Invasion Dynamics of a Non-indigenous bivalve, *Nuttallia obscurata*, (Reeve 1857), in the Northeast Pacific

by

Sarah Elizabeth Dudas
B.Sc., University of Guelph, 1997

A Dissertation Submitted in Partial Fulfillment
of the Requirements for the Degree of

DOCTOR OF PHILOSOPHY

in the Department of Biology

University of Victoria

Supervisor: Dr. John F. Dower

ABSTRACT

This thesis describes how life history characteristics of the varnish clam (*Nuttallia obscurata*), and interactions with the physical environment and other species, have contributed to its successful invasion in coastal British Columbia. Lab and field experiments were conducted to investigate varnish clam larval ecology (i.e. larval rearing experiments), adult population dynamics (i.e. annual population surveys, mark-recapture and length-frequency analysis, growth modeling) and ecological interactions with native species (i.e. predator/prey preference feeding trials). Using these results, a matrix demographic model was developed to determine which life history stage contributes the most to varnish clam population growth.

Larval rearing experiments indicated that temperature and salinity tolerances of varnish clam larvae are comparable to native species, however the planktonic phase is slightly longer (3-8 weeks). Based on local oceanographic circulation, varnish clam larvae have the potential to disperse throughout their entire geographic range in just one reproductive season. Varnish clam population surveys revealed spatiotemporal variation in density and size. No relationships were evident between varnish clam density and the number or density of co-occurring bivalve species. Length-frequency analysis suggested that recruitment varies among sites, with high post-settlement mortality coinciding with high recruitment. The presence of similar recruitment pulses at geographically separate sites indicates regional scale processes may influence recruitment. Individual growth rates varied among sites, with higher growth corresponding to lower population densities and water temperature. Monthly survival rates ranged from 0.81 – 0.99 and were lower for clams 10-30 mm. Predator/prey preference feeding trials showed that crabs prefer varnish clams to local species when clam burial depth is limited. Crabs therefore have the potential to influence varnish clam distributions, particularly on beaches where the varnish clam is unable to bury deeply. Based on matrix demographic analysis, adult survival (e.g. clams ≥ 40 mm) is the most crucial factor for varnish clam population growth, and drives the observed population growth differences between sites. This study of the varnish clam invasion demonstrates that its success lies in both species (e.g. lengthy planktonic phase, high survival) and regional (e.g. favourable ocean circulation patterns for rapid dispersal) characteristics. Measures to reduce introductions should be targeted in areas where introductions are likely to have the furthest reaching impacts.

Supervisor: Dr. John F. Dower, (Department of Biology)

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

I would like to thank the following funding sources: National Sciences and Engineering Research Council of Canada, University of Victoria, Bamfield Marine Sciences Centre, University of British Columbia, Fisheries and Oceans Canada, Aquaculture Association of Canada, Randy Baker Memorial Scholarship, and Parks Canada for allowing me to join their bivalve surveys in Pacific Rim National Park.

Without volunteer assistance this project would not have been possible, their support and enthusiasm has been invaluable. Special thanks go to Jennifer Mersereau, Megan Foss, Dan Curtis, Alli Griffiths, Tara Brown and Caroline Fox.

Thanks to the Dower Lab, Rob Campbell, Rana El-Sabaawi, Tom Bird, GC Kim, Jonathan Rose and Akash Sastri for helpful advice and discussion; Guy White, Neil Bourne, Louis Gosselin, Andre Martel, Jon Schnute and Graham Gillespie for their guidance; and my friends, Janine Beckett, Dana Haggarty and Jenn Yakimishyn for discussion, field support and sanity checks.

Thanks to my committee at UBC for help in the original project design, to my committee at UVic, Brad Anholt, Louise Page, Tom Tomascik and Verena Tunnicliffe for their direction and new ideas, and to my supervisor, John Dower, who has provided constant support, guidance and inspiration.

Finally, a special thanks to my family, Jane, Frank and Jake Dudas whose love, support and editing, have been unfailing, and James Mortimor, who has been involved in every aspect of this project from start to finish and has spent endless hours listening, editing, and digging.

Chapter 1. Introduction

Non-indigenous species (NIS) have become a significant threat to native ecosystem biodiversity and function on a global scale in recent decades (Carlton and Geller, 1993; Cohen and Carlton, 1998; Ruiz et al., 1997). The number of invasions by non-indigenous marine species continues to increase, with approximately 400 invaders currently known along the Pacific and Atlantic coasts of the United States (Ruiz et al., 1997). The increase in marine invasions is due largely to increased transport of non-indigenous species via vectors such as shipping and aquaculture (Ruiz et al., 1997). Impacts of invasions by non-indigenous species range from benign to severe, such as the zebra mussel invasion in the Great Lakes (Neary and Leach, 1992) that has resulted in dramatic changes in the complexity of benthic habitats (Beekey et al., 2004), or the invasion of the green crab that can significantly decrease numbers of bivalve prey (Floyd and Williams, 2004). These invasions can also have significant economic impacts, in some cases exceeding hundreds of millions of dollars (Pimental et al., 2000). Understanding the dynamics of NIS invasions is therefore crucial for identifying additional species that may be poised to invade, and which are likely to become established and have negative impacts on native species in recipient regions.

Coastal British Columbia has experienced an increasing number of marine and estuarine invasions over the past few decades (Fig. 1.1, Levings et al., 2002). Whether this increase is the result of increasing anthropogenic vectors such as shipping, or an increase in research effort to identify non-indigenous species is difficult to discern; it is likely the result of both. To date however, very few systematic surveys have been conducted in the region, making it difficult to determine exactly when (and where) a particular invader arrived. At present, about 90 marine and estuarine invaders have been documented in coastal BC, consisting primarily of invertebrates (73%) and algal species (Levings et al., 2002). Vectors of introduction for these species include aquaculture, ballast water transfer, the release of live seafood and fish, plant nurseries and releases due to research and teaching activities (Levings et al., 2002). Historically, the most important vector for the introduction of non-indigenous marine species in coastal BC has been the aquaculture industry, which has introduced seven species intentionally and at least 12 species accidentally as “hitchhikers” (Levings et al., 2002). Canada has recently introduced regulations to prevent further introductions via this pathway.

Currently, the vector of greatest concern is the transfer of ballast water from vessels entering coastal BC waters and ports. Juan de Fuca Strait is the busiest shipping waterway in North America, with China, Japan and Korea currently being the principal trading partners (http://www.portvancouver.com/statistics/). It is therefore not surprising that 42% of non-indigenous marine invaders in coastal BC are originally native to Asia. With the increasing size (and speed) of ships, and the ever-increasing volumes of shipping traffic, a growing number of marine invertebrates are being introduced. This increased frequency of introduction (and re-introduction in some cases) therefore raises the likelihood that their larval stages will eventually survive and adults will become established (Carlton, 1985; Moyle, 1991). Although regulations have been put in place to minimize such introductions in Canadian waters (e.g mandatory ballast water exchange

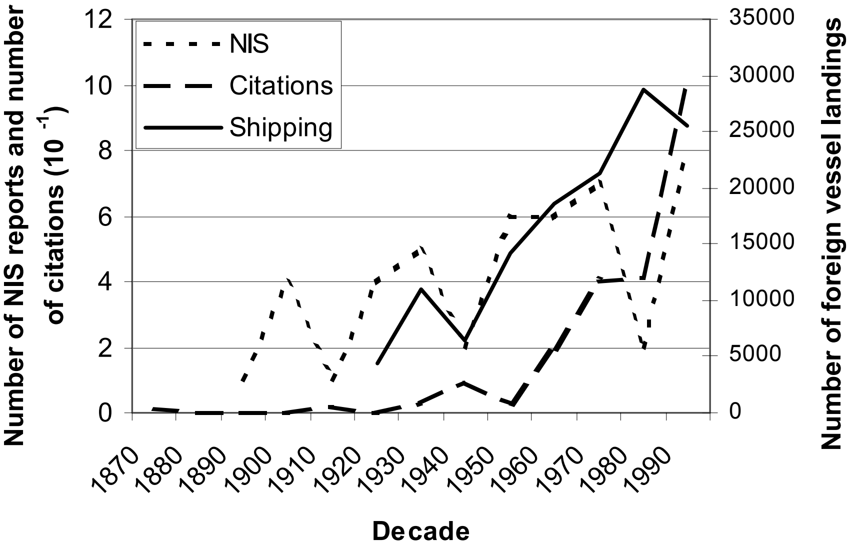


Fig. 1.1. Non-indigenous marine invertebrate species reported in British Columbia from 1890-1999 compared to foreign vessel records for the Port of Vancouver (1920-1990) and number of citations listed in Anderson's 1999 marine non-indigenous species report for BC.

before ships enter coastal waters), these measures are both difficult to enforce and not entirely efficient (Locke et al., 1993).

To date there have been only a few reports on effects of marine invasions in BC ecosystems, suggesting either that the introductions have generally been benign or have resulted in (as yet) undetectable changes (Levings et al., 2002). The main exceptions to this have been the Pacific oyster (*Crassostrea gigas*), the Manila clam (*Venerupis philippinarum*), and the recently introduced varnish clam (*Nuttallia obscurata*). The Pacific oyster, which was intentionally introduced back in the 1900's (Quayle, 1989), has since become well established around much of southern coastal BC and, where abundant, can increase the availability of epibenthic shelter for other species. Human activities associated with its culturing can further alter the intertidal environment (e.g. removal of rocks; Levings et al., 2002). The Manila clam was introduced accidentally with the Pacific oyster, and has since become the main target species in the wild harvest intertidal clam fishery and in culture (Harbo et al., 1997), therefore representing a significant economic effect. Part of its success may be attributed to its ability to survive higher in the intertidal zone than native clam species.

The varnish clam has become abundant throughout much of southern BC over the past decade and often occurs on Manila clam farms, raising concerns that it might compete with (or displace) Manila clams. To date, however, there has been no evidence to support this claim. Other non-indigenous species of particular concern in coastal BC include the Japanese Oyster drill (*Ceratostoma inornatum*) which was introduced accidentally as a hitch-hiker on the Japanese oyster and which is a potential major predator on cultured oysters (Levings et al., 2002). The green crab (*Carcinus maenas*), which has recently been reported from the west coast of Vancouver Island and Victoria, is also of concern because it is a voracious predator (particularly on juvenile bivalves) and has the potential to significantly alter any ecosystem that it invades (Cohen et al., 1995). Despite these concerns regarding marine non-indigenous species in BC, however, little research on their invasion dynamics has been conducted to date.

As a starting point for understanding factors that regulate the dynamics of invasions by non-indigenous species in coastal BC, this thesis uses the relatively recent invasion of the varnish clam as a ‘model’ system, and as a means for addressing some fundamental questions in invasion ecology. These include:

1. *What attributes make a non-indigenous species a successful invader?*
2. *What attributes make particular sites more (or less) vulnerable to invasion?*
3. *How do non-indigenous species invasions influence local ecological interactions (e.g. predator-prey)?*

Invertebrate invaders with complex life cycles (i.e. alternation between benthic and pelagic stages) also provide the opportunity to investigate the role of larval dispersal in marine invasion dynamics. Through this approach, we can gain insight into the degree of connectivity between neighbouring populations by observing where (and how fast) the varnish clam spreads in relation to its suspected point of introduction.

History of the invasion: The varnish clam (*Nuttallia obscurata*; Reeve, 1857) was first reported from the Northeast Pacific in Semiahmoo Bay (Washington), near Vancouver BC in 1991 (Forsyth, 1993), and was likely first introduced in English Bay (Neil Bourne, pers. comm.). The varnish clam is a member of the Psammobiidae family, synonyms include *Nuttallia olivacea*, *N. solida* (Roth, 1978) and the common names, "purple" or "dark mahogany clam" and the "savoury clam". The sunset clam, *Gari californica* is the only other Psammobiidae clam found in BC however, it has a much whiter shell than the varnish clam. There are no other species in BC with the varnish clams' combination of morphology and colouration. Since its introduction, the varnish clam has spread rapidly throughout the Strait of Georgia, northward along the west coast of Vancouver Island, and southward along the Washington and Oregon coasts. Currently, the geographic limits of the invasion are Smith Sound on the mainland of BC (across from the northern tip of Vancouver Island) in the north, and Alsea Bay, Oregon, in the south (Fig. 1.2). The varnish clam's range expanded rapidly after its detection in 1991, appearing in Puget Sound by 1993, Barkley Sound by 1995, Alsea Bay (its southern limit) by 1999, Brooks Peninsula (its northern limit on the west coast of Vancouver Island) by 2002 and Smith Sound (its northern limit on the mainland) by 2004 (Gillespie and Bourne, in press). Empty varnish clam shells have recently been reported north of Brooks Peninsula and are suspected to have populations there although no live varnish clams have yet been documented.

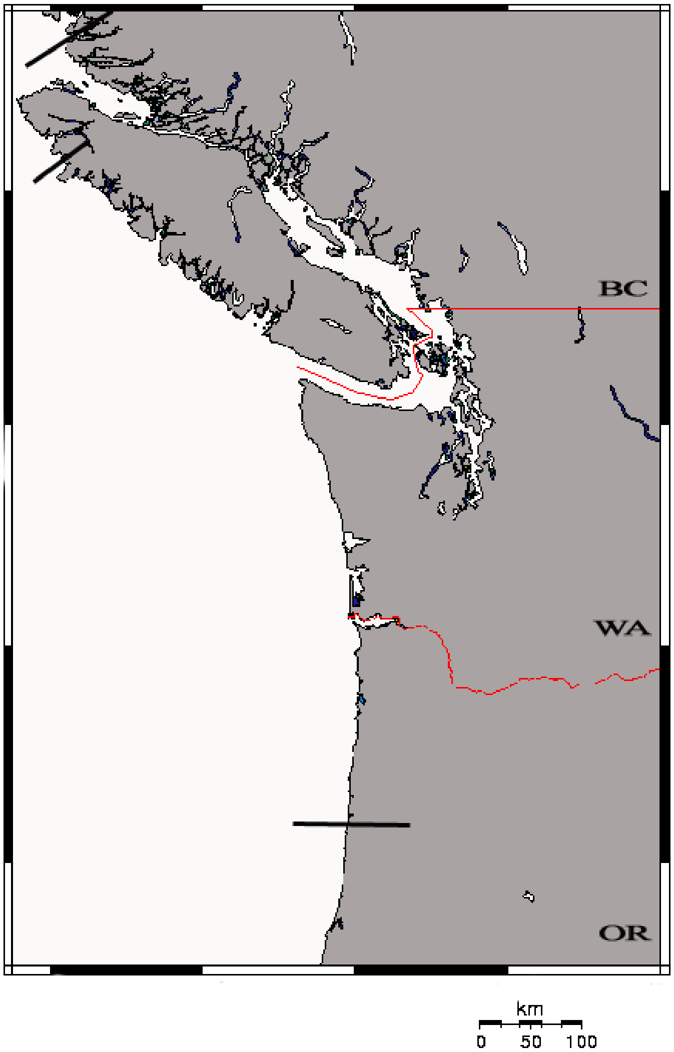


Fig. 1.2. Current distributional limits (black bars) of the varnish clam in the Northeast Pacific.

Originally a native of Korea, China and southern Japan, the varnish clam is suspected to have been introduced to coastal BC via ballast water disposal in Vancouver Harbour (Gillespie et al., 1999). The varnish clam is generally found intertidally in sand and gravel substrates (being most abundant in the high intertidal zone), and co-occurs with other bivalves such as the Manila clam (*V. philippinarum*) and the Pacific littleneck clam (*Protothaca staminea*; Heath, 1998). Adult varnish clams exhibit three different feeding modes: suspension feeding and two types of pedal feeding (locomotory and sweep-feeding; M. Parker, University of Victoria, unpublished manuscript). In its native range, the varnish clam is a broadcast spawner with planktonic larvae (Miyawaki and Sekiguchi, 1999); however, little is known about its life history or dispersal potential in the Northeast Pacific.

The primary focus of this thesis was to determine how the life history characteristics of the varnish clam, and its interactions with the physical environment (and with other species), have contributed to its distribution, dispersal and success as an invader in the Northeast Pacific. To achieve this objective, I have adopted a multidisciplinary approach that integrates aspects of larval ecology, population dynamics and empirical observations of ecological interactions with native species. In Chapter two, I document the first account of the developmental and environmental tolerances of varnish clam larvae in the Northeast Pacific and the implications for regional dispersal. This chapter has been accepted for publication in the Marine Ecology Progress Series (with co-author JF Dower). In Chapter three, I examine the spatial and temporal variation of adult population dynamics including population size and densities, recruitment, growth and survival rates. In Chapter four, I investigate the prey preference of locally abundant crab predators, and the varnish clam's morphological and behavioural predator refuges. This chapter is currently in press at the Journal of Experimental Marine Biology and Ecology (with co-authors IJ McGaw and JF Dower). In Chapter five, I combine the life history data using a matrix demographic model to determine the life history stage most crucial to varnish clam population growth, and its subsequent invasion success. This represents one of the first times that such an approach has been applied in a marine invasion context. Finally, in Chapter six, I discuss the keys to the varnish clams invasion success, based on species and region characteristics, potential invasion impacts and practical implications. In order to facilitate future research on the varnish clam invasion in British Columbia, the data collected during the course of this research are archived at the University of Victoria and are freely available. Please contact Sarah Dudas (sdudas@canada.com) or John Dower (dower@uvic.ca) in the Department of Biology at the University of Victoria should you like a copy of any of the data sets.

Chapter 2. Reproductive ecology and dispersal potential of the varnish clam and comparison to native bivalve species in southern British Columbia

2.1 Introduction

Characteristics typical of successful invaders include: short generation time, broad diet, the ability to establish colonies from even a single individual (i.e. asexual or hermaphroditic) and broad environmental tolerances (Ehrlich, 1986). Characteristics that limit an invader may change over the course of the invasion, in that characteristics that facilitate successful colonization (e.g. high fecundity, young age-at-maturity) may not be the same as those that facilitate dispersal and long term population maintenance (e.g. timing of spawning, lengthy planktonic phase, regular supply of immigrants; Vermeij, 1996).

The invasibility of the recipient region will also influence progression of an invasion. Factors suspected to increase invasibility include low species diversity (Stachowicz et al., 1999), disturbance (Hobbs and Huenneke, 1992) and human activities (Ruiz et al., 1997). The recipient region must also have a favourable climate and appropriate habitat (Swincer, 1986). For marine invertebrates with a planktonic larval stage, the regional oceanography of the recipient region will be important, not only because of the ‘climate’ (i.e. temperature and salinity), but also because of mesoscale circulation patterns.

The varnish clam is a broadcast spawner in its native range (Miyawaki and Sekiguchi, 1999) with a peak spawning period occurring in the spring and sexual maturity occurring in just one year (Hushan, 1994). Laboratory studies in the Northwest Pacific indicate that the planktonic larvae can develop in temperatures of 15-25°C and can metamorphose in waters from 10-30°C (Hushan et al., 1988). In BC, however, the varnish clam may experience cooler average temperatures (i.e. 10-12°C) and, thus, might be expected to have both slower growth and a longer planktonic phase.

This study examines the reproductive and early life history characteristics that may have contributed to the rapid spread of the varnish clam in coastal BC. Characteristics examined include (1) adult sex ratios and fecundity, (2) timing of spawning, (3) larval development, (4) influence of temperature and salinity on larval growth and metamorphosis and (5) dispersal potential in BC based on planktonic larval duration and regional oceanography. We also compare the varnish clam to co-occurring native bivalve species in order to highlight the life history advantages that may have contributed to its success. Knowledge of the early life history of this species is essential for understanding its dispersal dynamics in the Northeast Pacific and how far (and to what extent) it will spread in the future.

2.2 Methods

2.2.1 Sex ratio and timing of spawning

Adult varnish clams were collected from two beaches – Robbers Passage, in Barkley Sound on the west coast of Vancouver Island, and Bamberton Provincial Park (Bamberton, hereafter) in Saanich Inlet on the east coast of Vancouver Island, BC (Fig.

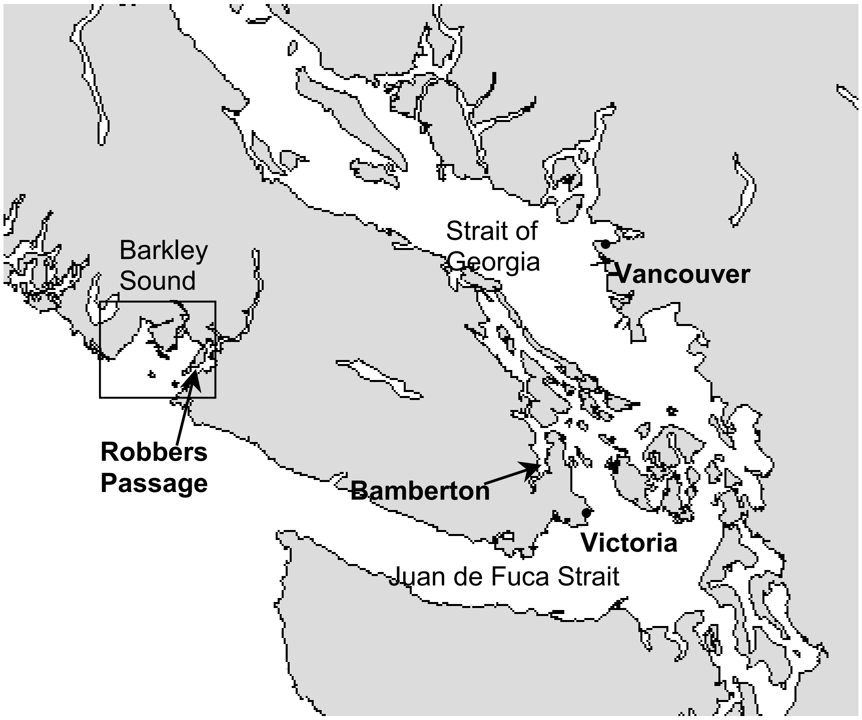


Fig. 2.1. Region of study – Southern Vancouver Island, British Columbia. Bamberton Provincial Park site is located in Saanich Inlet, Robbers Passage site in Barkley Sound.

2.1). Collections were made on a monthly basis during the winter (approximately 12 clams per site), and weekly during spring and summer (approximately 12-25 clams per site) from May 2002 to January 2004. In the laboratory, dissections and gonad smears were conducted on male and female clams spanning the size range present at each site, in order to determine gonad presence and sex.

Timing of spawning was estimated by observing the percentage of clams (> 3cm) with visible gonads at each site. Varnish clam "egg puddles" were also observed at Robbers Passage around the periphery of siphon holes at low tide during the spawning season. Egg puddle observations were recorded on a weekly basis during the reproductive season to better constrain estimates of peak spawning time at Robbers Passage. In 2002, seawater temperature and salinity were measured every 10 minutes at Robbers Passage with an InterOceans Inc. S4 current meter deployed for the duration of the spawning season. Oceanographic conditions at Bamberton were not measured directly at the adult population site. As a proxy for local temperature conditions we used temperature data collected hourly by a permanent oceanographic buoy moored in Saanich Inlet, approximately 6 km from the site, provided by the Institute of Ocean Sciences in Sidney, BC.

2.2.2 Fecundity

Varnish clam gonadal tissue was dissected from ripe females from both beaches throughout the spawning season. Eggs were teased apart from the surrounding tissue to facilitate counting. Eggs were then suspended in seawater and several subsamples counted using a Sedgewick Rafter counting cell. Clam size and fecundity relationships were compared between the two beaches using analysis of covariance (ANCOVA) to compare linear regressions according to Zar (1984). GraphPad Prism (www.Graphpad.com) was used to conduct the analysis, and to test slopes for linearity using the 'runs' test to determine if the regressions differed from significantly from a straight line (www.graphpad.com).

Flesh weights were also compared between sites. Flesh was excised from shells and both were dried at 60°C until weight was constant. Clam size and flesh weight relationships were compared between the two beaches with ANCOVA as stated above.

2.2.3 Larval development

Sexually mature adult varnish clams were collected from Robbers Passage and held in 12°C running seawater at the Bamfield Marine Sciences Centre (BMSC). All spawning trials and experiments were conducted using 0.45 µm filtered seawater. To induce spawning, clams were placed in aquaria with 12°C seawater and fed a suspension of algal paste. After 2 hours, the water was replaced with 25°C seawater. Once spawning began, clams were moved to tanks with clean, filtered, 15°C seawater. Egg and sperm sizes were recorded using an ocular micrometer. Upon evidence of fertilization, eggs were filtered gently onto a 20 µm sieve and transferred to 2 L culture vessels. Cultures were held at 15°C and developmental stage and embryo lengths (longest axis) were recorded approximately every 4 hours until they reached the trochophore stage, after which measurements were taken twice a day until the first larval shell (prodissoconch I), had developed.

2.2.4 Temperature and salinity larval rearing experiments

Once the majority of larvae had developed into D-stage veligers (approximately 48 hours), equal numbers of larvae were distributed into duplicate temperature treatments (~500 per replicate) at 9, 15 and 20°C (held at an ambient salinity of 31-32 PSU), and duplicate salinities of 10, 15 and 20 PSU (held at an ambient temperature of 15°C) in 1 L culture vessels. Cultures were lightly aerated and water was changed 2-3 times a week. All cultures were maintained under an 18 hr light: 6 hr dark photoperiod cycle to simulate natural conditions. Larvae were fed a mix of cultured algae (*Isochrysis galbana* and *Pavlova lutheri*) at a rate of 40 000 cells/L per day (Strathmann, 1987). In cases where bacterial contamination was observed, cultures were treated with a mixture of penicillin and streptomycin sulfate (Strathmann, 1987), which has previously been shown to have no effect on larval growth (Hushan et al., 1997). Larval shell length and height were measured twice weekly (using 15 individuals per culture). Metamorphosis was defined as the point at which the larval velum was lost and only a foot remained, indicating preparation for the ontogenetic shift from planktonic to benthic existence. Larval period/planktonic duration was defined as the time from fertilization to metamorphosis. Experiments were continued until all larvae had either metamorphosed or died. Larval growth rates between treatments were compared using ANCOVA. Photomicrographs were taken throughout the larval rearing experiments to document the different developmental stages.

A separate experiment was conducted to determine whether laboratory growth rates were comparable to those observed in the field. Equal numbers of recently fertilized varnish clam eggs were split between a “field rearing chamber” and a 2 L larval rearing vessel held at 15°C and 31 PSU in the lab. The field rearing chamber consisted of a capped section of PVC pipe (approximately 20 L in volume) with two large windows covered in 53 µm mesh which was anchored off the BMSC dock at approximately 1.5 m depth. A StowAway Tidbit data logger was attached to the field rearing chamber to monitor temperature during the experiment. Lab and field growth rates were compared using ANCOVA.

2.3 Results

2.3.1 Sex ratio and timing of spawning

Sex ratios differed between the two populations. The female:male:hermaphrodite ratio in Robbers Passage was 0.46**:**0.49**:**0.05, while at Bamberton the ratio was 0.39:0.57:0.04, (with the high proportion of males at Bamberton deviating significantly from a 1:1 sex ratio, chi-square = 22.6, $P < 0.0001$). The smallest female clam observed (across an overall size range of 1.4 –6.8 cm) was 2.3 cm in length and the smallest male was 1.6 cm.

All clams (> 3 cm) observed at both beaches possessed reproductive tissue (Fig. 2.2) from June – August 2003 and May - September 2002 (when only Robbers Passage was observed). The first evidence of spawning occurred as temperature began to rise in June, and tapered off as temperature began to fall towards September (Fig. 2.3). Egg puddle observations indicated that spawning events did occur between late May and the end of August in 2002. During 2003, evidence of spawning (i.e. presence of egg puddles) first appeared in early June and continued through early September. This suggests an extended spawning period that runs from June-September in Robbers Passage and from June-August at Bamberton. Varnish clams also appear to be dribble or intermittent spawners throughout the season.

2.3.2 Fecundity

Clams of equivalent size contained approximately 1.5 times more eggs in Robbers Passage than at Bamberton ($F=5.36$, $DF=1,116$, $P < 0.05$, Fig. 2.4). Egg numbers ranged

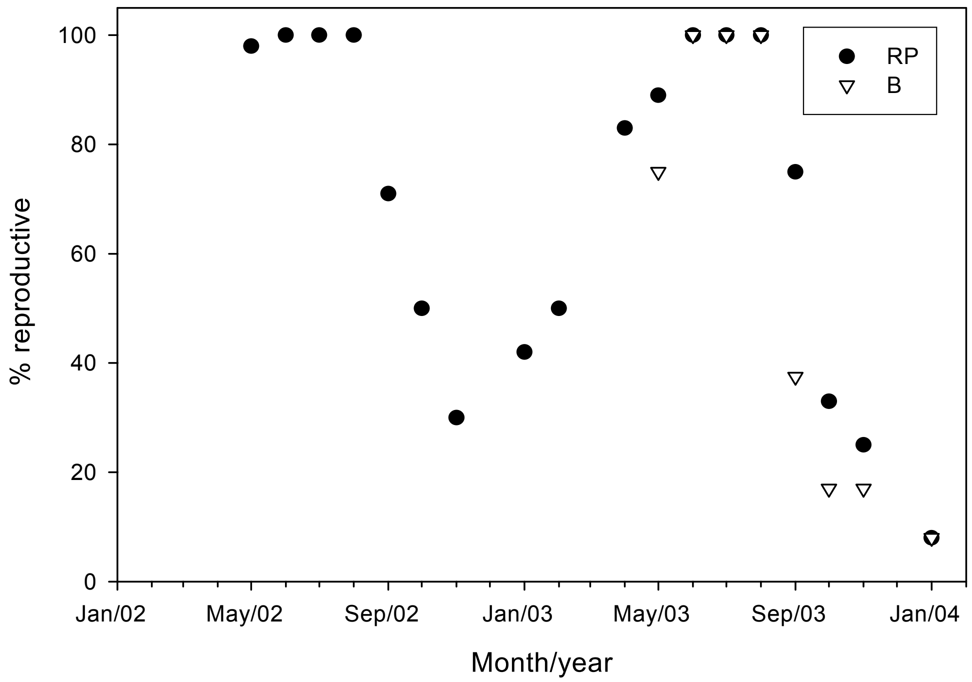


Fig. 2.2. Percent of varnish clams with gonads observed at Robbers Passage (RP) and Bamberton (B) from May 2002-Jan 2004.

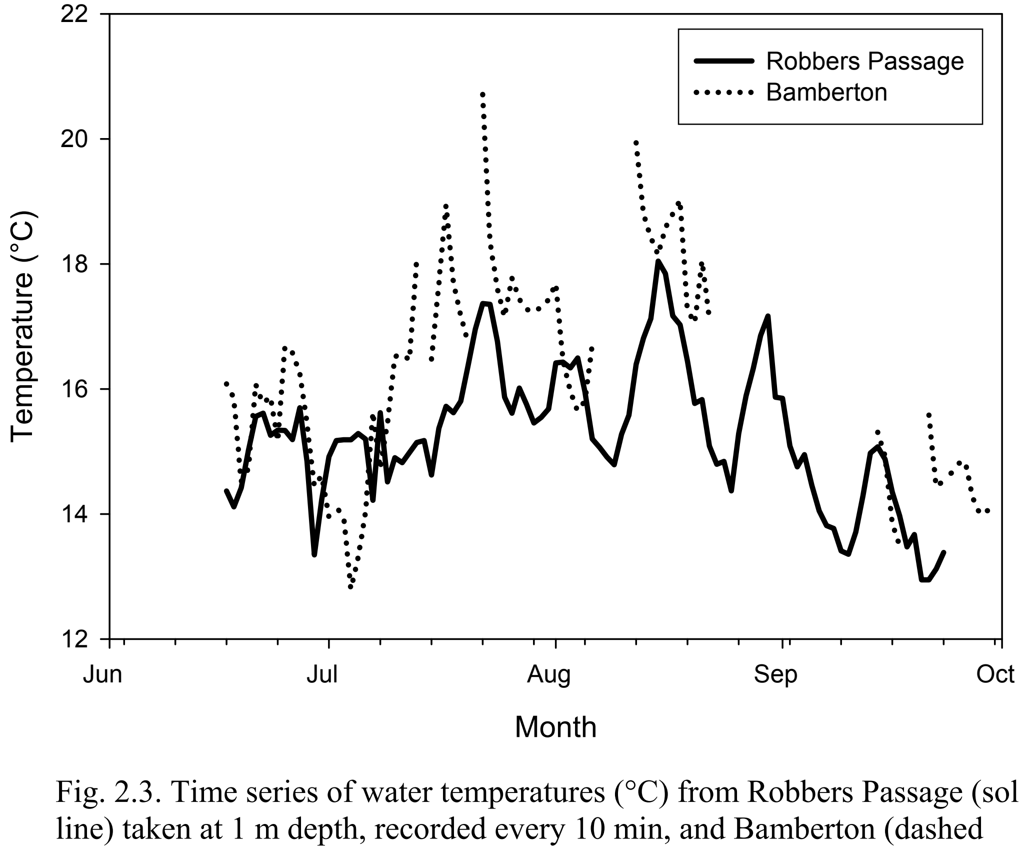


Fig. 2.3. Time series of water temperatures (°C) from Robbers Passage (solid line) taken at 1 m depth, recorded every 10 min, and Bamberton (dashed line), taken at approximately 1 m depth, every hour from June-Sept 2002. Bar at bottom indicates spawning season in Robbers Passage.

from 9×10^4 to 6×10^6 per female at Robbers Passage and 4×10^4 to 4×10^6 at Bamberton. Egg numbers were highly variable even among clams of the same length (e.g. 5 cm clam could have $2\text{-}3 \times 10^6$ eggs).

Flesh weight comparisons showed that, on average, Robbers Passage clams contained approximately twice as much flesh as Bamberton clams of the same shell size (Fig. 2.5, F=58.28, DF = 1, 200, $P < 0.05$).

2.3.3 Larval development

Average oocyte diameter was approximately 55 µm and sperm were approximately 7.5-10 µm long (not including the flagellum). Sperm were released in a steady stream and were visible as a milky white fluid. Eggs were released in a similar manner but were less conspicuous. By three hours post-fertilization, eggs were in the 2-3 cell stage with unequal cleavages (Fig. 2.6a). By 6 hours, the blastomere had developed into a round ball of multiple cells (70-80 µm), and at 16 hours the larvae had developed into free swimming, acorn-shaped, trochophore larvae. By 43 hours, each larva had developed a straight-hinge, D-shaped shell (70-90 µm) and a ciliated velum, a stage typical of marine bivalves and known as the D-stage or straight-hinge veliger (named for the shape of the first larval shell, the prodissoconch I; Ackerman et al., 1994). Food was also evident in the larval gut by this stage. The different stages of development are illustrated in Fig 2.7.

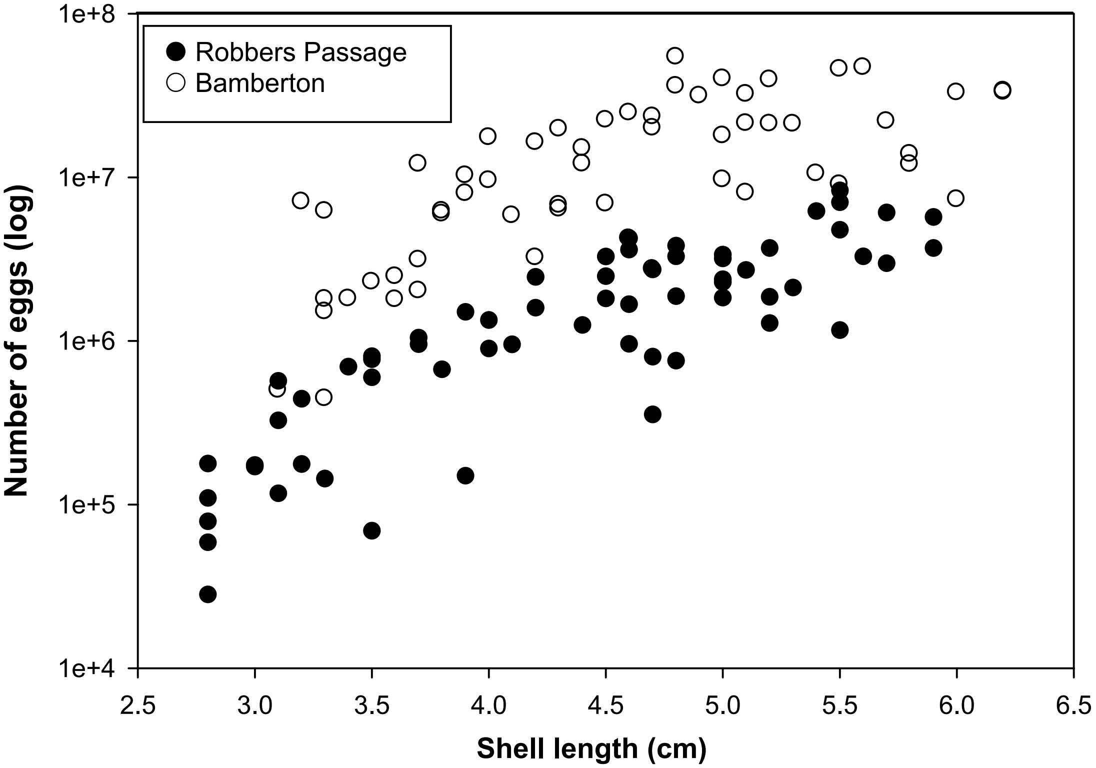


Fig. 2.4. Shell length (cm) versus log number of eggs of varnish clams collected in Robbers Passage and Bamberton.

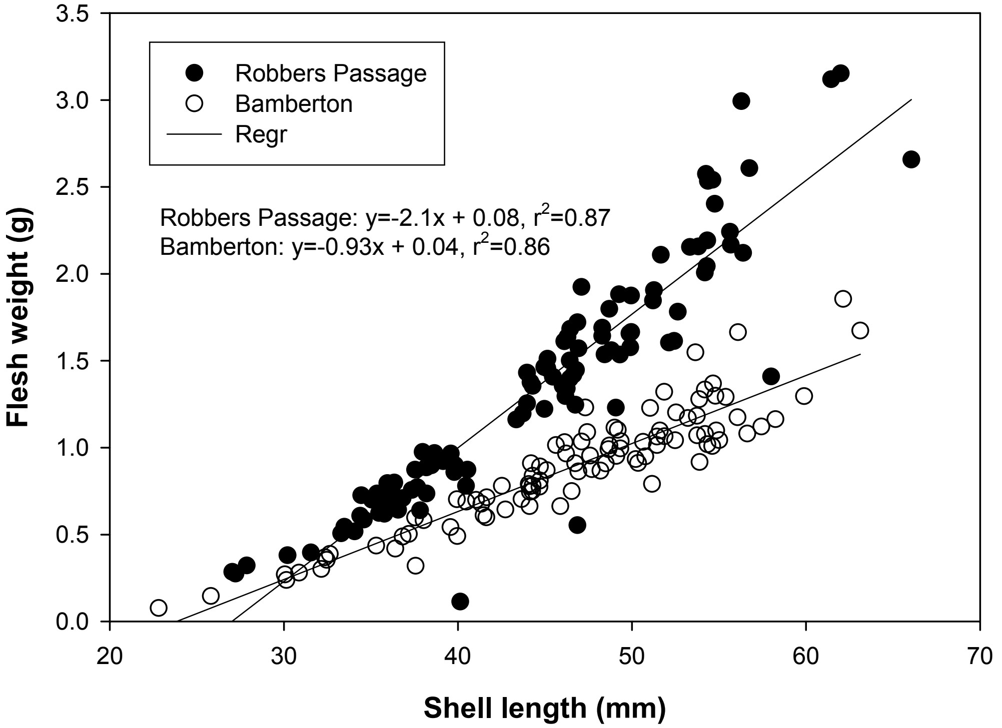


Fig. 2.5 Shell length (mm) versus flesh weight (g) for varnish clams collected in Robbers Passage and Bamberton. Lines are linear regressions.

2.3.4 Temperature and salinity experiments

When larvae were reared at 20ºC, the umbo appeared by day 12 (170 µm), the larvae developed into pediveligers by day 15 and settled out beginning on day 19 (180-200 µm; Fig. 2.6b). In the 9°C treatment, larval development was extremely slow and only the presence of the umbo was observed by day 36 (120 µm; Fig. 2.6b). Larvae in the 9°C did not survive long enough to develop further.

At a temperature and salinity approaching ambient field conditions (i.e. 15°C, 31 PSU), the umbo began to appear by day 15 (shell length of 120 µm, signifying the beginning of
At a temperature and salinity approaching ambient field conditions (i.e. 15°C, 31 PSU), the umbo began to appear by day 15 (shell length of 120 µm, signifying the beginning of
the second larval shell, the prodissoconch II, which was completely laid down by day 21 (130 µm). At approximately 27 days (and an average pediveliger length of 180 µm), the foot became evident (Fig. 2.6b). By day 33, the larvae in this treatment were at >180 µm in length and possessed only a foot, completing metamorphosis.

In the salinity treatments, larvae reared at 10 PSU did not survive past the D-stage veliger (even after 30 days in culture). Among larvae reared at 15 PSU, the umbo appeared at day 30 (150 µm), but no larvae survived past this stage (Fig. 2.6c). In the 20 PSU treatment, larval development progressed at a rate similar to ambient ocean conditions (i.e. 15°C, 31 PSU), with the umbo laid down at 20 days (160 µm), progression to the pediveliger by day 27 (length = 180 µm), and metamorphosis at ~day 31 (length = 180-210 µm).

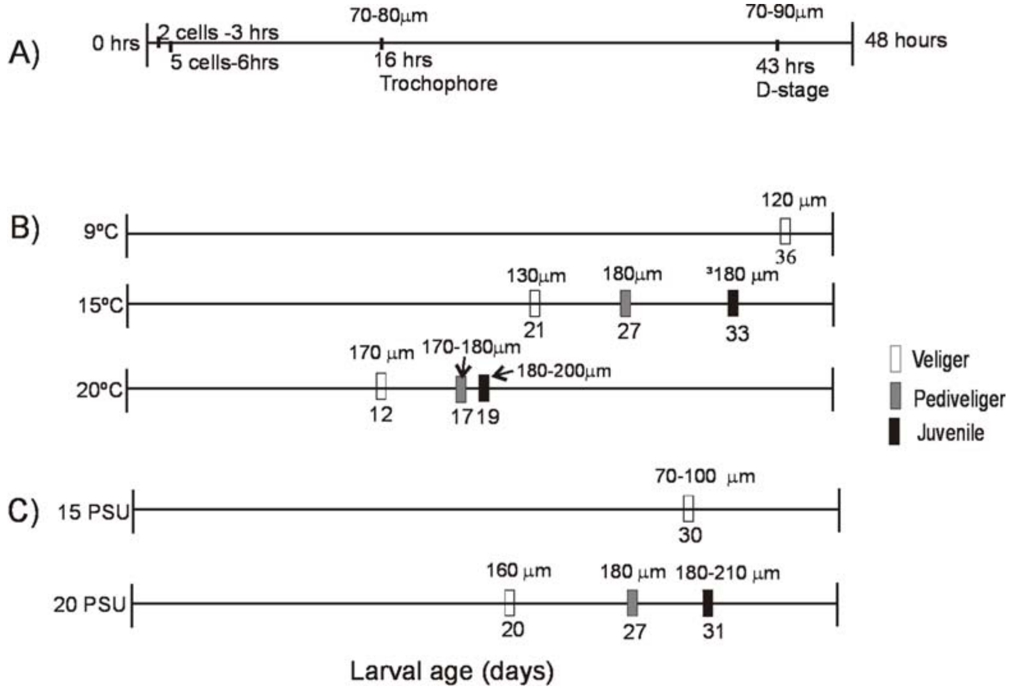


Fig. 2.6. Varnish clam development trajectories based on larval rearing experiments for A) the first 48 hrs at ambient temperature and salinity (15ºC, 31 PSU), and 2-40 days at B) 9-20ºC and C) 15-20PSU. Bars denote developmental stage: veliger with velum only (clear bar), pediveliger with velum and foot (gray bar) and juvenile with foot only (black bar). Numbers above bars represent larval size (in µm) at that stage, numbers below bars show the day on which the developmental stage was reached

Larval growth rates differed significantly among temperature treatments (ANCOVA, F=583, DF=3,1107, $P < 0.0001$). At 20°C and 15°C, the larval growth rates were 8 and 3 times faster than those observed at 9°C (Fig. 2.8a). The increase in growth rate corresponding to a 10ºC increase in temperature (i.e. Q10) was 4.9, indicating strong temperature dependence. Larval growth rates also differed significantly among salinity treatments (ANCOVA, F=31.3, DF=2, 870, $P < 0.0001$), with the fastest growth rate observed at 20 PSU, five times higher than at 10 PSU (Fig. 2.8b). The Q10 for salinity was 3.5 indicating strong salinity dependence for growth rate (although not as

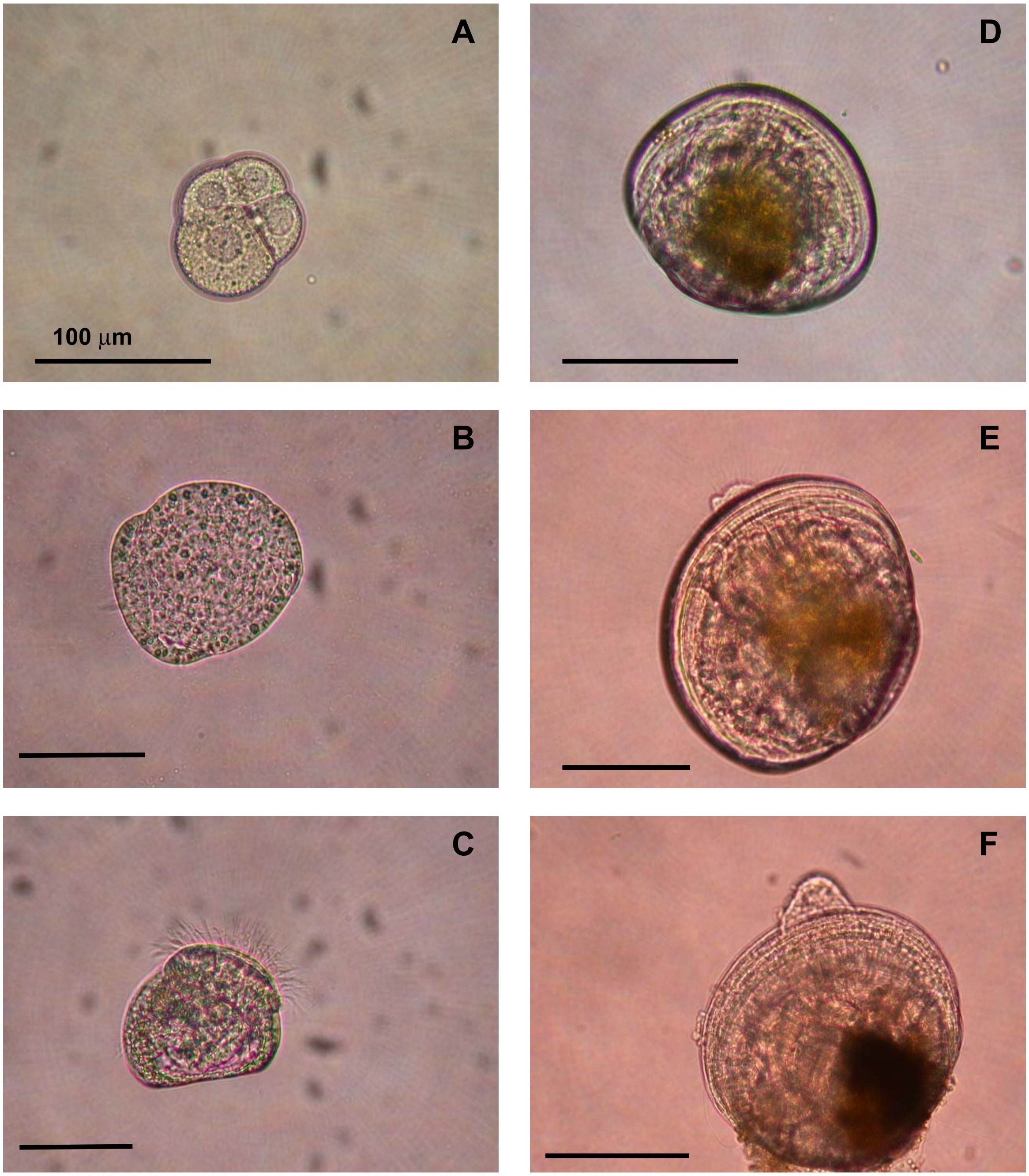


Fig. 2.7. Photomicrographs of the varnish clam during its development just after fertilization (A) to juvenile (F). 100 µm scale bars are included in each panel to show approximate length.

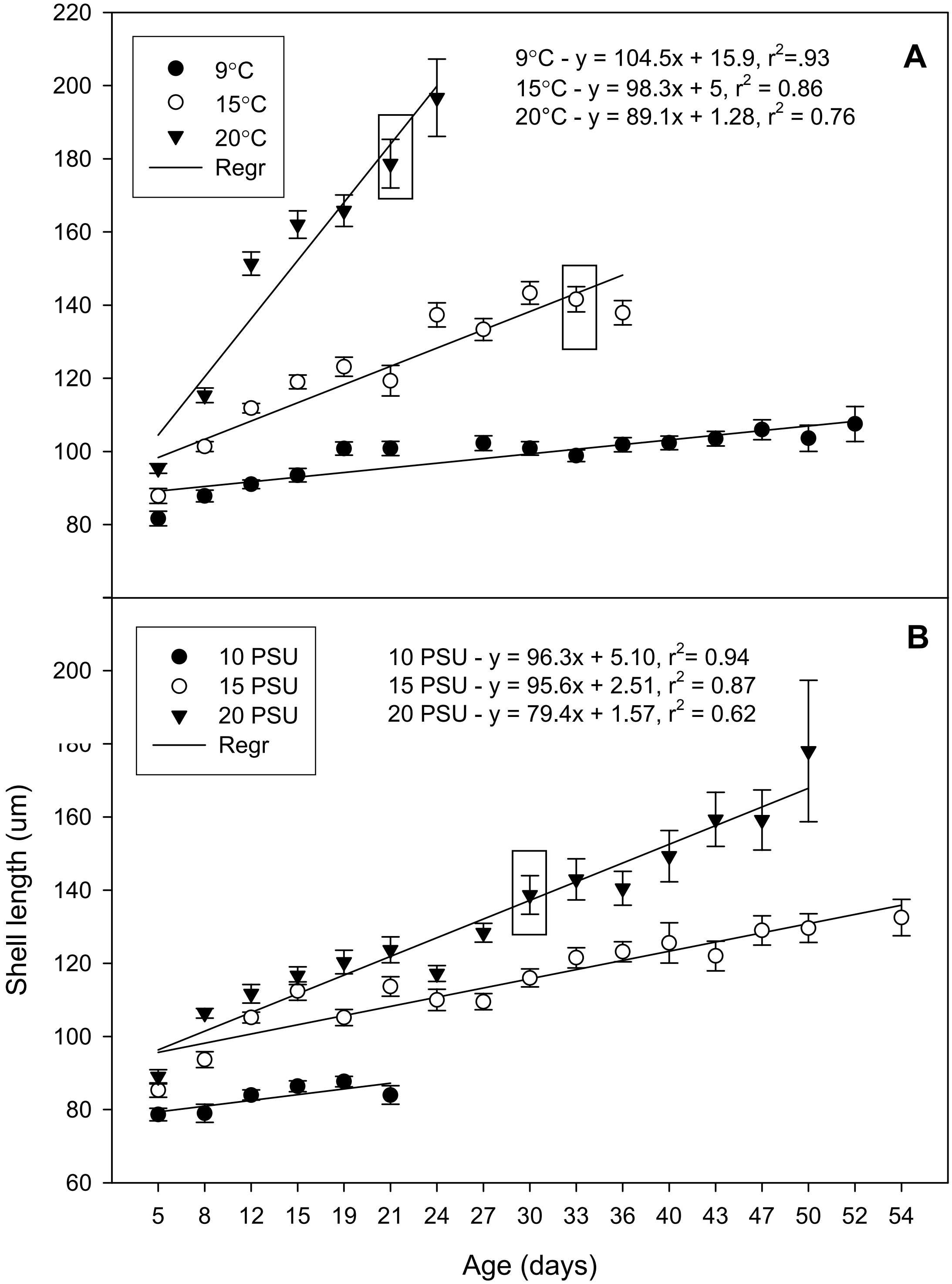


Fig. 2.8. Larval age (days) versus average shell length (in µm) of varnish clams for (A) temperature (°C) at 31 PSU and (B) salinity (PSU) at 15°C trials. Bars represent standard errors. Lines are linear regressions, n=15. Boxed points represent age when larvae began to metamorphose. Data are shown for duration of experiment.

pronounced as for temperature). Larval size at settlement was ~180 µm with settlement occurring as early as day 19 (at 20°C). The oldest larvae observed with a velum were 59 days old (from the 15°C treatment) however we were unable to observe settlement therefore these larvae might not have been competent. These results suggest a planktonic duration of at least 3 and possibly up to or greater than 8 weeks.

Larval growth rates in the field and the lab were not significantly different over the first 11 days of culture (ANCOVA, F=7.8, DF=1,147, P = 0.176) despite the fact that field temperatures varied considerably (13-22°C) while larvae in the lab were held at a constant 15°C. After the 11th day, temperatures in the field treatment decreased and the larvae experienced heavy mortalities leaving insufficient numbers to permit further comparison with lab cultures.

2.4 Discussion

The varnish clam population at Bamberton in Saanich Inlet had significantly more males than females, which is unusual for gonochoristic (i.e. separate sexes) species in which the sex ratio is usually either close to 1:1 or slightly skewed towards females (Mackie, 1984). Male-skewed sex ratios are generally uncommon, although they have been observed in some other dioecious bivalve species (Gaspar and Monteiro, 1999). In protandric bivalves, food levels may influence sex determination, with sperm production occurring at lower food levels and egg production at high food levels (Sastry, 1968). If this extends to gonochoristic species, then the differences in sex ratios observed in this study could be indicative of different feeding conditions at the two sites. Differences in food availability are also supported by the higher flesh content observed for Robbers Passage among clams of equal length.

Other factors known to skew sex ratios towards males include temperature (Lee et al., 2003), differential development rates, or different maximal lengths (e.g. with males usually being smaller; Baghurst and Mitchell, 2002; Marsden, 1999) or differential mortality (Valenzuela, et al, 2003). Temperature differences between the two sites in this study are unlikely to favor the production of males because Saanich Inlet typically has warmer temperatures than Barkley Sound. No significant differences in male and female lengths or morphology, occurred at either of the two sites, making differential developmental and mortality rates an unlikely explanation as well. The presence of pinnotherid (pea) crabs in bivalves has been associated with sex ratios skewed towards males (Christensen and McDermott, 1958). Accordingly, pea crabs were only observed in Bamberton clams and may have contributed to the higher abundance of males. A varnish clam population located about 100 km north of Bamberton also had sex ratios skewed towards males and no evidence of hermaphrodites (L. Genn, University of Victoria, unpublished data). In Genn's study, males dominated the smaller size classes but the sex ratio leveled off to 1:1 in larger size classes, suggesting protandry. Whether the skewed sex ratio observed in varnish clam populations at these select sites is due to protandry, environmental differences, pea crab infestation, or a combination remains unclear.

The presence of functional hermaphrodites in varnish clam populations would be advantageous for an invasion, potentially enabling even one individual to establish a population. Hermaphrodites occurred in both populations at higher frequencies than those observed (usually ~0.1%) among other dioecious bivalves (Eversole, 1986). However, it is unlikely that these individuals were functionally hermaphroditic since the gonads did not appear to be regionally distinct or in separate zones (Mackie, 1984).

Small size-at-maturity enables varnish clams to reproduce quickly after settling, further increasing the chance of a successful invasion. The smallest varnish clams observed with eggs and sperm were 2.3 cm and 1.6 cm, respectively. A more detailed reproductive study of varnish clams reported reproductive clams as small as 0.8 cm (L. Genn, University of Victoria, unpublished data). Assuming that 1.6-2.2 cm varnish clams are 1 year old (Choi, 2001), then most of the varnish clams in the Bamberton and Robbers Passage populations reach maturity in their first year. This is quite young compared to co-occurring native bivalves that typically do not reach maturity until 2-3 years (Appendix, Table 2.1.). Early maturation and high fecundity should provide further advantages to the varnish clam in the early stages of establishment (Bohn et al., 2004), and have most likely contributed to its rapid increase in abundance. The fecundity of varnish clams is comparable to similar-sized local species at Robbers Passage and Bamberton (Appendix, Table 2.1).

Similar to native bivalves in coastal BC, varnish clams spawn from late spring to early fall (Appendix, Table 2.1.). The spawning period occurs when temperatures begin to increase, indicating that larvae are likely developing in waters from 13-15°C. The Eggs puddles on the sand has been observed for several species in BC, in addition to varnish clams (Helm et al., 2004). Varnish clam eggs on the sand remain viable (S.E. Dudas, unpublished data) despite their exposure, allowing them to be fertilized on both outgoing and incoming tides, and potentially provide an advantage for increasing fertilization success.

The varnish clam exhibits a larval development pattern typical of marine bivalves (Ackerman et al., 1994; Quayle and Bourne, 1972; Sastry, 1979). Its size at settlement is comparable to, or smaller than, other similar sized, soft-bottom bivalves with which it occurs (Appendix, Table 2.2.). Differences in larval rearing temperatures and salinities make it difficult to directly compare larval growth rates between species, however there is no evidence that varnish clam larvae exhibit significantly faster growth than local bivalve species (Appendix, Table 2.2.). Varnish clam larvae reared in a Japanese laboratory study grew faster (Sun et al., 1997) than the growth rates observed here, likely the result of colder average temperatures experienced at the higher latitudes of the new environment.

Temperature had a stronger effect on growth of larval varnish clam larvae than did salinity (Q10 of 4.09 versus 3.5), similar to local bivalve larvae (Culliney et al., 1974). In their native range, varnish clam larvae develop at salinities of 24 - 31 PSU . In coastal BC, however, the larvae are able to develop at salinities as low as 20 PSU, and at growth rates equivalent to those observed at ambient salinity (30 PSU) at the same temperature.

Varnish clam larvae have a wide range of temperature and salinity tolerances and a lengthy planktonic duration similar to many native species (Appendix, Table 2.2.).

The varnish clam's lengthy larval planktonic duration has implications for its dispersal in coastal BC. Figure 2.9 shows the surface circulation patterns around Vancouver Island (Thomson, 1982). Thus, assuming that larvae behave as passive particles (i.e. lacking any vertical migratory behaviour), even a 10 cm sec^{-1} current would be enough to disperse them 180 km in just three weeks (at 20 cm sec^{-1} this range increases to 378 km). Timing of spawning indicates that the larvae are likely to be in the water column when temperatures are approximately 15°C, corresponding to a planktonic larval duration of at least three (and possibly up to eight weeks assuming the larvae remain competent). Under these conditions and assumptions varnish clam larvae have the *potential* to disperse hundreds of kilometers in just one reproductive season. Given this dispersal potential, the fact that varnish clams are not found on all beaches with suitable habitat, indicates that more localized oceanographic features (e.g. eddies) may influence larval supply to beaches.

Assuming the vicinity of Vancouver Harbour to be the point of introduction (Gillespie et al., 1999), the varnish clam has already traveled 570 km to reach its current northern limit on the WCVI and over 900 km to its southernmost population in Oregon. The water mass movement in this region during the spawning period likely facilitated the varnish clam invasion, by dispersing the larvae throughout regions where suitable habitat is abundant (i.e. the Strait of Georgia).

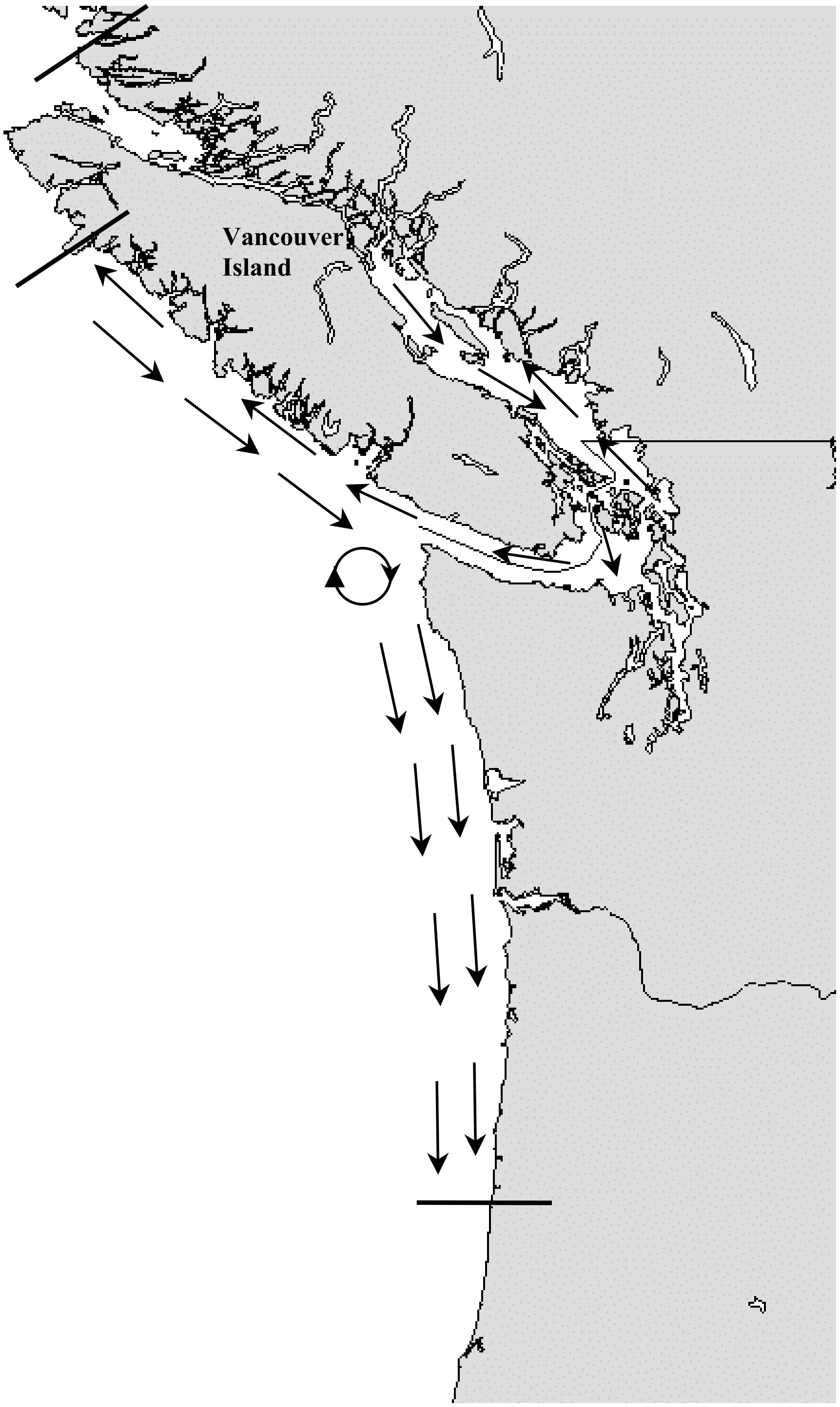


Fig. 2.9. Generalized summer surface circulation patterns in coastal British Columbia. Arrows represent surface current direction. Circle represents the surface eddy off the mouth of Juan de Fuca. Bars represent the current distributional limits of known varnish clam populations. Based on data from Thomson (1982), Gillespie et al., (2001) and Gillespie and Bourne (2004).

These oceanographic circulation patterns have played a role in past exotic species introductions as well. The Manila clam (*Venerupis philippinarum*), a native of Japan, followed a similar invasion route in the 1930s (Bourne, 1982), after its introduction to Ladysmith Harbour on Vancouver Island. The port of Vancouver is particularly susceptible to introductions, due to its location in relation to currents, and the fact that it is one of the endpoints for shipping traffic entering the Strait of Juan de Fuca the (the busiest shipping corridor in North America). When invertebrate species with extended planktonic larval stages are introduced into this area they are likely to be rapidly dispersed not only throughout BC but also southwards towards Washington and Oregon.

This study provides the first account of the development and environmental tolerances of varnish clam larvae in the Northeast Pacific. The two main steps in any invasion are initial introduction and successful establishment of the species, followed by the expansion of populations in the new region (Vermeij, 1996; Williamson and Fitter, 1996). For the varnish clam, small size-at-maturity likely also contributed to its rapid establishment, allowing new settlers to reproduce within one year. Likewise, its high fecundity, lengthy planktonic phase and the favourable regional ocean currents (see Fig. 2.9) have also contributed to the rapid range expansion, dispersing larvae to the large number of suitable shellfish beaches in the Strait of Georgia. The varnish clam invasion of the Northeast Pacific demonstrates how quickly an invader can establish and spread, when it possesses life history characteristics suited for both establishment and dispersal. Particularly, when these characteristics are supplemented with ocean circulation patterns that favour dispersal throughout the recipient region.

2.5 Appendix

Table 2.1. Egg size, fecundity, Size/age-at-maturity and timing of spawning of the varnish clam and co-occurring species

Spp.	**Egg size**	**Fecundity/size**	**Size/age-at-maturity**	**Timing of spawning**	**References**
Nuttallia obscurata	46-55 um	4x10^{4}-6x10^{6}, 2.8-6.2 cm	1.6 cm, 1 yr		1,2
Venerupis philipinnarum	60-75 um	1.9x10^{5}-2.4x10^{6}, 1.9-4 cm	2-2.5 cm, 2-3 yrs	late spring-summer	3,4,5,6,7
			1.5 cm, 1.5 yrs		N.Bourne, pers. comm.
Mya arenaria	68-73 um	2.4x10^{4}-7.2x10^{5}, 4-8.5 cm	5 yrs		8,9,7
Panopea abrupta		7-10x10^{6}	4.5-7.5 cm, 3 yrs	June-July	10,11
Saxidomus giganteus			4 cm, 3-4 yrs	late spring	5
Protothaca staminea			2.2-3.5 cm, 2-3 yrs	late spring-summer	5,12
Clinocardium nuttalli	80 um		2 yrs	late spring	5,13
Tresus capax	60-70 um		7 cm, 3-4 yrs	late Feb, early March	5, 14
Macoma balthica	101-108 um		0.6-0.65 cm, 3 yrs		15,16

1. (Choi, 2001), 2. L.Genn Unpublished data, 3. (Ponurovsky and Yakovlev, 1992), 4. (DFO, 1999b), 5. (Quayle and Bourne, 1972), 6. (Bourne, 1982), 7. (Loosanoff and Davis, 1963), 8. (Brousseau and Baglivo, 1982), 9. (Abraham and Dillon, 1986) 10. (Goodwin and Pease, 1989) 11. (DFO, 2000), 12. (DFO, 1999a), 13.(Strathmann, 1987) 14. (Bourne and Smith, 1972) 15. (Harvey and Vincent, 1989), 16. (Honkoop and van der Meer, 1997)

Table 2.2. Developmental time (from fertilization) comparisons for bivalves co-occurring with varnish clams in BC

Spp	Temp. (°C)	Sal (PSU)	Trochophore Length (um) / Time (d/h)	D-Stage Length (um)/ Time (d)	Veliger Length (um)/ Time (d)	Pediveliger Length (um)/ Time (d)	Settlement Length (um)/ Time (d)	References
Nuttallia obscurata	15	31	70-90 µm /48 h	70-90 µm /48 h				
	9	31			120 µm/ 36 d			
	15	31			130 µm / 21 d	180 µm /27 d	>180 µm /33 d	
	20	31			170 µm 12 d	170-180 µm /17 d	180-200 µm / 19 d	
	15	10			none survived			
	15	15			150 µm/ 30 d			
	15	20			160 µm /20 d	180 µm /27 d	180-210 µm /31 d	
Venerupis philipinarum	20	-		95 µm	120 – 140 µm		175-220 µm /14 d	1
	25	20-30					165-180 µm /19 d	2
	14	20-25					29d	2
	14	30					none survived	2
	19	20-30				19-22 d		2
	10	10-30					none survived	2
	10-30	10-15					none survived	2
	21	29-32		88-96 µm		200-220 µm /15-17 d		3
	13-16						21-28 d	4
			1 d	95 µm	140 µm			4
Mya arenaria	20			86-90 µm	123-155 µm	165	170-228 28	1
	cold		12 h	24-36 h	2-6 wks		28-42 d	5
Macoma balthica	4		2-3 d	5 d				6
	10						235-268 µm /22-32 d	7
	15						240-272 µm /17-25 d	7
	20						220-270 µm /15-22 d	7
Panopea abrupta	16						400-1500 16 –35 d	8
	14			111 µm /48 h	120 µm / 6d			9
	9							
	14						381 µm /47 d	10
			80-100 µm/24 h	110 µm /48 h	165-400 µm	300 µm		
Protothaca staminea			60-80 µm/12 h	24 hrs	14 d		260-280 µm /21 d	11
Tresus capax	13	28-29	24 h	75 µm /48 h	140-150 µm	200-210 µm	260-280 µm	12
Saxidomus giganteus	18	25-31	24 h	142 µm /48 h	224 µm /16 d		311 µm /22-30 d	13
	15-20	20-29					230-250 µm/20-25d	14
Clinocardium nuttallii	15			18 hr				4

1. (Loosanoff and Davis, 1963) 2. (Robinson and Breese, 1984) 3. (Laing and Utting, 1994) 4. (Strathmann, 1987), 5. (Abraham and Dillon, 1986), 6. (Pekkarinen, 1986), 7. (Drent, 2002), 8. (Goodwin and Pease, 1989), 9. (Goodwin, 1973a; 1973b), 10. (Goodwin et al., 1979), 11. (Chew and Ma, 1987; Quayle and Bourne, 1972; Shaw, 1986) , 12. (Bourne and Smith, 1972), 13. (Breese and Phibbs, 1970), 14. (Bourne, 1971)

Chapter 3. Varnish clam (*Nuttallia obscurata*) population demographics in the Strait of Georgia and Barkley Sound

3.1 Introduction

The varnish clam (*Nuttallia obscurata*) first appeared in the Northeast Pacific in 1991 (Forsyth, 1993), and has since spread rapidly throughout most of southern coastal British Columbia (BC), Canada and southwards to Oregon, USA (Gillespie, 1995). The presence of several distinct age classes observed in BC populations in 1994 indicates that the introduction occurred a few years prior to its detection (Merilees and Gillespie, 1995). Varnish clams have since been reported from more than one hundred beaches in coastal BC, often at high densities (i.e. 800/m^2). They are typically found in the mid-high intertidal zone, in mixed sand, gravel and mud, with highest abundances often occurring higher in the intertidal zone than any other native bivalve species (Gillespie, 1995). Adult varnish clams are capable of suspension and deposit feeding (including siphonal deposit feeding and pedal locomotory and sweep feeding; M. Parker, University of Victoria, unpublished manuscript). In BC, varnish clams are included in both recreational and commercial fisheries. A separate varnish clam commercial fishery is under development (Gillespie et al., 2001) however, they are currently harvested along with other economically valuable species that co-occur with them (e.g. *Venerupis philippinarum*).

Data on varnish clam populations in the Northeast Pacific are limited. Studies in the Strait of Georgia (SoG hereafter), BC and Puget Sound (Selleck, 2003), Washington, have investigated its distribution and co-occurrence and competition with commercially important bivalve species (Gillespie et al., 2001). However, almost nothing is known about population densities and size structure of varnish clams elsewhere in the Northeast Pacific. Likewise, individual growth and survival rates are currently unknown. The purpose of this study was to determine: (1) population densities, size-structure and substratum type for varnish clam populations in the SoG and on the west coast of Vancouver Island (WCVI hereafter), (2) document spatial and temporal changes in size-structure, (3) explore correlations between varnish clam density, tidal height and co-occurring species, (4) explore relationships between shell length, shell thickness, flesh weight and burial depth, and (5) determine varnish clam growth and survival rates.

Examining varnish clam populations in different geographical regions of BC can help determine whether these populations are the result of isolated invasion events (usually indicated by a single size class in length-frequency distribution), or repeated recruitment events (i.e. multiple size-classes). A time series of annual surveys can also indicate whether varnish clam populations are increasing in size or density, and reveal any changes in co-occurring bivalve species. Comparison of growth and survival rates at different sites can provide information on local environmental influences, and enable comparison with native species. Finally, knowledge of the population dynamics of this species, and how local populations vary spatially and temporally, is crucial to understanding whether the varnish clam will impact soft-bottom native intertidal communities in coastal BC and for developing management plans for a sustainable commercial fishery (Gillespie et al., 2001).

3.2 Methods

3.2.1 Population density, size, and substratum type

Varnish clam population surveys were conducted annually at one site in the Strait of Georgia (Jericho Beach) and four sites in Barkley Sound (Robbers Passage, Hand Island, Dodd Island and, Toquart Bay) from 2001-2003 (Fig. 3.1). Bamberton Provincial Park in Saanich Inlet was also surveyed in 2003. Preliminary surveys were conducted at each site to determine the areas within the beach that varnish clams were present. These limits were recorded and annual surveys targeted regions of the beaches with varnish clams. Survey methodology, length-frequency distributions, population size and density calculations followed the methods for random and stratified random sampling as described in Gillespie and Kronlund (1999). This sampling methodology entails dividing

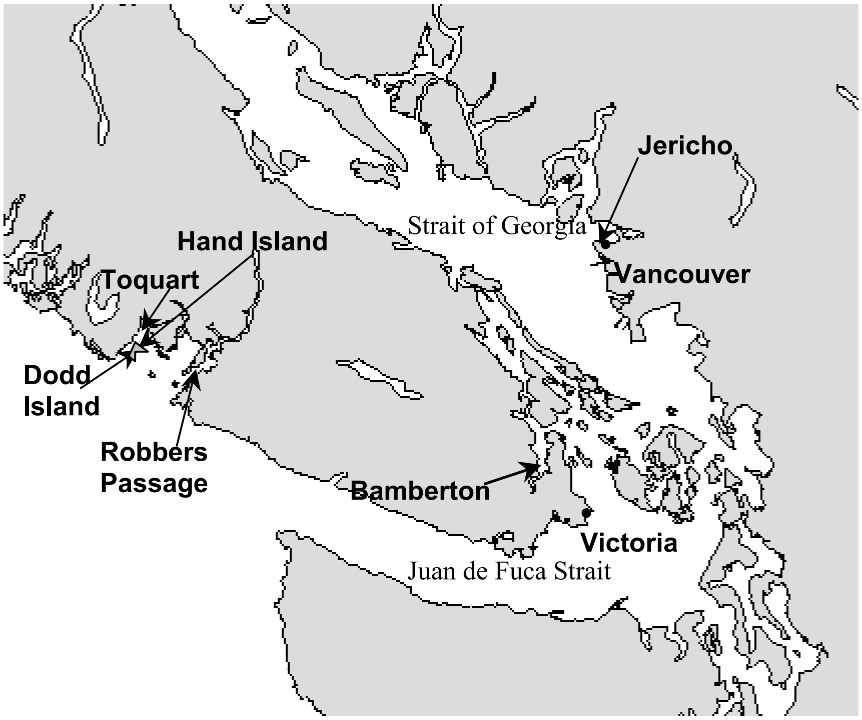


Fig. 3.1. Population survey sites for varnish clams in the Strait of Georgia (Jericho, Bamberton) and Barkley Sound (Robbers Passage, Hand and Dodd Islands and Toquart).

the beach into different areas, or strata, that are known to have clams. Quadrats are then sampled randomly within each stratum. Each year the same strata on each beach were sampled. The number of quadrats sampled per site was dependent on beach area such that a minimum of 30 quadrats per hectare area was sampled (Gillespie and Kronlund, 1999). Intertidal heights were determined for each quadrat sampled (0.25 m^2) using a hand level and a metre stick. This height was then added to the tidal height at the exact time of measurement to determine the height above mean lower low water. All bivalve species in each quadrat were identified, and their lengths, widths and heights measured to the nearest millimeter using digital calipers according to the dimensions shown in (Harbo, 1997). Quadrats were excavated by hand (using a small spade) for all surveys. In 2002-2003, sampling was supplemented with 2 mm mesh screening for 50% of the quadrats at each site (determined by what was feasible within one tide). Because clams could not be removed from Hand and Dodd Islands in Pacific Rim National Park no screening was conducted at these sites. Relationships between varnish clam density, intertidal height, and number and density of co-occurring species were determined using regression analysis.

Substratum samples were collected for six of the survey sites in 2003 using a cylindrical poly-vinyl chloride core (20 cm in length, 10 cm diameter, 1570 cm^3). Three to twelve samples were collected per site (dependent on survey area), over the tidal range surveyed (which varied from 0.75-3.1 m between sites). Substratum samples were frozen shortly after collection for later analysis. Sediment characteristics were determined following Buchanan's (1984) method for clean beach sand. Sediments were categorized according to Table 3.1. Statistics (i.e. sorting, grain size) were calculated using the program GRADISTAT (Blott and Pye, 2001).

3.2.2 Length-frequency analysis

Length-frequency distributions were measured monthly from spring to fall, and every other month during the winter, for Robbers Passage and Bamberton Provincial Park from 2001-2003. Randomly placed quadrats (0.25 m^2) were dug to 30 cm depth, at approximately 1.6 m tidal height, until a total of at least 300 clams had been measured. In 2002 quadrats were screened using a 2 mm mesh. Due to the presence of a large number of clams <10 mm in length at Bamberton (i.e. the number was so large that measuring all of the clams in a 0.25 m^2 quadrat was not feasible), the quadrat size was reduced to 0.09 m^2 when screening was implemented.

Table 3.1. Sediment category and grain size (Blott and Pye, 2001)

Sediment Category	Grain size (mm/µm)	
Fine gravel	4-8 mm	Gravel
Very fine gravel	2-4 mm	
Very coarse sand	1-2 mm	Sand
Coarse sand	0.5-1 mm	
Medium sand	250-500 µm	
Fine sand	125-250 µm	
Very fine sand	63-125 µm	
Mud	<63 µm	Silt

3.2.3 Relationship between shell length, shell weight, flesh weight and burial depth

Approximately 100 varnish clams were removed for dissection from June-August 2003 from each of Jericho Beach, Robbers Passage, Toquart Bay and Bamberton. In January 2004, an additional 100 clams were taken from Robbers Passage and Bamberton. Flesh was excised from the clams and placed in pre-weighed aluminum boats, the corresponding shells were placed in aluminum trays, and both were dried to constant weight at 60°C. Cubic regression equations were used to describe the observed relationships between shell length and flesh and shell weights.

Varnish clam burial depths were measured in the field at Robbers Passage and Toquart Bay. Troughs were excavated in the sand to expose one side of buried varnish clams. The distance from the top of each clam to the surface was then measured to the nearest centimeter with a clear plastic ruler.

3.2.4 Growth and survival rate analysis

Mark-recapture methods were used to calculate growth rates of varnish clam populations at Robbers Passage and Bamberton. Approximately six hundred 10-65 mm clams were marked at each site in May 2003 using Sharpie® permanent markers and then sealed with cyanoacrylate glue. Clams ≥30 mm in length were marked and reburied in the field on the same day. Clams <30 mm in length were marked in the lab, placed in flowing seawater once the marks had dried, and then returned to the field the following day. Clams were recaptured and their growth increments measured (to the nearest millimeter) in September and May of each year until 2005. Large clams were recaptured by carefully digging the mark-recapture plot with hand spades. Small clams (i.e. <30 mm) were excavated by hand and the substratum was sieved to 2 mm to ensure that very small clams were not missed. Mark-recapture plots were checked the day following each recapture exercise to confirm that excavation and reburial did not substantially increase mortality rates (i.e. by altering the substratum), and revealed mortalities <0.05%.

Annual growth increments were determined from the recapture data and modeled using four growth functions (Table 3.2). These included three determinate, asymptotic growth functions (the specialized and generalized von Bertalanffy models and the Gompertz model), and one non-asymptotic, indeterminate growth model (the Tanaka model).

Models were fit iteratively using the ordinary least squares method in SigmaPlot. The most appropriate model was then determined by comparing values of the Akaike Information Criterion (AIC). The AIC identifies the most parsimonious model by balancing the need to decrease bias in estimates (by increasing the number of parameters) against the need to increase precision by decreasing the number of parameters (Burnham et al., 1995). AIC values were calculated using formulae from Quinn and Keough (2002):

$$\mathrm{AIC} = n[\ln(SS_{residual})] + 2(p+1) - n\ln(n)$$

where:

p = number of parameters

n = number of observations

Lower AIC values indicate more parsimonious models. Because the AIC is scored on a relative scale, AIC differences are often more informative than absolute scores, and can thus be used to rank a group of models (Burnham and Anderson, 1998). The larger the ΔAIC (i.e. difference between the model with the lowest AIC and the model being compared), the less plausible the model, and less support for selecting one model over another. Models with $\Delta AIC \leq 2$ both have substantial support and should both be considered when making inferences about the data. Models with ΔAIC 4-7 have considerably less support and indicate there is a real difference between the models, and those with $\Delta AIC > 10$ have essentially no support and provide strong evidence for model differences (Burnham and Anderson, 1998).

Table 3.2. Equations for the various determinate and indeterminate growth functions used to model varnish clam size-at-recapture from the Robbers Passage and Bamberton populations.

Model	Equation	Parameter definitions	Reference
Specialized von Bertalanffy	$L_2 = L_1 (L_\infty - L_1)(1 - e^{-kt})$	L_2 = size at recapture L_1=size at marking L_∞=asymptotic size k =rate of decrease in growth rate t =time interval	(Brey, 2001; Fabens, 1965)
Generalized von Bertalanffy	$L_2 =[L_\infty^{1/D} (1 - e^{-kt})+ L_1(e^{-kt})]^D$	L_2, L_1, L_∞, t, k as above D = determines shape of curve	(Brey, 2001; Fabens, 1965)
Gompertz	$\ln(L_2) = \ln (L_\infty)(1-e^{-kt}) + \ln (L_1)(e^{-kt})$	same as above	(Brey, 2001)
Tanaka	$L_2 = 1/(\sqrt{f}) \times [2G + 2 \sqrt{(G^2 + fa)}] + d$ $G = (E/4) - [(fa)/E] + f$ $E = e^{(\sqrt{f})(L1-d)}$	$1/\sqrt{a}$ = maximum growth rate d = shifts body size of maximum growth f = measures rate of change of growth rate	(Tanaka, 1982), (Brey, 2001; Ebert et al., 1999)

In order to directly compare growth rates between Robbers Passage and Bamberton varnish clam populations, growth increment data were first transformed ($\log_e$) to linearize the data, and then analyzed using analysis of covariance (ANCOVA). To facilitate comparison of varnish clam growth rates with native species for which only size-at-age data are available, a size-at-age key was made for varnish clams based on the growth increment data and the assumption that a 15 mm clam is one year old (Choi, 2001). For example, if a 15 mm clam had an average growth increment of 15 mm over one year then a 30 mm clam is two years old and so forth.

Survival rates were determined using capture-mark-recapture (CMR) methods (Lebreton et al., 1992) from the software program MARK (White and Burnham, 1999). In CMR analysis, live recaptures can be used to determine survival and recapture rates using the Cormack-Jolly-Seber (CJS) model. The CJS model assumes that: (1) all individuals have the same probability of recapture, (2) all individuals have the same probability of survival from one interval to the next, (3) marks are not lost between captures or missed during recapture, and (4) all samples are instantaneous and each release is made immediately after the sample (Pollock et al., 1990). To ensure that my data satisfied these assumptions, I used the bootstrap routine in MARK to run a fully size- and time-dependent model for each site (using two size groups, < 30 mm and ≥ 30 mm, for each site). The bootstrap routine simulates recapture histories that meet these assumptions and then compares these to the observed data (White and Burnham, 1999). By calculating the ratio of the simulated deviance from the bootstrap values to the observed deviance in the actual data, one can quantify the degree of lack of fit, or the amount of overdispersion (i.e. greater than binomial 'noise' or variation) in the data, the variance inflation factor, known as $\hat{c}$ (Cooch and White, 2004). Deviance is calculated as the difference between -2log(Likelihood) of the current model and -2log(Likelihood) of the saturated model, where the saturated model is the model for which the number of parameters is equal to the sample size (White and Burnham, 1999). The variance inflation factor can be calculated as:

$$\hat{c} = \text{observed deviance}/\text{expected deviance}$$

I conducted more than 500 bootstrap simulations to determine $\hat{c}$ for each population separately and then adjusted the variances and confidence intervals to account for this overdispersion.

The CJS model can also be expanded to include a "movement" parameter to examine how individuals move between different "states" (Brownie et al., 1993). These states can be any one of a variety of characteristics including location, reproductive condition, or size class (Cooch and White, 2004). In the present study, the "states" were 5 size classes. I used the multi-state CMR model to investigate size, site, and time dependence in survival rates, recapture rates, and growth transition rates (i.e. movement from one size class to another). Although goodness-of-fit tests are being developed for this type of model (Pradel et al., 2003), they are not yet well established. I therefore used the averaged $\hat{c}$ values from the bootstrap simulations of each population separately to account for overdispersion.

The global model (i.e. containing all the parameters thought to influence survival, recapture and growth transitions) included full time-dependence in size, site and growth transitions. Because clams can only grow from one size class to the next (i.e. they cannot shrink to smaller size classes), only these particular transitions were allowed (and all other transition parameters were set to zero). The first step with the global model was to determine whether the influence of site had a consistent (additive) effect over time. Once this was established, I used reduced versions of the global model (i.e. holding one or more parameters constant) to investigate differences in survival, recapture and growth transitions between sites. The corresponding AIC, Δ AIC, and AIC weights were used to assess model fit. The AIC was calculated as:

$$AIC = -2\ \ln(L) + 2\ K$$

where:

L = model likelihood

K = number of parameters

The ΔAIC values can also be used to calculate Akaike weights to calibrate the models and provide an index of 'relative plausibility' (Burnham and Anderson, 1998). The AIC weights, *w*, were calculated as:

$$w = \left[\exp\left(\frac{-\Delta AIC}{2}\right) \Big/ \sum \exp\left(\frac{-\Delta AIC}{2}\right) \right]$$

Akaike weights are used to quantify how well each model is supported by the data (e.g. a model with a weight of 0.4 versus 0.2 is twice as well supported; Cooch and White, 2004). The AIC can be further modified to account for overdispersion in the data ($QAIC_C$) as shown below (Burnham and Anderson, 1998). As ĉ increases, the contribution of the model likelihood to the $QAIC_C$ decreases, thus the penalty for increasing the number of parameters (K) also increases. Therefore, as ĉ increases, the $QAIC_C$ will favour models with fewer parameters (Cooch and White, 2004).

$$QAIC_C = \frac{-2\ln(L)}{\hat{c}} + 2K + \frac{2K(K+1)}{n-K-1}$$

where:

L = model likelihood

n = sample size

K = number of parameters

3.3 Results

3.3.1 Population density, size, co-occurring species and substratum type

Population density and size (Table 3.3) varied both spatially and temporally between sites (Fig. 3.2). The Jericho Beach and Robbers Passage varnish clam populations both appeared to decrease in size and density, while the Hand Island population increased in size and density. The Dodd Island and Toquart populations increased in size and density in 2002 and then decreased in 2003. The largest populations were found on the largest beaches (i.e. Jericho, Bamberton and Toquart; Table 3.3.). Length-frequency distributions also varied spatially and temporally (Fig. 3.3), with average sizes ranging from 29 mm (Toquart) to 49 mm (Dodd). There appears to have been a pulse of new recruits (i.e. individuals that have survived to a size large enough to be detected in the adult population surveys) in 2002 at Jericho, Robbers Passage, Dodd and Hand Islands.

Table 3.3. Site, year, area surveyed within the beach, varnish clam population size with 95% confidence limits, and mean density based on annual population surveys

Site	**Year**	**Area Surveyed (m^2)**	**Estimated Population Size per beach***	**+/- 95% Confidence Interval**	**Mean density per m^2**
Robbers	2001	1311	280806	575094	214
	2002	1215	214116	653236	168
	2003	1215	167058	440059	133
Jericho	2001	8509	1851511	150065	237
	2002	8509	1465803	126363	172
	2003	7804	1204325	93229	154
Toquart	2001	9298	2392576	810849	257
	2002	9298	3328634	6148756	358
	2003	9298	3149627	8799754	339
Hand	2001	735	130268	121925	177
	2002	797	185678	176981	233
	2003	797	229695	118753	288
Dodd	2001	1319	213570	336031	174
	2002	1319	276420	125803	210
	2003	1319	234797	115696	192
Bamberton	2003	6045	264640	740493	438

* Note screening began in 2002 for Robbers, Jericho and Toquart populations

Although screening for smaller individuals began in 2002, this pulse was not observed in the 2003 data, suggesting that the pulse was not a sampling artifact. This pulse was not observed at Toquart, however, which appeared to receive regular annual recruitment based on the persistence of small individuals.

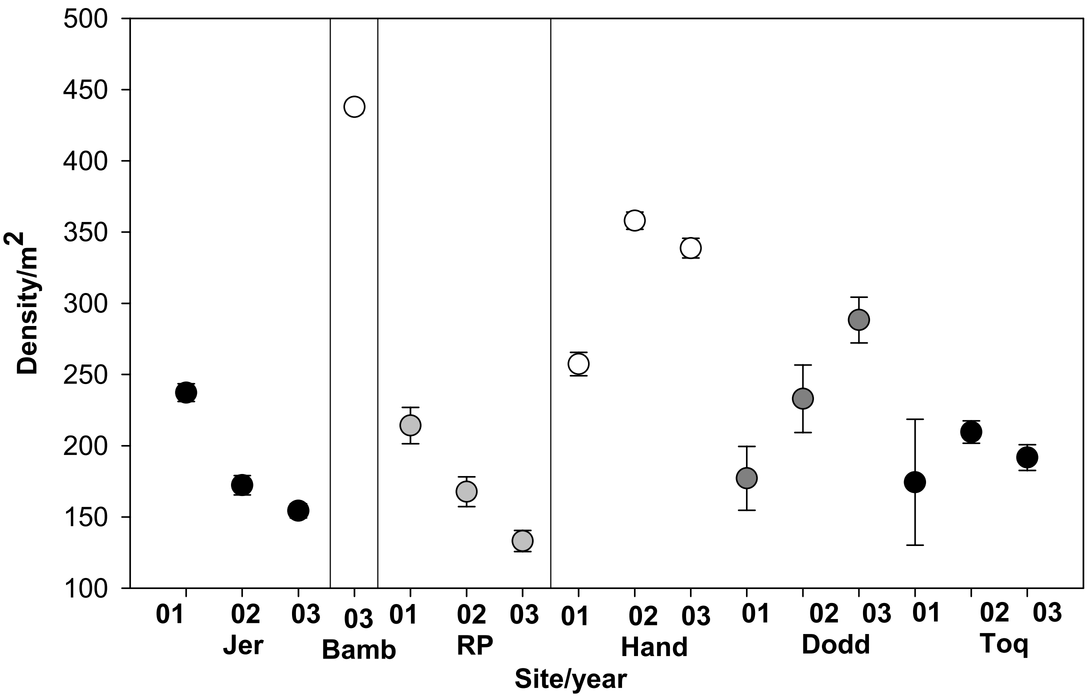


Fig.3.2. Varnish clam densities (individuals per m^2 quadrat) from the annual population surveys in the Strait of Georgia (Jericho=Jer, Bamberton=Bamb) and Barkley Sound (Robbers Passage=RP, Hand and Dodd Islands and Toquart=Toq) from 2001-2003 with standard error bars. For 2001 this includes varnish clams approximately ≥ 2 cm, for 2002-2003 ≥ 0.2 cm for all populations except Dodd and Hand Island.

Density of various varnish clam populations does not appear to be significantly related to either intertidal height or number (or density) of co-occurring species ($P > 0.05$), however the highest varnish clam densities were usually observed above 2 m (Fig. 3.4). There appeared to be a slight decrease in number of species observed with increasing intertidal height: a significant negative relationship was observed in 2002 for Robbers Passage and Dodd ($P < 0.05$, $r^2 = 0.89$ and 0.58 respectively) and for all sites in 2003 ($P < 0.05$, r^2 ranged from 0.14-0.44). Among the 274 quadrats sampled only 43% had co-occurring

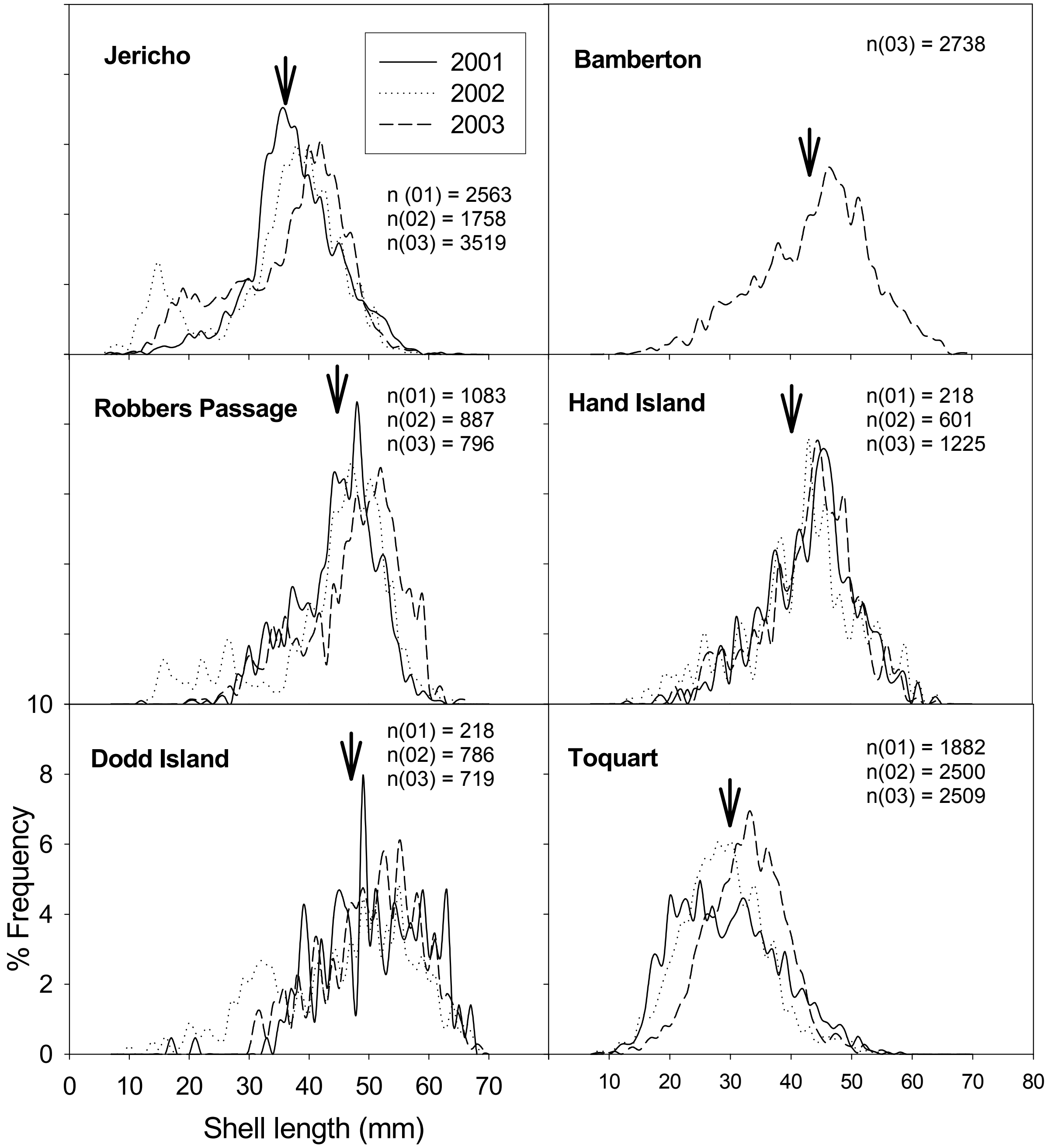


Fig. 3.3. Annual length-frequency distributions for varnish clam populations in the Strait of Georgia (i.e. Jericho and Bamberton) and Barkley Sound (Robbers Passage, Hand Island, Dodd Island and Toquart) for 2001 (—), 2002 (·····) and 2003 (---). Arrows indicate average shell length for the population; sample sizes for each site and year are indicated in panels. Figures were generated using raw data.

species, the most common being the Manila clam (*Venerupis philipinarum*) and the Pacific Littleneck clam (*Protothaca staminea*, Fig. 3.5).

Varnish clams were found in poorly sorted substratum with mixed gravel and sand (Table 3.4., Fig. 3.6). The Robbers Passage and Hand Island sampling sites were composed of a variety of substratum types, unlike the other sampling sites, which were dominated largely by coarse or medium sand.

3.3.2 Length-frequency analysis

Differences in recruitment patterns are also apparent in the length-frequency analyses. Robbers Passage had two dominant modes at 20-30 mm and 40-60 mm (Fig. 3.7). The 20-30 mm mode appeared to merge with the 40-60 mm mode by October 2003. These results are consistent with the observation of a pulse of recruitment observed in the 2002 annual population survey. In contrast to Robbers Passage, the length-frequency distribution at Bamberton has one dominant mode from 30-60 mm (Fig. 3.8). Prior to screening, beginning in 2003, a small percentage of 20-30 mm individuals moved through the size classes (before gradually merging into the 30-60 mm mode). A pronounced difference in the length-frequency distribution was observed following implementation of screening in May 2003, with the addition of a second dominant mode at 10 mm (providing evidence of annual recruitment at this site).

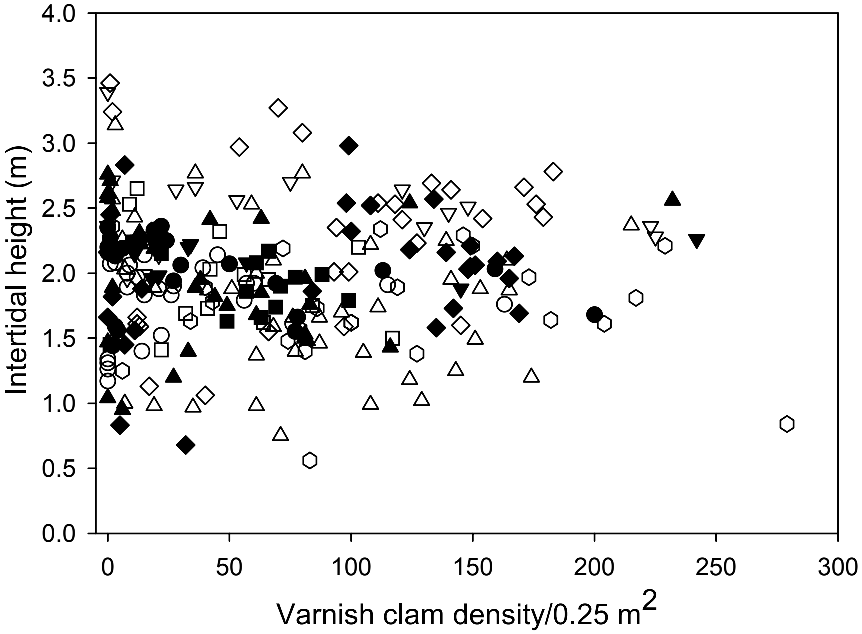


Fig 3.4. Varnish clam density/0.25 m^2 versus intertidal height for Robbers Passage ●, Hand ▼and Dodd ■ Islands, Toquart ◆, Jericho ▲ , and Bamberton ⬢ beaches for 2002 (filled symbols) and 2003 (empty symbols).

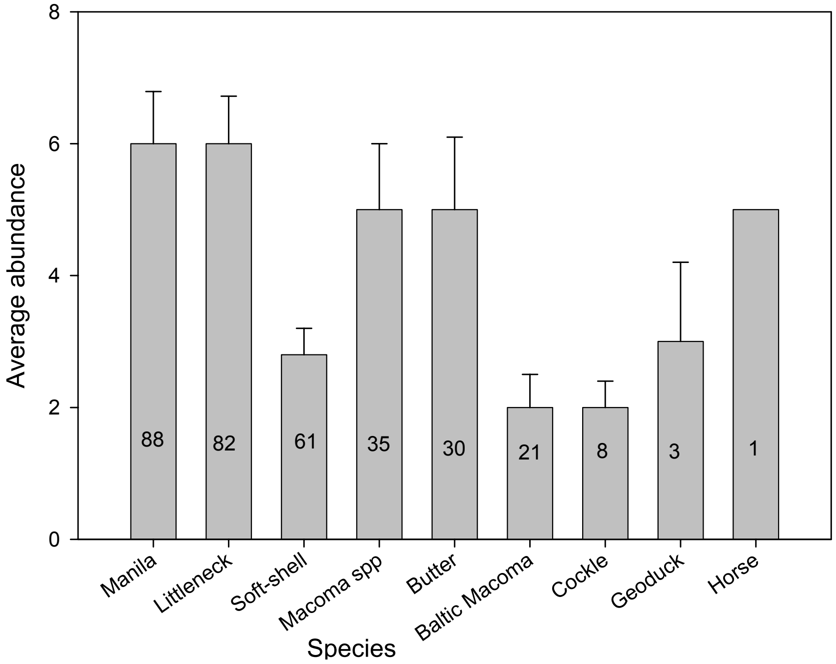


Fig. 3.5. Average abundance of bivalve species that co-occur with varnish clams (with standard error). Numbers inside bars represent the number of quadrats the species co-occurred with the varnish clam (out of a potential 117). For example, Manila clams were found in 88 of 117 quadrats with co-occurring species, at an average density of 6/quadrat. Data are pooled across sampling sites. Note – the Horse clam has no standard error because the species was observed in one quadrat only.

Table 3.4. Mean grain size and sorting index with standard deviations for Robbers passage, Hand and Dodd Islands, Toquart Bay, Bamberton and Jericho varnish clam beaches. Sorting values 0.7-1.0 = moderately sorted, 1.0-2.0 = poorly sorted and 2.0-4.0 = very poorly sorted.

Site	Mean grain size	Std Dev	Sorting	Std Dev
Robbers Passage	1147.1	352.6	3.2	0.36
Hand Isl.	742	104.9	3.6	0.21
Dodd Isl.	617.6	346.4	1.9	0.29
Toquart Bay	545.2	194.2	2.2	0.32
Bamberton	441.2	58.7	2.0	0.15
Jericho	1046.7	412.1	2.4	0.41

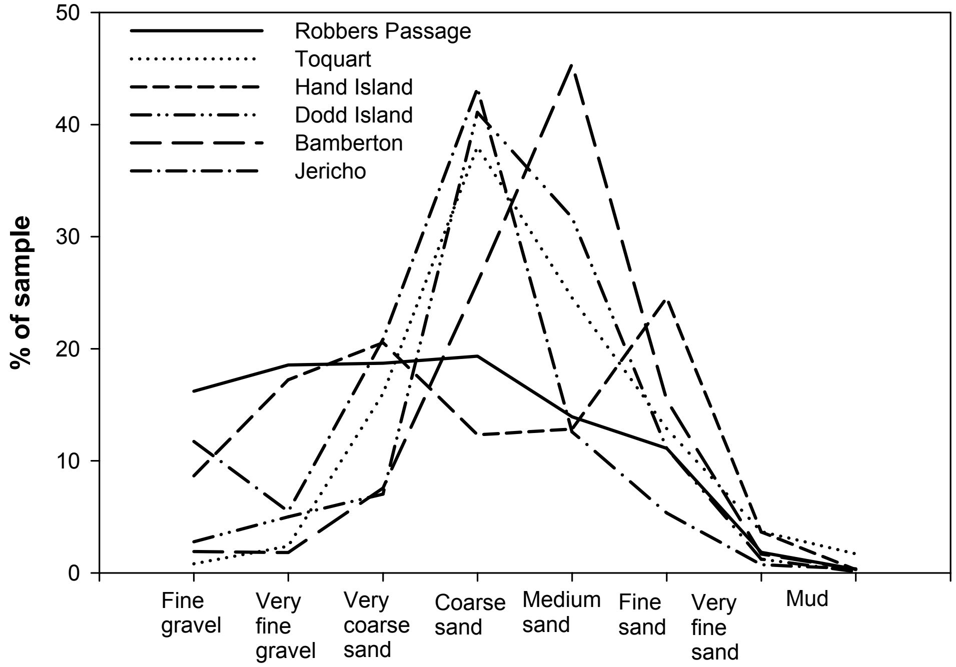


Fig. 3.6. Percent composition of sediment types in substratum samples from Robbers Passage, Toquart, Hand and Dodd Islands, Bamberton and Jericho. Error bars have been omitted to make dominant sediment types more visible.

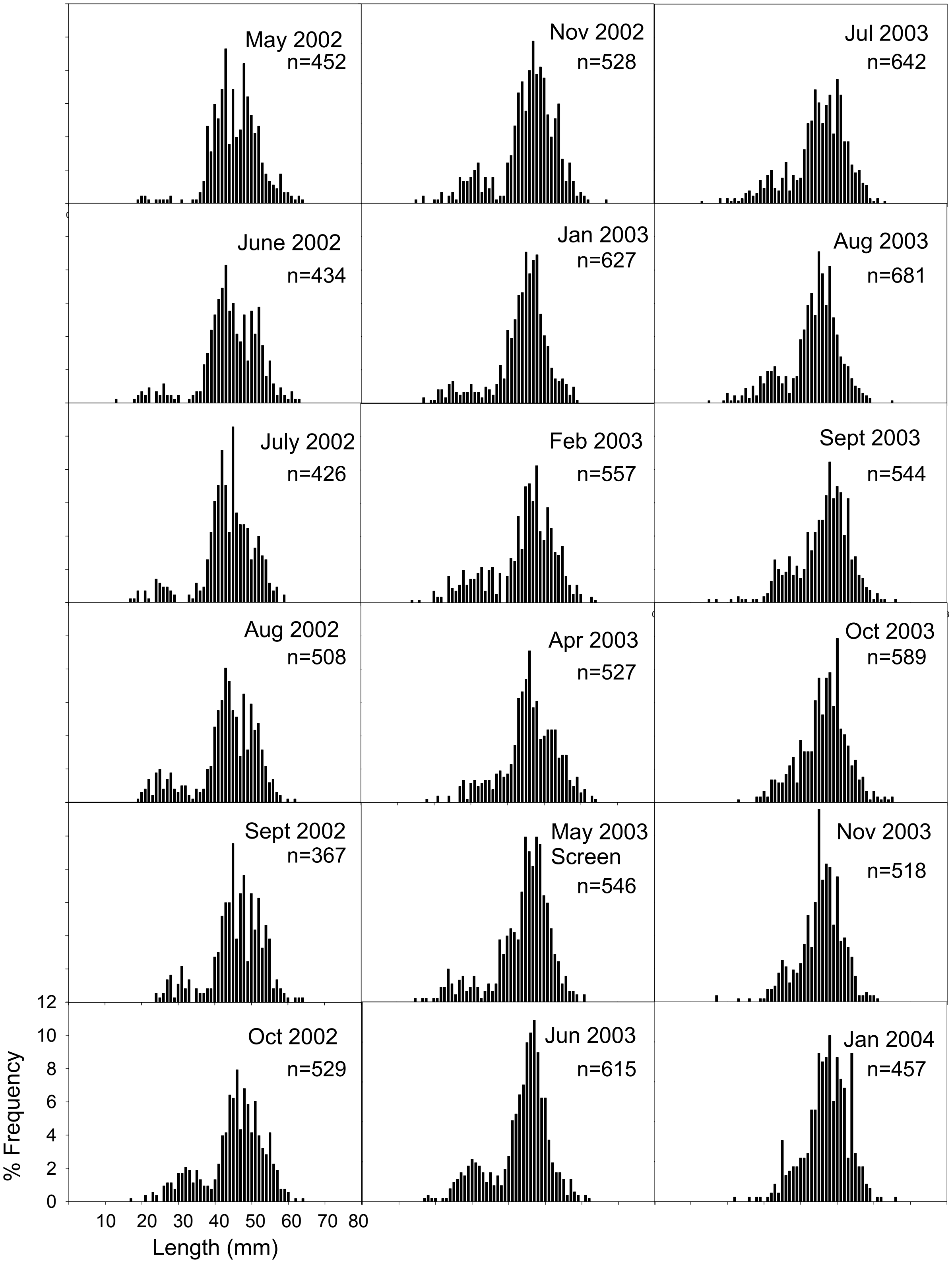


Fig. 3.7. Monthly length-frequency distributions of varnish clams from Robbers Passage without substratum screening with 2 mm mesh (May 2002 – April 2003 and with screening (May 2003 onwards).

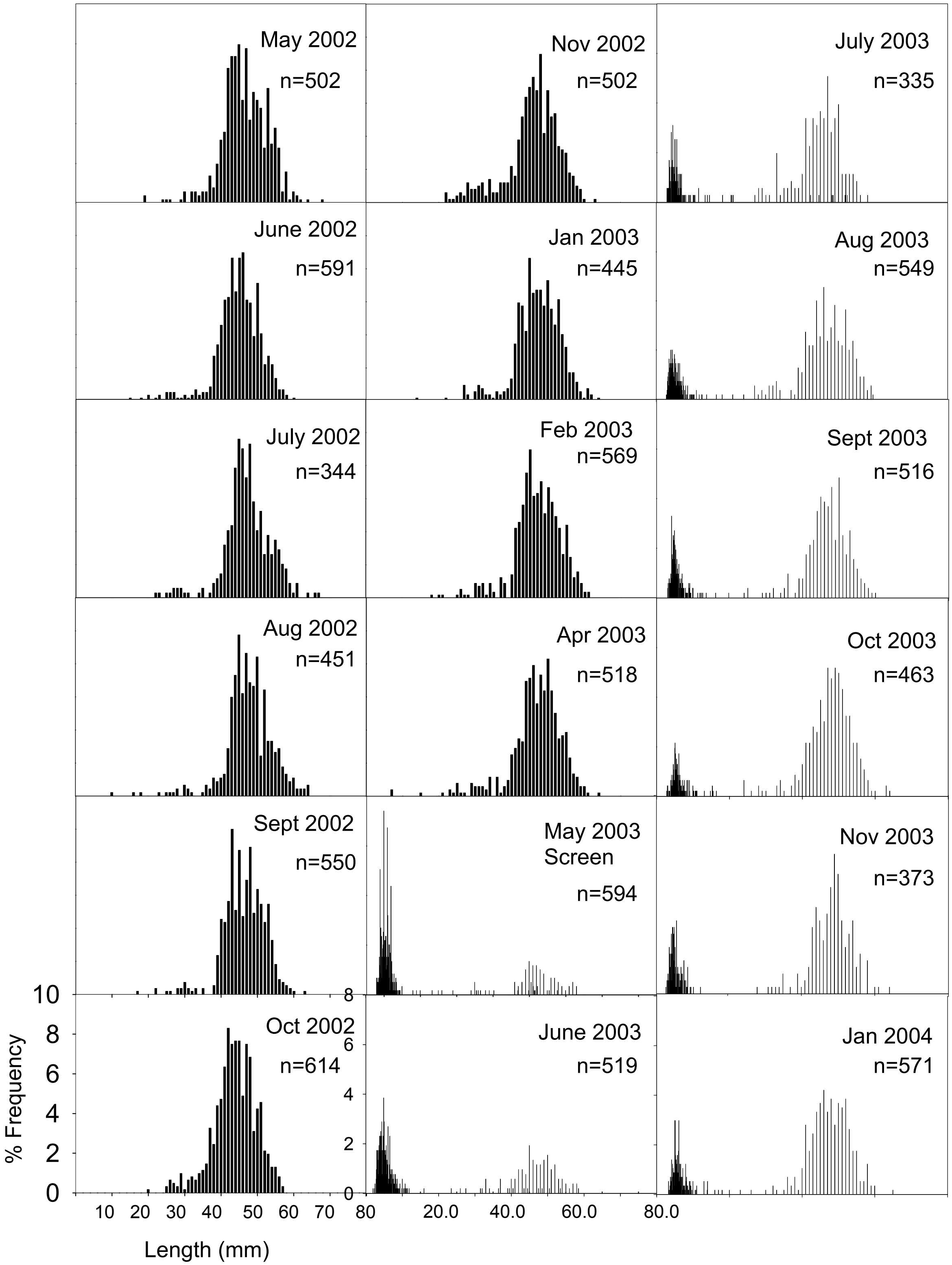


Fig. 3.8. Monthly length-frequency distributions of varnish clams from Bamberton without substratum screening with 2 mm mesh (May 2002-Apr 2003) and with screening (May 2003 onwards). Note the increase in precision of length, and corresponding scale change, with screening (to 0.1 mm).

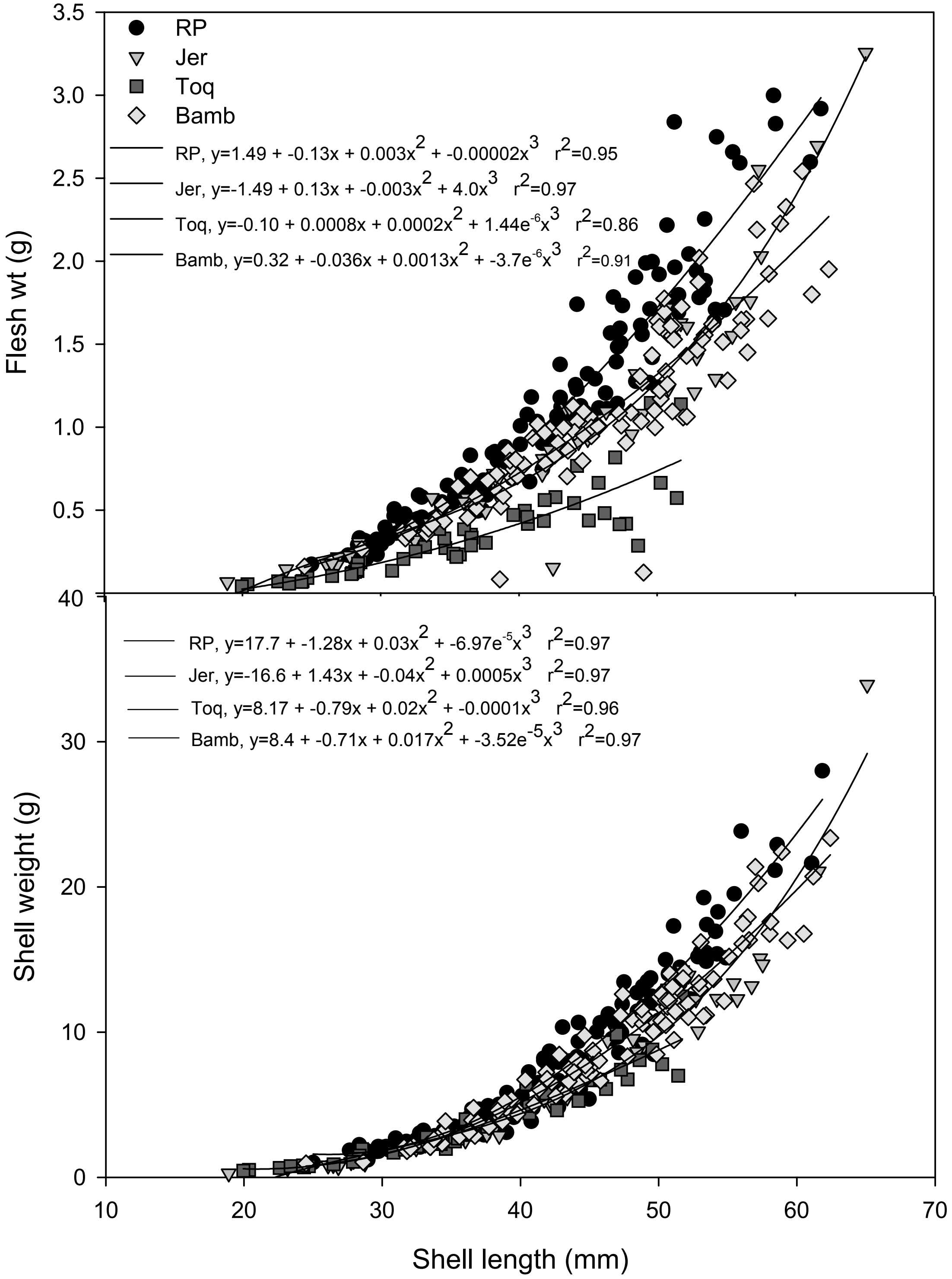


Fig. 3.9. Varnish clam shell length versus flesh weight (g), upper panel, and shell weight (g), lower panel, for Robbers Passage, Jericho, Toquart and Bamberton for June samples. Lines show regressions and corresponding equations.

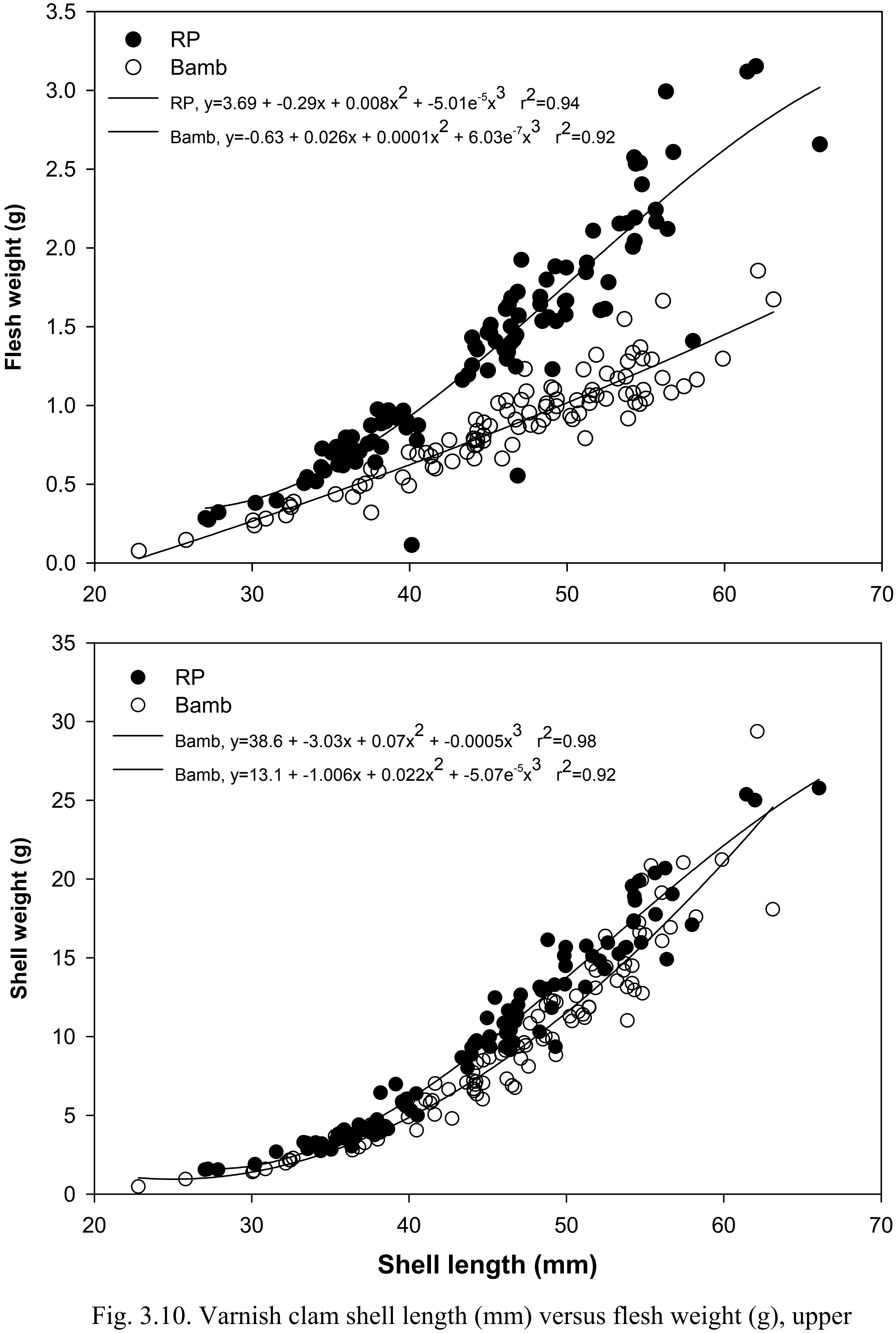


Fig. 3.10. Varnish clam shell length (mm) versus flesh weight (g), upper panel, and shell weight (g), lower panel, for Robbers Passage and Bamberton for January samples. Lines represent regressions and corresponding equations.

3.3.3 Relationship between shell length, shell weight, flesh weight and burial depth

Robbers Passage varnish clams from the June 2003 dissections had slightly higher flesh and shell weights compared to the other sites. Toquart clams had the lowest flesh weights observed (Fig. 3.9). To eliminate flesh weight differences caused by gonad maturation, only the January 2004 collections from Robbers Passage and Bamberton were separately compared. Robbers Passage varnish clams have approximately twice the flesh weight of Bamberton clams and slightly higher shell weights (Fig. 3.10).Varnish clams less than 30 mm in length appeared to bury slightly shallower than larger clams. For varnish clams larger than 30 mm there appeared to be no clear relationship between burial depth and shell length (Fig. 3.11).

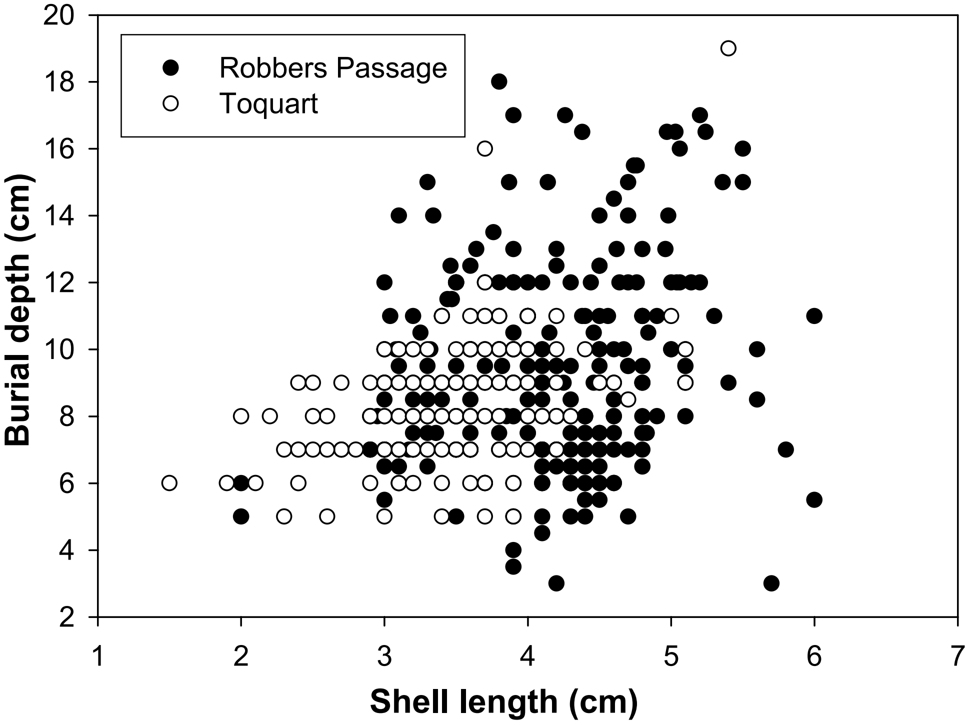


Fig. 3.11. Varnish clam shell length (cm) versus burial depth (cm) at Robbers Passage (n=177) and Toquart 2001 (n=167). Note that many points directly overlap each other.

3.3.4 Growth and survival rate analysis

The Tanaka growth model provided the best fit for varnish clam growth in both the Robbers Passage and Bamberton populations, followed by the generalized von Bertalanffy and the Gompertz model (Fig. 3.12, Table 3.5). All of asymptotic models underestimated the observed maximum size (70 mm). Between-site comparisons of the Tanaka growth function estimates indicate that Robbers Passage varnish clams grow faster, with the maximum growth rate occurring at a larger size (Table 3.6). Differences between the two sites were also evident in the direct comparison of the linearized growth increment data (Fig. 3.13). ANCOVA showed significantly different slopes between sites ($F = 722.2$, $P < 0.0001$, DF=1, 1003).

The bootstrap goodness-of-fit simulations from the survival rate analysis indicated moderate overdispersion in both data sets, although both populations still satisfied the CJS assumptions; Robbers Passage $P = 0.102$, Bamberton $P = 0.180$, based on rank of the observed deviance within the bootstrap data set. The average $\hat{c}$ for Robbers Passage and Bamberton (1.61) was used to adjust for this overdispersion in the multi-state CMR model that included both populations. To ensure that overdispersion did not change model rank, I experimented with increasing $\hat{c}$ values and found that rank remained consistent for $\hat{c}$ values up to 2.2.

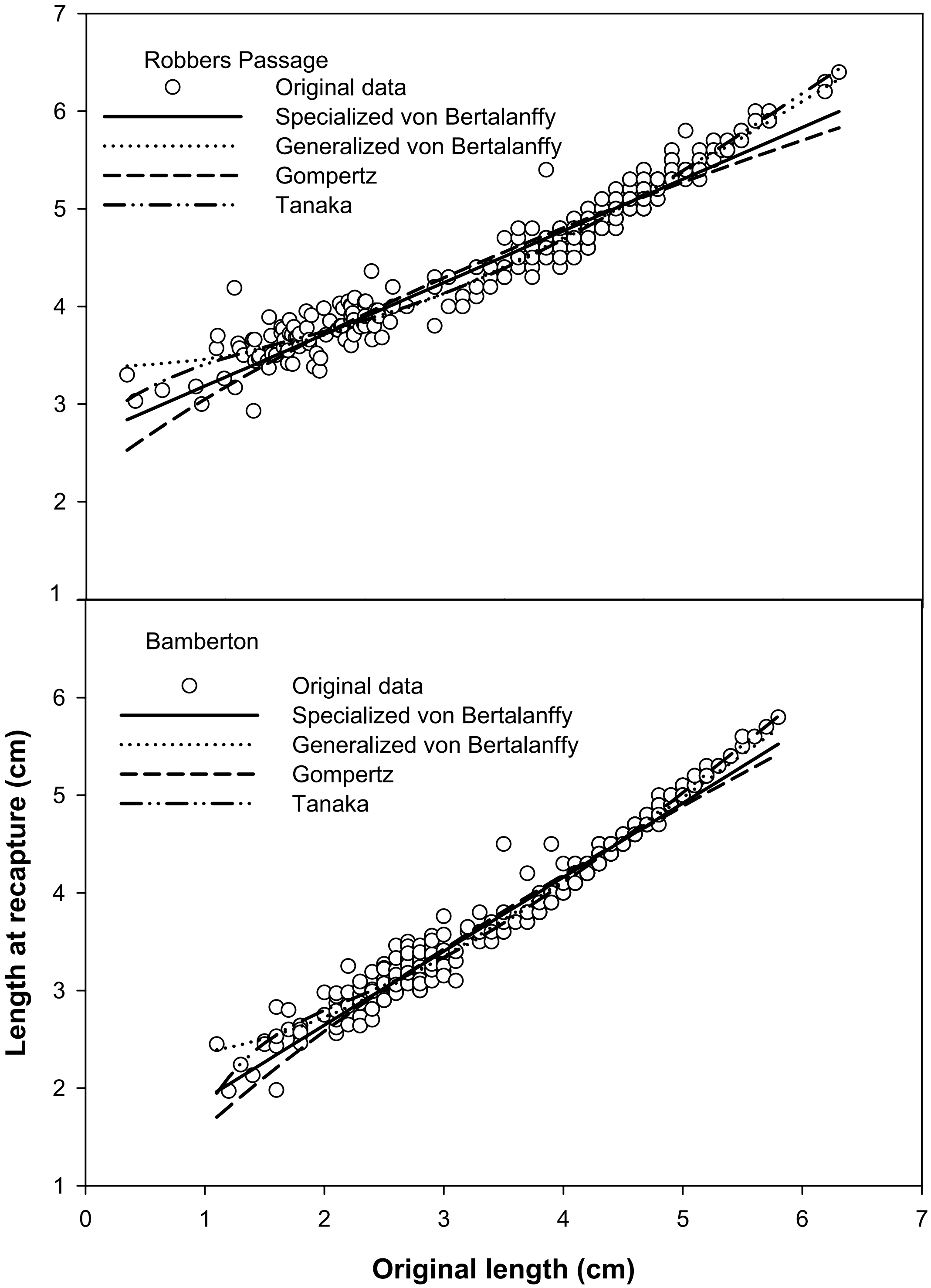


Fig. 3.12. Specialized von Bertalanffy, Generalized von Bertlanaffy, Gompertz and Tanaka growth model fit to varnish clam original length versus length at recapture (cm) for Robbers Passage and Bamberton populations.

Table 3.5. Varnish clam growth models and corresponding Akaike Information Criterion (AIC) values and ranked differences in AIC values (ΔAIC) for Robbers Passage and Bamberton

	Robbers Passage		Bamberton	
Model	**AIC**	**ΔAIC**	**AIC**	**ΔAIC**
Tanaka	-1698	0	-2146	0
Generalized von Bertalanffy	-1674	-25	-2096	-50
Specialized von Bertalanffy	-1529	-170	-1979	-117
Gompertz	-1397	-301	-1832	-146

Table 3.6. Varnish clam Tanaka growth function parameter estimates for a measure related to maximum growth rate (a), rate of change in growth rate (f) and size at maximum growth rate (d), for Robbers Passage (RP) and Bamberton (B) and corresponding standard errors (SE)

	Estimate			
Model Parameters	**RP**	**SE**	**Bamb**	**SE**
a	0.24	0.03	0.92	0.07
f	1.27	0.08	2.01	0.16
d	2.04	0.03	1.20	0.05

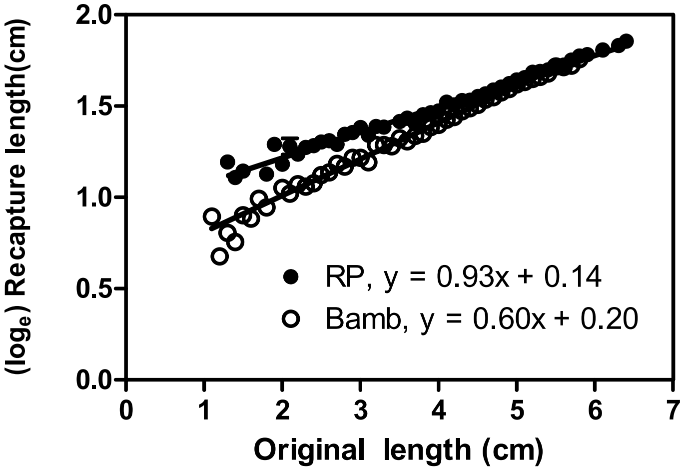


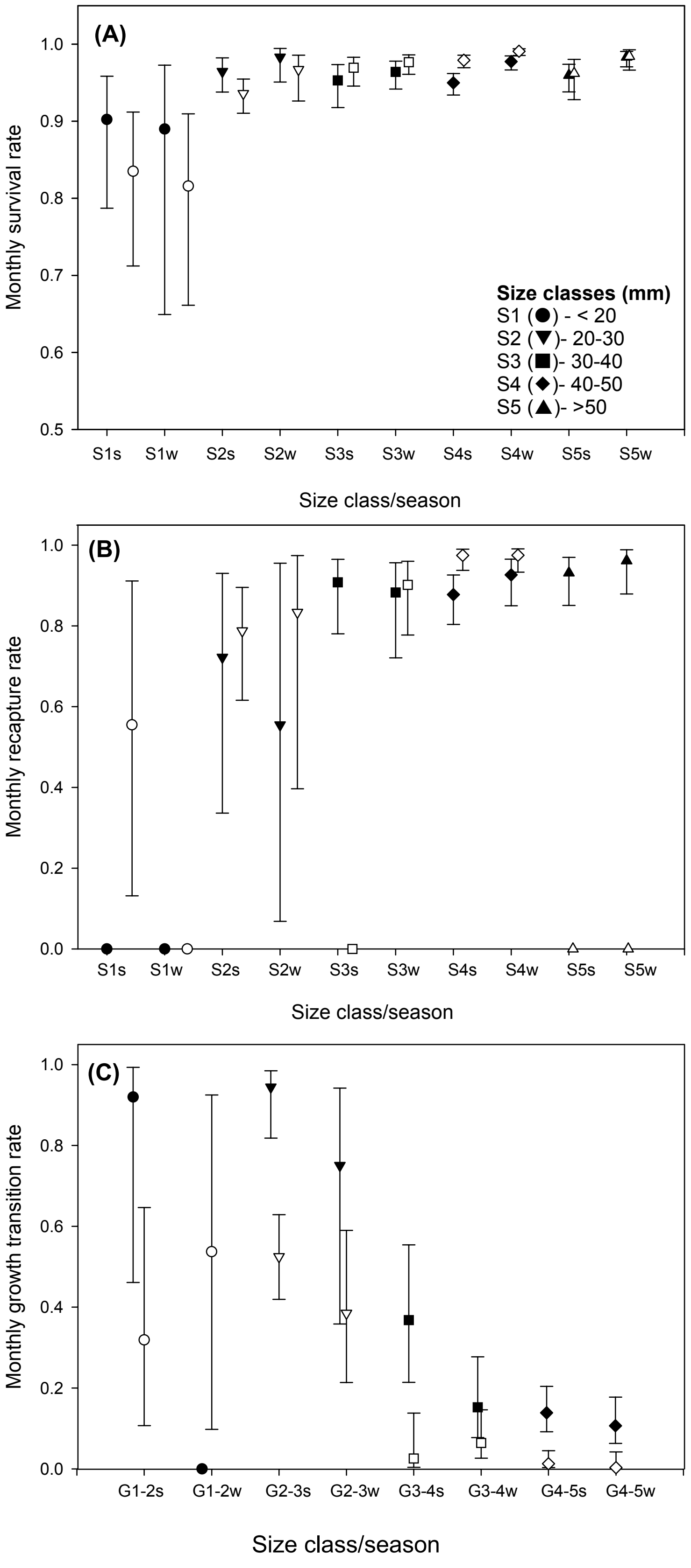
Fig. 3.13. Initial clam length (cm) at capture versus $\log_e$ length at recapture of varnish clams from Robbers Passage and Bamberton. Lines represent linear regressions.

Model selection showed that survival, recapture and growth transitions were all size-, site- and time-dependent, with the effects of site and time consistent (additive) over time for survival (Table 3.7). Comparison of survival rates (Fig. 3.14a) between sites shows higher survival for clams < 30 mm in length at Robbers Passage and higher survival for clams ≥ 30 mm in length at Bamberton. Recapture rates differed slightly between sites, with higher rates occurring at Bamberton (Fig. 3.14b). All growth transition estimates were higher at Robbers Passage, providing further evidence of faster growth rates at this site (Fig. 3.14c).

Table 3.7. Factors included in multi-state models for varnish clam capture-mark-recapture analysis adjusting for overdispersion ($\hat{c}$=1.61), and their corresponding number of parameters (K), and adjusted deviance (QDeviance), Akaike Information Criterion (QAIC) values, AIC value differences (ΔQAIC), AIC weights (*w*).

Survival	Recapture	Transition	K	QDeviance	QAIC	ΔQAIC	*w*
site+time	site*time	site*time	57	112	3332	0	0.87
time	site*time	site*time	51	142	3350	17	0.00
constant	site*time	site*time	44	166	3360	27	0.00
site+time	time	site*time	57	134	3355	23	0.00
site+time	site	site*time	56	118	3336	4	0.13
site+time	constant	site*time	51	142	3350	18	0.00
site+time	site*time	time	56	282	3501	168	0.00

Fig. 3.14. Varnish clam monthly survival rates (A), recapture rates (B) and growth transition rates (C) for Robbers Passage (filled symbols) and Bamberton (empty symbols). ‘s’ =summer months from May-Sept., ‘w’= winter months Oct.-Apr. In panel C, G1-2 represents growth from size class 1 to 2 for Bamberton and 1 to 3 for Robbers Passage. G2-3 represents growth from size class 2 to 3, and so forth. Rates are offset for viewing clarity. Bars represent 95% confidence intervals. Parameters that were not estimable are shown as zero values.



3.4 Discussion

3.4.1 Population density, size, co-occurring species and substratum type

Varnish clams have established dense populations in both the Strait of Georgia and on the west coast of Vancouver Island, with population densities and sizes that vary both spatially and temporally. All populations occurred in mixed gravel and sand substratum, similar to other varnish clam populations in the region (Byers, 2002a; Dinnel, 2000; Heath, 1998, M. Barker and R.G. B. Reid, UVic, unpublished manuscript). Surveyed populations appear to have resulted from several recruitment events, as there were a range of size classes present in each of length-frequency distributions. This indicates that these varnish clam populations are well established and are likely to be sustainable.

The high average densities observed (132-436 varnish clams > 20 mm /m^2) are similar to those found elsewhere in the Northeast Pacific (Dinnel, 2000). Densities in coastal BC appear to be lower than those reported from its native range (e.g. 10,000/m^2; Miyawaki and Sekiguchi, 1999), however those studies included individuals 1.0 mm and larger while my study only included individuals >10mm. Another study of varnish clams in the SoG that included clams 2.0 mm and larger observed densities as high as 6392/m^2 (L. Genn, University of Victoria, unpublished data). Varnish clams in the Pacific Northeast appear to be larger (up to 70 mm) than in their native range (up to 53 mm), which is consistent with findings from other marine invertebrate invasions that show that body size often increases in new ranges (Grosholz and Ruiz, 2003). Mechanisms that explain this size increase are not clear. Possible explanations include greater resources in the recipient region, or reduced predation and/or parasites (Grosholz and Ruiz, 2003). In the varnish clam invasion, the most plausible explanation is reduced predation due to its deep burial depth rather than parasitism, because the varnish clam is host to many parasites that are also found in local bivalves (Marshall et al., 2003). The varnish clam may, however, experience lower levels of parasitism compared to its native range, which could contribute to the larger body size.

Spatial and temporal differences in varnish clam population size and density, combined with differences in size-structures between sites, suggest that local factors (e.g. predation, competition, temperature, wave exposure) are important influences on adult population dynamics. With the exception of Toquart (where most clams were between 20-40 mm), the populations were dominated by larger size classes (40-50 mm). This suggests that Toquart received regular annual recruitment and that juvenile survival rates are likely high, given the dominance of smaller individuals. In contrast, the lack of small individuals in other populations indicates that recruitment is either extremely low or episodic, or that high post-settlement mortality results in few individuals surviving to larger sizes.

A recruitment pulse was observed in four of the five surveyed populations in 2002. The presence of this pulse in such geographically separated populations (i.e. the Strait of Georgia and the west coast of Vancouver Island) indicates that regional processes also influence recruitment. Warmer temperatures and decreased precipitation provide optimal conditions for varnish clam settlement (Miyawaki and Sekiguchi, 1999). In 2001 (when the settlement event would have occurred to produce the observed pulse of 20-30 mm clams in 2002), both temperature and precipitation were slightly lower than normal (i.e. precipitation was 30-85% of the normal amount based on the average from 1971-2000).

The persistence of smaller (i.e. <10 mm) clams at Bamberton suggests that varnish clams settle annually at this site. These smaller clams appear to suffer high mortality, however, few are seen to move through the size classes (suggesting that post-settlement processes may be important). In contrast, the Robbers Passage adult population appears to receive either very low (but steady) recruitment or episodic pulses such as the one observed in the annual 2002 survey. The monthly length-frequency distributions show this pulse moving through the size classes as the clams grow, indicating that a large portion of the newly settled clams survived.

No relationships between varnish clam density and the number of co-occurring bivalve species, co-occurring species density or intertidal height were evident in any of the populations sampled. Varnish clams do not appear to be causing decreases in either the number of co-occurring species or their densities. Given their deeper burial depths (i.e. approximately 3 times that of Pacific littleneck and Manila clams they are found with) and the ability to both filter and deposit feed, varnish clams seem unlikely to exert intense competition pressure (i.e. for space or food) on adult co-occurring species (Gillespie et al., 1999). This may explain the absence of any statistically significant relationships between varnish clam density and the number or density of other species.

A slight decrease in the number of species was observed as intertidal height increased, which is expected given the increased temperature and desiccation stress higher in the intertidal zone (Nybakken, 1993). Varnish clams most commonly occurred with Manila clams and Pacific littlenecks, in agreement with other studies in BC and WA (Byers, 2002a; Gillespie et al., 1999; Sasaki et al., 2002; Yates, 1999). At intertidal heights greater than 2.5 m the varnish clam was usually the only bivalve observed and no other species maintained comparably high densities at these heights. Previous studies have reported similar intertidal heights above which only varnish clams were found (Byers, 2002a). Its ability to deposit feed utilizing a variety of modes (e.g locomotory and pedal sweep feeding) may enable the varnish clam to survive quite high in the intertidal zone (i.e. at heights where filter feeding is limited by short submersion time each day; M. Parker, University of Victoria, unpublished manuscript).

3.4.2 Shell length, shell weight, flesh weight and burial depth

Relative to the other sites, varnish clams in Robbers Passage had higher flesh and shell weights (and some of the lowest densities observed). The opposite trend was observed at Toquart, which had the lowest flesh weights and highest densities. These findings indicate that density-dependent processes may be influencing individual growth in these populations. This is commonly observed in other bivalves, with increased density often resulting in decreased growth rates and gonad weights (Lee, 1996; Peterson and Black, 1988). This conclusion is further supported by comparisons between Robbers Passage and Bamberton. Varnish clams from Robbers Passage had more flesh than Bamberton clams of the same size (and which live at almost three times the density). The presence of pinnotherid (pea) crabs at Bamberton (but not at Robbers Passage) could also contribute to differences in growth. Pea crabs have been associated with gill damage in oysters that interferes with growth (Dame, 1996) and have been found to decrease weight gain in scallops (Narvarte and Saiz, 2004). Pea crabs are also thought to influence sex ratios in oysters, resulting in more males (Dame, 1996). Similarly, Bamberton also had a male-skewed sex (unlike Robbers Passage which had a more equal sex ratio, Chapter 2). This provides further indication that pea crabs may be influencing clam condition (and potentially growth) at Bamberton.

Bivalves with longer shell lengths are typically found at deeper burial depths (Zaklan and Ydenberg, 1997), however this relationship is not pronounced for varnish clams (Fig. 3.11). Although varnish clams <30 mm in length appear to bury slightly shallower, clams ≥30 mm showed no clear relationship between shell length and burial depth. The absence of a relationship between burial depth and shell length has also been documented for varnish clam populations in Puget Sound (Yates, 1999).

Varnish clams are able to bury deeper than bivalve species with which they are usually found (Manila and Pacific littleneck clams bury up to 10 cm; Harbo, 1997). In its native habitat, the majority of varnish clams <10 mm in length are found in the first 5 cm of sediment, few are found at 10-15 cm, and individuals >25 mm bury up to 15-20 cm deep (Ito and Okata, 1995). In the Northeast Pacific, varnish clams <10 mm also appear to be constrained to the top layers of substratum.

3.4.3 Growth and survival rates

The indeterminate growth function (the Tanaka model) provides the best fit for growth increment data for both Bamberton and Robbers Passage populations. Many studies have used the von Bertalanffy function to describe bivalve growth (Appleyard and Dealteris, 2001; Bradbury and Tagart, 2000; Chicharo and Chicharo, 2001; Hoffman et al., 2000; Richardson et al., 1993; Yap, 1977). It appears to be a sufficient model for species that reach a maximum asymptotic size and for data sets that include only large individuals. However, this function is known to be insufficient for describing early growth (Rogers-Bennett et al., 2003). Recent studies have shown that the Tanaka function is more appropriate for growth increment data that span a wide range of sizes (Ebert et al., 1999; Rogers-Bennett et al., 2003). Evidence from field observations and length-at-annulus measurements (Gillespie and Bourne, 2004) suggests that the varnish clam does not reach an asymptotic size, therefore making the Tanaka function a plausible model not only statistically, but biologically as well.

Comparison of model parameters showed that varnish clam growth is faster at Robbers Passage than at Bamberton. This is further supported by the initial size-at-marking versus size-at-recapture data that show ANCOVA results that show significant differences between the sites (Fig. 3.13). The observed growth rates may be influenced by density differences between the sites. While the mark-recapture plots had approximately equal densities, the individual clams were collected from areas with different densities. Individuals that have previously been stressed by crowding have been shown to be more vulnerable to mortality from physical disturbance (Peterson and Black, 1988). This 'ghost of densities past' could have influenced the growth rates observed in this study.

Environmental differences between the sites may also be influential. Due to its sheltered location in Saanich Inlet, Bamberton experiences both higher water (Fig. 2.3, Chapter 2) and air (e.g. mean monthly air temperature for July and August is ~4ºC higher; http://www.climate.weatheroffice.ec.gc.ca) temperatures than Robbers Passage, a feature that may increase thermal stress and result in decreased growth rates.

Varnish clams appear to have growth rates similar to native bivalve species, despite their high intertidal height and deeper burial depths (Fig. 3.15). Decreased growth rates have

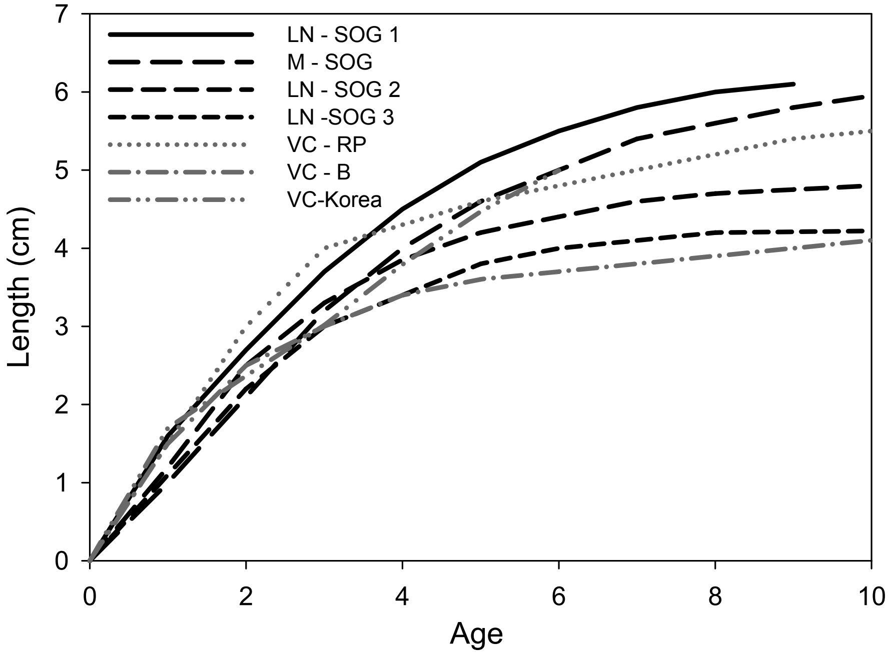


Fig.3.15. Approximate length-at-age comparisons between local clams (LN=Pacific littleneck, M=Manila) and varnish clams (VC) at various locations. SoG=Strait of Georgia, LN-SOG 1 and M – SOG are data are approximated from Quayle and Bourne (1972), LN-SOG 2 and 3 from Gillespie and Kronlund (1999), and VC-Korea from Choi (2001).

been observed for other suspension feeding clams that bury more deeply (Ahn et al., 1993; Byers, 2005). The decrease in growth is caused by the increased cost of having to develop longer siphons and transporting food over a longer distance (Zaklan and Ydenberg, 1997). Multiple feeding modes of the varnish clam may therefore enable it to succeed in this stressful environment. Growth rates in the Northeast Pacific are slower than those reported in its native habitat in Korea where water temperatures range from 10.5 – 23.5ºC (Choi, 2001). Slower growth observed for larger individuals in BC may be the result of persistent cooler water temperatures. For smaller clams (9-20 mm), annual growth rates from a mark-recapture study in Japan ranged from 12.14-13.49 mm per year across a temperature range of 5-27ºC (Ito et al., 2001). These findings are similar to my results for clams <20 mm that showed annual growth increments ranging from 0.92 – 15.60 mm.

Monthly varnish clam survival rates were quite high, varying from 0.81 for clams 10-20 mm, to 0.98 for clams >50 mm. Survival appears to be size-, time- and site-dependent, with small clams (i.e. < 30 mm) suffering higher mortalities at both sites. Because smaller clams cannot bury as deeply, this increases their exposure to predation and thermal and dessication stress. The higher surface area to volume ratio for smaller clams will also increase their vulnerability to heat stress (Nybakken, 1993). Survival rates for small clams were higher at Robbers Passage than at Bamberton. For larger clams (>30 mm), however, survival was higher at Bamberton. The higher survival rates for small clams at Robbers Passage may be due in part to faster growth rates observed at this site.

This enables clams to reach larger sizes quickly, making them less vulnerable to predators and abiotic stressors (e.g. by burying deeper).

The slightly lower survival rates for clams ≥ 30 mm at Robbers Passage may be the result of anoxia mortalities. In September 2003 a large number of intact shells in the Robbers Passage mark-recapture plot were found in blackened substratum, indicating that the deaths were caused by anoxia (Byers, 2005). Mortalities from algal smothering by *Ulva* spp. have previously been observed in clam beds (Bartoli et al., 2001; Dow and Wallace, 1961) and given the presence of large amounts of *Ulva* spp. at this site, this may have been a factor in the deaths at Robbers Passage .

Mark-recapture analysis shows that Robbers Passage varnish clams have higher growth transition rates at all size classes (Fig. 3.14c), providing further evidence of faster growth at this site. For instance, at Robbers Passage clams, individuals that were 10-20 mm in length grew to the third size class (30-40 mm) in one year. This is much faster than the Bamberton clams that grew only to the second size class (20-30 mm) during the same period.

Varnish clams have well-established sustainable populations in both the Strait of Georgia and the west coast of Vancouver Island. Their high densities, fast early growth rates and high survival rates will likely result in their continued success and further range expansion in this region. The varnish clam seems unlikely to have a significant direct competitive impact on native bivalve communities due to its location high in the intertidal, its limited spatial overlap with other species, its deeper burial depth and its diversity of feeding modes. Nonetheless, it seems plausible that high densities of varnish clams may alter sediment characteristics due to bioturbation (from burrowing and deposit feeding) and biodeposition. Bioturbation has been found to increase sediment oxygen and water content, which decreases sediment stability (Ahn et al., 1993; Vaughn and Hakenkamp, 2001). Increased bivalve densities have also been shown to increase the silt content of the sediment (Widdows et al., 2004) and decrease microalgal biomass (Lelieveld et al., 2004). By mixing material into the sediment (Widdows et al., 2004), bioturbation from bivalves can also influence nutrient fluxes (Lelieveld et al., 2004; Vaughn and Hakenkamp, 2001), and alter the chemical properties of the sediments (Lenihan and Micheli, 2001). Nutrient dynamics will also be influenced by excretion and biodeposition of faeces and pseudofaeces which can alter the composition of benthic communities (Vaughn and Hakenkamp, 2001), and potentially decrease the growth of other species (Ahn et al., 1993). Furthermore, bioturbating activities are thought to have a negative impact on suspension feeders (Wilson, 1991). This could have important implications for the economically valuable suspension feeders that occur on the same beaches as varnish clams. Given the high densities and large population size of varnish clams throughout the region, it is likely that the varnish clam will eventually impact the physical and chemical composition of the sediment and nutrient fluxes, which in turn may affect infaunal species occurring on the same beaches. Future studies should focus on addressing these issues in order to determine what impact varnish clams will have on these processes, and identify those species most likely to be affected. These studies could compare the sediment nutrients, organic content and stability between beaches with similar substrate types, with and without varnish clams, to determine the impact of their presence.

Chapter 4. Selective crab predation on native and introduced bivalves in British Columbia

4.1 Introduction

Introduced predators may significantly decrease native prey populations (Grosholz et al., 2000; Walton et al., 2002) and conversely, *native* predators may decrease the abundance of *introduced* prey (Reusch, 1998). Native predators may act as natural biological controls for introduced species (Harding, 2003) and, by preying on non-indigenous species, may actually alleviate predation pressure on native prey and thus decrease competition for limited resources (Wilbur et al., 1983). The physical properties of the invaded habitat that influence prey encounter probabilities and prey value, may also affect a predator's prey preference (Mascaro and Seed, 2000a). Prey may find refuge in size or morphology, low population densities, or because they occupy inaccessible habitat (Seitz et al., 2001). Selective foraging can have impacts on prey abundance and distribution (Mascaro and Seed, 2000a), and may influence invasion dynamics. Natural control of an invader may provide the community with some sort of ecological resistance (Elton, 1958) to the impacts of invasion (Reusch, 1998). Our study investigates cancrid crab predators as a mortality agent and potentially natural control for an introduced bivalve, the varnish clam (*Nuttallia obscurata*), in coastal British Columbia (BC).

The varnish clam, a suspected ballast water introduction, is native to Korea, China and Japan (Gillespie, 1995). In coastal BC it co-occurs with several native species, most commonly the two littleneck species – the native Pacific littleneck (*Protothaca staminea*) and the non-native Manila clam also known as the Japanese Littleneck (*Venerupis philippinarum*) that was introduced accidentally in the early 1900's (Quayle, 1964). Both species are of economic importance, with the Japanese littleneck clam being the main species harvested in the intertidal clam fishery for the past two decades (Harbo et al., 1997). The varnish clam differs from the littleneck species in morphology and behaviour. Relative to the littleneck species, varnish clams have thinner, flatter shells and bury up to 30 cm deep, compared to the 10 cm burial depth of littleneck clams (Harbo, 1997).

Cancrid crabs are well known predators in intertidal ecosystems of the northeast Pacific (Boulding, 1984; Carroll and Winn, 1989; Pauley et al., 1986; Zaklan and Ydenberg, 1997). Clams represent an important food source for Dungeness crab (*Cancer magister*) and red rock crabs (*Cancer productus*; Carroll and Winn, 1989; Pauley et al., 1986). Cancrid crabs have been observed to prey on both littlenecks (Boulding, 1984) and varnish clams (Byers, 2002a). The thinner, flatter shells of varnish clams could make them more vulnerable to crab predation, although their deeper burial may provide a spatial refuge. Our goal was to address both of these issues and determine if the crabs would prefer varnish clams to littleneck clams and whether burial depth provides a predation refuge.

For these experiments, 'preference' was defined as any deviation from random prey consumption (Chesson, 1978), and therefore encompasses all the biological aspects of predation that influence encounter and capture rates (e.g. handling time, prey density, availability etc.; Krebs, 1994). Measures of preference have also been constructed to isolate the influence of these various aspects of predation such as availability (Rapport and Turner, 1970) and handling time (Fairweather and Underwood, 1983; Liszka and Underwood, 1990; Underwood et al., 2004). For our purposes, however, we were interested in the result of all of these predation aspects combined that could result in non-random patterns of varnish clam or littleneck clam mortalities.

Our hypothesis was that, when accessible, the varnish clam should be preferred by crabs because of its thinner (i.e. easier to crack) shell, that should result in shorter handling times, lack of size refuge and increased profitability. We also predicted a continued preference for varnish clams when burial depth was limited (as both species would be equally accessible), and a switch in preference to littlenecks in 'unlimited' burial depth when the varnish clams were expected to bury deeper than the littlenecks.

4.2. Materials and methods

Experiments were conducted at the Bamfield Marine Sciences Centre, British Columbia, Canada from June - August 2001. Intermoult male Dungeness crabs (*Cancer magister*) and red rock crabs (*Cancer productus*) were collected in Barkley Sound. Pacific littleneck (*Protothaca staminea*), and Manila/Japanese littleneck (*Venerupis philippinarum*) clams were collected in Barkley Sound and the Strait of Georgia. The Japanese littleneck and the Pacific littleneck typically co-occur and have similar morphologies (Richardson, 1985). Preliminary feeding trials (I.J. McGaw, unpublished data) indicated that crabs did not distinguish between the two littleneck species. Because equal proportions of the littleneck species are often found with varnish clams, approximately equal numbers of each species were used in our experiments, in attempts to mimic the natural systems the crabs are most likely to encounter. Hereafter, we collectively refer to the two species as "littlenecks". Crabs and bivalves used in the experiments were held in running seawater (10-12°C and 32 PSU) for at least a week prior to experimentation. Crabs were fed fish every other day, but were starved for 4 days prior to the experiments to standardize hunger levels, and to ensure feeding during trials. Clams were fed an algae paste suspension daily.

4.2.1. Clam size and species preference

Ten, 6 hr feeding trials, on each of two size classes of two crab species, were conducted to determine the preferred and edible size-classes of clams. This time period was chosen to approximate the duration of water cover in the mid-high intertidal (where varnish clams are most abundant). Crabs were assigned to two size classes: small Dungeness (110-140 mm), large Dungeness (170-200 mm), small red rock (100-130 mm), and large red rock (150-180 mm). Crabs were held in individual compartments without substratum (45 cm x 40 cm) in aerated running seawater of 20 cm depth. Each crab was presented with 5 littleneck clams of three size ranges, small (20-30 mm), medium (30-40 mm) and large (40 – 50 mm). At 2 hr intervals any eaten clams were recorded and replaced with new clams of equal size. This experiment was repeated with small (25-35 mm), medium (35-45 mm) and large (45-55 mm) varnish clams. Crabs were used in only one feeding trial. Size preference was determined using Manly's α (as described below).

In a separate series of experiments, the maximum edible size of each clam species was determined. One littleneck or varnish clam was presented in each feeding trial and observed at the end of the 6 hr period. This was repeated with increasing clam size until the crab could no longer consume the clam. This enabled us to determine if clam size provided a refuge from predation for either species of clam.

To determine clam species preference in the absence of substratum, 10 crabs of each size and species were offered 3 small, medium and large clams of each species (i.e. 18 clams total). At 2 hr intervals, eaten clams were recorded and replaced with new clams of equal size until the end of the 6 hr period.

Feeding trials to determine clam species preference in natural substratum were conducted in circular tanks (0.5 m depth and 1.8 m diameter), with running seawater and 5 cm (= limited burial) or 15 cm (= 'unlimited') of locally collected fine sand. To establish burial depths in the lab, lengths of fishing line were glued to 50 clams of each species, which were then allowed to bury overnight in 15 cm of sand. The length of exposed line was then recorded to determine burial depth. Burial depths were compared using a Mann-Whitney Test. The burial depths observed in this trial were assumed to be representative of the burial depths in the proceeding crab feeding trials. Prior to each feeding trial 50 clams of each species, 25 medium (3-4 cm for littleneck, 3.5-4.5 cm for varnish) and 25 large (4.1-5 cm for littlenecks, 4.6-5.5 cm for varnish) were randomly planted foot first. A grid temporarily placed over the tank was used to randomize clam species and size distribution. Clams that failed to bury within one hour were replaced with new clams and those that did not bury overnight were recorded and removed. If the 50:50 ratio of each species changed as a result of these removals additional clams were removed to restore the ratio. For each feeding trial 5 starved crabs of a single species (carapace width 140 – 170 mm) were introduced to a tank and allowed to feed for 6 hrs. Five trials were conducted for each species of crab. The tanks were surrounded by black plastic sheeting to minimize disturbance. At the end of each trial, the sand was sifted to recover the remaining clams and cracked shells. The number consumed was determined by counting the number and species of live clams left.

Manly's α was used as an index of preference (Manly, 1974) for constant prey populations (feeding trials without substratum) and variable prey populations (feeding trials with substratum where eaten clams were not replaced). This index has been well established in the feeding preference literature (Manly, 1993; Manly et al., 2002) and has been used in similar preference experiments (Pattinson et al., 2003; Uthicke and Karez, 1999). This index was used for both size and species preference. Equations for constant and variable prey populations can be found in Krebs (1994) and the resulting α values for the index are described as follows:

$\alpha_i = 1/m$ = no preference for species *i*

$\alpha_i > 1/m$ = preference for species *i*

$\alpha_i < 1/m$ = avoidance of species *i*

where *m* = number of prey types (e.g. species or size)

For size preference experiments, an α value of 0.33 indicates no preference, > 0.33 indicates preference and < 0.33 indicates avoidance. For prey preference, an α value of

0.5 indicates no preference, > 0.5 indicates preference and < 0.5 indicates avoidance. Preference or avoidance was considered to be significant if the 95% confidence limits did not overlap 1/*m* of prey types.

4.2.2. Clam handling time and pick-up success

Twelve crabs were housed in individual compartments without substratum, in aerated seawater of 20 cm, and offered one medium sized varnish or littleneck clam. Crabs were observed throughout the feeding period and opening time (i.e. time from first clam pick-up to first bite of flesh) and feeding time (i.e. from first bite of flesh to abandonment of shell) were recorded. The sum of these two parameters constitutes the total handling time (excluding digestion). Handling times for each clam species were compared using t-tests. Square root data transforms were conducted when data did not meet assumptions of homogeneity of variance and normality. When the transformation did not correct for this a Mann-Whitney Test was employed.

To determine clam pick-up success, ten small and 10 large crabs of each species were housed individually and provided a mix of 10 medium and large clams of each species. Each crab was monitored for one hour during which observations of successful (clam eaten) and unsuccessful (clam abandoned) clam pick-ups were made. Eaten clams were replaced. The number of successful pick-ups was compared using statistical analysis as described above.

4.2.3. Relationship of shell length to flesh weight, profitability and shell thickness

To determine the relationship between shell length and flesh weight, clams were measured to the nearest 0.1 mm using digital calipers, shucked and then dried at 60°C in pre-weighed aluminum boats for 48 hours and then weighed (to the nearest 0.1 mg) on an analytical scale. Flesh weights between species were compared for all size classes using t-tests. Data that violated assumptions of normality and/or equal variance were log transformed. Profitability was determined following Elner and Hughes (1978) and expressed as the net energy intake (flesh) per unit handling time. Varnish and littleneck clam profitabilities were compared for each size and species of crab using t-tests. Profitabilities were only calculated for medium sized clams because only one size was used in the handling time experiments.

To determine the relationship of littleneck and varnish clam shell length to shell thickness (see Fig. 4.4. for dimension descriptions), over 200 clams were measured as above and compared using linear regression analysis.

4.3. Results

4.3.1. Clam size and species preference

When varnish and littleneck clams of 3 sizes were offered separately, large Dungeness crabs showed significant preference for medium littleneck clams ($\alpha = 0.46$, $P < 0.05$, Fig. 4.1a). Large littleneck and large varnish clams were also preferred though this preference proved to be statistically insignificant (Fig. 4.1a, b). Small Dungeness crabs showed significant preference for medium varnish clams ($\alpha = 0.46$, $P < 0.05$), and weaker preference for small and medium littlenecks and large varnish clams, and avoidance of large littlenecks and small varnish clams (Fig. 4.1a, b, Table 4.1). Large red rock crabs showed significant preference for medium littlenecks ($\alpha = 0.45$, $P < 0.05$) and weaker preference for medium and large littlenecks and large varnish clams. Small red rock crabs showed significant preference for small littlenecks ($\alpha = 0.58$, $P < 0.05$), and weaker preference for small and medium varnish clams and weaker avoidance of medium and large littlenecks (Fig. 4.1c,d, Table 4.1). Large red rock and Dungeness crabs significantly avoided small sizes of both littleneck ($\alpha = 0.16$ red rock, $\alpha = 0.17$ Dungeness, $P = 0.05$) and varnish clams ($\alpha = 0.16$ red rock, $\alpha = 0.13$ Dungeness, $P = 0.05$).

Almost 30% of the clam size preference data did not follow a normal distribution due to the presence of multiple zero or one values, indicating strong avoidance or preference. The crab size class that showed significant avoidance and a non-normal distribution (large Dungeness feeding on small varnish clams) also had an average α of 0.13 indicating that the statistical significance, despite the violation of normality, is likely real. Other size classes that violated this assumption (small Dungeness feeding on large littleneck, large and small varnish clams; small red rock feeding on medium and large littlenecks and small varnish clams) were not significant. Thus, although the sensitivity of the test may be decreased, this should not change the overall result.

For varnish clams, there was no size refuge from predation – both sizes and species of crab were able to crack the largest varnish clams offered (up to 64 mm). For large crabs of both species, the upper size limit for littlenecks was 50-52 mm. The maximum size of littleneck clam small crabs could consume was 45 mm.

In the experimental trials without substratum (Fig.4.2a), large and small Dungeness and large red rock crab showed significant preference for varnish clams ($\alpha = 0.63$ and 0.79 for Dungeness, $\alpha = 0.72$ for red rock, $p < 0.05$). Small red rock crabs, however, showed strong but statistically insignificant preference for varnish clams ($\alpha = 0.67$).

In the experimental trials with substratum, varnish clams buried significantly deeper than littleneck clams (*t*-test, $t = 5.58$, $P < 0.001$). Differences in burial depths were comparable, though less pronounced, than those observed in the field (S.E. Dudas, unpublished data), with varnish clams burrowing approximately twice as deep (6 cm versus 3 cm). In the field, varnish clams will burrow up to 30 cm deep compared to the maximum depth of 10 cm observed for littleneck calms. The differences observed between field and laboratory burial depths may have been due to the 15 cm limit of substrate in the tanks. We were unable to provide more substrate due to logistical constraints. Dungeness and red rock crabs feeding in 5 cm of substratum showed preference for varnish clams, however only Dungeness crab preference was statistically significant ($\alpha = 0.76$, $P = 0.05$, Fig. 4.3).

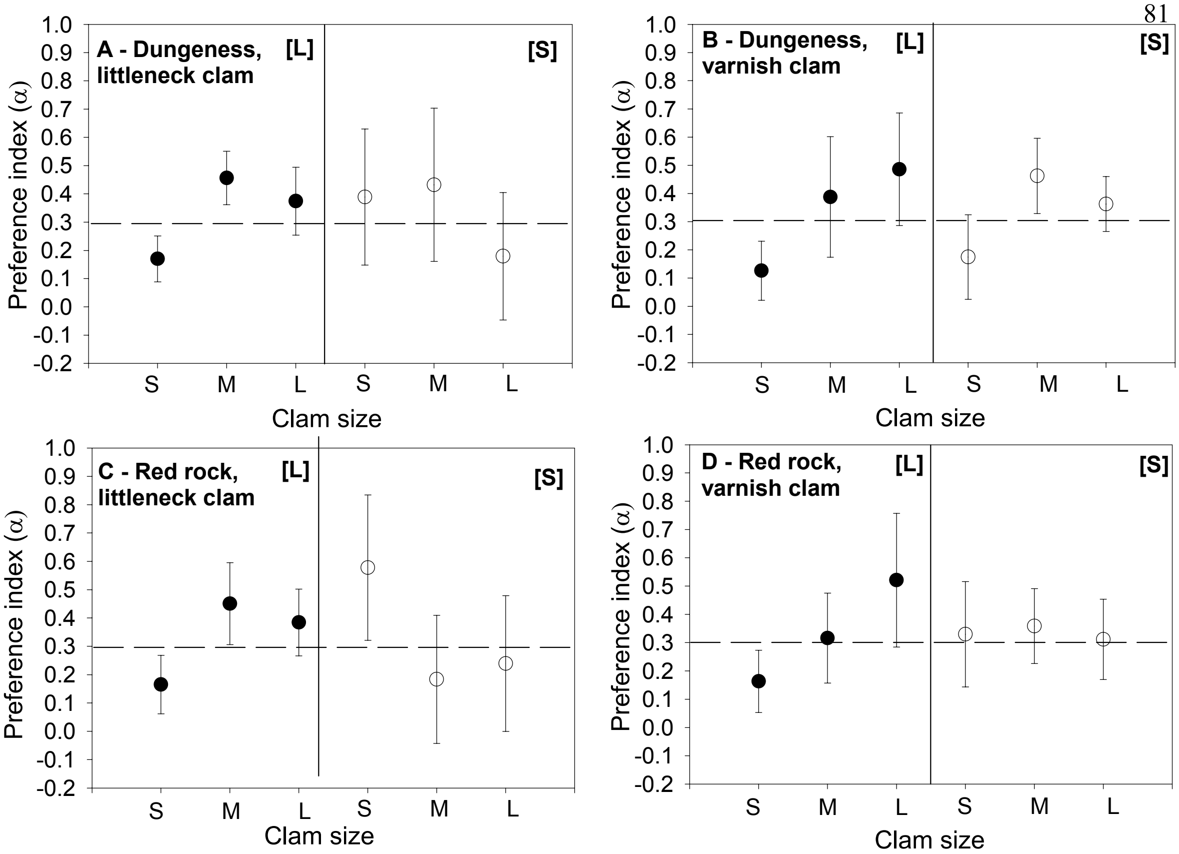


Fig. 4.1. Crab preference for different sizes of either littleneck or varnish clams. (A) Dungeness feeding on littleneck clam, (B) Dungeness feeding on varnish clam, (C) Red rock feeding on littleneck clam, (D) Red rock feeding on varnish clam. In each panel [L] and [S] refer to large and small crabs, while S, M, L on the x-axis denote small, medium and large size clams. Dashed line denotes value of zero preference (0.3), values above denote prey preference, values below, avoidance. Bars represent 95% CI. Where CI does not overlap the line preference is significant.

Table 4.1. Average Dungeness and red rock crab size preference for littleneck (LN) and varnish (V) clams. Alpha values above 0.3 indicate preference, values below indicate avoidance. Stars indicate significant preference or avoidance.

			Size preference (α)		
Crab sp.	**Crab size**	**Clam sp.**	**S**	**M**	**L**
Dungeness	Large	LN	0.17*	0.46*	0.37
		V	0.13*	0.38	0.49
	Small	LN	0.39	0.43	0.18
		V	0.18	0.46*	0.36
Red rock	Large	LN	0.17*	0.45*	0.38
		V	0.16*	0.32	0.52
	Small	LN	0.58*	0.18	0.24
		V	0.33	0.36	0.31

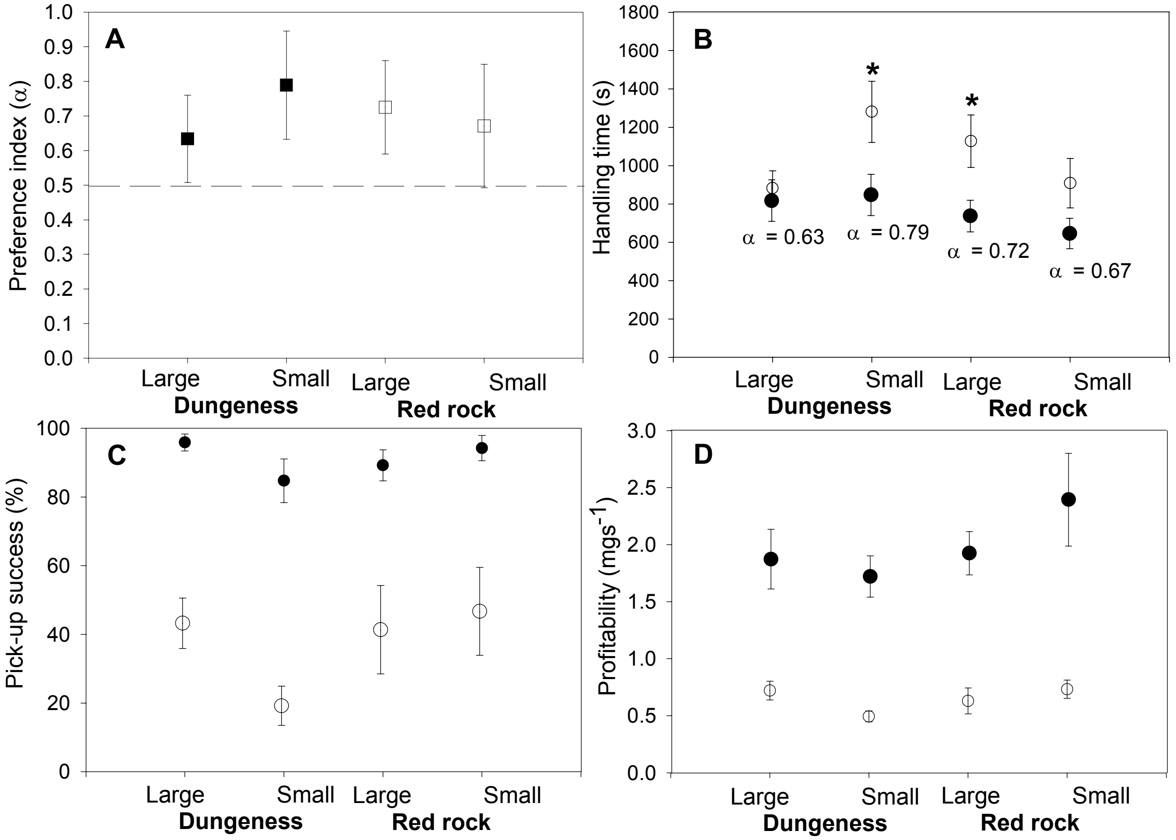


Fig. 4.2. (A) Dungeness (●) and red rock crab (○) preference (± 95% CI) for varnish clams. Dashed line represents zero preference (0.5). Values above dashed line indicate varnish clam preference and values below indicate littleneck preference. Where CI does not overlap the dashed line preference is significant. (B) Littleneck (○) and varnish (●) clam handling times for large and small Dungeness and red rock crabs (±SE). *denotes significant difference at 0.05 level. Alpha (α) values represent varnish clam preference values. Note that varnish clam preference increases as the differences between clam species handling times becomes greater. (C) Percent successful littleneck (○) and varnish clam (●) pick-ups (from total attempts) for Dungeness and red rock crabs (± SE). Differences between varnish and littleneck clams for both sizes and species of crab are significant at the 0.05 level. (D) Medium sized littleneck (○) and varnish (●) clam profitability (mgs^{-1}) for large and small Dungeness and red rock crabs. Differences between varnish and littleneck clam profitabilities are significant for both size and species of crab at the 0.05 level.

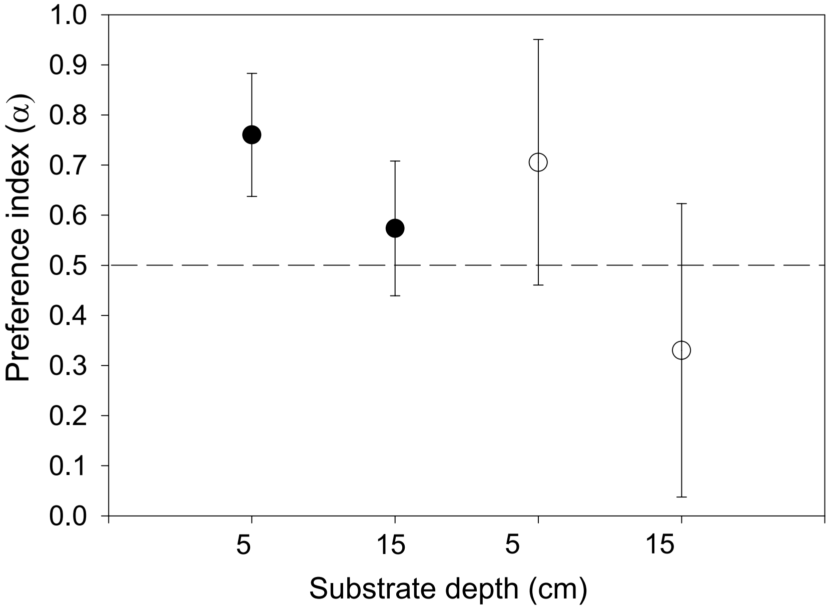


Fig. 4.3. Dungeness (●) and red rock crab (○) prey preference in 5 and 15 cm substratum (± 95% CI). Dashed line represents zero preference (0.5). Values above dashed line indicate varnish clam preference and values below indicate littleneck preference. Where CI does not overlap the dashed line prey preference is significant.

Dungeness crab preference for varnish clams decreased in the 15 cm substratum trial (α decreased from 0.76 to 0.57), and red rock crab preference switched to littleneck clams (α decreased from 0.70 to 0.33). However, no preferences in the 15 cm trial were significant.

4.3.2. Clam handling time and pick-up success

Small Dungeness and large red rock crabs had significantly longer handling times (up to approximately 50%) for littleneck clams than varnish clams ($t = 2.17$, $P = 0.041$, DF=22; $t = 2.33$, $P = 0.029$, DF=22), corresponding to the highest preference values (Fig. 4.2b). Large Dungeness and small red rock crabs appeared to have longer handling times for littleneck clams but they were not significantly different than the varnish clam handling times.

Littleneck and varnish clams were picked up with equal frequency, with the exception of small red rock crabs which picked up littlenecks significantly more often (*t*-test, $t = 2.19$, $P = 0.042$). All sizes and species of crabs also showed significantly higher successful varnish clam pick-ups (i.e. pick ups that resulted in feeding) compared to littlenecks (*t*-test, all $P \leq 0.011$, Fig. 4.2c).

4.3.3. Relationship of shell length to flesh weight, profitability and shell thickness

Dry flesh weights of the different size classes of clams, differed significantly between varnish clams and littlenecks (in medium and large size classes), with varnish clams yielding approximately 30% more flesh than littlenecks. Each size and species of crab obtained significantly more flesh per unit time when feeding on varnish clams (*t*-test, $P < 0.001$ for all). Correspondingly, varnish clams also represented significantly higher profitabilities, yielding approximately 1 mg/s more than littleneck clams ($P < 0.001$, Fig. 4.2d). Shell length versus shell thickness regressions showed that varnish clams have a more compressed shape with littlenecks being approximately 1.5 times thicker (Fig. 4.4).

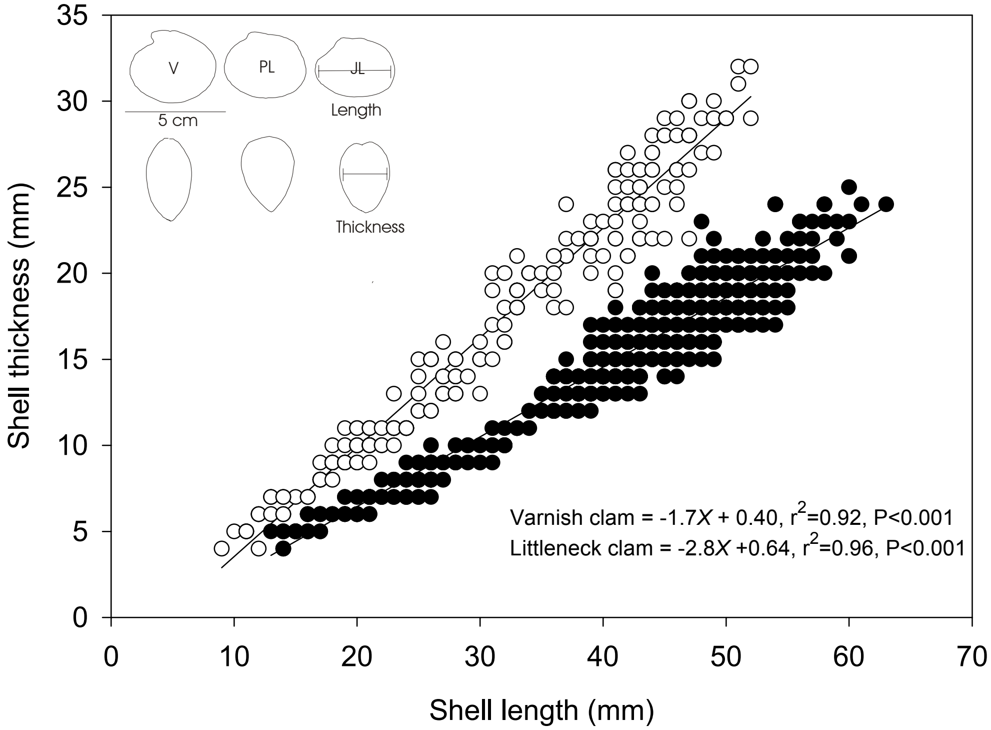


Fig. 4.4. Shell length versus thickness for littleneck (○) and varnish clams (●) and their corresponding linear regression equations. Inset shows shell dimensions for the varnish clam (V) and Pacific and Japanese littleneck clams (PL and JL).

4.4 Discussion

Given the high densities it attains on appropriate beaches, the varnish clam represents a significant prey source for native predators. Crabs can be an important structuring force in soft-benthic communities (Ebersole and Kennedy, 1995; Eggleston et al., 1992; Navarrete and Castilla, 1988; Pearson et al., 1981; Richards et al., 1999) and they appear to be taking advantage of the varnish clam as a new food resource (Byers, 2002a). Feeding trials without substratum show that the varnish clam is preferred over the co-occurring littleneck clam, supporting our hypothesis. This is likely the result of the decreased handling time of varnish clams (Fig. 4.2b). Shell shape is known to influence prey vulnerability (Mascaro and Seed, 2000b), with highly inflated morphologies requiring increased shell-breaking time (Boulding, 1984). With their compressed shape, varnish clams are easier for crabs to grip than the globular littleneck shells, which often slipped out of the chelae, resulting in unsuccessful pick-ups. Increased shell thickness has also been shown to confer resistance to crushing (Robles et al., 1990). The thin varnish clam shells require less force to crack, compared to the thicker shelled littleneck clam that requires up to 7-8 times the pressure (Byers, 2002a). Thus, shell morphology makes the varnish clam more vulnerable to predation than locally co-occurring species when crab predators have equal access to them.

Size preference trials showed a positive relationship between predator and prey size (larger crabs preferred larger prey, and smaller crabs preferred smaller prey). Neither crab species had a size limit for consuming varnish clams as originally predicted, and contrary to the littlenecks, crabs usually consumed larger sizes of varnish clams, likely because of the lack of a size refuge. Large crabs of both species showed significant avoidance of smaller clams. This may be due to the difficulty experienced when trying to pick up small items with their large chelae, which may also make it difficult to clean the flesh off the smaller shells (Elner and Hughes, 1978). Varnish clams are more vulnerable to predation because there is no size refuge from predation unlike the littleneck species, which can attain a refuge, when they reach a certain size (Boulding, 1984).

The varnish clam appears to be more profitable for crabs, yielding approximately 30% more flesh than similar sized littlenecks. This may have contributed to prey preference for varnish clams. Prey preference is likely the result of both active choice (i.e. based on profitability cues such as shell width and olfactory stimuli; Richards et al., 1999; Smith et al. 1999), and passive selection (i.e. based on the physical properties of the system such as substrate type; Mascaro and Seed, 2000a). In the present study it appears that varnish clam profitability, as well as tactile and mechanical issues (e.g. pick-up success), may contribute to it being the preferred prey. Furthermore, the degree of preference was found to increase according to differences in handling time; the longer it took to consume a littleneck clam, the greater the preference for the varnish clam. Handling time thus appears to influence not only the species preferred, but also the degree of preference. Although the compressed shape of the varnish clam may increase its vulnerability (i.e. by decreasing predator handling time), it also increases the ease of burrowing into the substratum, allowing it to bury deeply. This deeper burial may enable them to sustain high densities by decreasing their encounter rate with crab predators.

Besides relative abundance, the availability of different types of prey is the result of a predator's search and foraging methods (e.g. excavation of substratum), and prey properties that make them vulnerable to these methods (e.g. burial depth; Richardson, 1985). Both Dungeness and red rock crabs dig pits up to 30 cm deep to obtain bivalve prey, (Auster and Crockett, 1984; McGaw, 2004). Burial depth may thus be an important mechanism for soft-bottom bivalves (particularly soft-shell species) to decrease predation mortality (Blundon and Kennedy, 1982; Smith et al., 1999).

Varnish clams can bury at least twice as deep as littleneck clams (S.E. Dudas, unpublished data), potentially providing a refuge from predation by decreasing crab encounter rate and increasing excavation time. Excavation times for red rock crabs have been shown to increase with clam burial depth, and predation rates correspondingly decrease (Smith et al., 1999). Burial depth became a refuge from predation because of the increased time required to obtain the prey, which caused an overall decrease in the prey's profitability. Similarly, the deeper burial of the varnish clam could compensate for its increased vulnerability due to its morphology.

Feeding trials in limited substratum, show continued crab preference for varnish clams. In 'unlimited' substratum, however, all crabs showed reduced preference for varnish clams (and for red rock crabs a switch in preference to littleneck clams, Fig. 4.3). These findings generally support our original hypotheses.

Substratum type has been suggested as a limiting factor in determining where varnish clams can establish on a given beach (Byers, 2002a). Lower in the intertidal zone (where substratum is more compact), varnish clams cannot dig as deeply as in looser substratum that is typical of the high intertidal (Byers, 2002a). Varnish clams in more compact substratum are more vulnerable to predation (Byers, 2002a) because of their shallower burial depth. Therefore, the interaction between burial depth and substratum type will be influential in determining which beaches could harbour dense populations of varnish clams.

Implications of invasions for fisheries have not been fully recognized (Walton et al., 2002). The varnish clam often co-occurs with littleneck clams, which are important commercial species in coastal BC. Despite the deep burial of varnish clams, evidence of crab predation can be found on most beaches with varnish clams (S.E. Dudas, unpublished data). If crab predators choose the varnish clam over littlenecks this could potentially decrease littleneck mortalities. Alternatively, the abundance of prey items (e.g. varnish clams) could increase crab predator populations potentially resulting in increased mortalities. In addition to these potential biological effects, the varnish clam has already had an economic impact. As of 2002 the varnish clam can be harvested along with the littleneck clams, and the BC shellfish industry is currently trying to establish a market for them. Whether or not this invasion has improved or decreased the production of littleneck clams remains to be seen. Understanding these community interactions between varnish clams, co-occurring bivalves and their predators will provide useful information for determining the impacts this invasion has already had and what impacts may become evident as the invasion progresses.

Chapter 5. Invasion dynamics of the varnish clam (*Nuttallia obscurata*) in southern British Columbia: A matrix demographic modeling approach

5.1 Introduction

The number of invasions by non-indigenous marine invertebrate species in the Northeast Pacific has been increasing steadily over the last few decades, posing a threat to native biodiversity and ecosystem function (Kolar and Lodge, 2001). Because many marine invertebrates have complex life cycles (i.e. including both benthic and pelagic life history stages), once an invader has established it becomes almost impossible to prevent further spread of the species. Identifying the life history characteristics that contribute to invasion success is crucial to our understanding of why some invaders succeed (while others fail), and for identifying those species that may be poised to invade, and which might exert the greatest impacts.

Although matrix demographic analysis has long been a popular tool in population and community ecology, including studies of marine systems (Davis and Levin, 2002; Gotelli, 1991; Levin and Caswell, 1987; Miller, 2001; Nakaoka, 1997; Pascual and Caswell, 1992), only recently has its use been extended to study invasion dynamics (Neubert and Caswell, 2000; Parker, 2000; Ruesink, 2003). This approach allows one to determine vital population characteristics such as population growth rate, stable size distribution and reproductive contribution (Nakaoka 1997). In a size-structured matrix, the relative importance of the different life history stages for total population growth can be determined using sensitivity and elasticity analyses (See Section 5.2.3). Life table response experiments can also be conducted to decompose the effect of experimental treatments, different habitats or harvesting regimes (Miller, 2001) on the rate of population increase, into individual contributions from different vital rates (e.g. survival, reproduction; Caswell 2001).

In this chapter I use matrix demographic analyses to investigate the invasion of the varnish clam (*Nuttallia obscurata*) in coastal BC. I determined the vital rates contributing to its invasion success at two beaches in BC: Bamberton (in Saanich Inlet), a protected beach that was likely invaded shortly after the initial introduction near Vancouver, and Robbers Passage (in Barkley Sound), a more exposed site several hundred kilometeres away, and presumably the result of a later invasion. The main goals of the analyses were: (1) to determine which life history stage(s) is most crucial to population growth, (2) to compare the population growth rates between Bamberton and Robbers Passage and determine which life history stage(s) contributes to any observed differences and (3) to conduct population projections to investigate the plausibility of different recruitment scenarios.

5.2 Methods

5.2.1 Field Methods

Growth transition, survival rates and fecundity data were estimated from mark-recapture experiments and field collections conducted at Robbers Passage and Bamberton (see Chapter 3). Yearly growth and survival rates were calculated by eliminating timedependency in the multi-state capture-mark-recapture model (Chapter 3). Because all size-class 1 clams from Robbers Passage grew to size-class 3 in one year, the growth transition from 1-2 in this model actually represents the transition from size-class 1 to size-class 3 (Chapter 3, Fig. 3.14). Annual population survey data were available for Robbers Passage from 2001-2003 and from Bamberton for 2003. Monthly length-frequency distributions from both sites were available from May 2002-January 2004 (Chapter 3). The two sites appear to differ in recruitment dynamics; Robbers Passage having extremely low annual recruitment (or more episodic recruitment pulses), and Bamberton having higher levels of regular annual recruitment (Chapter 3). The sites also differ oceanographically, with Robbers Passage typically experiencing cooler temperatures (Chapter 2) and more wave exposure than Bamberton. Robbers Passage is also a smaller beach, approximately one-fifth the size of Bamberton, and its varnish clam density is only half as high.

5.2.2 Matrix model

Species life tables (which typically include size-specific growth, survival and reproduction rates) can be converted into a two-dimensional array, a matrix, where each column represents a life cycle stage, i (Heppell et al., 1999). The matrix elements, a_{ij}, represent the growth and/or survival transition probabilities or reproductive outputs of an individual in stage i at time t, to the number of individuals in stage j at time t+1 (Donovan and Welden, 2002). When a population vector (i.e. a column representing the number of individuals present in each size class) is multiplied by the matrix several times, it will reach a stable population size structure (i.e. where the abundance in each size class does not change) with an asymptotic population growth rate λ (Heppell et al., 1999). When the population reaches this stable size structure, matrix model sensitivities and elasticities can be calculated, based on the stable size distribution (*w*) and reproductive value (*v*) vectors. The reproductive value represents an individual's present and future reproduction contribution to population growth (Caswell, 2001). Sensitivities and elasticities show the relative importance of growth, survival and reproduction rates to the projected population growth rate. The calculations are described in the detailed model description below.

Size-class matrix models were developed for each site. Five size-classes were chosen based on size-dependent differences in survival and fecundity. Transitions between size-classes were described in a transition matrix (**A**) and projected according to the following equation (Caswell, 2001):

$$\mathbf{n}(t+1) = \mathbf{A}\cdot\mathbf{n}(t)$$

where:

$\mathbf{A}$ = a matrix of a_{ij}'s

$\mathbf{n}(t)$ = size-class abundance at time t

$\mathbf{n}(t+1)$ = size-class abundance at time t+1

A is the matrix of a_{ij}'s that represent the contribution of each size-class (i.e. in terms of growth, survival and fecundity) to the number of individuals at the next time step. The time-step for both sites was one year. The different a_{ij}'s, of the matrix (including fecundity, growth and survival) are shown as a life-cycle graph in Figure 5.1.

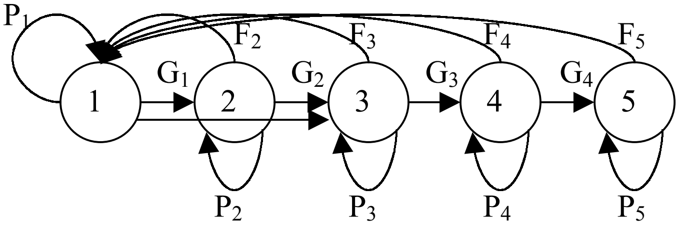


Fig. 5.1. Life cycle graph for the varnish clam transition matrix. G, P and F represent matrix elements of growth, survival and reproduction respectively.

where:

G_i = probability of surviving and growing to size-class $i + 1$ in one year (size class 1 also includes the probability of growing $i + 2$, $1 \rightarrow 3$)

P_i = probability of surviving and remaining in size-class i in one year

F_i = reproductive contribution size-class i

Population census is assumed to occur after reproduction. Therefore, 'F' represents the probability of fertilization and survival through larval and juvenile sizes to a size large enough to be detected in population surveys (~15 mm). To calculate 'F', I used fecundity and sex ratios calculated from previous experiments (see Chapter 2), multiplied by a conservative fertilization rate of 50% based on the literature (Grant et al., 1998; Marshall et al., 2004). For recruitment rate I also used literature values as a starting point. Bivalve studies report highly variable (but universally low) recruitment rates with only 0.001-0.0001% of larvae reaching settlement (Brousseau, 1978), and only 0.001-0.0001 recruits per egg spawned (Beukema et al., 1998). To determine a realistic recruitment estimate I projected the population by one year using the transition matrix and a range of recruitment rates (1 x 10^{-5} – 1 x 10^{-7}). I then compared the predicted size distribution to observed monthly length-frequency distributions. Because annual population surveys were also conducted at Robbers Passage I was able to utilize this information to construct more precise estimates of recruitment at this site. Previous researchers have calculated recruitment rates by assuming that the study population has reached a stable size structure, thereby enabling them to use the transition matrix to back-calculate the recruitment rates necessary to achieve the observed asymptotic state (Brousseau and Baglivo, 1982). In similar fashion, I used the three-year annual series of length-frequency distributions to determine the necessary recruitment levels to obtain the size structures observed. Using the observed size-class distributions and the predicted size-class distributions based on the transition matrix, I then used the SOLVER routine in Excel (which uses a nonlinear optimization code) to determine the recruitment rate that would minimize differences between observed and predicted size distributions. SOLVER was also used to vary both the growth transition (G) and the survival (P) rates to investigate the influence of uncertainty or variation in these estimates.

Like most other marine invertebrates, the varnish clam has a complex life history with both a planktonic larval stage and a benthic adult stage (Scheltma, 1986). Because of this, adult population dynamics may be de-coupled from larval dynamics, with local fecundity exerting only a minor effect on population growth and little influence on recruitment (Hughes, 1990). For my purposes, I assumed that the reproductive contribution of the adults (based on the site-specific adult fecundities and sex ratios and the assumed fertilization and recruitment rates) is representative of the contribution from all larval sources (i.e. both local and regional) from which the population receives recruits.

5.2.3 Matrix theory

The asymptotic population growth rate is represented by the dominant eigenvalue (i.e. λ, the latent root), of the transition matrix at the stable size distribution (Caswell, 2001). When $\lambda>1$ the population is increasing, when $\lambda<1$ the population is decreasing, and when $\lambda=1$ the population size remains constant (Donovan and Welden, 2002). By analysing the eigenvectors of the matrix at the stable size distribution, sensitivity and elasticity values can be calculated to determine the contribution of each size-class to population growth (Caswell, 2001; Davis and Levin, 2002). Sensitivity analysis demonstrates how small changes in the matrix elements a_{ij}, affect the population growth rate. High sensitivity of a vital rate implies that even a small change in its value has a large effect on the population growth rate (Horvitz and Schemske, 1995). For example, if the sensitivity for survival in size-class 2 (P_2) is 0.3, a small change in P_2 results in a population growth rate change (λ) by a factor of 0.3. The larger the sensitivity for a particular vital rate, the more sensitive population growth rate will be to changes in that rate. Sensitivity values are also useful for comparing the vital rates that are most important. For example if sensitivity for survival in size-class 2 is 0.3 and for size-class 1 it is 0.1, changes in size-class 2 have three times the effect of size-class 1.

Because the matrix elements (i.e. the vital rates) are often measured on different scales (e.g. fecundity and survival), proportional values can also be calculated. Elasticity analysis examines how population growth is affected by a proportional change in vital rates (Donovan and Welden, 2002). High elasticity implies that the vital rate in question has a high proportional contribution to the change in population growth rate, for a given proportional perturbation of that rate. For example, if the elasticity of P_2 was 0.3, a 10% increase in P_2 would result in a 3% increase in λ (i.e. 0.3 x 10%). The equations for sensitivity and elasticity are shown below.

Sensitivity is defined as:

$$S_{ij} = {(v_i w_j)} \big/ {\langle w, v \rangle}$$

where: *v, w* = first left and right eigenvectors

v_i, w_j = i^{th} and j^{th} elements of the left and right eigenvector

$\langle w,v \rangle$ = the scalar product of the right and left eigenvectors

Elasticity is defined as:

$$E_{ij} = (a_{ij} / \lambda) \times S_{ij}$$

where: a_{ij} = the matrix element

λ = dominant eigenvalue

S_{ij} = sensitivity

Sensitivities and elasticities were calculated for all matrix elements (i.e. F, P, G) and combined to determine the total sensitivity and elasticity for each size class. This analysis was done separately for each site.

To compare population growth rates from Robbers Passage and Bamberton, a life table response experiment was conducted. To conduct this analysis an average matrix of the sites is compared to the matrix of each site individually, and the differences in the population growth rates are decomposed into contributions from each vital rate/matrix element (Davis and Levin, 2002). Using this approach, one can thus determine which matrix elements are responsible for any observed differences in population growth rates (Caswell, 2001; Davis and Levin, 2002).

$$C_{ij} = \left(a_{ij}^{(s)} - a_{ij}^{(\cdot)}\right) \times S_{ij}\Big|_{\left(\mathbf{A}^{(s)}+\mathbf{A}^{(\cdot)}\right)/2}$$

where: C_{ij} = contribution of matrix element a_{ij}

a_{ij} = matrix element

S_{ij} = sensitivity

$\mathbf{A}^{(s)}$ = matrix for each site

$\mathbf{A}^{(.)}$ = average matrix

Because of their relatively young 'age' (i.e. the time since invasion) most invader populations may not have achieved their stable size distribution. Thus, it is useful to determine how far from this distribution the population might be. The rate of convergence to this distribution is determined by the eigenvalue with the second largest value. The ratio of the dominant eigenvalue to the subdominant value gives the "damping ratio" (Caswell, 2001):

$$\rho = \lambda_1 / \lambda_2$$

where: λ_1 = dominant eigenvalue

λ_2 = subdominant eigenvalue

The larger the dominant eigenvalue, the faster the population converges toward its stable size distribution. If a population is far from achieving this stable distribution it may exhibit transient behaviour that is different from asymptotic behaviour (Horvitz and Schemske, 1995). For example, the population growth rate and sensitivities for transient dynamics may differ from the asymptotic population growth rate and sensitivities. Therefore, it is not clear how well analytical results (e.g. sensitivities, elasticities) will represent population dynamics for populations that have not reached the stable distribution (Parker, 2000).

An index of proportional similarity (PS) was used to provide a measure of similarity between the observed size distributions and the stable size distribution (Horvitz and Schemske, 1995):

$$\mathrm{PS} = \sum_{n}^{i=1} \min(a_i, b_i) \times 100$$

where: a_i = proportion of individuals in the i^{th} size of the stable size distribution

b_i = proportion of individuals in the i^{th} size-class of the observed size distribution

All analyses were conducted using MATLAB (www.mathworks.com) and the PopTools add-in for Microsoft Excel (www.cse.csiro.au/poptools/).

5.2.4 Recruitment scenarios

Annual length-frequency distributions from Robbers Passage showed a distinct pulse of recruitment in 2002 (see Chapter 3, Fig. 3.3). To examine the influence of pulsed recruitment on size-class abundance, I therefore projected the population using varying transition matrices in Microsoft Excel, alternating years of zero recruitment with a range of recruitment pulse sizes ($1 \times 10^{-6} - 9 \times 10^{-8}$). I then compared observed length-frequency distributions against predicted distributions (to the nearest cm) using the proportional similarity (PS) index.

5.3 Results

5.3.1 Matrix analysis

The transition matrices and associated recruitment rates used to project populations for Robbers Passage and Bamberton are shown in Table 5.1. Holding recruitment constant for both sites (1.5×10^{-6}) yielded very different size-class abundance projections for the two beaches. Figure 5.2 shows length-frequency distributions obtained for Robbers

Passage and Bamberton from July 2003 and January 2004, along with predictions based on the matrix projection. Although projections based on a recruitment level of 1.5 x 10^{-6} produced a plausible size-class abundance distribution for Bamberton, this recruitment level was clearly too high for Robbers Passage. Robbers Passage appears to experience much lower levels of recruitment than Bamberton. In fact, the recruitment rate that provided the most accurate size-class abundance predications for Robbers Passage was less than 5% of the recruitment at Bamberton (Fig. 5.3). This recruitment level produces more plausible size-class abundances with a higher proportional similarity for 2001-2003 (43-48% and 87-90% for recruitment levels 1.5 x 10^{-6} and 7.4 x 10^{-8}, respectively). Based on these results I therefore used recruitment values of 1.5 x 10^{-6} (Bamberton) and 7.4 x 10^{-8} (Robbers Passage) to conduct the matrix demographic analysis.

The dominant eigenvalue (λ), which represents the asymptotic population growth rate, indicated that both populations are currently declining (Robbers Passage λ=0.73, Bamberton λ=0.84), with Robbers Passage declining at a faster rate. The stable size-class distributions had low PS relative to annual population survey size-class distributions observed for either population (35-58% for 2001-2003 for Robbers Passage, 59% for Bamberton). The damping ratios were also low (1.34 for Robbers Passage, 1.09 for Bamberton) indicating slow convergence to the stable size-class structure.

Table 5.1. Varnish clam transition matrices for Robbers Passage and Bamberton. The first matrix outlines what each matrix element in the data matrices represents. P_i=the probability of surviving and remaining in the size-class *i*. G_i = the probability of surviving and growing to size-class *i*+1 (G1+ represents probability of growing from size-class1 to 3). F_i = reproductive contribution to size-class 1. F values were calculated using a fertilization rate of 50% and a sex ratio and recruitment rate of 0.39 and 2×10^{-6} for Bamberton, and 0.46 and 7.4×10^{-8} for Robbers Passage.

Size-class	Size (mm)	Class 1	Class 2	Class 3	Class 4	Class 5
1	<20 mm	P1	F1	F2	F3	F4
2	20-29	G1	P2			
3	30-39	G1+	G2	P3		
4	40-49			G3	P4	
5	>50				G4	P5

Robbers Passage

Size-class	Size (mm)	Class 1	Class 2	Class 3	Class 4	Class 5
1	<2cm	0.02640	0.00153	0.00881	0.03393	0.06239
2	2.1-2.9	0	0.12603	0	0	0
3	3-3.9	0.32610	0.56409	0.42781	0	0
4	4-4.9	0	0	0.21117	0.54670	0
5	>5cm	0	0	0	0.09486	0.71646

Bamberton

Size-class	Size (mm)	Class 1	Class 2	Class 3	Class 4	Class 5
1	<2cm	0.01351	0.02226	0.12646	0.49558	0.7309
2	2.1-2.9	0.09666	0.27355	0	0	0
3	3-3.9	0	0.23264	0.64010	0	0
4	4-4.9	0	0	0.02436	0.83567	0
5	>5cm	0	0	0	0.00507	0.76627

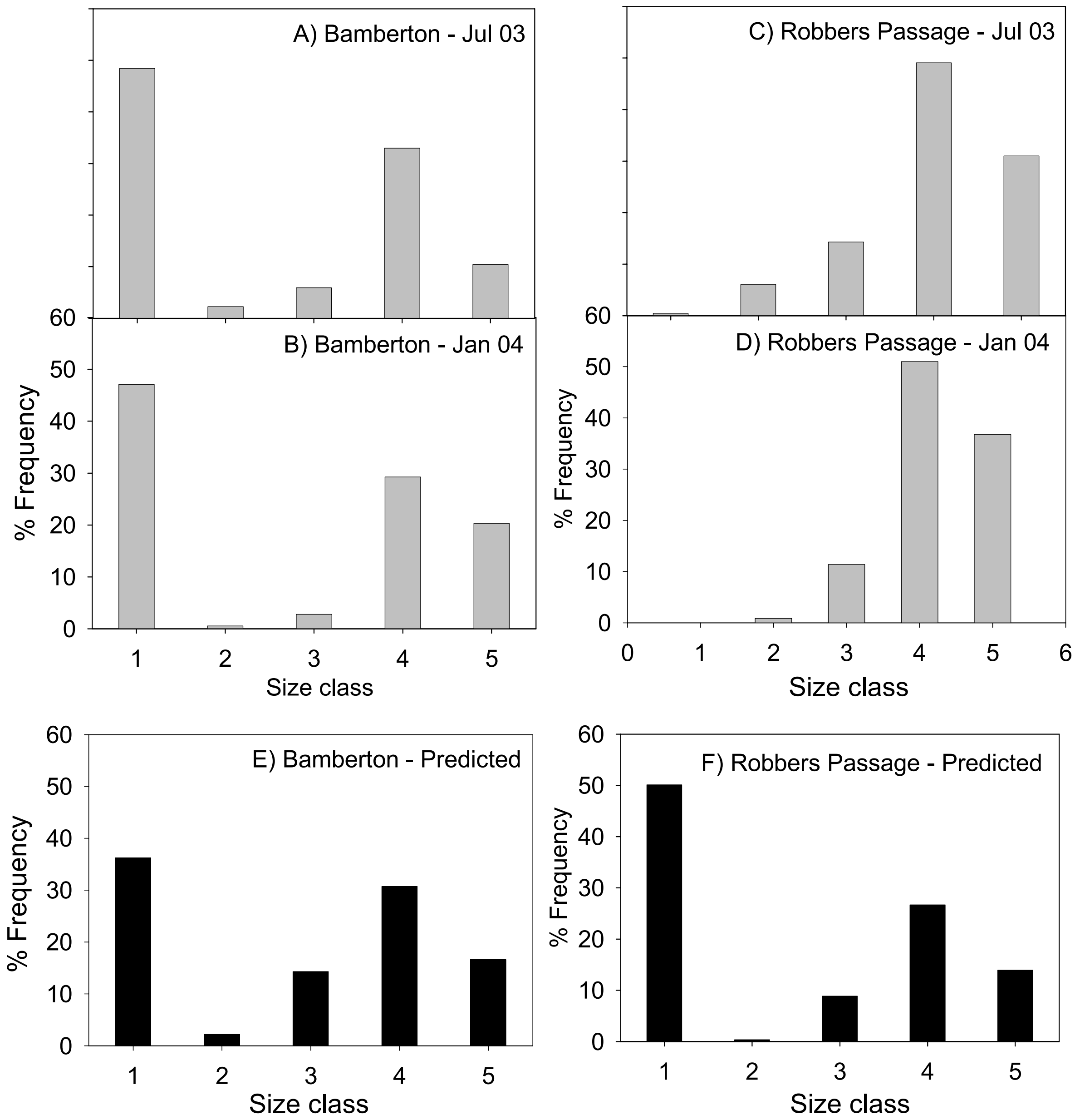
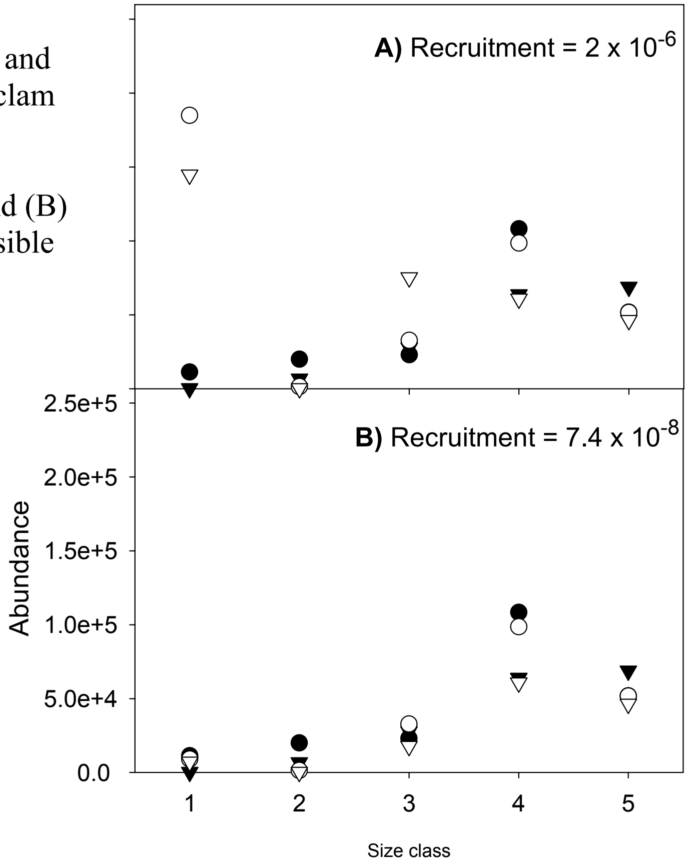


Fig. 5.2. Observed varnish clam size-class abundances for Bamberton, July 2003 (A), January 2004 (B) and Robbers Passage July 2003 (C), January 2004 (D) and predicted size-class abundances for Bamberton (E) and Robbers Passage (F) based on a recruitment level of 2 x 10^{-6} for both sites.

Fig. 5.3. Observed (filled symbols) and predicted (empty symbols) varnish clam size-class abundances for Robbers Passage for 2002 (●) – 2003 (▼) at recruitment levels of (A) 2 x 10^{-6} and (B) 7.4 x 10^{-8}. Some symbols are not visible because of the similarity between observed and predicted.



Survival rates of the largest size-classes (40-50 mm and ≥50mm) had the highest sensitivity and elasticity values for Robbers Passage and Bamberton respectively (Figs. 5.4a-b, 5.5a-b). Because of these high values, the larger size-classes also had the highest combined sensitivities and elasticities (Figs. 5.4c-d, 5.5c-d).

The life table response experiment showed that the largest difference between the two transition matrices occurred in the reproductive values (F) for the ≥50 mm size-class (Fig. 5.6a). However site differences in the survival of the 40-50 mm size-class had the largest contribution to between-site differences in population growth (Fig. 5.6b). Individual

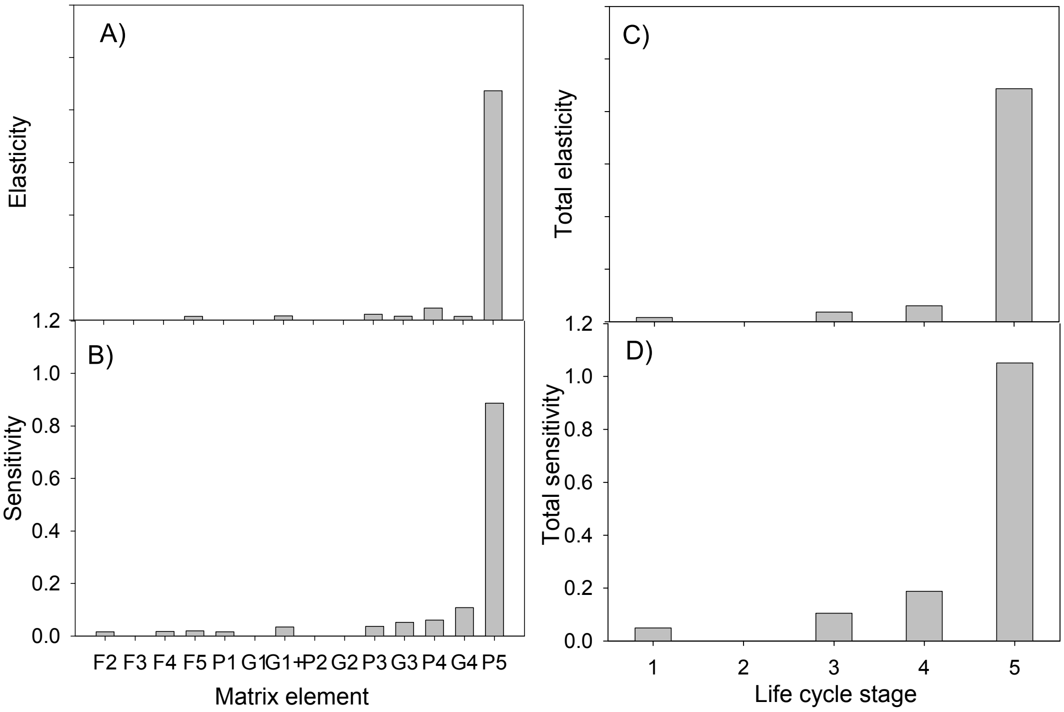


Fig. 5.4. Matrix element elasticity (A) and sensitivity (B) and total size-class elasticity (C) and sensitivity (D) for Robbers Passage. Fi = reproductive rate for size-class *i*, P*i* = survival rate for size-class *i*, G1+ =growth rate from size-class 1-3, G*i* = growth rate from size-class *i* to *i*+1.

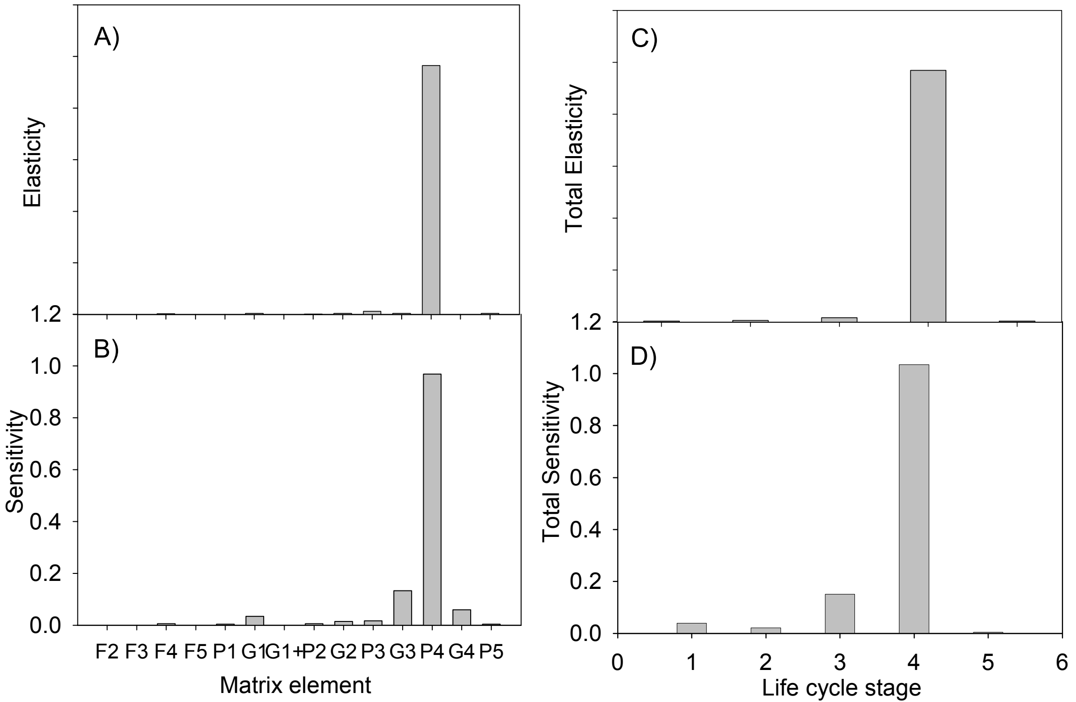


Fig. 5.5. Matrix element elasticity (A) and sensitivity (B) and total size-class elasticity (C) and sensitivity (D) for Bamberton. Fi = reproductive rate for size-class *i*, P*i* = survival rate for size-class *i*, G1+ =growth rate from size-class 1-3, G*i* = growth rate from size-class *i* to *i*+1.

growth and survival rates are likely to vary temporally, therefore I investigated how changes in these matrix elements would influence the results. To test the robustness of the sensitivities and elasticities to changes in growth and survival rates I used the SOLVER routine to vary these rates in the transition matrix to produce the most accurate size-class distribution predictions for Robbers Passage for 2001-2003. This produced the highest PS between observed and predicted size-class distributions (93-94% for 2002-2003). However, the rates that provided the best statistical fit (Table 5.2) were unrealistic (e.g. survival rate of 100% for small size-classes). Despite the changes in growth and survival rates, the larger size-classes maintained their highest sensitivities and elasticities.

Table 5.2. Varnish clam transition matrix obtained by varying all growth (G) and survival (P) probabilities to minimize the differences between the projected and the observed varnish clam size-class abundances for Robbers Passage from 2002-2003.

Size-class	**Size (mm)**	**Class 1**	**Class 2**	**Class 3**	**Class 4**	**Class 5**
1	<2cm	0	0.00153	0.00881	0.03393	0.06239
2	2.1-2.9	0	0.96490	0	0	0
3	3-3.9	1	0.03510	0.42396	0	0
4	4-4.9	0	0	0.57604	0.45537	0
5	>5cm	0	0	0	0.04846	1

5.3.2 Recruitment scenarios

The most accurate size-class abundance predictions for Robbers Passage resulted from a scenario in which a recruitment pulse in 2002 (with a recruitment level of 7.4×10^{-8} - 10×10^{-7}) was followed by a year of zero recruitment in 2003 (Fig. 5.7, PS=91%, 2002; PS=90%, 2003). Pulsed recruitment marginally increased the PS value for 2002 (the year in which the recruitment pulse was observed). However, decreasing the following year of

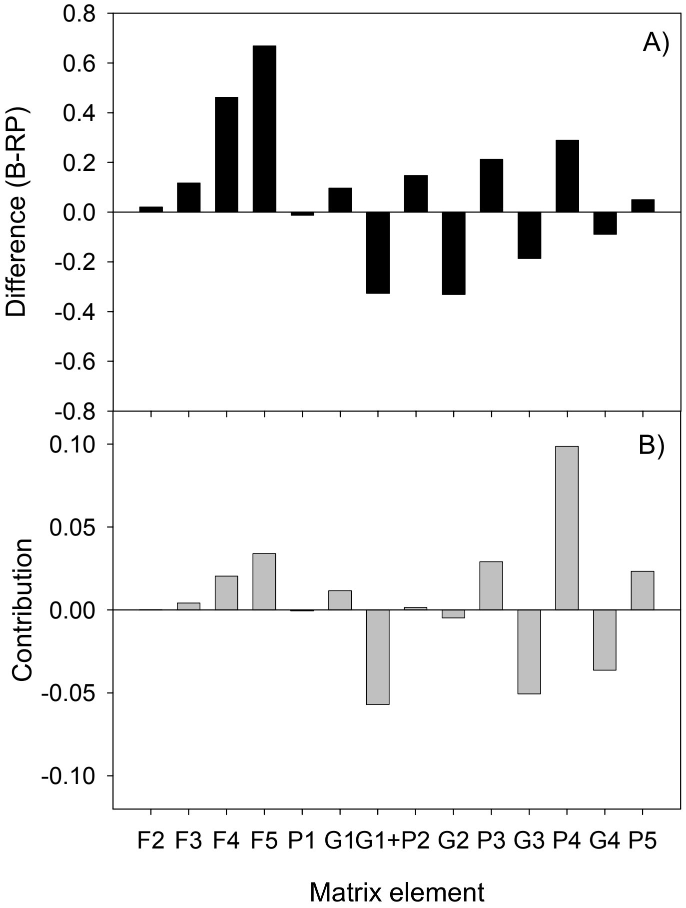


Fig. 5.6. Matrix element differences between Bamberton and Robbers Passage (A), and their contribution to differences in varnish clam population growth rate (B). Fi = reproductive rate for size-class *i*, P*i* = survival rate for size-class *i*, G1+ =growth rate from size-class 1-3, G*i* = growth rate from size-class *i* to *i*+1.

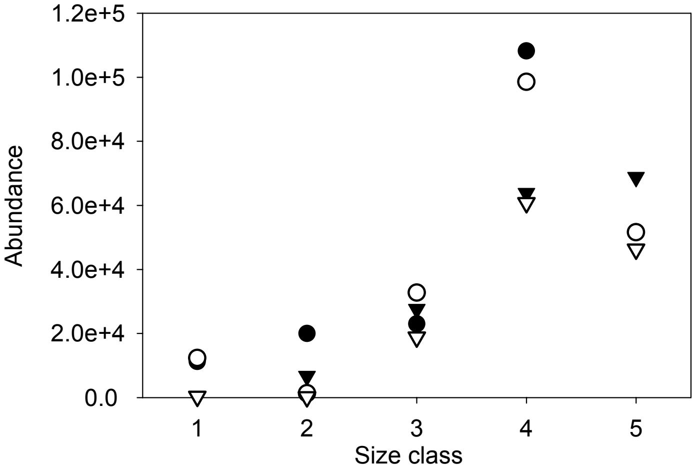


Fig. 5.7. Observed (filled symbols) and predicted (empty symbols) varnish clam size-class abundances for Robbers Passage from 2002 (●) and 2003 (▼) with a pulse of recruitment (1.0 x 10^{-7}) in 2002 and zero recruitment in 2003. Some symbols are not visible because of the similarity between the observed and predicted values.

recruitment to zero resulted in a 3% increase in the PS between observed and predicted size-class abundances for 2003. This suggests that interannual variability in recruitment at Robbers Passage is high.

5.4 Discussion

Identifying the most important life history characteristics for invasion success has been a key objective of invasion biologists for decades (Barrett and Richardson, 1986; Ehrlich, 1986). While characteristics such as fast growth rate, high fecundity, and a wide range of environmental tolerances (Ehrlich, 1986) are likely to apply to many invaders, identifying the most crucial life history stage for specific invasions is essential for addressing conservation and mitigation concerns (Caswell, 2001), and to determine where to focus future research efforts (Parker, 2000). In the case of the varnish clam invasion of coastal BC, the factor that contributes the most to population growth is the survival of the larger size-classes. This finding was consistent among sites, although the sensitivity and elasticity was highest for the survival of 40-50 mm clams for Bamberton, and ≥50 mm clams for Robbers Passage. The high sensitivities and elasticities corresponded to the highest survival rates at each site that also occurred in the same size classes (i.e. 0.83 for Bamberton clams 40-50 mm, 0.72 for ≥50 mm Robbers Passage clams). Stochastic matrix models of barnacles and bivalves have also found similar results, in which population dynamics are more sensitive to changes in survival than recruitment (Nakaoka, 1997; Svensson et al., 2004).

An invader may be successful either because it *shares* traits with local species, allowing it to survive in the new region by means similar to local species, or alternatively, because it *differs*, allowing utilization of different resources (Sakai et al., 2001). Given the importance of adult survival to population growth, it is the adult characteristics of the varnish clam that differ from those of local species that are the most influential. For instance, varnish clam morphology (i.e. thin shell, compressed shape) increases its vulnerability to predation (Chapter 4), but also increases its burial efficiency (Nel et al., 2001). Similarly, its deeper burial depth decreases the varnish clam's accessibility to predators (Chapter 4), while increasing its ability to live high in the intertidal zone, which consequently decreases its exposure to certain predators (e.g. those that can only feed when submerged, such as crabs and flatfish). These adult morphological and behavioural characteristics, because of their influence on adult survival, have likely played a dominant role in the invasion success of the varnish clam in coastal BC.

Varnish clam populations appear to receive variable levels of recruitment, ranging from regular annual recruitment (Bamberton), to relatively low levels of annual recruitment or, episodic pulses of recruitment interspersed with years of no recruitment (Robbers Passage). The ability of bivalves to sustain populations even in the face of highly variable recruitment levels has been demonstrated in studies of *Yoldia notabilis* (Nakaoka, 1993). Nakaoka (1993) conducted a long-term study of bivalve recruitment and showed that the population was maintained by occasional recruitment pulses (i.e. once every few years), large enough to cause increases in population size ($\lambda > 1$). Varnish clam recruitment is variable in Puget Sound (Selleck, 2003) and in its home range (Miyawaki and Sekiguchi, 2000), and presumably in coastal BC, as well. The varnish clam has a life span of at least 6 years, therefore populations are likely to be sustainable from occasional years of successful recruitment that increase λ.

Establishing the relative importance of pre- and post-settlement processes in driving adult population dynamics has been a central theme in marine ecology (Olaffson et al., 1994). The hypothesis that variation in larval recruitment causes variation in adult population size (Thorson, 1950; Fig. 5.8a) has been challenged by several studies suggesting that post-settlement processes (e.g. resource competition, predation, physical disturbance) are more important in structuring communities (Olaffson et al., 1994; Fig. 5.8b.). The low sensitivities and elasticities observed here for the reproductive values, 'F' (which also incorporate recruitment in the matrix model) indicate that post-settlement processes are influential for adult population dynamics of varnish clams for Bamberton and Robbers Passage. The *relative* importance of pre- and post-settlement processes may vary however, with larval settlement being more influential at low population and recruitment densities, and post-settlement processes becoming increasingly important at higher

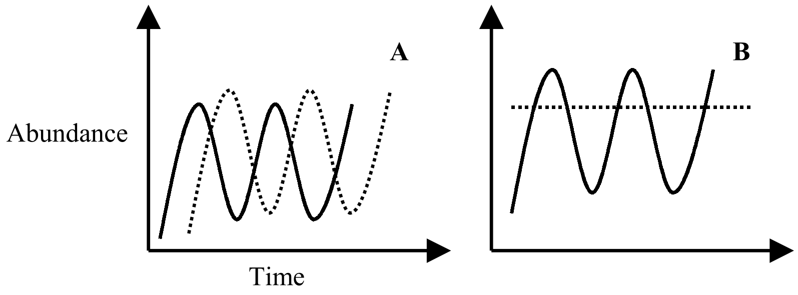


Fig. 5.8. Hypothetical relationship between time, larval recruitment (___) and population size (......) : (A) population size tracks larval recruitment variation, and (B) population size is de-coupled from larval recruitment.

population and recruitment densities (Caley et al., 1996; Morgan, 2001). Differences in the sensitivity and elasticity values for 'F' between the two populations support this suggestion, with sensitivities and elasticities for Robbers Passage (which experiences low recruitment) 6 and 27 times greater than the Bamberton population. This suggests that the adult population at Robbers Passage will be more sensitive to recruitment variations than the Bamberton population. Similarly, population studies of barnacles have shown that sites with low rates of larval settlement also have low adult abundance that varies greatly between years, whereas sites with high larval settlement have both a higher average adult abundance and lower interannual variability in abundance, regardless of differences in settlement (Gaines and Roughgarden, 1985).

My field observations support the matrix analysis results indicating that post-settlement processes are more influential at Bamberton compared to Robbers Passage. The monthly length-frequency distributions show evidence of higher post-settlement mortality at Bamberton (Chapter 3, Fig. 3.8). At Bamberton there are a large number of small individuals (<20 mm) however, they appear to suffer high mortalities because few are seen to grow through to the larger size-classes. Alternatively, at Robbers Passage there are few small clams (<20 mm). Nonetheless, a pulse of individuals is seen to survive and grow through the larger size-classes (Chapter 3, Fig. 3.7). Therefore, at Bamberton, where recruitment levels are high, post-settlement processes appear to be more influential (Fig. 5.9, solid line) relative to Robbers Passage (where recruitment levels are low), and pre-settlement processes (e.g. larval supply) are also important to adult population dynamics (Fig. 5.9, dashed line). Studies in the varnish clams native range also show that where larval supply and settlement are high, post-settlement processes determined adult population characteristics (Sekiguchi et al., 1995).

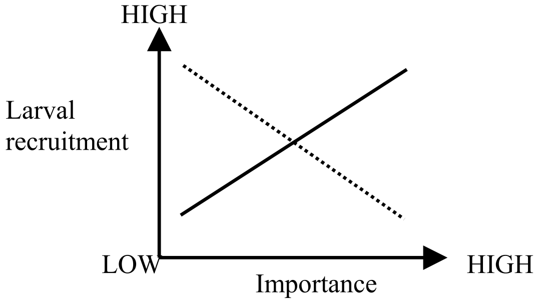


Fig. 5.9. Relative importance of pre- (......)and post-settlement (___) process and their relation to larval recruitment.

If adult population size is directly related to recruitment levels, then variable recruitment at each site may be the source of interannual variation in population size. However if population size is stable, despite variable recruitment, then density dependence among the adults may be influential (Caley et al., 1996). The abundance and size-structure of the Robbers Passage population appeared to be influenced by the pulse of recruits observed in 2002, suggesting that variable recruitment may contribute to population variation in size-structure and density. In contrast, the length-frequency distributions at Bamberton remained fairly consistent from year to year (Chapter 3, Fig. 3.8) despite high recruitment levels, indicating that density dependence may also influence the adult population at Bamberton, which has twice the density of Robbers Passage. The slower growth rates and lower fecundities at Bamberton (Chapter 2, 3) may be the result of density dependent influences on adults in this population. Slower growth rates may cause increased mortalities at small sizes because clams will take longer to reach a size of 30 mm, when they can bury more deeply to avoid predators and desiccation stress (Chapter 3). This could influence population size-structure, resulting in fewer individuals between 10-30 mm, as observed for the Bamberton length-frequency distributions (Fig. 3.8).

Based on population growth rates (λ=0.73, Robbers Passage; λ=0.84, Bamberton) both populations of varnish clams are currently declining. Correspondingly, annual population survey data from Robbers Passage showed a 24% and 22% decrease in 2002 and 2003. The slightly lower decrease in 2003 is likely the result of the recruitment pulse observed in 2002. Decreasing population growth rates have been observed in other invasions, with λ progressively declining as the invader becomes more established (Parker, 2000). Based on results from the life table response experiment, between-site differences in population growth rates are due to the contribution of differences in survival of clams that are 40-50 mm in length. Interestingly, the largest differences in the transition matrix elements occurred between reproductive values of clams that were ≥50 mm (Fig. 5.6.). Although the difference in reproductive values between the sites was twice that of the 40-50 mm clam survival rates (Fig. 5.6a), differences between survival rates at each site (Fig. 5.6b) had the largest contribution to the population growth rate differences. This demonstrates that the largest differences in vital rates between populations are not necessarily the largest contributors to differences in population growth.

Neither population appears to be close to achieving its stable size-class structure, which is to be expected given the fairly recent timeline of the invasion and the variability in recruitment levels. The Bamberton population (presumably the older population, given its closer proximity to Vancouver) had a smaller damping ratio, indicating that it is farther from reaching its stable size structure than is Robbers Passage (presumably the younger population). This may be the result of the difference in population growth rates. The damping ratio may have a negative correlation with λ, whereby faster growing populations converge toward their stable population structure more slowly (Caswell, 2001). The relatively small damping ratios of both populations indicate that these populations may be influenced by short-term behaviour or transient dynamics (i.e. varying size distributions) that may differ from asymptotic or long-term behaviour at the stable size distribution (Horvitz and Schemske, 1995). Therefore, the *current* populations at Bamberton and Robbers Passage may actually have different population growth rates, sensitivities and elasticities than the results (which are based on the asymptotic dynamics) suggest. In this study however, I was primarily interested in the asymptotic behaviour of the populations that represent the long-term population dynamics.

One drawback of deterministic matrix models is the assumption that vital rates remain constant over time (Caswell, 2001). Thus, uncertainty and plasticity in these rates are not accounted for (Miller, 2001). Stochasticity can be incorporated into these rates through matrix or element selection (Kaye, 2001), thereby allowing vital rates to vary temporally. The results of incorporating stochasticity can vary greatly depending on the choice of probability distribution that is assumed (Nakaoka, 1997). Because of the short duration of this study, however, I was unable to observe (and consequently incorporate) variation in vital rates. Nevertheless, the observed vital rates do appear to be robust against variation, given the consistently high sensitivities and elasticities observed for the large size-classes, even when growth transition and survival rates were allowed to vary.

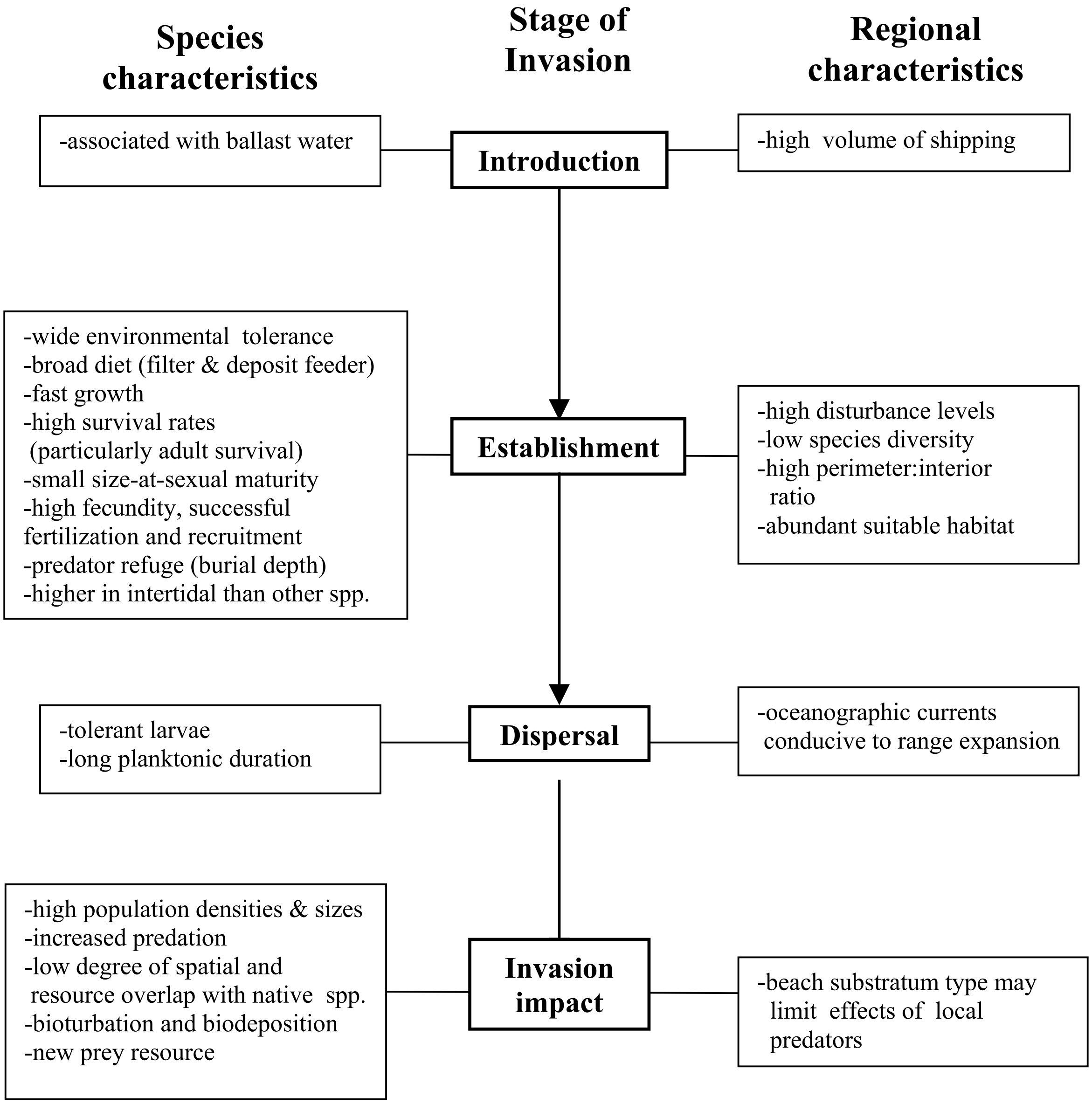
This study represents one of the first applications of a matrix demographic modeling approach to investigate marine invasion dynamics. Observed differences in recruitment, and corresponding population dynamics, provide evidence of the importance of post-settlement relative to pre-settlement processes, particularly for populations with high recruitment (Bamberton). Despite differences in growth and reproductive rates between the two sites, adult varnish clam survival is the most crucial vital rate for population growth at both Robbers Passage and Bamberton. Thus, any process that affects survival of large clams will therefore influence population growth. Because varnish clams must bury deeply in order to avoid predators (and keep survival rates high), varnish clams are unlikely to establish large populations on beaches with substratum that does not allow deep burial. Furthermore, harvesting of this species is likely to have an impact on its population growth not only by direct removal of clams, but also because the clams most likely to be removed (i.e. the largest individuals) are also those that are most crucial to population growth. Future research should therefore focus on factors influencing adult survival and determining the level of temporal variation in vital rates, in order to investigate the influence of stochasticity on population growth rates and size-class sensitivity and elasticity.

Chapter 6. Conclusions

The key to the success of the varnish clam invasion in the Northeast Pacific involves a combination of characteristics of both the species itself and the particular recipient region. The wide environmental tolerances of its larval form, its lengthy planktonic phase (Chapter 2), rapid early growth rate (Chapter 3) and small size-at-sexual-maturity have all contributed to the varnish clam's ability to establish and expand its range in coastal BC. A thin shell and compressed shape increase its vulnerability to local predators, but its deep burial provides a refuge (Chapter 4). This interaction between the varnish clams' life history characteristics, and the region it invaded, has played an essential role in its invasion success. Figure 6.1 summarizes the species and region characteristics that have been important during the different stages of the varnish clam invasion.

Life History Characteristics: Factors limiting populations can change over the course of an invasion. For instance, the characteristics that enable a species to be a good disperser may not be as helpful in ensuring successful establishment (Vermeij, 1996; With, 2002). The varnish clam has been successful since its introduction because its small size-at-maturity and fast growth rates have helped facilitate the 'establishment phase' of invasion while its long planktonic duration facilitated the 'dispersal phase' (Fig. 6.1). In addition, fertilization success (including spawning behaviour) and successful recruitment, while not studied here, has likely contributed to its establishment. In the early stages of an invasion, a life history that includes high growth rates, high reproductive investment and

Fig. 6.1. A generalized representation of the stages of an invasion (Sakai et al., 2001; With, 2002) adapted to illustrate the life-history traits and regional characteristics that influenced the varnish clam invasion in coastal BC.



early maturation are advantageous. However, in the later stages of an invasion (i.e. when the increased population density can lead to higher intraspecific competition), decreased reproductive investment (e.g. lower fecundity) and later maturation are often observed (Bohn et al., 2004). The lower fecundity and slower growth rates observed at the presumably ‘older’ invasion site at Bamberton may, therefore, be the result of a changing life history over the course of the invasion as the population density has increased.

In general, an invader may become successful because it shares common traits with local species that allow it to survive in the same habitat or, because it has different traits that allow it to occupy empty habitats (Sakai et al., 2001). The varnish clam (in addition to many other bivalve species) does both – its larval characteristics are similar to those of native bivalves while the adults have a different morphology (thinner shell, more compressed shape) than co-occurring native species.

As varnish clams approach a size of ~30 mm, survival rate increases and growth begins to decrease (Chapter 3, Fig. 3.14). This is also the size at which the weak relationship between shell length and burial depth disappears (Fig. 3.11). The importance of burial depth has implications for determining not only the maximum intertidal height that varnish clams can occupy, but also on which beaches it can become established (i.e. based on its ability to bury in the substrate type). Because varnish clams must bury deeply to avoid predators (and increase survival), they are unlikely to establish large populations on beaches (or areas within a beach) where substratum limits burial depth and predators are present. This interaction between substrate composition and burial depth therefore enables predators such as crabs to influence the distribution of varnish clams. If local predators preferentially feed on introduced prey (see Chapter 4), then the varnish clam invasion in coastal BC may serve to alleviate predation pressure on native bivalve species on beaches where varnish clam burial depth is limited. Alternatively, the invasion could result in increased predation pressure by providing another prey source for the crabs.

Matrix demographic analysis (Chapter 5) indicated that adult survival is the vital rate most crucial for varnish clam population growth and, consequently, invasion success. Characteristics that influence adult survival (e.g. shell morphology, burial depth) are therefore very important to population growth. Comparison of the Robbers Passage and Bamberton sites shows that even with different patterns of recruitment, adult survival remains important across sites. Both populations appear to be declining slowly at present. However it seems likely, with high varnish clam densities and large populations sizes observed, they will remain sustainable in the long term even with only episodic recruitment. A successful year of recruitment can result in an increase in population growth rate such that $\lambda > 1$. For Robbers Passage and Bamberton the recruitment levels required are 3.5×10^{-6} and 7×10^{-5}, both within the realm of observations for other bivalve populations (Brousseau, 1978). Bivalve populations can therefore be maintained by these successful recruitment events once every few years (Nakaoka, 1993).

Characteristics of the recipient region: Regional characteristics that have contributed to the varnish clam invasion of coastal BC include the availability of appropriate habitat and favourable oceanographic climate and current patterns (Fig. 6.1). Theory suggests that invasibility increases with higher perimeter:interior ratios (Byers et al., 2002). Coastal BC, with its numerous islands and inlets, has a very high perimeter:interior ratio, presumably increasing its susceptibility to invasion. The geographic complexity of BC's coastline also provides thousands of kilometres of coastline near major ports, further increasing the probability that invaders will reach suitable habitat. The regional landscape structure (i.e. abundant beaches) in BC was well suited to invasion by the varnish clam, and the particular point of introduction (i.e. the Port of Vancouver area) was ideally situated within the regional oceanographic setting for dispersal not only in coastal BC, but southwards toward the United States.

Disturbance can also influence invasibility (Byers, 2002). For instance, Baynes Sound (in the Strait of Georgia), an area where the varnish clam is already well established, is also an extensive shellfish farming area with many altered beaches (e.g. placement of predator netting to protect clam farms). Alteration of the beaches for shellfish farming practices, along with selective removal of harvested species, may have aided the invasion by protecting varnish clam larvae that settle under the predator netting and/or by making more resources available (i.e. with the selective removal of other species).

For an invasion to be successful, the recipient region must have a climate similar to the invader's native region (Vermeij, 1996). However, equally important for marine invaders are local and regional physical oceanographic patterns. The varnish clam invasion in coastal BC provides an excellent example of this, particularly in light of the similarity between its dispersal route and that of the Manila clam in the early 1900's (Quayle and Bourne, 1972). The velocity of local currents during the summer (i.e. when the larvae are in the water column) provide the varnish clam with the potential to disperse throughout its current distributional range in as little as one reproductive season (Chapter 2). The progressive spread of the varnish clam from the Strait of Georgia (SoG) to the west coast of Vancouver Island (WCVI), Washington and Oregon also indicates that the SoG may be an important source of larvae for populations on the WCVI and the coast of the United States. Similar length-frequency distributions from population surveys at several geographically separate sites (e.g. Robbers Passage, Hand Island, Dodd Island and Jericho) suggests that regional processes influence recruitment dynamics for some populations. This may be due, in part, to oceanographic connectivity between the SoG and the WCVI (indicating that the Strait of Juan de Fuca is an important larval transport corridor). This study thus highlights the importance of regional oceanographic circulation in invasion dynamics.

Another aspect of coastal BC that may increase its invasibility is its recent glacial history (i.e. as compared to other regions in the Northeast Pacific). Most of BC was covered by ice during the last glaciation approximately 15 000 years ago (Candy et al., 2002; Fulton, 1969). This glaciation was followed by a warming period that resulted in the northward retreat of the glacier (Candy et al., 2002). After deglaciation, sea level dropped and the intertidal zone was established at the approximate height it is today. The relatively recent deglaciation of BC has therefore left a shorter time period for colonization of the intertidal compared to southern regions, perhaps influencing current level of species diversity. One way to examine this possibility would be to compare the species diversity and frequency of invaders from coastal BC with a similar temperate system that had not been glaciated (or which had been deglaciated earlier). However, such an exercise is beyond the scope of this thesis.

The negative latitudinal gradient of marine species (i.e. species diversity generally decreases poleward; Hillebrand, 2004) may also play a role in region invasibility. As species diversity decreases with increasing latitude there may be more habitats and/or food resources available to new invaders that have not yet been colonized or utilized by native species, thereby increasing invasibility. However, there also appears to be a latitudinal gradient in non-indigenous species, with the number of non-indigenous species (which, in the Northeast Pacific, are often species native to warmer climates) decreasing at higher latitudes because of increasingly severe abiotic conditions (Sax, 2001). The potential increase in regional vulnerability, due to decreasing species diversity at higher latitudes, may therefore be negated by the accompanying harsher abiotic conditions.

Invasion Impacts: Currently, the varnish clam does not appear to be causing measurable declines in co-occurring bivalve species in coastal BC (Chapter 3). Varnish clams bury deeper than co-occurring species, decreasing competition for space, and use different feeding modes (suspension, deposit and pedal feeding), likely reducing direct competition for resources (Gillespie et al., 1999). Therefore, the varnish clam is unlikely to exert intense direct competitive pressure on local species (i.e. as compared to an invader species that occupies the same depth and utilizes identical food resources). However, if interspecific competition is currently low (e.g. perhaps due to the relatively recent nature of the invasion), then competitive effects on native species may simply not yet be detectable.

In their native range, varnish clams have been shown to decrease the organic content of the substratum by deposit feeding (Tsuchiya and Kurihara, 1980). Thus, if varnish clams can utilize food resources more effectively than native species in coastal BC, they may yet have a significant impact. Given their very high densities, varnish clam bioturbation and biodeposition activities may be substantial, and have the potential to change nutrient fluxes, chemistry, oxygen content and stability of beach sediments (Ahn et al., 1993; Lelieveld et al., 2004; Lenihan and Micheli, 2001; Vaughn and Hakenkamp, 2001). Through these activities, the varnish clam may alter the composition of the benthic communities they have invaded in BC (Vaughn and Hakenkamp, 2001). Moreover, if the varnish clam invasion begins to alter population-level processes (i.e. by reducing food abundance, changing the substratum), these impacts may even become ecosystem-level processes (Vitousek, 1990).

The impact of the varnish clam invasion in the Northeast Pacific will likely become more evident as the invasion progresses and its range expands. However, due to the lack of baseline ecological data from much of coastal BC, these impacts may prove difficult to quantify. Research focusing on the effect of varnish clam density on sediment characteristics (e.g. oxygen, stability, microalgal biomass) would be particularly valuable for assessing future invasion impacts, since changes in substratum composition are likely to influence the benthic community as a whole. The unique morphology and behaviour of the varnish clam decreases its space and resource overlap with native bivalves. This limited overlap, in combination with the extremely high densities that it attains, suggests that the varnish clam is likely to have a large *indirect* impact on native bivalve communities by altering the physical aspects of the habitat (i.e. changing substratum via bioturbation etc.).

Despite its potential to alter benthic community structure in the future, there may also be some positive impacts (to man) of the varnish clam invasion. Currently, a commercial varnish clam fishery is being developed in coastal BC. However, no positive economic impact of the invasion has emerged thus far. The market is being developed slowly, to allow sufficient time for consumer awareness to increase before varnish clams are marketed widely (i.e. in order to secure a higher value for the product). Processing issues, such as the purging of pea crabs before varnish clams go to market, will also need to be addressed (Gillespie et al., 2001). Therefore, it will likely be some years before any potential economic impacts will be noticeable.

Synthesis: Many invasion studies focus on individual aspects of invasions such as dispersal (Jamieson et al., 2002; Neubert et al., 2000), life history characteristics (Bohn et al., 2004; Devin et al., 2004; Rosecchi et al., 2001) or predator-prey dynamics (Grosholz et al., 2000; Reusch, 1998). However, to fully understand an invasion one needs to study aspects of both the invader and the recipient region, ideally over the course of the invasion as it progresses through the various stages. Doing this requires a truly multidisciplinary approach, incorporating numerous aspects of the invasion (e.g. larval ecology, adult population dynamics, species interactions), utilizing field and laboratory experimental and survey data (particularly if, as was the case with the varnish clam, very little was known about the species), and finally, interpreting the results within the context of the regional landscape.

Combining information from these different approaches in this study revealed findings that otherwise would not have been apparent. For example, integrating data on larval and reproductive life history with local oceanography provided information on not only planktonic duration, but also when (seasonally) and where the larvae may be dispersed (Chapter 2). By combining field observations of shell length, flesh weight and burial depth with mark-recapture experiments to determine survival and growth rates (Chapter 3), the importance of quickly achieving a size of 30 mm (i.e. where burial depth, and subsequently survival, increased) became evident. Using the species co-occurrence data from field surveys, laboratory predator/prey preference experiments were designed to incorporate the suite of prey species most likely encountered by local predators. As seen in Chapter 4, varnish clam co-occurrence with local bivalves can affect predator-prey interactions, demonstrating the potential of native predators to influence the varnish clam's distribution. Furthermore, although a number of different models have previously been used to investigate invader range expansions and dispersal (Hastings, 1996; Neubert et al., 2000), rarely has a matrix demographic approach been used for marine invasions. Although life history characteristics on their own provide useful information regarding the varnish clams' invasion success, using these data in a matrix demographic model clarified which specific vital rates and size-classes are most influential for population growth and therefore, invasion success (Chapter 5).

As a model system for studying marine invasion dynamics in coastal BC, the varnish clam introduction has highlighted the importance of Vancouver harbour area as a hot-spot for future introductions of other marine species with complex life-cycles, particularly in light of the regional oceanographic patterns which are highly conducive to the rapid spread of species that have a planktonic larval stage. At a larger scale, BC's structurally complex coastline structure provides a wide diversity of suitable shoreline habitats for many species, and the regional oceanography setting makes it a good 'source' region for dispersal to areas outside of BC.

Practical Implications: Invasive species are often detected only after their populations are already widespread and well-established, and by which point eradication is impossible. Early detection of new invaders may permit eradication or containment, thus limiting dispersal (Simberloff, 2003). Currently, there are no programs that focus specifically on detecting the arrival of non-indigenous marine species in coastal BC. There are, however, volunteer stewardship programs that monitor shorelines and the shallow subtidal in coastal BC to detect changes in species composition due to human activities. These programs could easily be expanded (indeed should be expanded) to include non-indigenous species monitoring as a fairly inexpensive means of providing an "early warning" that a new species may have arrived. Ballast water disposal models that are coupled with high-resolution physical circulation models (Larson et al., 2003) should also be used to identify beaches most likely to be inoculated by drifting larvae. Monitoring efforts could then be focused in these areas to increase the likelihood that invaders will be detected quickly. Furthermore, ballast water regulations and other measures that are intended to prevent non-indigenous species introductions should be targeted in areas where introductions are likely to have the farthest-reaching impacts, such as Vancouver Harbour.

The identification of adult survival as the most important vital rate to varnish clam population growth is of particular use to conservation and fisheries managers. Any management decision that influences the survival of adults may, subsequently, influence varnish clam population growth (e.g. the placement of predator netting on a beach to prevent predation on shellfish farms). For identifying marine conservation areas, where the goal is to preserve local species diversity, managers could, for instance, choose beaches that have substrate that limits varnish clam burial depth, thereby decreasing survival rates and the likelihood of varnish clams establishing large populations in the protected area.

LITERATURE CITED

Abraham, B.J., Dillon, P.L., 1986. Species profiles: life histories and environmental requirements of coasts and fishes and invertebrates (mid-Atlantic) -- softshell clam. U.S. Fish Wildl. Serv. Biol. Rep. 82 (11.68), 18pp.

Ackerman, J.D., Sim, B., Nichols, S.J., Claudi, R., 1994. A review of the early life history of zebra mussels (*Dreissena polymorpha):* comparisons with marine bivalves. Can. J. Zool. 72, 1169-1179.

Ahn, I., Lopez, G., Malouf, R., 1993. Effects of the gem clam *Gemma gemma* on early post-settlement emigration, growth and survival of the hard clam *Mercenaria mercenaria*. Mar. Ecol. Prog. Ser. 99, 61-70.

Anderson, E.A., Austin, W.C., Byers, S., Lipovsky, S., 2000. Literature review on the non-indigenous invertebrates of the Strait of Georgia. Edward Anderson Marine Sciences, Sidney, BC, pp. 96.

Appleyard, C.L., Dealteris, J.T., 2001. Modeling growth of the northern quahog, *Mercenaria mercenaria*. Abstracts of the 2000 Annual Meeting of the National Shellfisheries Association 20, 1117-1125.

Auster, P.J., Crockett, L.R., 1984. Foraging tactics of several crustacean species for infaunal prey. J. Shellfish Res. 4, 139-143.

Baghurst, B.C., Mitchell, J.G., 2002. Sex-specific growth and condition of the Pacific oyster (*Crassostrea gigas* Thunberg). Aquacult. Res. 33, 1253-1263.

Barrett, S.C.H., Richardson, B.J., 1986. Genetic attributes of invading species. In: Burdon, J.T. (Ed.), Ecology of biological invasions: An Australian perspective. Cambridge University Press, Cambridge, pp. 21-29.

Bartoli, M., Nizzoli, D., Viaroli, P., Turolla, E., Castaldelli, G., Fano, E.A., Rossi, R., 2001. Impact of *Tapes philippinarum* farming on nutrient dynamics and benthic respiration in the Sacca di Goro. Hydrobologia 455, 203-212.

Beekey, M.A., McCabe, D.J., Marsden, J.E., 2004. Zebra mussels affect benthic predator foraging success and habitat choice on soft sediments. Oecologia 141, 164-170.

Beukema, J.J., Honkoop, P.J.C., Dekker, R., 1998. Recruitment in *Macoma balthica* after mild and cold winters and its possible control by egg production and shrimp predation. Hydrobologia 375/376, 23-34.

Blott, S.J., Pye, K., 2001. Gradistat: a grain size distribution and statistics package for the analysis of unconsolidate sediments. Ear. Surf. Process. Landforms 26, 1237-1248.

Blundon, J.A., Kennedy, V.S., 1982. Refuges for infaunal bivalves from blue crab, *Callinectes sapidus* (Rathbun), predation in Chesapeake Bay. J. Exp. Mar. Biol. Ecol. 65, 67-81.

Bohn, T., Sandlund, O.T., Amundsen, P., Primicerio, R., 2004. Rapidly changing life history during invasion. Oikos 106, 138-150.

Boulding, E.G., 1984. Crab-resistant features of shells of burrowing bivalves: decreasing vulnerability by increasing handling time. J. Exp. Mar. Biol. Ecol. 76, 201-223.

Bourne, N., 1971. The effects of temperature, salinity and food on the development of the larvae of butter clams, (*Saxidomus giganteus*, Deshayes). Proc. Natl. Shellfish. Assoc. 61, 1.

Bourne, N., 1982. Distribution, reproduction, and growth of Manila Clam, *Tapes philippinarum* (Adams and Reeves), in British Columbia. J. Shellf. Res. 2, 47-54.

Bourne, N., Smith, D.W., 1972. The effect of temperature on the larval development of the horse clam, *Tresus capax* (Gould). Proc. Natl. Shellfish. Assoc. 62, 35-38.

Bradbury, A., Tagart, J.V., 2000. Modeling geoduck, *Panopea abrupta* (Conrad, 1849) population dynamics. II. Natural mortality and equilibrium yield. Abstracts of the 2000 Annual Meeting of the National Shellfisheries Association 19, 63-70.

Breese, W.P., Phibbs, F.D., 1970. Some observations on the spawning and early development of the butter clam, *Saxidomus giganteus* (Deshayes). Proc. Natl. Shellfish. Assoc. 60, 95-98.

Brey, T., 2001. Population dynamics in benthic invertebrates: a virtual handbook. Alfred Wegener Institute for Polar and Marine Research, Germany.

Brousseau, D.J., 1978. Population dynamics of the soft-shell clam *Mya arenaria*. Mar. Biol. 50, 63-71.

Brousseau, D.J., Baglivo, J.A., 1982. Estimation of equilibrium settlement rates for benthic marine invertebrates: its application to *Mya arenaria* (Mollusca: Pelecypoda). Fish. Bull. 80, 642-644.

Brownie, C., Hines, J.E., Nichols, J.D., Pollock, K.H., Hestbeck, J.B., 1993. Capture-recapture studeis for multiple strata including non-Markovian transitions. Biometrics 49, 1173-1187.

Buchanan, J.B., 1984. Sediment analysis. In: Holme, N.A., McIntyre, A.D. (Eds.), Methods for the study of marine benthos. Blackwell, Oxford, pp. 41-65.

Burnham, K.P., Anderson, D.R., 1998. Model selection and inference: a practical information-theoretic approach. Springer, New York.

Burnham, K.P., Anderson, D.R., White, G.C., 1995. Selection among open population capture-recapture models when capture probabilities are heterogeneous. J. Appl. Stat. 22, 611-624.

Byers, J.E., 2002a. Physical habitat attribute mediates biotic resistance to non-indigenous species invasion. Oecologia 130, 146-156.

Byers, J.E., 2002b. Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. Oikos 97, 449-458.

Byers, J.E., 2005. Marine reserves enhance abundance but not competitive impacts of a harvested nonindigenous species. Ecology 86, 487-500.

Byers, J.E., Reichard, S., Randall, J.M., Parker, I.M., Smith, C.S., Lonsdale, W.M., Atkinson, I.A.E., Seastedt, T.R., Williamson, M., Chornesky, E., Hayes, D., 2002. Directing research to reduce the impacts of nonindigenous species. Cons. Biol. 16, 63-640.

Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P., Menge, B.A., 1996. Recruitment and the local dynamics of open marine populations. Annu. Rev. Ecol. Syst. 27, 477-500.

Candy, J.R., Irvine, J.R., Parken, C.K., Lemke, S.L., Bailey, R.E., Wetklo, M., Jonsen, K., 2002. As discussion paper on possible new stock groupings (Conservation Units) for Fraser River chinook salmon. Canadian Stock Assessment Secretariat Research Document 2002/085.

Carlton, J.T., 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. Oceanogr. Mar. Biol. Ann. Rev. 23, 313-371.

Carlton, J.T., Geller, J.B., 1993. Ecological roulette: the global transport of nonindigenous marine organisms. Science 261, 78-83.

Carroll, J.C., Winn, R.N., 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Southwest) - brown rock crab, red rock crab, and yellow crab. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.117), U. S. Army Corps of Engineers,TR EL-82-4, 16 pp.

Caswell, H., 2001. Matrix population models: construction, analysis and interpretation. Sinauer Associates, Inc. Publishers, Sunderland, 722 pp.

Chesson, J., 1978. Measuring preference in selective predation. Ecology 59, 211-215.

Chew, K., Ma, A.P., 1987. Species profiles: life histories and environmental requirements of coasts and fishes and invertebrates (Pacific Northwest) -- common littleneck clam. U.S. Fish Wildl. Serv. Biol. Rep. 82 (11.78), 22pp.

Chicharo, L., Chicharo, M.A., 2001. Effects of environmental conditions on planktonic abundances, benthic recruitment and growth rates of the bivalve mollusc *Ruditapes decussatus* in a Portugese coastal lagoon. Fisheries Res. 53, 235-250.

Choi, S.H., 2001. The study of secondary production of *Nuttallia olivacea* in the shore of Dadaepo, Pusan. National University, Korea, Pukyong, pp. 32.

Christensen, A.M., McDermott, J.J., 1958. Life-history and biology of the oyster crab, *Pinnotheres ostreum* (Say). Biol. Bull. 114, 146-179.

Cohen, A.N., Carlton, J.T., 1998. Accelerating invasion rate in a highly invaded estuary. Science 279, 555-558.

Cohen, A.N., Carlton, J.T., Fountain, M.C., 1995. Introduction, dispersal and potential impacts of the green crab *Carcinus maenas* in San Francisco Bay, California. Mar. Biol. 122, 225-237.

Cooch, E., White, G., 2004. Program MARK: analysis of data from marked individuals. http://www.phidot.org/software/mark/docs/book/.

Culliney, J.L., Boyle, P.J., Turner, R.D., 1974. New approaches and techniques for studying bivalve larvae. In: Smith, W.L., Chanley, M.H. (Eds.), Culture of marine invertebrate animals. Plenum Publishing Corp., New York, pp. 257-271.

Dame, R.F., 1996. Ecology of marine bivalves: an ecosystem approach. CRC Press, New York.

Davis, J.L.D., Levin, L.A., 2002. Importance of pre-recruitment life-history stage to population dynamics of the woolly sculpin *Clinocottus analis*. Mar. Ecol. Prog. Ser. 234, 229-246.

Day, R., McEdward, L., 1984. Aspects of the physiology and ecology of pelagic larvae of marine benthic invertebrates. In: Steidinger, K., Walker, L.M. (Eds.), Marine plankton life cycle strategies. CRC Press, Boca Raton, Fla., pp. 93-113.

Devin, S., Piscart, D., Beisel, J., Moreteau, J., 2004. Life history traits of the invader *Dikerogrammus villosus* (Crustacea: Amphipoda in the Moselle River, France. Internat. Rev. Hydrobiol. 89, 21-34.

DFO, 1999a. Manila clam. DFO Science Stock Status Report C6-03 (1999).

DFO, 1999b. Native littleneck clam. DFO Science Stock Status Report C6-02 (1999).

DFO, 2000. Geoduck Clam. DFO Science Stock Status Report C6 05.

Dinnel, P.A., 2000. Biological and ecological assessments of *Nuttallia osbscurata* in north Puget Sound. Abstracts of the 2000 Annual Meeting of the National Shellfisheries Association.

Donovan, T.M., Welden, C.W., 2002. Spreadsheet exercises in ecology and evolution. Sinauer Associates Inc., Massachusetts, 556 pp.

Dow, R.L., Wallace, D.E., 1961. The soft-shell clam industry of Maine, U.S. Fish and wildlife service, Department of the Interior.

Drent, J., 2002. Temperature responses in larvae of *Macoma balthica* from a northerly and southerly population of the European distribution range. J. Exp. Mar. Biol. ecol. 275, 117-129.

Ebersole, E.L., Kennedy, V.S., 1995. Prey preference of blue crabs *Callinectes sapidus* feeding on three bivalve species. Mar. Ecol. Prog. Ser. 118, 167-177.

Ebert, T.A., Dixon, J.D., Schroeter, S.C., Kalvass, P.E., Richmond, N.T., Bradbury, W.A., Woodby, D.A., 1999. Growth and mortality of red sea urchins *Stronglocentrotus franciscanus* across a latitudinal gradient. Mar. Ecol. Prog. Ser. 190, 189-209.

Eggleston, D.B., Lipcius, R.N., Hines, A.H., 1992. Density-dependent predaiton by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. Mar. Ecol. Prog. Ser. 85, 55-68.

Ehrlich, P.R., 1986. Which animal will invade? In: Drake, J.A. (Ed.), Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, pp. 79-95.

Elner, R.W., Hughes, R.N., 1978. Energy maximization in the diet of the shore crab, *Carcinus maenas*. J. Anim. Ecol. 47, 103-116.

Elton, C.S., 1958. The ecology of invasions by animals and plants. Methuen and Co. Ltd., London.

Eversole, A.G., 1986. Reproductive biology of clam populations in North America: a review. J. Shellfish Res. 7, 117-118.

Fabens, A.J., 1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29, 265-289.

Fairweather, P.G., Underwood, A.J., 1983. The apparent diet of predators and biases due to different handling times of their prey. Oecologia 56, 169-179.

Floyd, T., Williams, J., 2004. Impact of green crab (Carcina maenas L.) predation on a population of soft-shell clams (Mya arenaria L.) in the Southern gulf of St. Lawrence. J. Shellfish Res. 23, 457-462.

Forsyth, R., 1993. *Nuttallia obscurata*, an introduced bivalve (Psammobiidae) in British Columbia. Vancouver Shell News 14, 9-12.

Fulton, R.J., 1969. Glacial lake history, southern interior Plateau, British Columbia. Geological Survey of Canada, Department of Energy, Mines and Resources Paper 69-37.

Gaines, S.D., Roughgarden, J., 1985. Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. Proc. Natl. Acad. Sci. 82, 3707-3711.

Gaspar, M.B., Monteiro, C.C., 1999. Gametogenesis and spawning int he subtidal white clam *Spisula solida*, in relation to temperature. J. Mar. Biol. Assoc. U.K. 79, 753-755.

Gillespie, G., 1995. Distribution and biology of the exotic varnish clam, *Nuttallia obscurata* (Reeve, 1857) in the Strait of Georgia, British Columbia. Abstracts of the 2000 Annual Meeting of the National Shellfisheries Association 20, 1196-1197.

Gillespie, G., Parker, M., Merilees, B., 1999. Distribution, abundance, biology and fisheries potential of the exotic varnish clam (*Nuttallia obscurata*) in British Columbia. Canadian Stock Assessment Secretariat Research Document 99/193, 39.

Gillespie, G., Rusch, B., Gormican, S.J., Marshall, R., Munroe, D., 2001. Further investigations of the fisheries potential of the exotic varnish clam (*Nuttallia obscurata*) in British Columbia. Canadian Stock Assessment Secretariat Research Document 2001/143.

Gillespie, G.E., Kronlund, A.R., 1999. A manual for intertidal clam surveys. Can. Tech. Rep. Fish. Aquat. Sci. 2270, 144p.

Gillespie, G.E., Bourne, N.F., 2004. Exploratory intertidal bivalve surveys. Can. Man. Rep. Fish. Aquat. Sci. In press.

Goodwin, C.L., 1973a. Subtidal geoducks of Puget Sound, Washington, Wash. Dept. Fisheries Tech. Rep.

Goodwin, C.L., 1973b. Effects of salinity and temperature on embryos of the geoduck clam (*Panope generosa* Gould.). Proc. Nat. Shellf. Assoc. 63, 93-95.

Goodwin, C.L., Pease, B., 1989. Species profiles: life histories and environmental requirements of coasts and fishes and invertebrates (Pacific Northwest) -- Pacific geoduck clam. U.S. Fish Wildl. Serv. Biol. Rep. 82 (11.120), 14pp.

Goodwin, L., Shaul, W., Budd, C., 1979. Larval development of the Geoduck calm (*Panope generosa*, Gould). Proc. Natl. Shellfish. Assoc. 69, 73-76.

Gotelli, N.J., 1991. Demographic models for *Leptogorgia virgulata,* a shallow-water Gorgonian. Ecology 72, 457-467.

Grant, C.M., Hooker, S.H., Babcock, R.C., Creese, R.G., 1998. Synchronous spawning and reproductive incompatibility of two bivalve species: *Paphies subtriangulata* and *Paphies australis*. Veliger 41, 148-156.

Grosholz, E.D., Ruiz, G.M., 2003. Biological invasion drive size increases in marine and estuarine invertebrates. Ecology Letters 6, 700-705.

Grosholz, E.D., Ruiz, G.M., Dean, C.A., Shirley, K.A., Maron, J.L., Connors, P.G., 2000. The impacts of a nonindigenous marine predator in a California Bay. Ecology 81, 1206-1224.

Harbo, R., Marcus, K., Boxwell, T., 1997. Intertidal clam resources (Manila, Littleneck and Butter Clam), Volume I: The west coast of Vancouver Island. Can. Man. Rep. Fish. Aquat. Sci. 2416, 116.

Harbo, R.M., 1997. Shells and shellfish of the Pacific Northwest. Harbour Publishing, Madeira, Park, 270 pp.

Harding, J.M., 2003. Predation by blue crabs, *Callinectes sapidus*, on rapa whelks, *Rapana venosa*: possible natural controls for an invasive species? J. Exp. Mar. Biol. Ecol. 297, 161-177.

Harvey, M., Vincent, B., 1989. Spatial and temporal variations of the reproduction cycle and energy allocation of the bivalve *Macoma balthica* (L.) on a tidal flat. J. exp. mar. biol. ecol. 129, 199-217.

Hastings, A., 1996. Models of spatial spread: a synthesis. Biol. Cons. 78, 143-148.

Heath, W.A., 1998. The varnish clam (*Nuttallia obscurata*): Another commercial species. Abstracts of the 2000 Annual Meeting of the National Shellfisheries Association 17.

Helm M.M., Bourne, N., Lovatelli, A. 2004. The hatchery culture of bivalves: a practical manual. Report No. 471, FAO Fisheries Technical Paper, Rome

Heppell, S.S., Crowder, L.B., Menzel, T.R., 1999. Life table analysis of long-lived marine species with implications for conservation and management. Amer. Fish. Soc. Symp. 23, 137-148.

Hillebrand, H., 2004. Strength, slope and variability of marine latitudinal gradients. Mar. Ecol. Prog. Ser. 273, 251-267.

Hobbs, R.J., Huenneke, L.F., 1992. Disturbance, diversity and invasion: implications for conservation. Cons. Biol. 6, 324-337.

Hoffman, A., Bradbury, A., Goodwin, C.L., 2000. Modeling geoduck, *Panopea abrupta* (Conrad, 1849) population dynamics. I. Growth. Abstracts of the 2000 Annual Meeting of the National Shellfisheries Association 19, 57-62.

Honkoop, P.J.C., van der Meer, J., 1997. Reproductive output of *Macoma balthica* populations in relation to winter-temperature and intertidal-height mediated changes of body mass. Mar. Ecol. Prog. Ser. 149, 155-162.

Horvitz, C.C., Schemske, D.W., 1995. Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. Ecology 65, 2, 155-192.

Hughes, T.P., 1990. Recruitment limitation, mortality and population regulation in open systems: a case study. Ecology 71, 12-120.

Hushan, S., 1994. On the sex gonad development and reproductive cycle of *Nuttallia olivacea*. Shangdong Fish. 11, 13-16.

Hushan, S., Gaojun, X., Weigang, W., Huanyu, L., 1988. Effects of salinity on embryonic development and growth of larvae of *Nuttallia olivacea*. Shangdong Fish. 15, 8-11.

Hushan, S., Yiyan, W., Wei, H., Xiaowei, D., 1997. The impact of two kinds antibiotics on the development of larval *Nuttallia olivacea*. Mar. Fish. 19, 160-163.

Ito, K., Okata, A., 1995. Functional relationships between benthic animals and their habitats in tidal flat. Tohoku J. Agricult. Res. 46, 47-60.

Ito, K., Sasaki, K., Omori, M., Okata, A., 2001. Growth rate of the bivalve *Nuttallia olivacea* measured by marking-recapture and caging. Jap. Jour. Benthology 56, 9-17.

Jamieson, G.S., Foreman, M.G.G., Cherniawsky, J.Y., Levings, C.D., 2002. European Green Crab (*Carcinus maenas*) dispersal: the pacific experience. Crabs in cold water regions: biology, management and economics, 561.

Kaye, T.N., 2001. Population viability analysis of endangered plant species: an evaluation of stochastic methods and an application to a rare prairie plant, Department of botany and plant pathology. Oregon State University, Corvallis, pp. 135.

Kolar, C.S., Lodge, D.M., 2001. Progress in invasion biology: predicting invaders. Trends Ecol. Evol. 16, 199-204.

Krebs, C.J., 1994. Ecology: the experimental analysis of distribution and abundance. Harper Collins College Publishers, New York.

Laing, I., Utting, S.D., 1994. The physiology and biochemistry of diploid and triploid manila clam (*Tapes philippinarum* Adams & Reeve) larvae and juveniles. J. Exp. Mar. Biol. Ecol. 184, 159-169.

Larson, M.R., Foreman, M.G.G., Levings, C.D., Tarbotton, M.R., 2003. Dispersion of discharged ship ballast water in Vancouver Harbour, Juan de Fuca Strait, and offshore of the the Washington coast. J.Environ. Eng. Sci. 2, 163-176.

Lebreton, J.D., Burnham, K.P., Anderson, D.R., 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studeis. Ecolog. Monogr. 62, 67-118.

Lee, H., Ban, S., Ikeda, T., Matsuishi, T., 2003. Effect of temperature on development, growth and reproduction in the marine copepod *Pseudocalanus newmani* at satiating food condition. J. Plank. Res. 25, 261-271.

Lee, S.Y., 1996. Distribution pattern and interaction of two infaunal bivalves, *Tapes philippinarum* (Adams and Reeve) and *Anomalocardia squamosa* (Linnaeus) (Bivalvia:Veneridae). J. Exp. Mar. Biol. Ecol. 201, 253-273.

Lelieveld, S.D., Pilditch, C.A., Green, M.O., 2004. Effects of deposit-feeding bivalve (*Macomona liliana*) density on intertidal sediment stability. New Zealand J. Mar. Fw. Res. 38, 115-128.

Lenihan, H.S., Micheli, F., 2001. Soft-sediment communities. In: Bertness, M., Gaines, S.D., Hay, M.E. (Eds.), Marine community ecology. Sinauer Associates, Inc., Sunderland.

Levin, L.A., Caswell, H., 1987. Demographic consequences of larval developmental mode: planktotrophy vs. lecithotrophy in *Streblospio benedicti*. Ecology 68, 1877-1886.

Levings, C.D., Kieser, D., Jamieson, G.S., Dudas, S., 2002. Marine and estuarine alien species in the Strait of Georgia, British Columbia. In: Claudi, R., Nantel, P., Muckle-Jeffs, E. (Eds.), Alien invaders in Canada's waters, wetlands and forests. Natural Resources Canada, Forest Service, Ottawa, pp. 19-28.

Liszka, D., Underwood, A.J., 1990. An experimental design to determine preferences for gastropod shells by a hermit-crab. J. Exp. Mar. Biol. Ecol. 137, 47-62.

Locke, A., Reid, D.M., van Leeuwen, H.C., Sprules, W.G., 1993. Ballast water excahnge as a means of controlling dispersal of freshwater organisms by ships. Can. J. Fish. Aquat. Sci. 50, 2086-2093.

Loosanoff, V.L., Davis, H.C., 1963. Rearing of bivalve mollusks. Adv. Mar. Biol. 1, 1-136.

Mackie, G.L., 1984. Bivalves. In: Tompa, A.S. (Ed.), The Mollusca: reproduction. Academic Press, Inc., New York, pp. 351-418.

Manly, B.F.J., 1974. A model for certain types of selection experiments. Biometrics 30.

Manly, B.F.J., 1993. Comments on design and analysis of multiple-choice feeding-preference experiments. Oecologia 93, 149-152.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2002. Resource selection by animals: Statistical design and analysis for field studies. Kluwer Academic Publishers, London.

Marsden, I.D., 1999. Reproductive cycles of the surf beach clam *Paphies donacina* (Spengler, 1793) from New Zealand. J. Shellfish Res. 18, 539-546.

Marshall, D.J., Semmens, D., Cook, C., 2004. Consequences of spawning at low tide: limited gamete dispersal for a rockpool anemone. Mar. Ecol. Prog. Ser. 266, 135-142.

Marshall, W.L., Bower, S.M., Meyer, G.R., 2003. A comparison of the parasite and symbiont fauna of cohabiting native (*Protothaca staminea*) and introduced (*Venerupis philippinarum*) and *Nuttallia obscurata*) clams in British Columbia. J. Shellfish Res. 22, 185-192.

Mascaro, M., Seed, R., 2000a. Foraging behavior of *Carcinus maenas* (L.): comparisons of size-selective predation on four species of bivalve prety. J. Shellfish Res. 19, 283-291.

Mascaro, M., Seed, R., 2000b. Foraging behavior of *Carcinus maenas* (L.): species-selective predation among four bivalve prey. J. Shellfish Res. 19, 293-300.

Matthews, M.A., McMahon, R.F., 1994. The survival of zebra mussels (*Dreissena polymorpha*) and Asian clams (*Corbicula fluminea*) under extreme hypoxia, The fourth international zebra mussel conference, Madison, Wisconsin.

McGaw, I.J., 2004. Ventilatory and cardiovascular modulation associated with burying behaviour in two sympatric crab species, *Cancer magister* and *Cancer productus*. J. Exp. Mar. Biol. Ecol. 303, 47-63.

Merilees, B., Gillespie, G., 1995. Two new exotic clams in Georgia Strait. Discovery 24, 143-145.

Miller, T.J., 2001. Matrix-based modeling of Blue Crab population dynamics with applications to the Chesapeake Bay. Estuaries 24, 535-544.

Miyawaki, D., Sekiguchi, H., 1999. Interannual variation of bivalve populations on temperate tidal flats. Fish. Sci. 65, 817-829.

Miyawaki, D., Sekiguchi, H., 2000. Long-term observations on larval recruitment processes of bivalve assemblages on temperate tidal flats. Benthos Res. 55, 1-16.

Morgan, S.G., 2001. The larval ecology of marine communities. In: Bertness, M., Gaines, S.D., Hay, M.E. (Eds.), Marine community ecology. Sinauer Associates, Inc., Sunderland.

Moyle, P.B., 1991. Ballast Water Introductions. Fisheries 16, 5.

Nakaoka, M., 1993. Yearly variation in recruitment and its effect on population dynamics in *Yoldia notabilis* (Mollusca: Bivalvia), analysed using projection matrix model. Res. Pop. Ecol. 35, 199-213.

Nakaoka, M., 1997. Demography of the marine bivalve *Yoldia notabilis* in fluctuating environments: an analysis using a stochastic matrix model. Oikos 79, 59-68.

Narvarte, M.A., Saiz, M.N., 2004. Effects of the Pinnotherid crab *Tumidotheres maculatus* on the Tehuelche scallop *Aequipecten tehuelchus* in the San Matias Gulf, Argentina. Fish. Res. 67, 207-214.

Navarrete, S.A., Castilla, J.C., 1988. Foraging activities of Chilean intertidal crabs *Acanthocyclus gayi* Milne-Edwards *et* Lucas and *A. hassleri* Rathbun. J. Exp. Mar. Biol. Ecol. 118, 115-136.

Neary, B.P., Leach, J.H., 1992. Mapping the potential spread of the zebra mussel (*Dreissena polymorpha*) in Ontario. Can. J. Fish. Aquat. Sci. 49, 406-415.

Nel, R., McLachlan, A., Winter, D.P.E., 2001. The effect of grain size on the burrowing of two *Donax* species. J. Exp. Mar. Biol. Ecol. 265, 219-238.

Neubert, M.G., Caswell, H., 2000. Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. Ecology 81, 1613-1628.

Neubert, M.G., Kot, M., Lewis, M.A., 2000. Invasion speeds in fluctuating environments. Proc. R. Sco. Lond. B 267, 1603-1610.

Nybakken, J.W., 1993. Marine biology: an ecological approach. HarperCollins College Publisher, New York.

Olaffson, E.B., Peterson, C.H., Ambrose, W.G., 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft-sediments: the relative significance of pre- and post-settlement processes. Oceanogr. Mar. Biol. Ann. Rev. 32, 65-109.

Parker, I.M., 2000. Invasion dynamics of *Cytisus scoparius*: a matrix model approach. Ecol. Appl. 10, 726-743.

Parker, M., Reid, R.G.B., unpublished manuscript. Aspects of the biology of Nuttallia obscurata, a Psammobiid bivalve recently introduced to the north-eastern Pacific. University of Victoria, Victoria, BC, pp. 8.

Pascual, M., Caswell, H., 1992. The dynamics of a size-classified benthic population with reproductive subsidy. Theoret. Pop. Biol. 39, 129-147.

Pattinson, K.R., Havel, J.E., Rhodes, R.G., 2003. Invasibility of a reservoir to exotic *Daphnia lumholtzi*: experimental assessment of diet selection and life history responses to cyanobacteria. Freshwater Biol. 48, 233-246.

Pauley, G.B., Armstrong, D.A., Heun, T.W., 1986. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest)--Dungeness crab. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.63), U. S. Army Corps of Engineers,TR EL-82-4, 20 pp.

Pearson, W.H., Woodruff, D.L., Sugarman, P.C., Olla, B.L., 1981. Effects of oiled sediment on predation on the littleneck clam, *Protothaca staminea,* by the dungeness crab, *Cancer magister*. Est. Coastal Shelf Sci. 13, 445-454.

Pekkarinen, M., 1986. Notes on the spawning, egg cleavage and early development of the bivalve *Macoma balthica*. Ann. Zool. Fennici. 23, 71-75.

Peterson, C.H., Black, R., 1988. Density-dependent mortality caused by physical stress interacting with biotic history. Amer. Nat. 131, 257-270.

Pimental, D., Lach, L., Zuniga, R., D., M., 2000. Environmental and economic costs associated with non-indigenous species in the United States. Bioscience 50, 53-65.

Pollock, K.H., Nichols, J.D., Brownie, C., Hines, J.E., 1990. Statistical inference for capture-recapture experiments. Wildl. Monogr. 107, 1-97.

Ponurovsky, S.K., Yakovlev, Y.M., 1992. The reproductive biology of the japanese littlenect, *tapes philippinarum*, (A. Adams and Reeve, 1850) (Bivalvia: veneridae). J. Shellfish Res. 11, 265-277.

Pradel, R., Wintrebert, C.M.A., Gimenez, O., 2003. A proposal for a goodness-of-fit test to the Arnason-Schwarz multistate capture-recapture model. Biometrics 59, 43-53.

Quayle, D.B., 1964. Distribution of introduced marine mollusca in British Columbia Waters. J. Fish. Res. Bd. Can. 21, 1155-1181.

Quayle, D.B., Bourne, N., 1972. The clam fisheries of British Columbia. Biological Station, Ottawa, pp. 70.

Quayle, D.B., Newkirk, G.F., 1989. Farming bivalve molluscs: methods for study and develpment. World Aquaculture Soceity, Ottawa, 294 pp.

Quinn, G.P., Keough, M.J., 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, 537 pp.

Rapport, D.J., Turner, J.E., 1970. Determination of predator food preference. J. Theor. Biol. 26, 365-372.

Reusch, T.B.H., 1998. Native predators contribute to invasion resistance to the non-indigenous bivalve *Musculista senhousia* in southern California, USA. Mar. Ecol. Prog. Ser. 170, 159-168.

Richards, M.G., Huxham, M., Bryant, A., 1999. Predation: a causal mechanism for variability in intertidal bivalve populations. J. Exp. Mar. Biol. Ecol. 241, 159-177.

Richardson, C.A., Seed, R., Al-Roumaihi, E.M.H., McDonald, L.M., 1993. Distribution, shell growth and predation of the New Zealand oyster, *Tiostrea* [=*ostrea*] *lutaria* Hutton, in the Menai Strait, North Wales. J. Shellf. Res. 12, 207-214.

Richardson, H., 1985. Availability of buried littleneck clams (*Venerupis japonica*) to northwestern crows (*Corvus caurinus*). J. Anim. Ecol. 54, 443-457.

Robinson, A.M., Breese, W.P., 1984. Gonadal development and hatchery rearing techniques for the manila clam *Tapes philippinarum* (Adams and Reeve). J. Shellfish Res. 4, 161-163.

Robles, C., Sweetnam, D., Eminike, J., 1990. Lobster predation on mussels: shore-level differences in prey vulnerability and predator preference. Ecology 71, 1564-1577.

Rogers-Bennett, L., Rogers, D.W., William, W.A., Ebert, T.A., 2003. Modeling red sea urchin (*Stronglocentrotus franciscanus*) growth using six growth functions. Fish. Bull. 101, 614-626.

Rosecchi, E., Thomas, F., Crivelli, A.J., 2001. Can life-history traits predict the fate of introduced species? A case study on two cyprinid fish in southern France. Freshwater Biol. 46, 845-853.

Roth, B., 1978. On the identificaiton of three Japanese species of *Nuttallia* (Mollusca: Bivalvia). Jap. Jour. Malac. 37, 223-229.

Ruesink, J.L., 2003. Hindcasting invasion impact based on species demography, Third International Conference on Marine Bioinvasions, La Jolla, California.

Ruiz, G.M., Carlton, J.T., Grosholz, E.D., Hines, A.H., 1997. Global Invasions of Marine and Estuarine Habitats by Non-indigenous Species: Mechanisms, Extent, and Consequences. Amer. Zool. 37, 621-632.

Rumrill, S.S., 1990. Natural mortality of marine invertebrate larvae. Ophelia 32, 163-198.

Sakai, A., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughmann, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N., Weller, S.G., 2001. The population biology of invasive species. Ann. Rev. Ecol. Syst. 32, 305-332.

Sasaki, K., Kudo, M., Tomiyama, T., Ito, K., Omori, M., 2002. Predation pressure on the siphons of the bivalve *Nuttallia olivacea* by the juvenile stone flounder *Platichthys bicoloratus* in the Natori River estuary, north-eastern Japan. Fisheries Sci. 68, 104-116.

Sastry, A.N., 1968. Relationships among food, temperature and gonad development of the bay scallop, *Aequipecten irradians* Lamarck. Physiol. Zool. 41, 44-53.

Sastry, A.N., 1979. Chapter 5 - Pelecypoda (Excluding Ostreidae). In: Giese, A.C., Pearse, J.S. (Eds.), Reproduction of marine invertebrates. Academic Press, New York, pp. 113-292.

Sax, D.F., 2001. Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. J. Biogeog. 28, 139-150.

Scheltma, R.S., 1986. On dispersal and planktonic larvae of benthic invertebrates: an eclectic overview and summary of problems. Bull. Mar. Sci. 39, 290-322.

Seitz, R.D., Lipcius, R.N., Hines, A.H., Eggleston, D.B., 2001. Density-dependent predation, habitat variation, and the persistence of marine bivalve prey. Ecology 82, 2435-2451.

Sekiguchi, H., Uchida, M., Sakai, A., 1995. Post-settlement processes determining the features of bivalve assemblages in tidal flats. Benthos Res. 49, 1-14.

Selleck, J.R., 2003. Comparative reproductive events of the invasive varnish clam, *Nuttallia obscurata*, and the fisheries littleneck clam, *Venerupis philippinarum*, Biology. Western Washington University, Bellingham, WA, pp. 45.

Shaw, W.N., 1986. Species profiles: life histories and environmental requirements of coasts and fishes and invertebrates (Pacific Southwest) -- common littleneck clam. U.S. Fish Wildl. Serv. Biol. Rep. 82 (11.46), 11pp.

Simberloff, D., 2003. How much information on population biology is needed to manage introduced species? Cons. Biol. 17, 83-92.

Smith, T.E., Ydenberg, R.C., Elner, R.W., 1999. Foraging behaviour of an excavating predator, the red rock crab (*Cancer productus* Randall) on soft-shell clam (*Mya arenaria* L.). J. Exp. Mar. Biol. Ecol. 238, 185-197.

Stachowicz, J.J., Whitlach, R.B., Osman, R.W., 1999. Species diversity and invasion resistance in a marine ecosystem. Science 286.

Strathmann, M.F., 1987. Reproduction and development of marine invertebrates of the Northern Pacific coast. University of Washington Press, Seattle, 670 pp.

Sun, H., Wang, W., Wang, Y., Yu, Z., 1997. The effects of temperature on embryonic development and growth of larvae of *Nuttallia olivacea*. Trans. Oceanol. Limnol. 2, 54-58.

Svensson, C.J., Jenkins, S.R., Hawkins, S.J., Myers, A.A., Range, P., Paula, J., O'Riordan, R.M., Aberg, P., 2004. Models of open populations with space-limited recruitment in stochastic environments: relative importance of recruitment and survival in populations of *Semibalanus balanoides*. Mar. Ecol. Prog. Ser. 275, 185-197.

Swincer, D.E., 1986. Physical characteristics of sites in relation to invasions. In: Groves, R.H., Burdon, J.J. (Eds.), Ecology of Biological Invasions. Cambridge University Press, Cambridge, pp. 67-76.

Tanaka, M., 1982. A new growth curve which expresses infinitive increase. Publ. Amakusa Mar. Biol. Lab. 6, 167-177.

Thomson, R.E., 1982. Oceanography of the British Columbia coast. Can. Spec. Publ. Fish. Aquat. Sci. 56, 291.

Thorson, G., 1950. Reproductive and larval ecology of marine bottom invertebrates. Biological Reviews 25, 1-45.

Tsuchiya, M., Kurihara, Y., 1980. Effect of the feeding behaviour of macrobenthos on changes in environmental condition of intertidal flats. J. Exp. Mar. Biol. Ecol. 44, 85-94.

Underwood, A.J., Chapman, M.G., Crowe, T.P., 2004. Identifying and understanding ecological preference for habitat or prey. J. Exp. Mar. Biol. Ecol. 300, 161-187.

Uthicke, S., Karez, R., 1999. Sediment patch selectivity in tropical sea cucumbers (Holothuriodea: Aspidochirotida) analysed with multiple choice experiments. J. Exp. Mar. Biol. Ecol. 236, 69-87.

Valenzuela, N., Adams, D.C., Janzen, F.J., 2003. Pattern does not equal process: exactly when is sex environmentally determined? Amer. Nat. 161, 676-683.

Vaughn, C.C., Hakenkamp, C.C., 2001. The functional role of burrowing bivalves in freshwater ecosystems. Freshwater Biol. 46, 1431-1446.

Vermeij, 1996. An agenda for invasion biology. Biol. Cons. 78, 3-9.

Vitousek, P.M., 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos 57, 7-13.

Walton, W.C., MacKinnon, C., Rodriguez, L., Proctor, C., Ruiz, G.M., 2002. Effect of an invasive crab upon a marine fishery: green crab, *Carcinus maenas,* predation upon a venerid clam, *Katelysia scalarina,* in Tasmania (Australia). J. Exp. Mar. Biol. Ecol. 272, 171-189.

White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46, S120-139.

Widdows, J., Blauw, A., Heip, C.H.R., Herman, P.M.J., Lucas, C.H., Middleburg, J.J., Schmidt, S., Brinsley, M.D., Twisk, F., Verbeek, H., 2004. Role of physical and biological processes in sediment dynamics of a tidal flat in Westerschelde estuary, SW Netherlands. Mar. Ecol. Prog. Ser. 274, 41-56.

Wilbur, H.M., Morin, P.J., Harris, R.H., 1983. Salamander predation and the structure of experimental communities: anuran responses. Ecology 64, 1423-1429.

Williamson, M., Fitter, A., 1996. The varying success of invaders. Ecology 77, 1655-1661.

Wilson, W.H., 1991. Competition and predation in marine soft-sediment communities. Annu. Rev. Ecol. Syst. 21, 221-241.

With, K.A., 2002. The landscape ecology of invasive spread. Cons. Biol. 16, 1192-1203.

Yap, W.G., 1977. Population biology of the Japanese Little-neck clam, *Tapes philippinarum* in Kaneohe Bay, Oahu, Hawaiian Islands. Pac. Sci. 31, 223-244.

Yates, E., 1999. Initial biological and ecological assessments of *Nuttallia obscurata* in North Puget Sound, Washington. Western Washington University, Bellingham, WA, 22pp.

Zaklan, S.D., Ydenberg, R.C., 1997. The body size-burial depth relationship in the infaunal clam *Mya arenaria*. J. Exp. Mar. Biol. Ecol. 215, 1-17.

Zar, J.H., 1984. Biostatistical analysis. Prentice-Hall Inc., Englewood Cliffs, NJ, 718 pp.