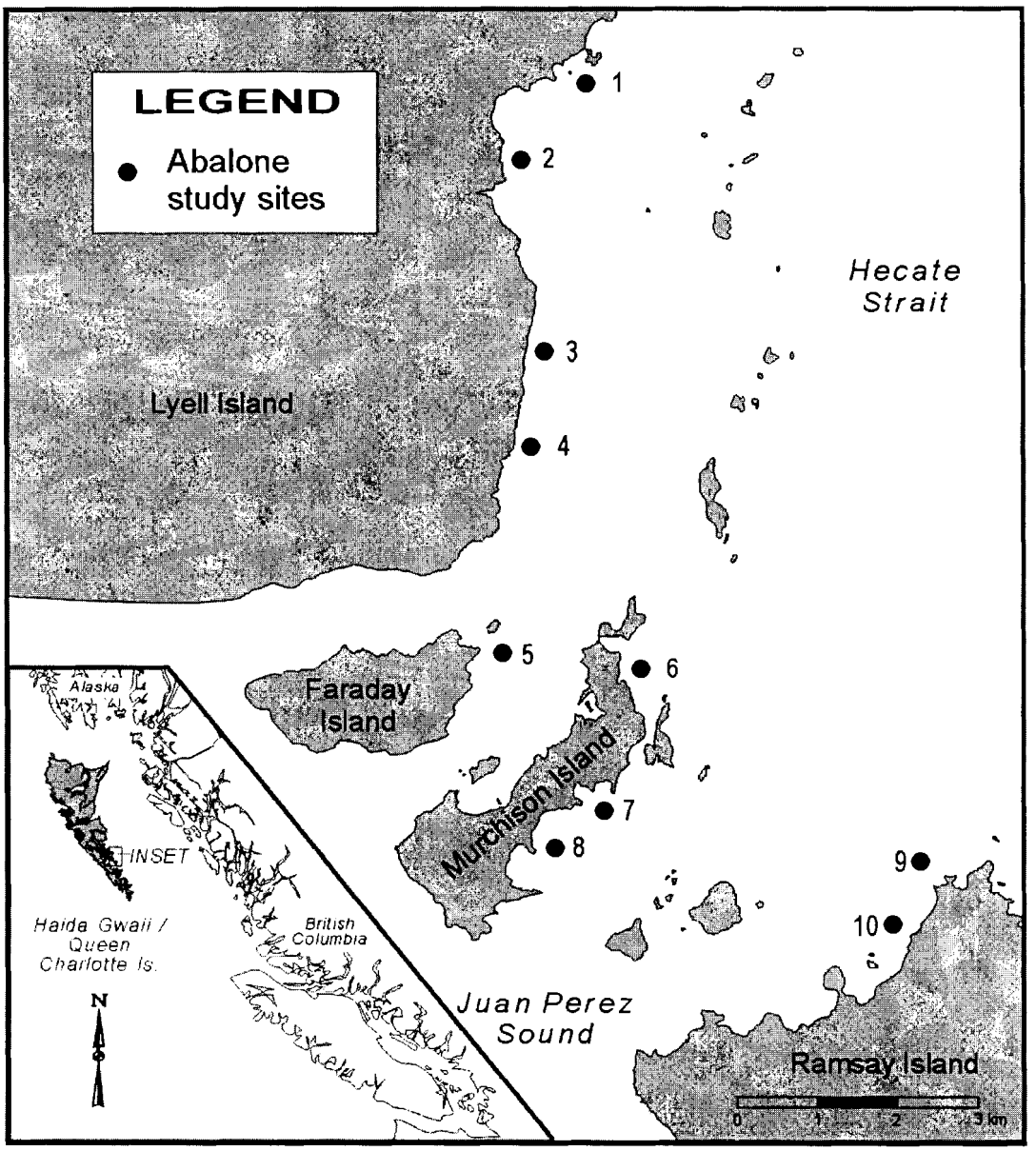

Figure 1.2. General location of abalone study sites, as mentioned in the text, within the research area.

Chapter 2

Manipulations of Mature Abalone Density

Introduction

Many species of benthic marine invertebrates form aggregations in their natural habitat. Examples of observed aggregations include abalone (Sloan and Breen 1988; Shepherd 1986*a*; McShane 1995a, 1995b; Shepherd and Partington 1995), asteroids (Babcock et al. 1994), holothurians (Babcock et al. 1994) and echinoids (Young et al. 1992, Levitan et al. 1992). Abalone may form aggregations to reproduce (Breen and Adkins 1980, Shepherd 1986*a*), feed (Shepherd 1973), or shelter (Hines and Pearse 1982, Shepherd 1986*b*, Tegner et al. 1989).

Sexually mature abalone display aggregative behaviour prior to and during the spawning season, but tend to be randomly distributed at other times of the year (Mottet 1978, Shepherd 1986*a*). This behaviour facilitates the synchronous release of gametes and likely increases the rate of successful egg fertilization (Breen and Adkins 1980, McShane 1995*b*). A significant reduction in adult spawner densities, such as those caused by commercial fishing, may therefore reduce egg fertilization success by dilution of gametes (Allee et al. 1949, Levitan and Sewell 1998). In controlled conditions, additional factors that may influence egg fertilization success include sperm-egg ratio, gamete age and the amount of time sperm and eggs are in contact (Baker and Tyler 2001). Reduced rates of egg fertilization can have the effects of reducing larval production and hence impact the ability of abalone populations to recover from critically low abundance.

The influence of mature northern abalone aggregation density on larval or juvenile recruitment has not been investigated (Breen 1986, Sloan and Breen 1988, Campbell 2000) and there have been no reported studies on other abalone species to determine egg fertilization rates in the wild (McShane 1995*a*). However, a reduction in the density of other benthic marine invertebrate spawners such as echinoids (Pennington 1985, Levitan 1991, Levitan et al. 1991), asteroids (Babcock et al. 1994), hydroids (Yund 1990), and corals (Oliver and Babcock 1992) has demonstrated reduced egg fertilization rates due primarily to the dilution of gametes. For free-spawning organisms in general, fertilization efficiency increases when populations are large, at high density and spawn synchronously (Levitan and Sewell 1998).

In Australia, two studies examined the relationship between adult abalone densities and the production of abalone larvae. In the first study, Prince et al. (1987, 1988) decreased the density of mature *Haliotis rubra* within a portion of coastline and found that larval recruitment was significantly lower inside the area from which spawning stock were removed and correlated with the density of breeding stock outside the adult removal areas. In the second study, Shepherd et al. (1992) increased or decreased mature *Haliotis laevigata* densities within 100 m wide sections of coast and found that larval recruitment was independent of adult density but varied according to features of coastal topography. These contrasting studies on the relationship between mature abalone densities and larval recruitment highlight our limited understanding of abalone larval behaviour and how factors such as temperature, hydrodynamics, coastal topography, settlement cues, and predation interact (Beaudry 1983; Morse and Morse 1984; Denny and Shibata 1989; McShane 1992; Slattery 1992; Roberts 2001; Sasaki and Shepherd 2001).

In Japan, transplanting abalone away from poor quality habitats to improve growth rates is fairly common practice (Mottet 1978, Saito 1979). In B.C., transplanting northern abalone from exposed habitats to more sheltered ones also improved growth rates (Breen 1986, Emmett and Jamieson 1988). In California, Henderson et al. (1988) transplanted pink abalone (*Haliotis corrugata*) and Tegner (1992) transplanted green abalone (*Haliotis fulgens*) in order to concentrate spawning stocks and enhance reproductive potential. In the abalone transplant studies of B.C. and California, researchers revisited transplant sites over time and searched the area for marked abalone shells to determine transplanted abalone survival and growth but no efforts were made to measure the density or dispersal rates of transplanted abalone at the release site.

In this study, I examined the hypothesis that northern abalone population abundance may be too low to successfully reproduce and therefore maintain a sustainable population (Campbell 2000; Toole et al. 2002; Atkins et al. 2004). To test this hypothesis, I established subtidal plots where mature northern abalone densities were artificially increased early in the spawning season and measured mature abalone densities within both aggregation plots and an equal number of control plots over time. If the abundance of abalone populations were below a critical threshold required for successful reproduction, I predicted that during the spawning season, artificially aggregated abalone would remain in significantly higher densities than in control plots

because of the greater reproductive potential of larger abalone (Campbell et al. 2003) and aggregated groups (Levitan and Sewell 1998).

Additional objectives of this study were to: (i) gauge the reproductive potential of transplanted abalone by visually grading gonad condition; (ii) examine factors that may contribute to maintaining spawner aggregation densities; and (iii) discuss the feasibility of this technique as a tool for abalone stock restoration.

Materials and Methods

Study sites and experimental design

This study occurred within the northern abalone research area previously described (Fig. 1.1). A total of 8 subtidal study sites were established along east Lyell Island (sites 1-4), south Murchison Island (sites 7-8) and north Ramsay Island (sites 9-10) from February 22 to March 2, 2002. The specific locations of study sites have been filed with the Shellfish Section of Fisheries & Oceans Canada at the Pacific Biological Station and are not presented to deter potential human interference at the sites. Study sites were systematically distributed within pre-surveyed areas that possessed suitable northern abalone habitat and average densities of all-sized emergent northern abalone similar to those found during DFO index surveys in 1998 (Campbell et al. 2000). Sites were selected haphazardly by examining the rocky shoreline for distinct landmarks used to aid in relocating the site.

Each of the 8 replicate sites measured approximately 15,000 m^2 (300 m of shore length x 50 m) and contained a control transect with plot where no northern abalone density manipulations occurred and a treatment transect with plot where mature northern abalone densities were increased by ~2.0/m^2 (Fig. 2.1). The 2 transects within a site were spaced approximately 250 m apart and oriented parallel to one another and perpendicular to shore. Each control and treatment transect bisected a 10 m x 10 m unmarked plot that was randomly located between a depth of 1-5 m datum, where 75% of all abalone are located (B. DeFreitas, unpublished). Marked transects were designed to guide the placement of plots and estimate ocean floor slope (change in depth/distance), whereas control and treatment plots were designed to focus sampling efforts within a feasible area where differences in northern abalone densities could be measured.

All plots were surveyed prior to the addition of abalone transplants during May 2-9, 2002 (week 0) and then surveyed again during July 7-24, 2002 (week 12) and May 1-5, 2003 (week 53).

Establishing transects and plots

Each of the 2 transects within a site were made from lead-core line marked at 1 m intervals, up to a maximum length of 50 m. Transects were established by randomly throwing one end of the line into the shallow water and using the dive tender boat to lay the line perpendicular to depth contours, from approximately 0-9 m below chart datum. A pair of divers then inspected the transect line to determine if the following criteria were met: substrate composition was mainly bedrock with boulders and cobble; presence of algal food for northern abalone (i.e., *Nereocystis luetkeana*, *Laminaria* spp., *Alaria* spp., encrusting red coralline algae); and moderate abundance of red sea urchins (*Strongylocentrotus franciscanus*) and common northern abalone predators (i.e., *E. dofleini*; *P. helianthoides*; *C. productus*; *Sebastes* spp.; family Cottidae).

If the selection criteria were met, divers consulted tide height tables (Tides and Currents Pro for Windows 3.0, Sedgwick Bay harmonic station) to help locate the transect line's shallow end at 0 m depth at datum. Visual markers were installed at approximately 5 m intervals along the transect length to ensure the exact location could be resurveyed over time. White PVC markers (15 cm x 15 cm x 0.64 cm with 0.95 cm centre hole) were attached to the substrate using a pneumatic hammer drill modified for use with standard SCUBA tanks and two types of metal anchors. Metal anchors included stainless steel concrete anchor bolts (12.7 cm x 0.95 cm) for rock substrates and galvanized steel corkscrews (45 cm x 0.95 cm) for cobble, gravel, shell or sand substrates. Each transect marker was labelled with circular (3 cm diameter) plastic tags to indicate its distance in metres relative to the shallowest marker and aid diver orientation. The maximum transect length was 50 m if water depth did not exceed 9 m depth and suitable abalone habitat was continuous. Transect lengths were <50 m on steeper slopes where depths quickly exceeded 9 m or if suitable abalone habitat was no longer present (i.e., continuous sand).

Control and treatment plots along transects were established by graphing the depth profile of each transect and using the Microsoft Excel (Microsoft Office Excel 2000) function "randbetween" to generate a random number within the range of distances along the transect that were 1-5 m deep. Marked distances along the transect line were

the only visual reference to indicate the plot's deep or shallow boundaries. A simple coin toss was used to select either of the 2 transects and plots within a site as the control or treatment.

Surveying plots

During the course of this study, control or treatment plots were surveyed 3 times: (1) May 2-9, 2002, (2) July 17-24, 2002, and (3) May 1-5, 2003 (Table 2.1). Surveys occurred within a number of 1 m^2 metal quadrats that served as the secondary sample unit, whereas the primary sampling unit was the sum of all quadrat samples within a plot. The position of quadrat samples was determined randomly in advance and always progressed from deep to shallow water in order to follow safe diving practices.

Approximately half the area of each plot was surveyed by sampling five 1 m x 5 m strips on each half of the plot (Fig 2.1). The location of each strip was determined by using the Microsoft Excel (Microsoft Office Excel 2000) function "randbetween" to generate 5 random numbers which corresponded to sample strip starting points on each side of the plot. Divers started plot surveys at the seaward end of the plot's left side and placed the first quadrat sample adjacent to the distance measurement markings on the transect line. The next 4 quadrats were flipped perpendicular to the transect line to complete a single sample strip. Divers returned to the transect to position the first quadrat of each sample strip and completed all strips on the left side of the plot before attempting to survey strips on the right side.

Data collection

During plot surveys, a plastic clipboard and waterproof data sheet was used to record the following variables within each 1 m^2 quadrat sample: quadrat location; time of day (Pacific Standard Time); gauge depth (ft); substrate type; abalone shell length (mm SL); the number of red sea urchins; the number of common abalone predators; and the percent abundance of common brown, red and green macroalgae.

The position of each quadrat sample was recorded to aid in monitoring the movements of tagged abalone and assist in mapping unique site features such as octopus dens or kelp forest boundaries. The time of day and gauge depth were recorded to calculate the depth at datum of each sample and overall transect slope (change in depth/distance). The first, second and third dominant substrate types in each sample were recorded as number codes that referred to bedrock (2), boulders (3), cobble (4), gravel (5), sand (7), and shell (8).

All northern abalone found within quadrat samples were measured for maximum shell length (mm) using custom built aluminum calipers and recorded on data sheets as exposed, tagged or recently dead. Exposed abalone were those visible on the surface of bedrock or boulders; tagged abalone were those transplanted to treatment plots after initial surveys in May 2002; and recently dead abalone were empty shells that did not crumble after a firm hand squeeze.

To measure additional components of kelp forest community structure, the number of red sea urchins (*S. franciscanus*), number of common abalone predators (i.e., *P. helianthoides, E. dofleini, C. productus*), and percent abundance of common brown, red and green macroalgae within each quadrat sample was recorded. Common algae species included: *Nereocystis luetkeana; Macrocystis integrifolia*; *Laminaria* spp.; *Costaria costata*; *Cymathere triplicata*; *Pleuophycus gardneri*; *Pterygophora californica*; *Desmarestia* spp.; *Alaria* spp.; *Egregia menziesii*; articulated coralline red algae; *Phyllospadix scouleri*; and *Ulva fenestrate*.

All diving operations followed an approved safety plan that included detailed procedures in case of emergency and contact information for the nearest medical aid. Underwater work was conducted by 2 divers using the buddy system and supported by a designated boat tender that recorded dive times. Several different diving vessels were used throughout the duration of the study and included two 5.8 m custom built aluminum skiffs and Canadian Coast Guard operated rigid hull inflatable zodiacs. All participating divers were trained in marine algae identification and dive survey techniques prior to conducting surveys. Diver training included mock surveys that built up skill levels and acclimatized individuals to work safely within thick kelp forests.

Collecting, marking and transplanting abalone

A total of 1600 northern abalone were collected from within the research area, marked with a unique identification tag and transplanted to 8 replicate treatment plots during May 4-9, 2002. The specific locations of abalone collection sites have been filed with the Shellfish Section of Fisheries & Oceans Canada at the Pacific Biological Station.

Divers collected abalone by searching pre-surveyed areas and removing approximately every 5th abalone encountered. Abalone were carefully removed from rocks without the use of any tools such as pry bars that may potentially damage the animal's delicate foot. On occasion, divers utilized live *P. helianthoides* to dislodge abalone that were tightly adhering to rocks by instigating the abalone's natural predator

avoidance response (Emmett and Jamieson 1988). Divers placed collected abalone into mesh bags and transferred them to 53 L plastic containers filled with fresh sea water for transport to the support vessel. Once onboard the ship, abalone were transferred to 500 L plastic containers lined with nylon mesh and filled with constant flow seawater.

Each collected abalone was measured for maximum shell length using calipers, examined to estimate sex and gonad condition, and marked with a unique identification tag. A flat wooden stick was used to move aside the abalone's epipodium and visually examine the gonad to determine its sex and grade reproductive condition. Dark green colored gonads were classified as female and pink or beige colored gonads were classified as male. The reproductive stage of each gonad was roughly estimated by recording whether it appeared completely deflated, mildly swollen or completely swollen. Abalone were prepared for marking by cleaning off a portion of the shell with a small wire brush and then drying the shell with pressurized air. A small amount of Z-Spar A-788 splash zone marine epoxy was then used to attach a 95 mm diameter, uniquely numbered vinyl disk tag (Floy Tag, Seattle Washington, USA) to the shell.

Tagged abalone were placed on plastic trays inside of 53 L plastic containers filled with pumped sea water. Each plastic tray held 25 abalone and each 53 L container held 2 plastic trays. After 4 containers were filled with 200 tagged abalone, they were promptly transported to the release site where a team of divers physically placed abalone within the centre of the pre-surveyed treatment plot. The 200 abalone transplanted to each treatment plot corresponded to a density increase of ~2.0/m^2. Each abalone was examined to ensure the tag had been properly applied and that the animal was firmly attached to the rock substrate. Abalone transplanted to treatment plots were observed opportunistically during the days immediately following their release.

Data analysis

All gauge depths were converted to depth (m) at datum using predicted tide heights (Tides and Currents Pro, 2000) with Sedgwick Bay harmonic station properties. All analyses, unless stated otherwise, were performed using JMP statistical software (JMP, 2001).

For comparative analyses of abalone densities within each treatment or control plot over time, the 50 quadrat samples that comprise the ten 1 m x 5 m sample strips were treated as separate samples. For comparative analyses of abalone densities within all

treatment or control plots during one sample period, all quadrat samples were pooled together and considered a single sample.

In the presentation of changes in abalone abundance over time, week 0 = surveys during May 2-9, 2002; week 1 = the addition of marked abalone to treatment plots immediately after initial surveys; week 12 = surveys during July 17-24, 2002; and week 53 = surveys during May 1-5, 2003 (one year after the addition of marked abalone to treatment plots). Mature northern abalone are defined as those measuring ≥70 mm.

Results

General survey summary

During the 12-month study, a total of 1515 exposed abalone were measured in 2400 quadrat samples of abalone habitat. Approximately 59 person hours of dive time were required to complete plot surveys (Table 2.1).

The mean transect length was 43 m (Min. 20 m, Max. 50 m) and the mean transect depth range was -0.2 m to 7.5 m (Min. -0.9 m, Max. 10.1 m). The average transect slope, measured as the change in depth over distance, was 18% (Min. 8%, Max. 38%). The average minimum and maximum plot depth was 1.6 m to 4.4 m (Min. -0.3 m, Max. 4.4 m). Bedrock, boulders and cobble were the most common substrates in plots (Table 2.2).

Pre-treatment summary

Prior to the addition of transplanted abalone, the mean abalone SL within control and treatment plots was 77.0 mm (Fig. 2.2). Control plots contained significantly larger abalone (79.1 mm ± 1.4 SE) than treatment plots (73.4 mm ± 2.1 SE), (Mann-Whitney test, $P<0.032$). Approximately 66% ($n=169$) of all exposed abalone in control plots and 62% ($n=91$) of those in treatment plots measured ≥70 mm and were considered to be mature.

For the initial survey, the mean density of all sized abalone within control and treatment plots was $0.51/m^2 \pm 0.10$ SE. The mean density of mature abalone within control and treatment plots was $0.33/m^2 \pm 0.06$ SE. There was no significant difference between the density of mature abalone within control plots ($0.42/m^2 \pm 0.11$ SE) and treatment plots ($0.23/m^2 \pm 0.05$ SE) (Mann-Whitney test, $P>0.32$) (Table 2.3).

The mean density of common predators of abalone within control and treatment plots was $0.07/m^2 \pm 0.01$ SE. There was no significant difference in predator densities

between control and treatment plots (Mann-Whitney test, P>040). Within control plots, abalone predator densities were higher than average at sites 1, 3, & 10 and lower than average at sites 2, 7, 8 & 9. Within treatment plots, abalone predator densities were higher than average at sites 1, 2, & 3 and lower than average at sites 4, 7, 8 & 9 (Table 2.3).

Transplanted abalone population characteristics

The mean SL of abalone collected from each of the 6 collection sites ranged from 79.6 mm to 98.9 mm. The mean SL of all 1600 transplanted abalone was 93.8 mm (Min. 47.9 mm, Max. 140.2 mm) (Fig. 2.3). The mean SL of abalone transplanted to each of the 8 experimental sites ranged from 78.8 mm at site 1 to 103.4 mm at site 3 (Fig. 2.4).

The collected abalone populations was comprised of 43% females and 57% males (Table 2.4, 2.5). Approximately 56% of all abalone with undeveloped or deflated gonads were female whereas the majority (67%) of abalone with fully developed or swollen gonads were male. Total female abalone (n=684) gonad condition was predominately rated as "mildly swollen" (43%) and the remaining females were either "completely deflated" (19%) or "fully swollen" (19%). In contrast, total male abalone (n=915) gonad condition was predominately rated as either "fully swollen" (43%) or "mildly swollen" (41%) and the remaining males were "completely deflated" (17%) (Table 2.6).

Approximately 12% of all abalone collected were youth sized <70 mm SL (n=191). In this size class, 29% females (n=28) and 19% males (n=18) were found to have "completely deflated" gonads.

Post treatment summary – mature abalone abundance

For all replicate sites combined, mature abalone densities within control plots remained stable without any significant differences for the duration of the study (Kruskal-Wallis ANOVA test, P>0.977) (Fig. 2.5). Twelve weeks after the addition of transplants, the mean density of mature abalone within treatment plots was $0.83/m^2 \pm 0.30$ SE, a non-significant increase of ~$0.60/m^2$ (Kruskal-Wallis ANOVA test, P>0.140) above pre-treatment densities (Fig. 2.5). One year after the addition of transplants, the mean density of mature abalone ($0.25/m^2 \pm 0.04$ SE) within treatment plots was similar to pre-treatment levels ($0.23/m^2 \pm 0.05$ SE) (Fig. 2.5).

Twelve weeks after the addition of transplants, significant increases (Tukey-Kramer HSD test) in mature abalone density were detected within treatment plots at sites 2, 3, 4 & 9 (Table 2.8, Fig. 2.6). The mean density of mature abalone within these high transplant retention sites was 1.49/m^2 ± 0.37 SE, which corresponds to a density approximately 6.8 times greater in magnitude than original densities. In stark contrast, the mean density of mature abalone within low transplant retention sites (1, 6, 7 & 10) was 0.18/m^2 ± 0.07 SE, approximately 1.3 times less than original densities.

Approximately 61% of all abalone found within treatment plots at sites 2, 3, 4 & 9 during week 12 were transplanted (tagged) abalone, whereas the remaining treatment plots contained approximately 25% transplanted (tagged) abalone (Table 2.9). During week 53, approximately 13% of all abalone found within treatment plots at sites 2, 3, 4 & 9 and approximately 7% of all abalone found at the remaining sites were transplanted (tagged) abalone (Table 2.9).

There were no significant changes in mean abalone density at 7 of the 8 control plots, with the exception of site 3 where a significant decrease (Tukey-Kramer HSD test) in mature abalone densities was detected (Table 2.8, Fig. 2.6). One year after the addition of abalone transplants, the treatment plot at site 3 was the only location that continued to have a significantly greater density of mature abalone than the initial density measured in May 2002.

Post treatment summary – size of abalone

In July 2002, approximately 12 weeks after the addition of transplanted abalone, the mean abalone SL at both control and treatment plots had increased (Table 2.7, Fig. 2.7). Abalone within control plots were non-significantly larger, (+2.3 mm, Mann-Witney test, $P>0.323$) whereas abalone within treatment plots were significantly larger (+15.6 mm, Mann-Witney test, $P<0.001$). In July 2002, abalone within treatment plots were also significantly larger than those within control plots (Mann-Witney test, $P<0.001$). In subsequent surveys during 2003, although there was no significant difference in mean abalone SL between control and treatment plots (Mann-Witney test, $P>0.051$), the size of abalone had decreased significantly in both control (Mann-Witney test, $P>0.002$) and treatment plots (Mann-Witney U test, $P<0.001$) (Fig. 2.7).

Predator abundance and transplant mortalities

To investigate whether the abundance of predators of abalone in treatment plots increased in response to the addition of transplanted abalone, predator densities in control and treatment plots during May 2002 and July 2002 were compared. Within control plots, mean predator density increased significantly (+ 0.08/m^2, *t*-test, t=-2.463, df=14, *P*>0.027) between May and July but within treatment plots, there was no significant difference (*t*-test, t=0.813, df=14, *P*>0.429) in predator densities between the two sample periods.

The density of predators within high abalone transplant retention plots (sites 2, 3, 4 & 9) were compared with the remaining treatment plots during the initial survey and at 12 weeks to examine if predators contributed to abalone transplant retention. During both time periods, there was no significant differences in predator densities between high abalone retention sites and low retention sites (week 0, *t*-test, t=-1.362, df=6, *P*>0.222; week 12, *t*-test, t=-1.242, df=6, *P*>0.261).

During opportunistic visits to treatment plots in the days immediately following the release of abalone transplants, a total of 20 (1.3%) transplanted abalone were found dead (Table 2.10). In July 2002, 12 weeks after transplants were completed, a total of 311 (19.4%) tagged abalone and 68 (4.3%) empty shells were found during plot surveys. The highest rate of recovery for transplanted abalone was 54.5% (*n*=109) at site 9 and the lowest was 4.4% (*n*=8) at site 1. One full year after transplants were completed, only 30 (1.9%) live tagged abalone and 25 (1.6%) empty tagged shells were recovered (Table 2.10).

Red sea urchin abundance

The density of red sea urchins (Table 2.11) within high abalone transplant retention plots (sites 2, 3, 4 & 9) were compared with the remaining treatment plots during the initial survey and at 12 weeks to examine if urchin abundance contributed to abalone transplant retention. During the initial survey, red sea urchin densities were significantly greater at high retention sites than low retention sites (t-test, t=-2.235, df=14, *P*>0.042) but during the second survey, there was no longer a detectable difference (t-test, t=-1.226, df=14, *P*>0.241).

Discussion

Overview

This study did not support the hypothesis that the current density of abalone populations are below a critical threshold required for successful reproduction, as transplanted abalone dispersed from enhanced densities during the spawning season. However, the study also indicated that artificially aggregated abalone dispersed at slower rates from some sites and that transplanted animals may influence population structure and theoretical reproductive potential when combined with resident abalone. There was no clear relationship between treatment site features and the retention of transplanted abalone to differentiate a 'good' from a 'poor' transplant site.

Prior to the addition of transplanted abalone, the mean density of all sized abalone within control and treatment plots was 0.51/m^2 ± 0.10 SE and the mean abalone SL was 77.0 mm. These results are very similar to the 1998 DFO survey in southeast Haida Gwaii where Campbell et al. (2000) reported a mean density of 0.51/m^2 at 128 sites and a mean abalone SL of 76.6 mm. This suggests that abalone populations within the research area were representative of those measured along the entire southeast coast of Haida Gwaii and that abalone abundance within the region had stabilized to levels approximately 17% of those recorded in 1978 (2.93/m^2, Breen and Adkins 1979).

Mature abalone abundance

During the 3 sample periods, mean densities of mature abalone within all replicate control plots changed very little (Min. ~0.41/m^2, Max. ~0.47/m^2) and there was no significant differences in mean densities of mature abalone within all replicate treatment plots (Min. ~0.23/m^2, Max. ~0.83/m^2) (Fig. 2.5). In general, these results suggested that transplanted abalone did not remain in enhanced densities for the duration of the reproductive season but instead dispersed at different rates until original densities were obtained. If the original density of abalone were below a critical threshold required for reproductive success, as suggested in the national recovery strategy (Toole et al. 2002), mature abalone at all transplant sites would have benefited from larger aggregations that increase egg fertilization rates (Giese and Pearse 1974, Shepherd 1986*a*, Denny and Shibata 1989).

Although this study did not support the hypothesis of impaired reproductive ability due to low population abundance, several findings suggest that artificial aggregations are a viable method to increase the theoretical reproductive potential of abalone during

the spawning season. First, the density of mature abalone within treatment plots at sites 2, 3, 4 & 9 was significantly higher (~6.8 times) than original levels 12 weeks after the addition of transplants (Fig 2.6). Second, transplanted abalone comprised ~60% of all abalone within treatment plots at sites 2, 3, 4, & 9 and ~25% at the remaining sites during week 12 (Table 2.9). Third, transplanted abalone increased the mean abalone SL within treatment plots at week 12 and hence increased the fecundity of the spawning population (Fig. 2.7). The actual benefits of these artificially created spawning aggregations composed of large animals can only be implied because egg fertilization rates were not directly measured. However, recent studies on abalone (Clavier 1992; McShane 1995a, 1995b; Shepherd and Partington 1995; Babcock and Keesing 1999) and sea urchins (Pennington 1985, Levitan 1991, Levitan et al. 1992, Levitan and Sewell 1998) have pointed to reduced fertilization success caused by dilution of gametes through reduced adult spawner densities. Additionally, the reproductive contribution of a few large females may be greater than several smaller females (Campbell et al. 1992, 2003). For free-spawning marine invertebrates in general, egg fertilization is enhanced by the aggregation of spawners, synchrony of gamete release, and sperm volume (Giese and Pearse 1974).

Factors influencing transplanted abalone retention

Within treatment plots, transplanted abalone dispersed from enhanced densities at variable rates and densities returned to pre-treatment levels one year later. These results imply specific sites possessed certain features that supported higher than average abalone densities during the summer spawning season. Numerous physical and biological factors may have contributed to retaining transplanted abalone and include: handling stress; tag loss; food availability; predator abundance; red sea urchin abundance; exposure to wave energy; substrate composition; and plot depth, size, or slope. Due to this study occurring in the field, it was impossible to effectively control for these variables and determine with certainty which factors played a greater role in retaining transplanted abalone. However, a discussion of these various factors based on observations and analysis of available data is warranted.

Each transplanted abalone was initially removed from the water and processed prior to placement in treatment plots. Although care was taken to minimize stress due to handling, it is reasonable to assume that each animal may have been affected negatively to some degree. This was most apparent at site 1, the initial release site,

where 18 animals were found dead several days after transplanting. The specific cause of these mortalities was not known but appeared to be stress due to handling that consequently made the animals more susceptible to natural predation.

The loss of identification tags may have contributed to the incorrect identification of transplanted abalone. A total of 160 abalone (10%) were doubled marked with a second tag to test for tag loss but all double tagged animals that were found in subsequent surveys did not lose any tags. Due to generally low tag recapture rates, the possibility of tag loss remains an issue.

Food availability within each study site was assumed to be equal during each sample period because all sites contained a superabundance of attached and drift macroalgae. The composition or abundance of food for abalone within plots was not analyzed because the data collection technique of recording percent abundance of common brown, red and green macroalgae within each quadrat sample was insufficient to standardize the subjective observations of 14 different divers.

The abundance of common predators of abalone did not appear to contribute to the retention of transplanted abalone as there was no significant difference in predator densities between high and low abalone transplant retention sites. During this study, the most significant predators of mature abalone were octopus (*E. dofleini*), who forage largely at night, and frequently return to a den to feed (Hartwick et al. 1981). This highly mobile predator was rarely observed during plot surveys but likely played a greater role of influencing the retention of transplanted abalone, as several tagged shells were found discarded in middens at the mouth of octopus dens. Other significant predators of mature abalone, such as sea otters (*E. lutris*) and human divers, are rarely sighted within the abalone research area and therefore thought to have a negligible impact on transplanted abalone retention.

The abundance of red sea urchins also did not appear to contribute to the retention of transplanted abalone as urchin densities were significantly greater at high retention sites than low retention sites during week 12 but not significantly different during week 53. The relationship between abalone and red sea urchins is unknown but commonly thought to be either competitive because the two species share food and space or symbiotic because urchin grazing prevents kelp overgrown of encrusting red coralline algae, the abalone larval settlement substrate (Sloan and Breen 1998).

Study sites were systematically dispersed within the semi-exposed eastern portion of the abalone research area in an effort to minimize wave exposure variability. There

were no observed differences in algae type or abundance between different study sites to indicate differences in wave exposure. Similarly, substrate composition did not appear to influence transplanted abalone retention because all sites contained a combination of rock substrates (i.e., bedrock, boulders, and cobble) that provided suitable shelter and drift algae entrapment habitat for mature abalone.

Preliminary surveys indicated that 97% of all abalone were at depths between 0-9 m and that 75% of all abalone were at depths between 1-5 m. The relatively small mean plot depth range (Min. 1.4 m, Max. 3.9 m) minimized the variability of depth within the 16 plots and did not appear to influence transplanted abalone retention. In contrast, the size and slope of plots may have contributed to variability in measurements of transplanted abalone retention. The 10 m x 10 m plot size may have been too small to effectively 'capture' transplanted abalone during surveys, as any animals that travelled >5 m in any direction would not have been recorded within quadrat samples. There was no statistical relationship between the slope of the plot and transplanted abalone retention; however it is worth noting that site 9 had both the highest slope (38%) and the highest density of transplanted abalone (~1.72/m^2) at week 12. This suggests that transplanted abalone may have been initially confined by a limitation of habitat outside the plot, as there is less available habitat within the 1-5 m depth range at greater slopes.

Future studies

As a potential northern abalone stock restoration technique, I offer the following recommendations for future trials in this area so that maximum theoretical benefits to reproduction are obtained.

First, transplanted abalone should originate from areas containing extremely low densities, poor habitat quality or susceptible to high predation. Transplanting abalone away from areas of low density will result in the removal of widely dispersed individuals who likely may not encounter another individual for the remainder of their reproductive life. Transplanting abalone away from areas of poor habitat quality (i.e., turbulent surf zones) will increase growth rates and result in increased fecundity (Breen 1986, Emmett and Jamieson 1989). Transplanting abalone away from areas susceptible to high predation (i.e., sea otter range expansion or poaching) may extend the animal's life and allow for participation in more numerous spawning events.

Second, collected abalone need not be tagged prior to transplanting as this process generally involves great time commitments and excessive handling that may contribute

to animal stress. Tagging studies can be beneficial for monitoring growth, movement or survival of transplanted abalone but are ancillary to the primary objective of creating dense spawning aggregations.

Third, the transplant site should be located in high quality abalone habitat that is confined by natural features that limit abalone dispersal. For northern abalone, high quality habitat includes: high rugosity rock substrates (i.e., bedrock with crevices or boulder gardens); an abundance of macroalgae for food and attenuating water currents that help retain larvae; an abundance of encrusting coralline algae for larval settlement and juvenile food; water depths that range from 1-5 m datum; and the presence of herbivorous grazers (i.e., sea urchins, limpets and chitons) that 'farm' the coralline algae surface. Natural features that form boundaries around transplant sites, such as sandy beaches or muddy bays, will limit abalone dispersal and aid in maintaining dense spawning aggregations.

Fourth, transplants should occur at the onset of the spawning season and ideally, be repeated at least once during the spawning season. According to hatchery studies the timing of the main spawning season will depend primarily on the water temperature (~12^{0}C) (Pearce 2003). And finally, the transplant study will need to be repeated annually.

Table 2.1. Plot survey effort summary.

Survey Dates		No. of Quadrats	Dive time (hr:min)	Effort (min/quad)
May 2-9, 2002	(week 0)	800	22:39	1.7
July 17-24, 2002	(week 12)	800	18:04	1.4
May 1-5, 2003	(week 53)	800	18:24	1.4
Total		2400	59:07	

Table 2.2. Summary of transect and plot physical features at control (C) and treatment (T) sites. The most common substrates are listed (1=first, 2=second, 3=third) where substrate code 2=rock, 3=boulders, 4=cobble, 5=gravel, 7=sand, and 8=shell. Percent slope is calculated as the change in depth / transect length. All depths are in metres and converted to datum.

Site	Control or Treat.	Substrate			Transect Length (m)	% Slope	Transect Depth		Plot Ctr. Location (m)	Plot Depth	
		1	2	3			Min	Max		Min	Max
1	C	3	4	8	35	19	0.3	7.0	12	0.6	3.8
	T	3	4	7	50	11	0.1	5.9	22	2.5	4.6
2	C	2	4	5	35	29	-0.9	10.1	10	1.4	5.8
	T	3	4	7	40	15	1.0	6.9	15	2.1	4.1
3	C	2	4	7	50	13	-0.5	6.4	11	1.7	4.4
	T	2	4	8	50	8	-0.2	4.1	38	3.0	4.2
4	C	3	8	7	50	17	0.3	8.8	9	2.1	4.8
	T	2	7	4	50	14	-0.8	6.6	18	0.8	4.6
7	C	3	4	5	40	17	0.1	7.8	11	0.7	2.1
	T	3	4	8	30	30	-0.8	8.9	8	1.4	4.8
8	C	4	7	8	50	15	-0.7	6.9	27	2.3	3.8
	T	2	4	8	50	10	0.3	5.5	34	2.0	3.5
9	C	2	7	7	40	21	-0.7	8.1	8	0.7	4.7
	T	2	7	4	20	38	-0.9	8.7	5	-0.3	5.7
10	C	3	4	8	50	16	0.4	8.8	16	2.2	5.0
	T	2	8	4	50	17	0.6	9.4	22	3.1	4.6

Table 2.3. Summary of abalone and common predators of abalone densities (#/m^2) in control (C) and treatment (T) plot surveys during week 0 (May 2002), prior to the addition of transplanted abalone.

Site	Control or Treatment	Abalone density (#/m^2)			Predator density
		<70mm SL	≥70mm SL	Total	
1	C	0.22	0.54	0.76	0.12
	T	0.04	0.14	0.18	0.10
2	C	0.20	0.28	0.48	0.04
	T	0.04	0.36	0.40	0.12
3	C	0.12	0.34	0.46	0.08
	T	0.18	0.12	0.30	0.16
4	C	0.00	0.28	0.28	0.06
	T	0.14	0.08	0.22	0.06
7	C	0.36	0.78	1.14	0.02
	T	0.36	0.34	0.70	0.04
8	C	0.00	0.04	0.04	0.04
	T	0.10	0.40	0.50	0.00
9	C	0.56	0.94	1.50	0.00
	T	0.22	0.32	0.54	0.06
10	C	0.32	0.18	0.50	0.10
	T	0.04	0.06	0.10	0.08
Mean	C	0.23 ± 0.07	0.42 ± 0.11	0.65 ± 0.17	0.06 ± 0.01
	T	0.14 ± 0.04	0.23 ± 0.05	0.37 ± 0.07	0.08 ± 0.02

Standard errors shown are for all site groups combined (n = 8)

Table 2.4. Sex and gonad condition of 1600 abalone sampled from collection sites during May 4-9, 2002. Sex was determined by gonad color where males are pink/beige and females are green. Gonad condition code 1=completely deflated, 2=mildly swollen and 3=fully swollen. Values are percents of collected population at each of 6 sites.

Collection Site	No. of Abalone	Proportion Female	Female gonad condition			Male gonad condition		
			1	2	3	1	2	3
A	235	0.44	0.16	0.17	0.12	0.11	0.19	0.26
B*	505	0.42	0.15	0.15	0.11	0.12	0.25	0.21
C	166	0.42	0.11	0.23	0.08	0.12	0.27	0.19
D	109	0.39	0.07	0.20	0.12	0.06	0.29	0.25
E	298	0.43	0.12	0.20	0.11	0.08	0.24	0.25
F	287	0.45	0.07	0.19	0.19	0.05	0.18	0.32
Mean	267	0.43	0.12	0.18	0.12	0.09	0.23	0.25

* Unable to determine the sex of 1 abalone collected from site B.

Table 2.5. Sex and gonad condition of 1600 abalone transplanted to each site during May 4-9, 2002. Sex was determined by gonad color where males are pink/beige and females are green. Gonad condition code 1=completely deflated, 2=mildly swollen and 3=fully swollen. Values are percents of transplanted population (n = 200) at each of 8 sites.

Transplant Site	No. of Abalone	Proportion Female	Female gonad condition			Male gonad condition		
			1	2	3	1	2	3
1	200	0.44	0.17	0.16	0.12	0.13	0.17	0.27
2	200	0.43	0.11	0.16	0.17	0.03	0.19	0.35
3*	200	0.41	0.24	0.16	0.02	0.19	0.30	0.11
4	200	0.46	0.12	0.19	0.15	0.11	0.26	0.18
7	200	0.38	0.07	0.22	0.09	0.11	0.30	0.22
8	200	0.42	0.14	0.19	0.09	0.11	0.25	0.23
9	200	0.43	0.08	0.23	0.13	0.06	0.22	0.29
10	200	0.47	0.07	0.18	0.23	0.03	0.19	0.32
Mean	200	0.43	0.12	0.18	0.12	0.09	0.23	0.25

* Unable to determine the sex of 1 abalone transplanted to site 3.

Table 2.6. Gonad condition of 1599 female and male abalone in each of 3 size classes. Gonad condition code 1=completely deflated, 2=mildly swollen and 3=fully swollen. Values are proportion of each sex in each size class.

Size Class	Sex	No. of Abalone	Gonad Condition		
			1	2	3
<70 mm SL	Female	96	0.29	0.36	0.34
	Male	95	0.19	0.35	0.46
70 - 99 mm SL	Female	298	0.23	0.44	0.33
	Male	430	0.13	0.38	0.50
≥100 mm SL	Female	290	0.34	0.44	0.22
	Male	390	0.20	0.45	0.35
Total	Female	684	0.29	0.43	0.29
	Male	915	0.17	0.41	0.43

Table 2.7. Summary of size frequency data for all exposed abalone measured (mm SL) within control (C) and treatment (T) plots during week 0 (May 2002), week 12 (July 2002) and week 53 (May 2003).

Statistic	Week 0		Week 12		Week 53	
	C	T	C	T	C	T
Mean shell length	79.1	73.4	81.4	89.0	74.7	70.8
Median	83.0	77.0	86.0	93.0	78.5	70.0
Std error	1.4	2.1	1.3	1.0	1.5	1.6
Upper 95%	81.9	77.6	84.0	91.1	77.6	74.0
Lower 95%	76.2	69.3	78.8	87.0	71.4	67.5
Total number	258	147	263	395	252	194

Table 2.8. Mean density (#/m^2) of mature abalone (≥70 mm) within control (C) and treatment (T) plots during week 0 (May 2002), week 12 (July 2002) and week 53 (May 2003). Mean densities at sites followed by a common letter, in the same row, are not significantly different (P>0.05) and means in the same row with no common letters are significantly different (P<0.05) using the Tukey-Kramer HSD test.

Site	Control or Treatment	Abalone density (#/m^2)		
		Week 0	Week 12	Week 53
1	C	0.54 a	0.54 a	0.32 a
	T	0.14 a	0.10 a	0.28 a
2	C	0.28 a	0.38 a	0.36 a
	T	0.36 a	1.22 b	0.28 a
3	C	0.34 a	0.02 b	0.08 b
	T	0.12 a	1.14 b	0.34 c
4	C	0.28 ab	0.60 a	0.26 b
	T	0.08 a	1.00 b	0.10 a
7	C	0.78 a	1.02 a	1.06 a
	T	0.34 a	0.38 a	0.28 a
8	C	0.04 a	0.04 a	0.24 b
	T	0.40 a	0.12 a	0.18 a
9	C	0.94 a	0.98 a	0.62 a
	T	0.32 a	2.58 b	0.40 a
10	C	0.18 a	0.14 a	0.36 a
	T	0.06 a	0.12 a	0.10 a
Mean	C	0.42 ± 0.11	0.47 ± 0.14	0.41 ± 0.11
	T	0.23 ± 0.05	0.83 ± 0.30	0.25 ± 0.04

Standard errors shown are for all site groups combined (n = 8)

Table 2.9. Percentage of transplanted (tagged) mature abalone (≥70 mm) within treatment plots at week 12 (July 2002) and week 53 (May 2003) after the addition of transplanted abalone.

Treatment Site	Percent tagged abalone	
	Week 12	Week 53
1	20.0	7.1
2	47.5	0.0
3	49.1	0.0
4	80.0	20.0
7	31.6	21.4
8	16.7	0.0
9	66.7	30.0
10	33.3	0.0
Mean	43.1	9.8
Std Error	7.8	4.3

Standard errors shown are for all site groups combined (n = 8)

Table 2.10. Total number of transplanted abalone found alive and dead (empty shells) at each treatment site during week 1 (May 2002), week 53 (July 2002) and week 53 (July 2003). Week 1 occurred in the days immediately following the addition of transplanted abalone during May 2-9, 2002.

Site	Week 1		Week 12		Week 53	
	Released	Dead	Alive	Dead	Alive	Dead
1	200	18	8	11	1	0
2	200	1	41	0	2	2
3	200	0	43	4	3	3
4	200	0	51	2	1	0
7	200	0	23	12	4	4
8	200	0	10	13	2	4
9	200	0	109	0	6	0
10	200	1	26	26	11	12
Total	1600	20	311	68	30	25
% Total	100	1.3	19.4	4.3	1.9	1.6

Table 2.11. Red sea urchin density (#/m^2) within control (C) and treatment (T) plots during week 0 (May 2002), week 12 (July 2002) and week 53 (May 2003).

Site	Control or Treatment	Red sea urchin density (#/m^2)		
		Week 0	Week 12	Week 53
1	C	11.28	17.56	9.36
	T	1.50	1.08	1.58
2	C	7.26	7.92	4.40
	T	6.22	7.02	2.88
3	C	12.32	11.50	7.36
	T	4.18	1.48	5.38
4	C	11.06	14.06	10.26
	T	16.26	13.10	15.12
7	C	8.34	13.24	8.40
	T	5.50	4.86	4.52
8	C	3.72	2.50	4.74
	T	5.94	2.72	5.48
9	C	8.42	6.08	8.08
	T	8.42	9.76	4.52
10	C	3.72	1.10	3.00
	T	2.60	1.86	3.54
Mean	C	8.27 ± 1.16	9.25 ± 2.06	6.95 ± 0.92
	T	6.33 ± 1.61	5.24 ± 1.55	5.38 ± 1.47

Standard errors shown are for all site groups combined (n = 8)

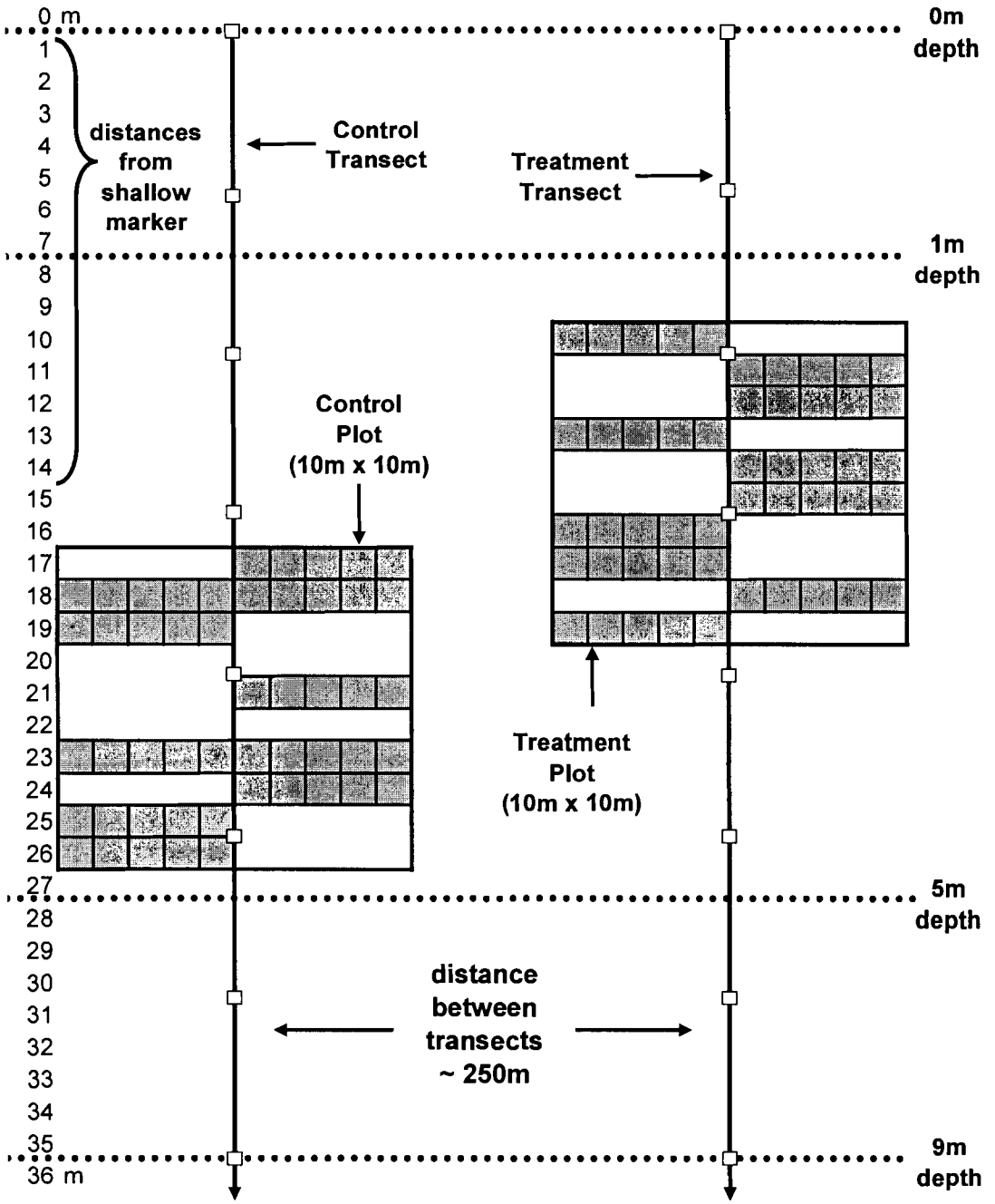

Figure 2.1. Schematic diagram of each study site. Each transect is marked at 5 m intervals and all distance measurements are referenced from the 0 m depth marker. Each transect bisects a 10 m x 10 m plot randomly located within a depth range of 1-5 m. A total of 10 randomly selected 1 m x 5 m strips are surveyed in each plot. Each grey square represents a 1 m^2 quadrat sample.

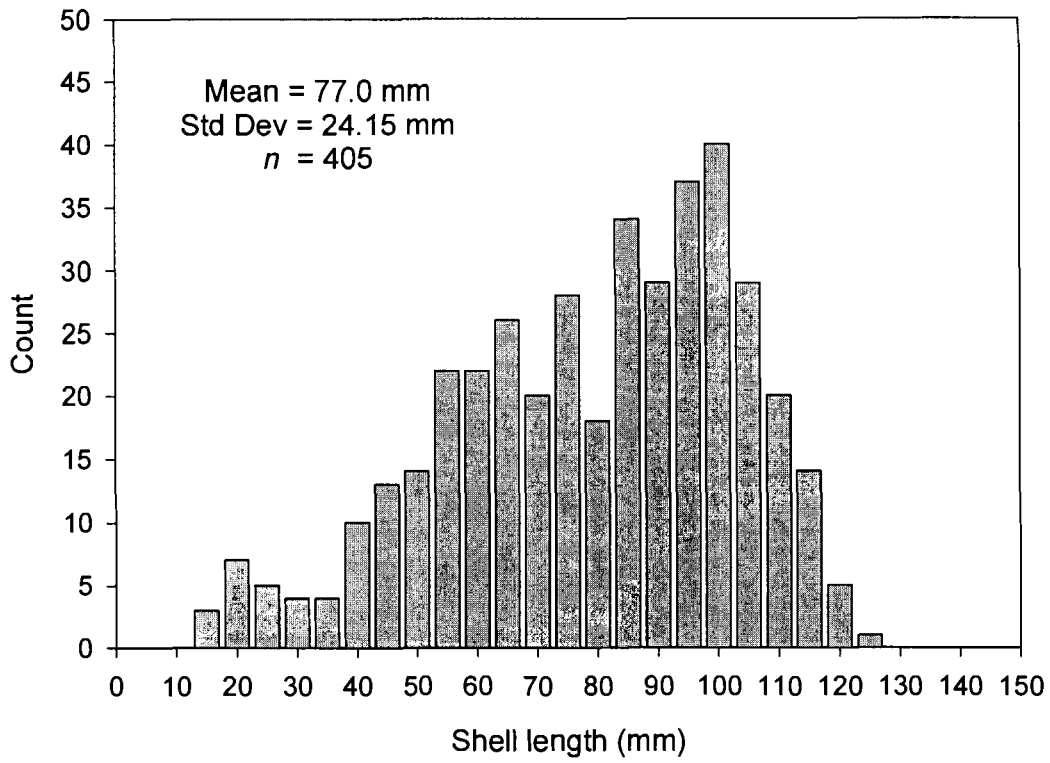

Figure 2.2. Size frequency distribution of all exposed abalone measured in control and treatment plots at 8 study sites during May 2-9, 2002, prior to the addition of transplanted abalone. Each bar indicates a 5 mm size group.

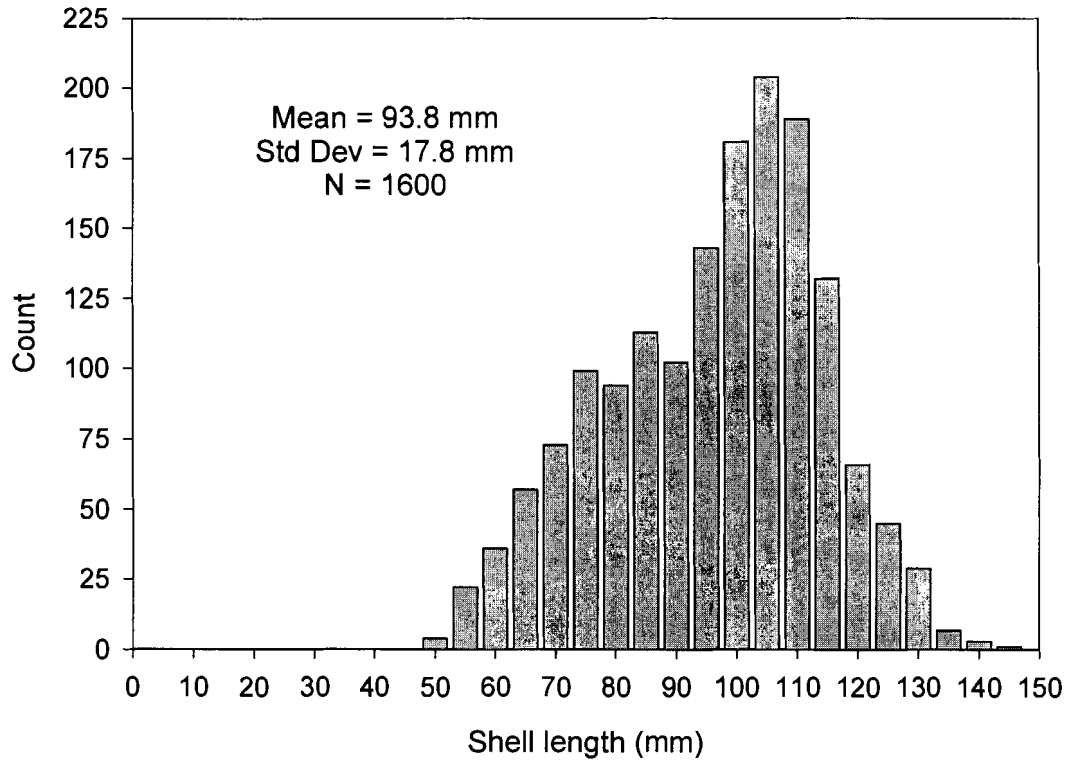

Figure 2.3. Size frequency distribution of 1600 abalone collected, marked and transplanted after initial surveys during May 2-9, 2002. Each bar indicates a 5 mm size group.

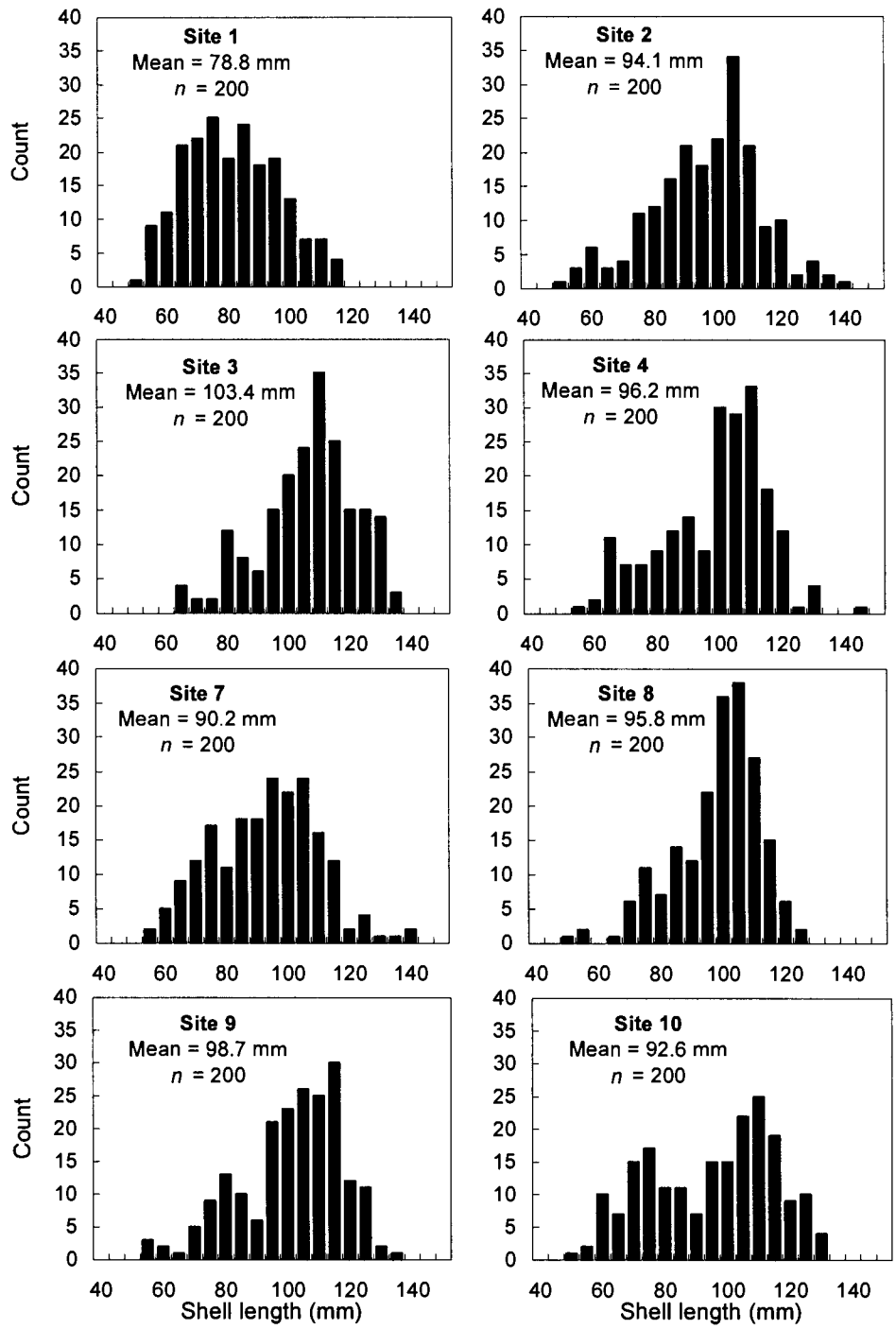

Figure 2.4. Size frequency distribution of 1600 abalone transplanted to sites 1-4 and 7-10 during May 2-9, 2002. Each bar indicates a 5 mm size group.

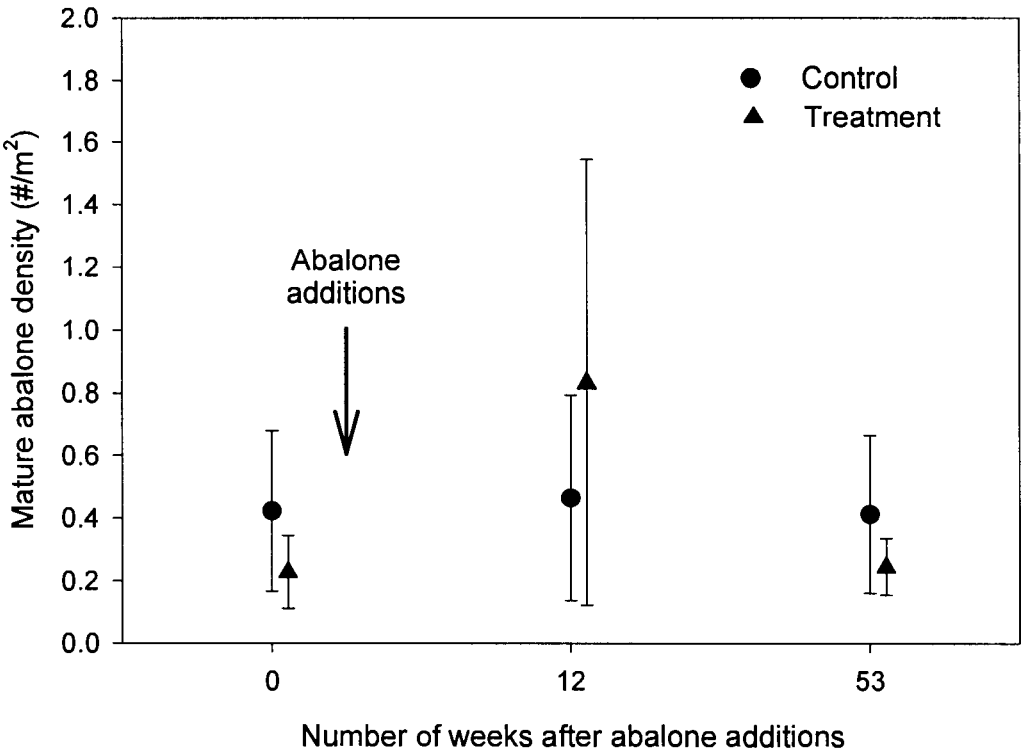

Figure 2.5. Mature abalone (≥70 mm) density (#/m^2) within 8 control (●) and treatment (▲) plots during week 0 (pre-treatment), week 12 (July 2002) and week 53 (May 2003). Vertical bars are 95% confidence intervals.

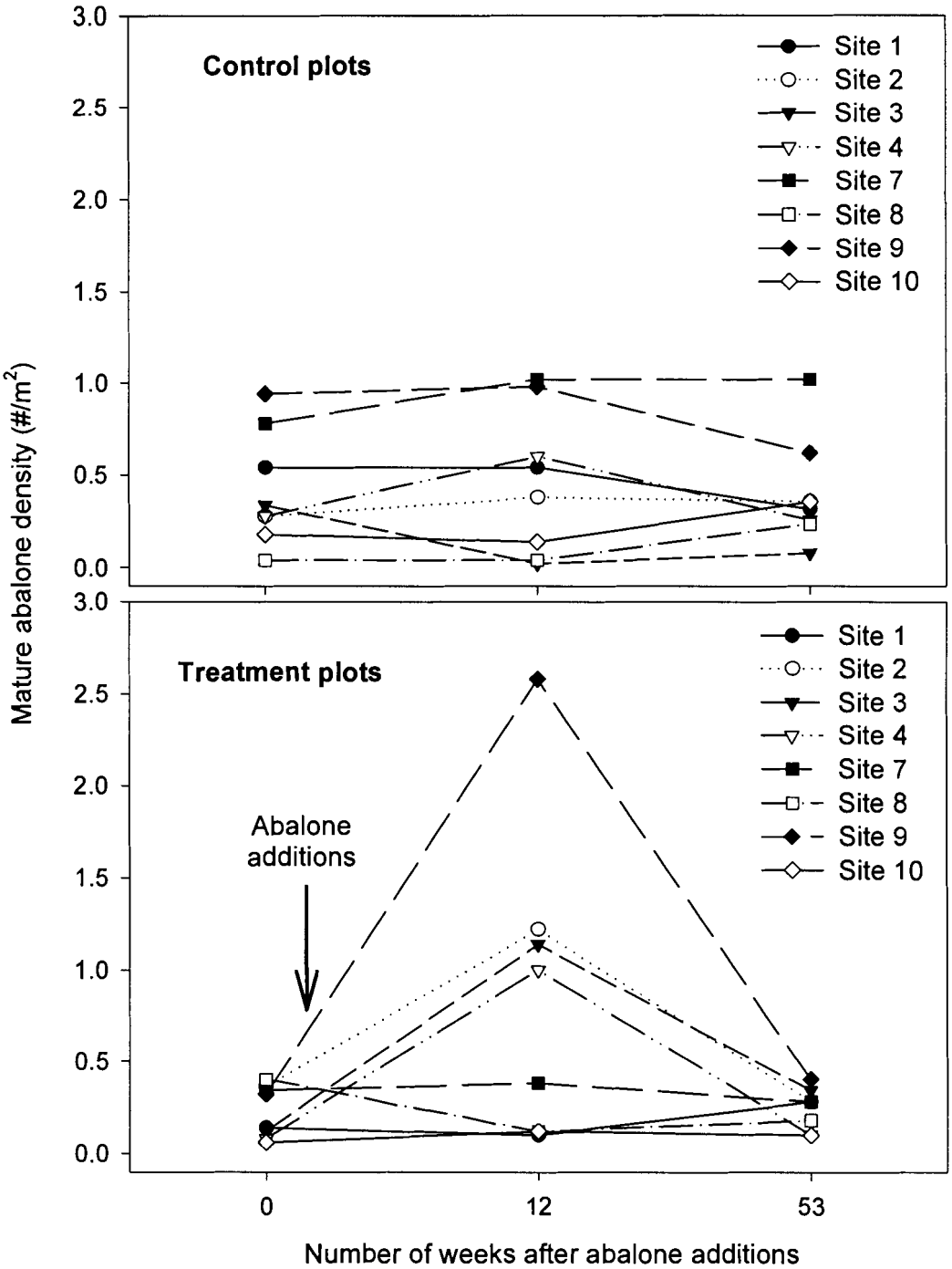

Figure 2.6. Mature abalone (≥70 mm) density (#/m^2) within control and treatment plots at each of 8 sites during week 0 (pre-treatment), week 12 (July 2002) and week 53 (May 2003).

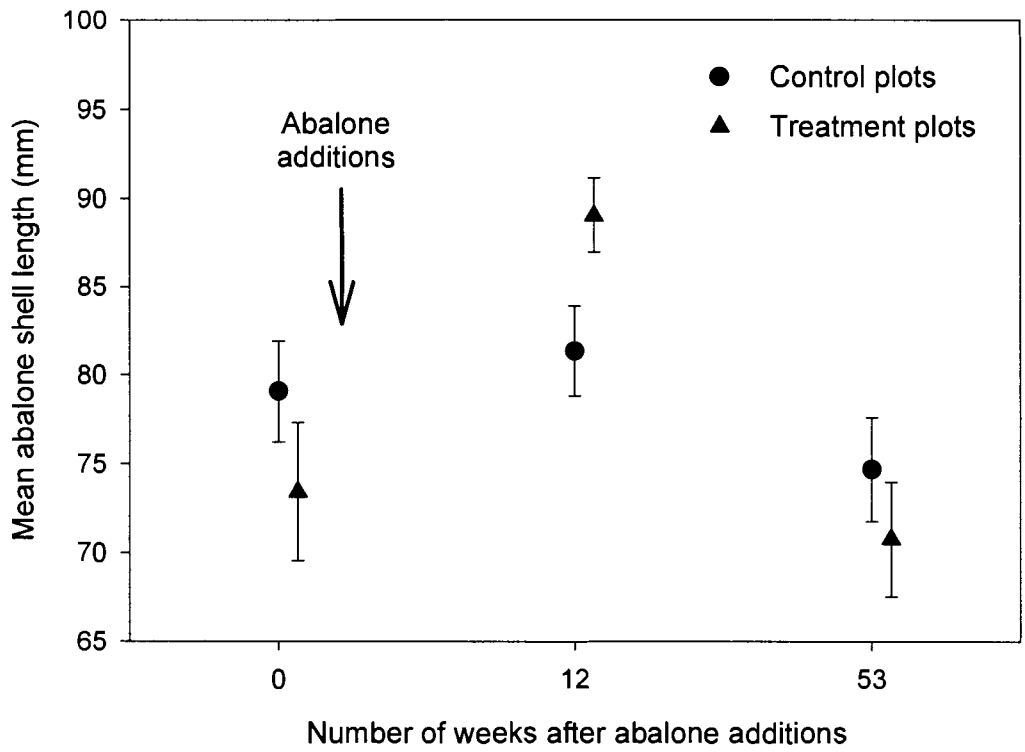

Figure 2.7. Mean abalone shell length (mm) within control (●) and treatment (▲) plots during week 0 (pre-treatment), week 12 (July 2002) and week 53 (May 2003). Vertical bars are 95% confidence intervals.

Chapter 3

Estimating Juvenile Abalone Abundance Using Artificial Habitats

Introduction

The most significant factors thought to be inhibiting northern abalone recovery are illegal harvests and poor recruitment (Campbell 2000, Toole et al. 2002). Recruitment defined as the number of juvenile abalone growing and surviving to the adult population each year, may be insufficient as a result of critically low adult densities (Shepherd and Brown 1993; Shepherd and Partington 1995) that reduce reproductive success due to low fertilization of gametes (Allee et al. 1949). Other processes that may reduce abalone recruitment include variation in timing and intensity of gamete production, larval predation and post-larval mortality (McShane 1992, 1995*a*). Recruitment processes for northern abalone are not well understood (Breen 1986, Sloan and Breen 1988).

Increasing the abundance of existing wild northern abalone populations in B.C. is the long-term goal of the national recovery strategy for northern abalone (Toole et al. 2002). One component of the strategy is to conduct abalone research and rebuilding experiments that may lead to increased breeding success, recruitment and population densities. In order to evaluate the success of various rebuilding experiments, it will be necessary to measure changes in abalone recruitment by quantifying the abundance of juveniles.

Artificial collectors have been successful at measuring the intensity of abalone larval settlement (Keesing et al. 1995, Nash et al. 1995) but require high maintenance, a considerable time investment to sort samples and appropriate larval identification expertise. Other larval settlement survey techniques such as underwater magnification (Shepherd and Turner 1985), anaesthesia (Prince and Ford 1985) and suction (McShane and Smith 1988) also require great diving and sample sorting efforts. Artificial habitats have been used to monitor abalone population fluctuations in Japan (Hayashi and Yamakawa 1988) and in California, Davis (1995) used artificial concrete block habitats that provided standardized sample areas to monitor juvenile abalone recruitment. Comparing results from previous juvenile abalone surveys that required the destruction of natural habitat (Tegner et al. 1989), Davis (1995) was able to provide surrogate juvenile abalone habitat and produce an index of abalone recruitment.

This chapter describes the design and testing of artificial concrete block habitats over a 12-month period at 6 sites in Haida Gwaii (Queen Charlotte Islands), B.C. The

objectives were to determine if concrete block habitats provided surrogate habitat for juvenile northern abalone and if so, the ability of artificial habitats to quantify juvenile abalone abundance in different locations. To determine if juvenile abalone abundance within artificial habitats was representative of nearby natural habitats, surveys of natural abalone habitats during the same time period were compared.

Materials and Methods

Study sites

Within the abalone research area (Fig. 1.1), twenty-four artificial concrete block habitats were tested at sites 1-6 (Fig 1.2). All study sites were located in the general area where previous abalone population surveys had determined a baseline of abalone densities (Campbell et al. 2000, Jones et al. 2003).

Artificial habitat design and deployment

The artificial habitat design utilized is a modification of that described by Davis (1995). Each habitat provides about 3.5 m^2 of surface area and consists of 24 concrete mini-blocks haphazardly oriented within a modified commercial crab trap (Fig. 3.1). Standard 20 cm x 20 cm x 40 cm concrete blocks were cut into quarters longitudinally to produce 4 individual mini-blocks. Discarded commercial crab traps measuring approximately 1.0 m in diameter and 0.3 m in height were altered by removing the central 'fishing' component, leaving a structurally effective frame of corrosive resistant metal enclosed with stainless steel mesh. Diamond-shaped openings within the wire mesh frames were approximately 66 mm x 91 mm and tested with empty shells to confirm their permeability to abalone <66 mm SL. Each structure also possessed a pre-fabricated entry or exit hole measuring 102 mm in diameter that was permeable to all abalone sizes and a hinged lid that allowed access to load, remove and examine concrete mini-blocks during artificial habitat deployment and sampling.

In July 2001, 24 habitats were deployed by belaying each intact unit from the dive support vessel to the ocean floor. Divers repositioned each structure with an industrial airlift bag. Within a site, 4 habitats were oriented parallel to shore in depths of 4-9 m and from 7-30 m apart. The habitats were randomly located within areas dominated by small boulders and cobble encrusted with red coralline algae. No anchoring mechanisms were utilized to secure the units in place, as each unit weighed approximately 120 kg and possessed a stable base.

Artificial and natural habitat surveys

Divers visually inspected artificial concrete habitats for structural integrity in February 2002 and thoroughly surveyed each unit *in situ* during May 2002, July 2002 and May 2003. A pair of divers sampled artificial habitats by removing and examining each concrete mini-brick for abalone. All abalone found were measured for maximum SL to the nearest millimeter and empty abalone shells were also measured and removed. After all bricks were examined, they were haphazardly repositioned within the metal frame. No special effort was made to remove or monitor abalone adhering to bricks as the bricks were replaced back into the wire mesh containers.

To estimate the abundance of juvenile abalone occupying natural habitats, sampling was conducted within 50 m^2 of area at 4 artificial habitat sites (sites 1-4) and 4 additional random sites (sites 7-10) during May 2002, July 2002 and May 2003 (Fig. 1.2). The fifty 1 m^2 quadrat samples of natural abalone habitat corresponded to the abalone density manipulation control plots discussed in Chapter 2 (Fig. 2.1). To estimate the abundance of juvenile abalone within natural habitats that may be cryptic (i.e., hiding underneath rocks or within crevices), divers invasively searched five randomly selected 1 m^2 quadrats (10% of total samples) at each site during each survey. The invasive searching method involved looking on the undersides of all movable rocks but did not include any destruction of natural habitat as care was taken to return any disturbed rocks to their original position. Diver efficiency in searching natural habitats was not measured.

Data analysis

All gauge depths were converted to depth (m) at datum using predicted tide heights (Tides and Currents Pro, 2000) with Sedgwick Bay harmonic station properties. All analyses, unless stated otherwise, were performed using JMP statistical software (JMP, 2001).

Each of the four artificial habitats within a site was treated as a single sample when examining differences in the same site over time or when examining differences between sites during the same survey period. The four artificial habitats within a site were combined and treated as a single sample when examining differences in all sites over time. Similarly, each of the 50 quadrat samples of natural abalone habitat were treated as a single sample when examining differences in the same site over time or when examining differences between sites during the same survey period.

In the analysis, I define juvenile abalone as ≤50 mm SL, youth abalone as 51-69 mm SL and mature abalone as ≥70 mm SL.

Results

Abalone abundance in artificial habitats

A total of 423 abalone and 35 empty shells were counted and measured within artificial habitats during the study (Table 3.1). The smallest and largest abalone SL measured in artificial structures was 15 mm and 100 mm, respectively. The average SL of all alive and recently dead abalone within artificial habitats was 42.8 mm and 56.6 mm, respectively (Fig. 3.2). Juvenile, youth and mature abalone represented 77%, 19%, and 4%, respectively, of all abalone found within artificial habitats.

Ten months after the installation of artificial habitats, during the first survey in May 2002, all 24 units contained juvenile or youth abalone (n=144, mean=6.0/unit ± 0.94 SE). During the second survey in July 2002, all but two artificial habitats contained juvenile or youth abalone (n=124, mean=5.2/unit ± 0.88 SE). During the final survey in May 2003, only one artificial habitat did not contain any juvenile or youth abalone (n=137, mean=5.70/unit ± 0.82 SE). The mean number of juvenile abalone occupying each artificial habitat was 4.5/unit ± 0.45 SE (Min. 0.0/unit, Max. 15.0/unit).

Comparing the three sample periods, there was no significant difference in the total number of juvenile abalone/unit (ANOVA F=0.11, df=2,15, P>0.892) or the total number of all sized abalone/unit (ANOVA F=0.16, df=2,15, P>0.858).

The mean density of juvenile, youth, mature and all-sized abalone within artificial habitats was 1.29, 0.31, 0.07 and 1.68/m^2, respectively (Table 3.2). Of the three abalone size groups, only juvenile abalone densities in artificial habitats were significantly different between sites (Tukey-Kramer HSD test, Table 3.2). Juvenile abalone densities within each site remained unchanged during the 3 sample periods (Tukey-Kramer HSD test), with the exception of site 5 that showed a significant decrease (P>0.038) from July 2002 to May 2003.

On average, each artificial habitat required 12.5 minutes for a pair of divers to completely survey.

Abalone abundance in natural habitats

A total of 773 abalone were counted and measured within natural habitat samples. The smallest and largest abalone found in natural habitats was 14 mm and 124 mm SL.

Juvenile abalone accounted for 13.3% (n=103) of all those measured, while 67.3% (n=520) were mature. The mean abalone SL was 78.4 mm (Fig. 3.4).

The mean density of juvenile, youth, mature and all-sized abalone measured with natural habitats was 0.09, 0.13, 0.43 and 0.64/m^2, respectively (Table 3.3). During the three sample periods, there was no significant differences in mean juvenile abalone density (ANOVA F=0.27, df=2,21, P=0.770) or mean density of all sized abalone (ANOVA F=0.01, df=2,21, P>0.995). Natural habitat samples were located at a mean depth of 2.58 m ± 0.03 SE (Min. = 0.1 m, Max. = 6.0 m).

At sites 1-4, where both artificial and natural habitat surveys were conducted within an area >15,000 m^2, juvenile abalone densities were significantly greater within artificial habitats (t-test, t=3.386, df=58, P>0.001) and youth abalone occupied artificial and natural habitats at similar densities (t-test, t=1.879, df=58, P>0.065) to natural habitats.

During the entire study, only 12 cryptic abalone were found during invasive searches of natural habitats. This corresponds to a total density of 0.1/m^2 or a mean density of 0.03/m^2. Of the total number of abalone found during invasive searches of natural habitats, 42% (n=5) were juvenile, 50% (n=6) were youth and 8% (n=1) were mature.

Discussion

The artificial habitat design tested in this study provided surrogate habitat for juvenile and youth northern abalone. Within ten months of installation, native juvenile and youth northern abalone had discovered and occupied each of the 24 artificial habitats. During subsequent surveys in July 2002 and May 2003, the mean number of juvenile and youth abalone occupying all artificial habitats remained similar. This suggested that concrete blocks provided surrogate shelter throughout the summer months when surrounding food abundance is high and good quality alternative natural habitats were available; and that once artificial materials are conditioned and attract abalone, they maintain a relative number or density of juvenile abalone.

The specific length of time required for artificial materials to condition and attract abalone was difficult to determine due to the limited number of sample periods. The concrete materials appeared to be suitable for northern abalone within seven months based on observations of abalone occupying most artificial habitats during structural inspections in February 2002. The conditioning time of this material was consistent with

Davis (1995) who found "juvenile native *H. rufescens* and *H. corrugata* inhabited artificial habitats within four months of deployment" in California.

As indicated in Fig. 3.2, juvenile northern abalone were the most abundant size class occupying artificial habitats. Both the small mesh size and high substrate complexity may have contributed to the size selectivity by limiting access and suitable shelter for abalone ≥70 mm SL. Juvenile abalone densities measured within artificial habitats were significantly different between sites but similar within sites. This apparent ability of artificial structures to quantify juvenile abalone abundance within standardized sample areas at different locations may provide the feedback required to gauge the success of future stock restoration experiments. Benefits of the modular artificial habitat design tested here included the low cost of construction, ease of deployment, durability within high energy subtidal environments, and most importantly, their ease of being dismantled and reconstructed by divers *in situ*, without the destruction of natural habitat.

Specific factors that made the artificial structures attractive to abalone were not investigated experimentally but were likely due to the consistent and availability of good quality sheltered habitat provided by the concrete blocks. Based on observations, additional factors that may have influenced the abundance of abalone in artificial habitats included easily accessed algal food growing on concrete bricks, and a mesh frame that may have excluded large predators such as sunflower seastars (*P. helianthoides*).

The measured abundance of juvenile abalone within artificial habitats may have been at their annual spring peak, as surveys were only conducted during May and July, a similar time of year that Davis (1995) measured a peak in abalone recruitment. In order to calibrate artificial habitats into better juvenile abalone abundance instruments, it will be necessary increase the number of surveys and monitor fluctuations in abalone abundance throughout the year. Only by comparing the changes in abalone abundance from winter to summer can the magnitude of localized recruitment events be determined.

In this study, juvenile abalone recruitment measured within artificial habitats was not representative of recruitment measured within nearby natural habitats. At sites 1-4, juvenile abalone abundance measured within artificial habitats was significantly greater than natural habitat samples, ranging in magnitude from 10 times greater at site 3 to 30 times greater at sites 1, 2 and 4. Although each natural habitat sample was randomly located within good quality juvenile abalone habitat and the mean juvenile abalone density found within natural habitats was similar to Campbell et al. (2000), natural

habitats provided little consistency with substrate composition and hence, the lower abundance of sheltered habitat. The significantly greater abundance of juvenile abalone found within artificial structures as compared to natural habitats suggests that abalone populations are not suffering from recruitment failure due to low population abundance. Instead, it appears that traditional survey techniques in natural habitats are unable to recognize or effectively detect juvenile recruitment due to the cryptic behaviour of juvenile abalone.

The use of artificial habitats as a standardized sampling instrument to estimate the abundance of cryptic juvenile abalone was supported by this research. The haphazardly oriented concrete blocks provided preferred habitat for juvenile abalone and the metal frame covered with wire mesh provides structural integrity and allowed each sampling unit to be quickly deployed or repositioned. A pair of divers could easily sample units *in situ*, with no destruction to either natural habitat or abalone adhering to concrete bricks.

As a juvenile northern abalone recruitment monitoring tool, several conditions improve the use of artificial habitats. In an area or coastline of interest, artificial structures should be installed at the same time so that conditioning of the materials is equal amongst units. The specific length of material conditioning time was not determined in this study but seven months appears to be sufficient. To better gauge any spatial or temporal differences in relative juvenile abalone abundance, surveys should be conducted at intervals of one-two months. As a northern abalone stock restoration tool, artificial habitats appear most suitable as a means to quantify relative changes in juvenile recruitment that may be due to experimental stock enhancement, an enhancement over non-rugose substrates (i.e., smooth bedrock), or an initial release site for cultured juveniles.

Table 3.1. Total number of abalone found in 4 artificial habitats at each site surveyed between May 2002 and May 2003.

Site	May 2002		July 2002		May 2003	
	Alive	Dead	Alive	Dead	Alive	Dead
1	17	1	24	1	46	2
2	44	1	38	4	25	8
3	5	2	3	2	14	0
4	12	0	10	1	8	0
5	37	3	31	0	27	5
6	37	3	20	1	25	1
Total	152	10	126	9	145	16

Table 3.2. Mean number and densities (#/m^2) of abalone at each artificial habitat site surveyed between May 2002 and May 2003. Means followed by the same letter were significantly different ($P<0.05$), using a Tukey-Kramer HSD test.

Site	No. of Abalone	Abalone density (#/m^2)			
		≤50 mm	51-69 mm	≥70 mm	All sizes
1	29.0	1.60a	0.48a	0.00a	2.07a
2	35.7	2.00a	0.45a	0.10a	2.55a
3	7.3	0.26b	0.21a	0.05a	0.52b
4	10.0	0.40b	0.17a	0.14a	0.71b
5	31.7	1.83a	0.31a	0.12a	2.26a
6	27.3	1.67a	0.26a	0.02a	1.95a
Mean	23.5	1.29	0.31	0.07	1.68
SE	4.8	0.31	0.05	0.02	0.35

Standard errors shown are for all sites combined (n = 6)

Table 3.3. Mean number and densities (#/m^2) of abalone at each natural habitat site surveyed between May 2002 and May 2003.

Site	No. of Abalone	Abalone density (#/m^2)			
		≤50 mm	51-69 mm	≥70 mm	All sizes
1	33.3	0.05	0.15	0.47	0.67
2	27.7	0.07	0.15	0.34	0.55
3	11.0	0.03	0.05	0.15	0.22
4	21.3	0.01	0.03	0.38	0.43
7	59.7	0.03	0.21	0.95	1.19
8	6.3	0.01	0.01	0.11	0.13
9	79.3	0.44	0.30	0.85	1.59
10	19.0	0.05	0.11	0.23	0.38
Mean	32.2	0.09	0.13	0.43	0.64
SE	8.9	0.05	0.03	0.11	0.18

Standard errors shown are for all sites combined (n = 8)

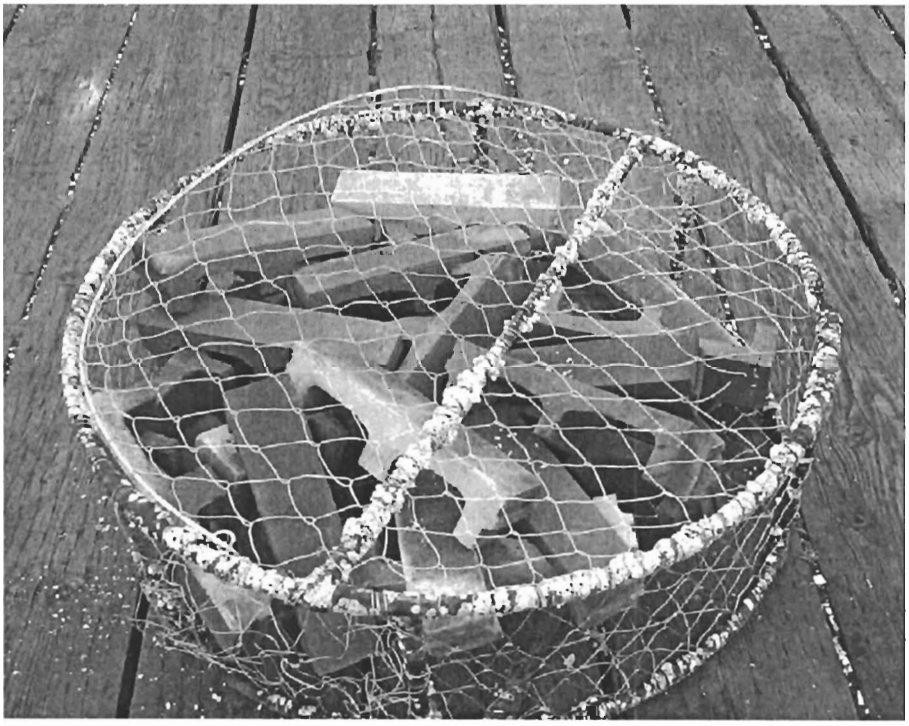

Figure 3.1. Artificial habitat design.

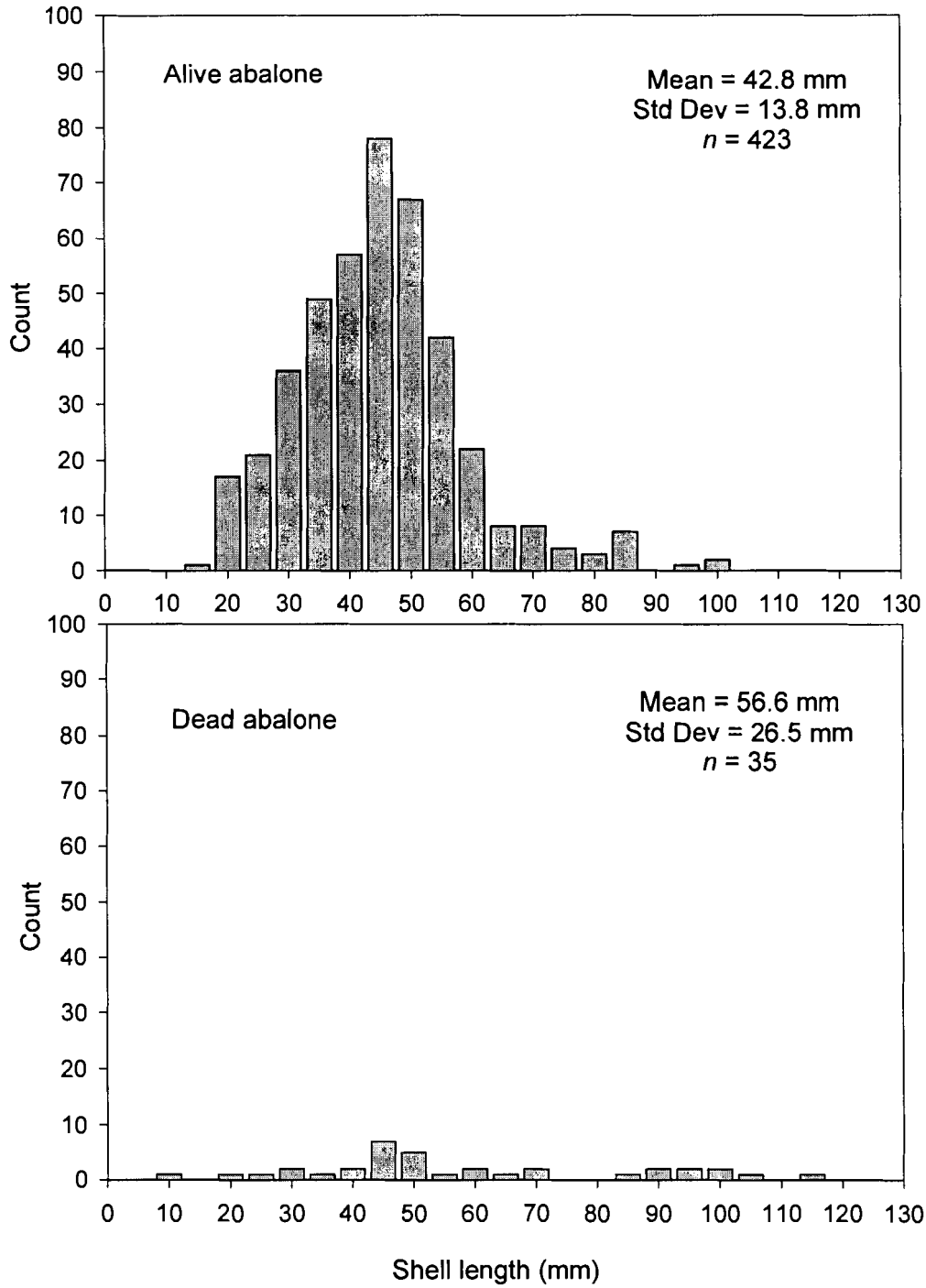

Figure 3.2. Size frequency distributions of alive and dead abalone measured within artificial habitats at sites 1-6 between May 2002 and May 2003. Each bar indicates a 5 mm size group.

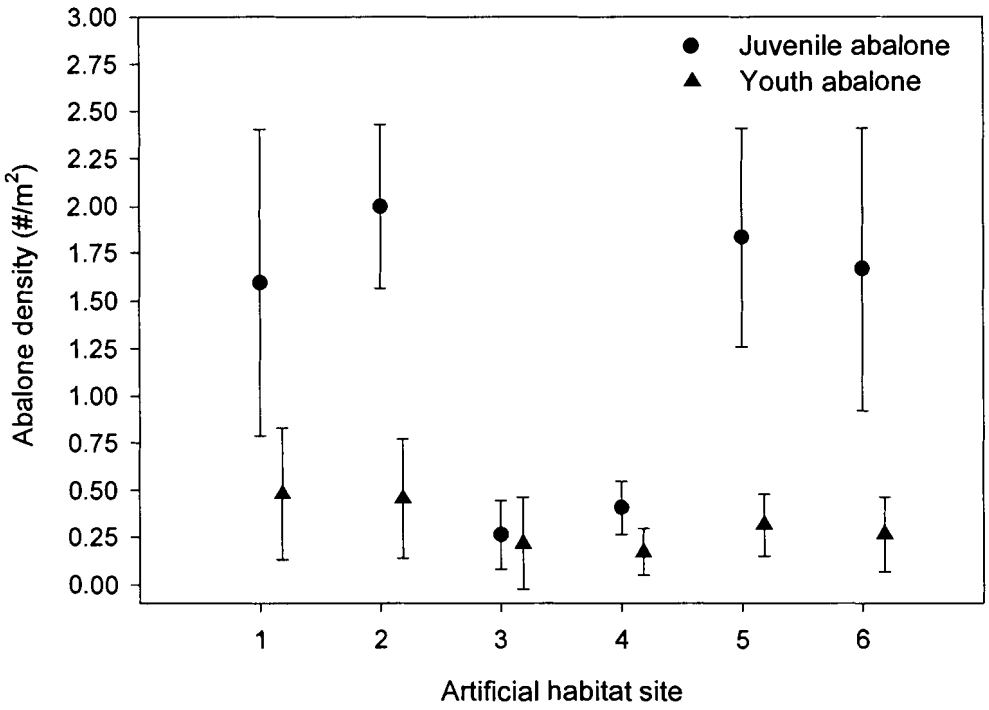

Figure 3.3. Mean juvenile (≤ 50 mm) (●) and youth (51-69 mm) (▲) abalone density measured within artificial habitats at sites 1-6 between May 2002 and May 2003. Vertical bars are 95% confidence intervals.

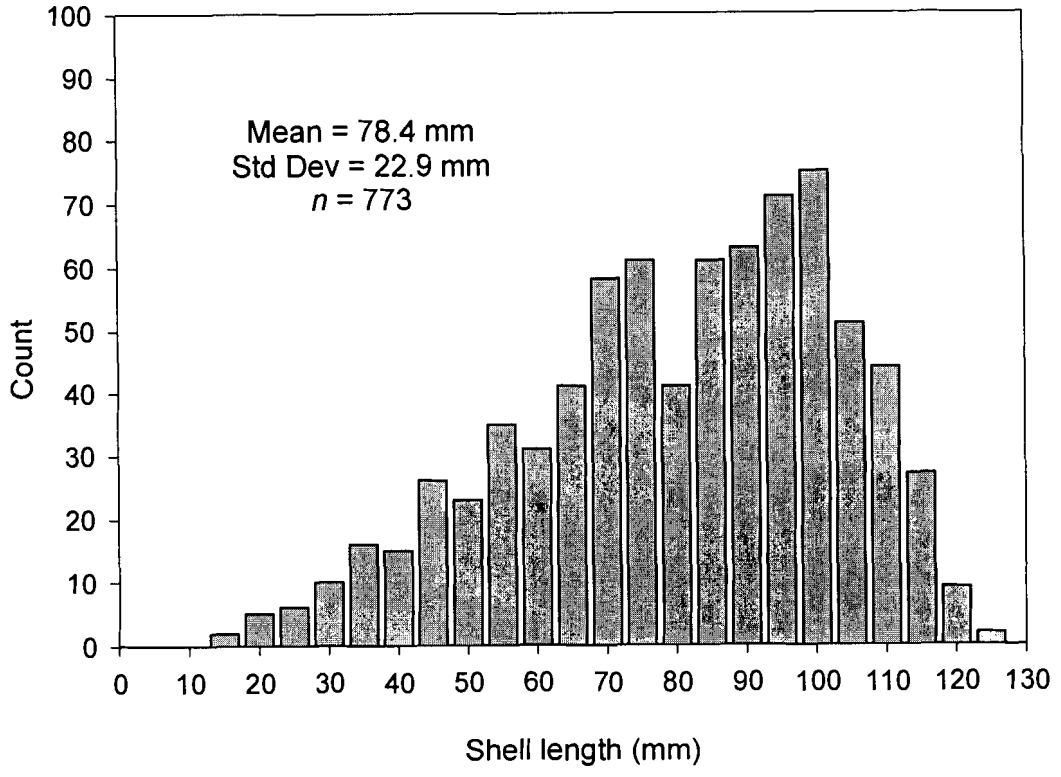

Figure 3.4. Size frequency distributions of abalone measured within natural habitats at sites 1-4 and 7-10 between May 2002 and May 2003. Each bar indicates a 5 mm size group.

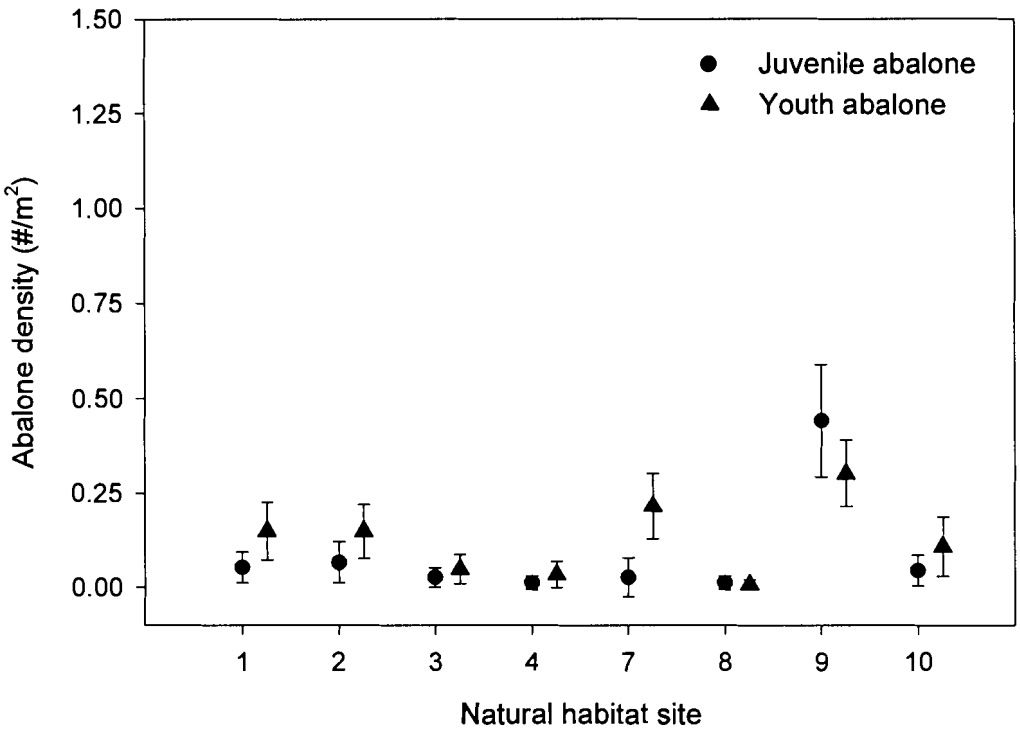

Figure 3.5. Mean juvenile (≤ 50 mm) (●) and youth (51-69 mm) (▲) abalone density measured within natural habitats at sites 1-4 and 7-10 between May 2002 and May 2003. Vertical bars are 95% confidence intervals.

Chapter 4

General Discussion and Conclusion

The lack of recovery of northern abalone populations in B.C., fifteen years after the fishery closure in 1990, is attributed primarily to illegal harvests and low-recruitment (Campbell 2000, Toole et al. 2002). This national concern is shared by other nations who face similar challenges in rebuilding exploited abalone populations. Wild abalone populations in Alaska (Woodby et al. 2000), California (Tegner et al. 1992, Karpov et al. 2000), South Africa (Tarr 2000), New Zealand (Schiel 1992), Australia (Prince et al. 1992), and Mexico (Guzmán del Próo 1992) are all threatened by an increasing market demand and low capital fishing costs. Struggling to keep up with this global demand is our research on abalone biology and ecology in order to better understand population processes critical to halting the decline of wild populations, and ultimately, their restoration.

The results from the most recent DFO index survey in southeast Haida Gwaii indicate that mature abalone densities are only ~12% of those measured in 1978 (Breen and Adkins 1979, Atkins et al. 2004). With this significant reduction in spawner density, the potential for continued population collapse due to insufficient reproduction is considered likely (Toole et al. 2002, Atkins et al. 2004). However, in this thesis, I was unable to find any evidence to support the hypothesis of impaired reproductive abilities due to low abundance of spawners. In chapter 2, I examined the behavioural response of mature northern abalone that were transplanted into dense aggregations early in the spawning season to determine if they remained in elevated densities for the duration of the reproductive period, with implied benefits to reproduction. I found that aggregated mature abalone dispersed from enhanced densities and many factors may contribute the rate at which they disperse. In chapter 3, I examined if artificial concrete block habitats provided surrogate shelter for cryptic juvenile abalone and if so, could these structures determine relative abundance within different areas or reflect abundance in surrounding natural habitats. I found that juvenile abalone occupied standardized artificial habitats at ~25% times greater density than natural habitats and confirmed that natural habitat surveys are an ineffective methodology to detect juvenile recruitment. But how might these studies contribute to northern abalone stock restoration?

The study on artificial aggregation of mature abalone indicated that transplanted abalone are capable of modifying the population structure of resident abalone by

significantly increasing both the density and size of animals at certain locations. As stated previously, these factors contribute to a greater reproductive potential during the spawning season based on results from other fertilization efficiency studies (Pennington 1985; Yund 1990; Levitan 1991; Levitan et al. 1991; Oliver and Babcock 1992; Babcock et al. 1994). These reproductive benefits apply not just too northern abalone, but all free-spawning marine invertebrates that have greater egg fertilization efficiency when populations are large, at high density and spawn synchronously (Levitan and Sewell 1998). For future applications in northern abalone stock restoration, this technique appears most beneficial for relocating abalone from areas containing extremely low densities, poor habitat quality or susceptible to high predation.

Very little is known about northern abalone recruitment (Sloan and Breen 1988, Campbell 2000), primarily due to the numerous highly variable and unpredictable processes that may influence the production and survival of larvae (McShane 1995*a*). As reviewed in chapter 1, these processes include: gamete production (i.e., fecundity of different sized abalone or variation in timing and intensity of spawning); egg fertilization success (i.e., concentration of gametes or sperm-egg ratio); larval dispersal (i.e., coastal hydrodynamics); larval settlement (i.e., suitable habitat); and predation from benthic filter feeders. Additionally, the various techniques developed to measure abalone larval settlement (Shepherd and Turner 1985; Prince and Ford 1985; McShane and Smith 1988; Keesing et al. 1995; Nash et al. 1995) are useful for determining the spatial and temporal differences in the relative numbers of larvae but not relating these abundance estimates to a visible life stage that will soon contribute to the next population.

My investigations into estimating relative juvenile northern abalone abundance using artificial habitats were aimed at measuring the recruitment of a visible life stage that has already survived the above mentioned larval processes. As juvenile northern abalone will mature in <3 years and join the world of broadcast spawners, determining the abundance of this life stage provides a better approximation of both near-future reproductive potential and reproductive output of currently established mature animals. The results from surveys of artificial abalone habitats indicated that these structures not only provided surrogate habitat to juvenile abalone, but preferential shelter as compared to invasively searched natural habitats. These findings also imply that current dive survey techniques of sampling natural habitats to measure juvenile abundance are inefficient due the high variability of natural substrates and large number of samples required to detect site differences. For future applications in northern abalone stock

restoration, artificial habitats appear most suitable as a means to quantify juvenile recruitment, an enhancement over non-rugose substrates (i.e., smooth bedrock), or an initial release site for cultured juveniles.

A fundamental question that remains unaddressed is "how do we define northern abalone stock restoration?" In the context of fisheries management, 'stock' implies a distinct population regarded as an entity for management or assessment. An additional definition of 'stock' that may apply to northern abalone is any animals kept for use or profit (i.e., livestock). These definitions imply that our current concerns about northern abalone are not because they are "a species that is likely to become endangered if limiting factors are not reversed" (www.cosepec.gc.ca), but because the abundance of large abalone (≥100 mm SL) is significantly lower than densities measured during the 1970's and they remain unable to support a commercial fishery 15 years after the coast-wide fishery closure. It is my impression that the biology of northern abalone, particularly their low or sporadic recruitment; slow growth; longevity; sedentary nature; and location in the food chain as prey for sea stars; octopus; crabs; fish; birds; humans and rapidly expanding sea otter populations, will prohibit the restoration of northern abalone populations to abundances measured during the 1970's.

In conclusion, I found that artificially aggregated mature abalone may remain in dense spawning groups for the duration of the spawning season, and that juvenile abalone abundance can be easily estimated using artificial habitats. These findings provide additional knowledge to help understand northern abalone biology, and may be applied towards trials in 'stock restoration'.

List of References

Allee, W.C., A.E. Emerson, O. Park, T. Park, and K.P. Schmidt. 1949. Principles of animal ecology. Saunders, Philadelphia. 837p.

Atkins, M., J. Lessard, and A. Campbell. 2004. Resurvey of northern abalone, *Haliotis kamtschatkana*, populations in southeast Queen Charlotte Islands, British Columbia, April 2002. Can. Manuscr. Fish. Aquat. Sci. 2704:37p.

Babcock, R.C., C.N. Mundy, and D. Whitehead. 1994. Sperm diffusion models and *in situ* confirmation of long distance fertilization in the free spawning asteroid *Acanthaster planci*. Bio. Bull. 186:17-28.

Babcock, R.C., and J. Keesing. 1999. Fertilization biology of the abalone *Haliotis laevigata*: laboratory and field studies. Can. J. Fish. Aquat. Sci. 56:1668-1678.

Baker, M.B., and P.A. Tyler. 2001. Fertilization success in the commercial gastropod *Haliotis tuberculata*. Mar. Ecol. Prog. Ser. 211:205-213.

Beaudry, C.G. 1983. Survival and growth of the larvae of *Haliotis kamtschatkana* Jonas at different temperatures. J. Shellfish Res. 3:109-110.

Boutillier, J.A., W. Carolsfeld, P.A. Breen, S. Farlinger, and K. Bates. 1985. Abalone resurvey in the southeast Queen Charlotte Islands, July 1984. Can. Manuscr. Rep. Fish. Aquat. Sci. 1818:87p.

Breen, P.A. 1980. Muscled mollusc: the northern abalone. Diver 6 (6):26-28.

Breen, P.A. 1986. Management of the British Columbia fishery for northern abalone (*Haliotis kamtschatkana*). Can. Spec. Publ. Fish. Aquat. Sci. 92:300-312.

Breen, P.A., and B.E. Adkins. 1979. A survey of abalone populations on the east coast of the Queen Charlotte Islands, August 1978. Fish. Mar. Serv. Manuscr. Rep. 1490:125p.

Breen, P.A., and B.E. Adkins. 1980. Spawning in a British Columbia population of northern abalone, *Haliotis kamtschatkana*. Veliger 23:177-179.

Breen, P.A., and B.E. Adkins. 1981. Abalone surveys and tagging conducted during 1979. Can. Manuscr. Rep. Fish. Aquat. Sci. 1623:88p.

Butman, C.A. 1989. Larval settlement of soft-sediment invertebrates: the spatial scales of patterns explained by active habitat selection and the emerging role of hydrodynamic processes. Oceanogr. Mar. Biol. Ann. Rev. 25:113-65.

Calderwood, M.E. 1985. Technological advances in the field of abalone mariculture. Final Prep. (1982-1985) Pacific Trident Mariculture Ltd. Victoria, B.C. 125p. Contract to Dep. of Supply and Services, Canada, No. 053B FP 501-2-005.

Campbell, A. 1996. An evaluation of abalone surveys off southeast Queen Charlotte Island. Can. Tech. Rep. Fish. Aquat. Sci. 2089:111-131.

Campbell, A. 2000. Review of northern abalone, *Haliotis kamtschatkana* stock status in British Columbia. Can. Spec. Publ. Fish. Aquat. Sci. 130:41-50.

Campbell, A., I. Manley, and W. Carolsfeld. 1992. Size at maturity and fecundity of the abalone, *Haliotis kamtschatkana*, in British Columbia. Can. Manuscr. Rep. Fish. Aquat. Sci. 2169:47-65.

Campbell, A., I. Winther, B. Adkins, D. Brouwer, and D. Miller. 1998. Survey of northern abalone (*Haliotis kamtschatkana*) in the central coast of British Columbia, May 1997. Can. Stock Assessment Secretariat Res. Doc. 98/89. Fisheries and Oceans Canada, 200 Kent Street, Ottawa, Ont. K1A 0E6, Canada. 28p.

Campbell, A., D. Brouwer, J. Rogers, and D. Miller. 2000. Abalone resurvey in southeast Queen Charlotte Islands, 1998. Can. Manuscr. Rep. Fish. Aquat. Sci. 2528:30p.

Campbell, A., J. Lessard, and G.S. Jamieson. 2003. Fecundity and seasonal reproduction of northern abalone, *Haliotis kamtschatkana*, in Barkley Sound, Canada. J. Shellfish Res. 22:811-818.

Carolsfeld, W., S. Farlinger, B.C. Kingzett, N.A. Sloan, and G. Thomas. 1988. Abalone resurvey in the southeast Queen Charlotte Islands, June 1987. Can. Manuscr. Rep. Fish. Aquat. Sci. 1966:90p.

Clavier, J. 1992. Fecundity and optimal sperm density for fertilization in the ormer (*Haliotis tuberculata* L.). *In* Abalone of the world: biology, fisheries and culture. *Edited by* S.A. Shepherd, M.J. Tegner, and S.S. Guzmán del Próo. Fishing New Books, Oxford. 86-92p.

Davis, G.E. 1995. Recruitment of juvenile abalone (*Haliotis* spp.) measured in artificial habitats. Mar. Freshwater Res. 46:549-554.

DeFreitas, B. 2003. Estimating juvenile northern abalone (*Haliotis kamtschatkana*) abundance using artificial habitats. J. Shellfish Res. 22:819-823.

Denny, M.W., and M.F. Shibata. 1989. Consequences of surf-zone turbulence for settlement and external fertilization. American Naturalist 134:859-889.

Ebert, E.E., and J.L. Houk. 1984. Elements and innovations in the cultivation of red abalone, *Haliotis rufescens*. Aquaculture. 39:375-92.

Emmett, B., and G.S. Jamieson. 1988. An experimental transplant of northern abalone, *Haliotis kamtschatkana,* in Barkley Sound, British Columbia. Fish. Bull. 87:95-104.

Fedorenko, A.Y., and P.E. Sprout. 1982. Abalone biology, fishery regulations, commercial catch (1952-1980), and current state of resource in British Columbia. Can. Manuscr. Rep. Fish. Aquat. Sci. 1658:74p.

Farlinger, S., G.A. Thomas, and W. Carolsfeld. 1991. Abalone resurvey in the Estevan group and Aristazabal Island, June 1989. Can. Manuscr. Rep. Fish. Aquat. Sci. 2104. 39p.

Fletcher, W.J. 1987. Interactions among subtidal Australian sea urchins, gastropods, and algae: effects of experimental removals. Ecol. Monogr. 57:89-109.

Giese A.C., and J.S. Pearse 1974. Introduction: general principles. *In* Reproduction of marine invertebrates. Volume 1: Acoelomates and Pseudocoelmate Metazoans. *Edited by* A.C. Giese and J.S. Pearse) Academic Press, New York. 1-49p.

Guzmán del Próo, S.A. 1992. A review of the biology of abalone and its fishery in Mexico. *In* Abalone of the world: biology, fisheries and culture. *Edited by* S.A. Shepherd, M.J. Tegner, and S.S. Guzmán del Próo. Fishing New Books, Blackwell Sciences Ltd., Oxford, U.K. 341-360p.

Hartwick, B., L. Tullock, and S. Macdonald. 1981. Feeding and growth of *Octopus dofleini* (Wülker). Veliger 24:129-138.

Hayashi, I., and H. Yamakawa. 1988. Population fluctuations of three sympatric species of *Haliotis* (Mollusca: Gastropoda) in artificial habitats at Kominato, central Japan. Aquaculture 73:67-84.

Hines, A.H., and J.S. Pearse. 1982. Abalones, shells, and sea otters: dynamics of prey populations in central California. Ecology 63:1547-60.

Henderson, K.C., D.O. Parker, and P. Haaker. 1988. The survival and growth of transplanted adult pink abalone, *Haliotis corrugata*, at Santa Catalina Island. California Fish and Game 74:82-86.

JMP. 2001. Version 4.0. SAS Institute Inc. Cary, NC, USA.

Jones, R., B. DeFreitas, N. Sloan, L. Lee, K. von Boetticher, and G. Martin. 2003. Abalone stewardship in Haida Gwaii: forging a long-term commitment. Can. Tech. Rep. Fish. Aquat. Sci. 2482:5-19.

Karpov, K.A., P.L. Haaker, I.K. Taniguchi, and L. Rogers-Bennett. 2000. Serial depletion and collapse of the Califomia abalone (*Haliotis* spp.) fishery. *In* Workshop on rebuilding abalone stocks in British Columbia. *Edited by* A. Campbell. Can Spec. Pub. Fish. Aquat. Sci. 130:11-24.

Keesing, J.K., R. Grove-Jones, and P. Tagg. 1995. Measuring settlement intensity of abalone: results of a pilot study. Mar. Freshwater Res. 46:539-543.

Leighton, D.L. 1972. Laboratory observations on the early growth of the abalone *Haliotis sorenseni*, and the effect of temperature on larval development and settlement success. Fish. Bull. 70:373-81.

Levitan, D.R. 1991. Influence of body size and population density on fertilization success and reproductive output in a free-spawning invertebrate. Biol. Bull. 181:261-268.

Levitan, D.R., and M.A. Sewell. 1998. Fertilization success in free-spawning marine invertebrates: review of the evidence and fisheries implications. *In* Proceedings of the north pacific symposium on invertebrate stock assessment and management. *Edited by* G.S. Jamieson and A. Campbell. Can. Spec. Pub. Fish. Aquat. Sci. 125:159-164.

Levitan, D.R., M.A. Sewell, and F. Chia. 1991. Kinetics of fertilization in the sea urchin *Strongylocentrotus franciscanus*: interaction of gamete dilution, age, and contact time. Bio. Bull. 181:371-378.

Levitan, D.R., M.A. Sewell, and F. Chia. 1992. How distribution and abundance influence fertilization success in the sea urchin *Strongylocentrotus franciscanus*. Ecology 73:248-254.

McLean, J.H. 1966. West American prosobranch gastropoda: Superfamilies Patellacae, Pleurotomariacea and Fisurellacea. Ph.D. dissertation, Stanford University, CA. 255p.

McShane, P.E. 1992. Early life history of abalone: a review. *In* Abalone of the world: biology, fisheries and culture. *Edited by* S.A. Shepherd, M.J. Tegner & S.A. Guzmán del Próo. Fishing New Books, Blackwell Science Ltd., Oxford. U.K. 120-138p.

McShane, P.E. 1995*a*. Recruitment variation in abalone: its importance to fisheries management. Mar. Freshwater Res. 46:555-70.

McShane, P.E. 1995*b*. Estimating the abundance of abalone: the importance of patch size. Mar. Freshwater Res. 46:657-662.

McShane, P.E., and M.G. Smith. 1988. Measuring recruitment of *Haliotis rubra* Leach (Gastropoda:Haliotidae): comparison of a novel method with two other methods. Aust. J. Mar. Freshwater Res. 39:331-336.

McShane, P.E., K.P. Black, and M.G. Smith. 1988*a*. Recruitment processes in *Haliotis rubra* (Mollusca:Gastropoda) and regional hydrodynamics in southeast Australia imply localized dispersal of larvae. J. Mar. Biol. Ecol. 124:175-203.

McShane, P.E. M.G. Smith, and K.H.H. Beinssen. 1988*b*. Growth and morphometry in abalone (*Haliotis rubra*) from Victoria. Aust. J. Mar. Fresh. Res. 39:161-6.

Microsoft Office Excel. 2000. Microsoft Corporation, Redmond, Washington, USA.

Mileikovsky, S.A. 1971. Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. Mar. Biol. 10:193-213.

Morse D.E., H. Duncan, N. Hooker, and A. Morse. 1977. Hydrogen peroxide induces spawning in mollusks, with activation of prostaglandin endoperoxide synthetase. Science, N.Y. 196:298-300.

Morse, A.N.C., and D.E. Morse. 1984. Recruitment and metamorphosis of *Haliotis* larvae induced by molecules uniquely available at the surface of crustose red algae. J. Exp. Mar. Biol. Ecol. 75:191-215.

Mottet, M.G. 1978. A review of the fishery biology of abalones. Wash. State Dept. Fish. Tech. Rep. 37:81p.

Nash, W.J., J.C. Sanderson, J. Bridley, S. Dickson, and B. Hislop. 1995. Post-larval recruitment of blacklip abalone (*Haliotis rubra*) on artificial collectors in southern Tasmania. Mar. Freshwater Res. 46:531-538.

Oliver J., and R. Babcock. 1992. Aspects of the fertilization ecology of broadcast spawning corals: sperm dilution effects and *in situ* measurements of fertilization. Bio. Bull. 183:409-17.

Olsen, S. 1984. Shellfish enhancement report. NOAA, NMFS, Final report for project 1-444-R. Wash. State Dep. Fish., Seattle, Wash. 85p.

Paine, R.T., and R.L. Vadas. 1969. The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. Limnol. Oceanogr. 14:710-19.

Paul, A.J., and J.M. Paul. 1981. Temperature and growth of maturing *Haliotis kamtschatkana* Jonas. Veliger 23:321-324.

Pearce, C.M., P. Agerup, A. Alabi, D. Renfrew, J. Rosser, G. Whyte, and F. Yuan. 2003. Recent progress in hatchery production of pinto abalone, *Haliotis kamtschatkana,* in British Columbia, Canada. Can Tech. Rep. Fish. Aquat. Sci. 2482:29-44.

Pennington, J.T. 1985. The ecology of fertilization of echinoid eggs: the consequences of sperm dilution, adult aggregation, and synchronous spawning. Bio. Bull. 169:417-430.

Prince, J.D., and W.B. Ford. 1985. Use of anaesthetic to standardize efficiency in sampling abalone populations (genus *Haliotis*; Mollusca:Gastropoda). Aust. J. Mar. Freshwater Res. 36:701-706.

Prince, J.D., T.L. Sellars, W.B Ford, and S.R. Talbot. 1987. Experimental evidence for limited dispersal of haliotid larvae. J. Exp. Mar. Biol. Ecol. 106:243-263.

Prince, J.D., T.L. Sellars, W.B Ford, and S.R. Talbot. 1988. Confirmation of a relationship between the localized abundance of breeding stock and recruitment for *Haliotis rubra* Leach (Mollusca: Gastropoda). J. Exp. Biol. Ecol. 122:91-104.

Prince J.D., and S.A. Shepherd. 1992. Australian abalone fisheries and their management. *In* Abalone of the world: biology, fisheries and culture. *Edited by* S.A. Shepherd, M.J. Tegner, and S.S. Guzmán del Próo. Fishing New Books, Blackwell Sciences Ltd., Oxford, U.K. 407-426p.

Quayle, D.B. 1971. Growth, morphometry and breeding in the British Columbia abalone (*Haliotis kamtschatkana* Jonas). Fish. Res. Board Can. Tech. Rep. 279:84p.

Roberts, R. 2001. A review of settlement cues for larval abalone (*Haliotis* spp.) J. Shellfish Res. 20:571-586.

Saito, K. 1979. Studies on propagation of ezo abalone, *Haliotis discus hannai* Ino – I. Analysis of the relationship between transplantation and catch in Funka Bay Coast. Bull. Jap. Soc. Sci. Fish. 45:675-704.

Sasaki, R., and S.A. Shepherd. 1995. Larval dispersal and recruitment of *Haliotis discus hannai* and *Tegula* spp. on Miyagi Coasts, Japan. Mar. Freshwater Res. 46:519-529.

Sasaki, R., and S.A. Shepherd. 2001. Ecology and post-settlement survival of the ezo abalone, *Haliotis discus hannai*, on Miyagi coasts, Japan. J. Shellfish Res. 20:619-626.

Schiel, D.R. 1992. The paua (abalone) fishery of New Zealand. *In* Abalone of the world: biology, fisheries and culture. *Edited by* S.A. Shepherd, M.J. Tegner, and S.S. Guzmán del Próo. Fishing New Books, Blackwell Sciences Ltd., Oxford, U.K. 427-437p.

Shepherd, S.A. 1973. Studies on southern Austrian abalone (genus *Haliotis*) I. Ecology of five sympatric species. Aust. J. Mar. Freshwater Res. 24:217-57.

Shepherd, S.A. 1986*a*. Studies on southern Australian abalone (genus *Haliotis*) VII. Aggregative behaviour of *H. laevigata* in relation to spawning. Mar. Biol. 90:231-236.

Shepherd, S.A. 1986*b*. Movement of the southern Australian abalone *Haliotis laevigata* in relation to crevice abundance. Aust. J. Ecol. 11:295-302.

Shepherd, S.A., and H.M. Laws.1974. Studies on southern Australian abalone. II. Reproduction of five species. Aust. J. Mar. Freshwater Res. 25:49-62.

Shepherd, S.A., and J.A. Turner. 1985. Studies on southern Australian abalone (genus *Haliotis*). VI. Habitat preferences and abundance and predators of juveniles. J. Exp. Mar. Biol. Ecol. 93:285-298.

Shepherd, S.A., D. Lowe, and D. Partington. 1992. Studies on southern Australian abalone (genus *Haliotis*) XIII: larval dispersal and recruitment. J. Exp. Mar. Biol. Ecol. 164:247-260.

Shepherd, S.A., and L.D. Brown. 1993. What is an abalone stock: implications for the role of refugia in conservation. Can. J. Fish. Aquat. Sci. 50:2001-2009.

Shepherd, S.A., and D. Partington. 1995. Studies on southern Australian abalone (Genus *Haliotis*). XVI. Recruitment, habitat and stock relations. Mar. Freshwater Res. 46:669-680.

Shepherd, S.A., D. Woodby, J.M. Rumble, and M. Avalos-Borja. 2000. Microstructure, chronology and growth of the pinto abalone *Haliotis kamtschatkana*, in Alaska. J. Shellfish Res. 19:219-228.

Slattery, M. 1992. Larval settlement and juvenile survival in the red abalone (*Haliotis rufescens*): an examination of inductive cues and substrate selection. Aquaculture 102:143-153.

Sloan, N.A., and P.A. Breen. 1988. Northern abalone, *Haliotis kamtschatkana*, in British Columbia: fisheries and synopsis of life history information. Can. Spec. Pub. Fish. Aquat. Sci. 103:46p.

Steneck, R.S. 1986. The ecology of coralline algal crusts: convergent patterns and adaptive strategies. Ann. Rev. Ecol. Syst. 17:273-303.

SYSTAT. 2004. Version 11. SPSS Inc., Chicago, IL, USA.

Tarr, R.J.Q. 2000. The South African abalone (*Haliotis midae*) fishery: a decade of challenges and change. *In* Workshop on rebuilding abalone stocks in British Columbia. *Edited by* A. Campbell. Can. Spec. Pub. Fish. Aquat. Sci. 130:32-40.

Tegner, M.J. 1992. Brood stock transplants as an approach to abalone stock enhancement. *In* Abalone of the world: biology, fisheries and culture. *Edited by* S.A. Shepherd, M.J. Tegner, and S.A. Guzmán del Próo. Fishing New Books, Blackwell Science Ltd., Oxford. U.K. 461-473p

Tegner, M.J., and R.A. Butler. 1985. Drift-tube study of the dispersal potential of green abalone (*Haliotis fulgens*) larvae in the southern California Bight: implications for the recovery of depleted populations. Mar. Ecol. Prog. Ser. 26:73-84.

Tegner, M.J., P.A. Breen, and C.E. Lennert. 1989. Population biology of red abalone, *Haliotis rufescens*, in southern California and management of red and pink, *H. corrugata*, abalone fisheries. Fish. Bull. 87:313-339.

Tegner, M.J., DeMartini, J.D., and Karpov, K.A. 1992. The California red abalone fishery: a case study in complexity. *In* Abalone of the world: biology, fisheries and culture. *Edited by* S.A. Shepherd, M.J. Tegner, and S.S. Guzmán del Próo. Fishing New Books, Blackwell Sciences Ltd., Oxford, U.K. 370-383p.

Thomas, G., S. Farlinger, and W. Carolsfeld. 1990. Abalone resurvey in southeast Queen Charlotte Islands in 1990. Can. Manuscr. Rep. Fish. Aquat. Sci. 2099:66-82.

Thomas, G., and A. Campbell. 1996. Abalone resurvey in Aristazabal Island, the Estevan group and Banks Island, June 1993. Can. Tech. Rep. Fish. Aquat. Sci. 2089:97-109.

Thompson, W.F. 1914. Report on the abalones of British Columbia (*Haliotis gigantae*, Chemnitz). [=*H. kamtschatkana* Jonas] Rep. B.C. Commissioner Fish., Victoria, B.C. (1913), 126-130p.

Tides and Currents Pro. 2000. Version 3.0. Nobeltec Corporation, Portland, Oregon, USA.

Toole, J., B. Adkins, E. Bornhold, J. Boutillier, G. Caine, A. Campbell, A. Castledine, L. Convey, C. Cote, P. Coulson, T. Down, K. Francis, H. Gill, R. Harbo, H. Holmes, B. Jubinville, D. Lawseth, B. G. Lucas, A. Morgan, G. Parker, and J. Rogers. 2002. National recovery strategy for the northem abalone (*Haliotis kamtschatkana*) in British Columbia. Fisheries and Oceans Canada. (www-comm.pac.dfo-mpo.gc.ca/pages/consultations/fisheriesmgmt/abalone/AbaloneRecovStrategy_e.htm). 22p.

Watson, J. 2000. The effects of sea otters (*Enhydra lutris*) on abalone (*Haliotis* spp.) populations. *In* Workshop on rebuilding abalone stocks in British Columbia. *Edited by* A. Campbell. Can. Spec. Pub. Fish. Aquat. Sci. 130:123-132.

Webber, H.H. 1977. Gastropoda: Prosobranchia. *In* Reproduction of marine invertebrates. Volume IV. Molluscs: gastropods and cephalopods. *Edited by* A.C. Giese and J.S. Pearse. New York: Academic Press 1977. 1-97p.

Winther, I., A. Campbell, G.A. Thomas, B.E. Adkins, and B.G. Clapp. 1995. Abalone resurvey in the southeast Queen Charlotte Islands, 1994. Can. Manuscr. Rep. Fish. Aquat. Sci. 2273. 46p.

Woodby, D., R. Larson, and J. Rumble. 2000. Decline of the Alaska abalone (*Haliotis* spp.) fishery and prospects for rebuilding the stock. *In* Workshop on rebuilding abalone stocks in British Columbia. *Edited by* A. Campbell. Can. Spec. Pub. Fish. Aquat. Sci. 130:25-31.

Young, C.M., P.A. Tyler, J.L. Cameron, and S.G. Rumrill. 1992. Seasonal breeding aggregations in the low-density populations of the Bathyal echinoid *Stylocidaris lineate*. Marine Biology 113:603-12.

Yund, P.O. 1990. An *in situ* measurement of sperm dispersal in a colonial marine hydroid. J. Exp. Zool. 253:102-6.