

Effects of Shell Abrasion and Aerial Exposure on
the Performance of Pacific Oysters *Crassostrea gigas*
(Thunberg, 1793) Cultured in Tasmania,
Australia.

Colleen Maree O'Meley
B.Sc. [Hons. (Chem.)]

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Declaration

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A handwritten signature in black ink, reading 'C. O'Mealey'. The signature is written in a cursive style with a large, looped 'C' and a stylized 'O'.

Colleen Maree O'Mealey
November, 1995

Abstract

Two of the major management strategies used by Tasmanian oyster farmers for grow-out of unattached (single-seed) Pacific oysters (*Crassostrea gigas*) are shell abrasion, occurring either deliberately or inadvertently during mechanised grading, and manipulation of intertidal growing height (degree of aerial exposure). Some farmers assert that these strategies can promote faster meat growth, and hence higher condition indices [meat weight relative either to shell cavity volume (CI_{vol}), or to shell weight (CI_{shell})]. These reports, however, are anecdotal and have not been substantiated in the literature. The present study was undertaken to evaluate the effects of shell abrasion and aerial exposure on the performance (growth, condition index, shell shape, glycogen content and gonad development) of Pacific oysters cultured in mesh baskets, in two separate experiments, on two commercial leases in Tasmania.

Pacific oysters in Experiment 1 were subjected to the following shell abrasion treatments; one-third were machine-graded twice (MM group), another third were machine-graded once (M group) and the last group were not machine-graded (C group, control). Their performance was measured over 81 d and in 87% of the 77 data sets (eleven performance indices measured on seven sample dates), shell abrasion was not a significant factor ($P>0.05$). It is suggested that this was because the available oysters had little 'shell frill' (fragile shell extensions on the outer margins).

Pacific oysters used in Experiment 2 had large shell frill extensions, prior to being treated as follows; two-thirds of the oysters were initially machine-graded (M group) and one-third was not (C group), and then half of the M group oysters were shaken in their baskets after six weeks, and twelve weeks (MB group) into the experiment. Oysters machine-graded once (M group) lost a mean of 3.3 ± 0.4 mm in shell height and 5.9 ± 1.0 mm in shell length (mean \pm s.e.; $n=13$). Additional shell frill was removed when oysters were shaken in their baskets (MB group). On the first occasion, the mean shell height and shell length were reduced by 3.4 ± 0.5 mm and 2.5 ± 0.4 mm (mean \pm s.e.; $n=29$), respectively. When the baskets were shaken again, six weeks later, reductions of 4.5 ± 0.6 mm in shell height and 2.9 ± 0.7 mm in shell length (mean \pm s.e.; $n=29$) were recorded.

The C group grew faster than the MB group, whilst results for the M group were usually intermediate. By the final sample (124 d) in Experiment 2, the

results ($P < 0.05$) were, for; whole weight (g oyster^{-1}) $C > M, MB$, shell height $C > M > MB$, shell length $C, M > MB$, shell depth $C > M, MB$, dry shell weight (g oyster^{-1}) $C > M, MB$, and for dry meat weight (g oyster^{-1}) $C > M$ but the MB group was not significantly different ($P > 0.05$) to the other two. Reduced shell growth relative to meat growth, is one of the major factors influencing condition index; the MB group had a higher mean CIvol than both M and C groups ($P < 0.05$), while the CIvol of the last two groups were not significantly different ($P > 0.05$) by the final sample. The trends in CIshell values were similar, but less pronounced, and by the final sample the mean CIshell values were similar ($P > 0.05$). Shell shape was significantly altered such that the MB group had a higher ($P < 0.05$) mean cup index [= (shell height \times shell length) $^{0.5}$ / shell depth] but lower ($P < 0.05$) mean roundness index (= shell length / shell height) compared to the other two groups. Throughout the experiment the mean glycogen content did not differ significantly ($P > 0.05$) amongst groups.

The range, for average daily aerial exposure treatments, was much greater in Experiment 1 (0-26% exposure d^{-1}) than in Experiment 2 (0-7% exposure d^{-1}). By the final sample in Experiment 1, the mean whole weight, shell height, shell length, shell depth and dry shell weight of subtidal (0% exposure d^{-1} ; L group) oysters were higher ($P < 0.05$) than those held at 26% exposure d^{-1} (H group). Because their dry meat weights were similar ($P > 0.05$), the H group developed a higher ($P < 0.05$) mean CIvol and CIshell than the L group. The H group had a higher ($P < 0.05$) mean cup index but lower ($P < 0.05$) mean roundness index compared to the L group, and the mean glycogen content of the H group was higher ($P < 0.05$) than in the L group.

Aerial exposure levels of 0% exposure d^{-1} (L group) compared 7% exposure d^{-1} (H group) did not significantly affect ($P > 0.05$) the mean whole weight, shell height, shell depth, dry shell weight or dry meat weight indices, although the shell length of the H group was higher ($P < 0.05$) than that of the L group by the final sample in Experiment 2. Compared to the L group, the H group had higher, but not significantly different ($P > 0.05$), mean CIvol and CIshell indices, and were slightly rounder but less cupped in shape. The H group did have a significantly higher ($P < 0.05$) mean glycogen content by the last sample.

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In neither experiment did shell abrasion or aerial exposure have a consistent effect on gonad development, or sex group ratio (male: female: indeterminate).

This study has shown that shell abrasion can retard shell growth, but improve the CIvol, CIshell and cup index for Pacific oysters which have substantial shell frill prior to abrasion. The roundness index and glycogen content, however, were not improved. Increased levels of aerial exposure led to an improved glycogen content, compared to subtidal oysters. Increased levels of exposure will also retard shell growth, but will improve the CIvol, CIshell and cup index, but not the roundness index. As such they are useful management tools but they do not promote faster meat growth.

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1. Introduction

1.1 Review

This review aims to introduce the reader to the literature covering the taxonomy, distribution, marketing, site selection and cultivation methods for Pacific oysters (*Crassostrea gigas*). Where possible, specific studies which may be relevant to the effects of shell abrasion and aerial exposure on oysters are emphasised.

1.1.1 Production and value of Pacific oysters

Oysters are an important aquaculture product. In 1991, oysters accounted for 31% by weight (t) of the world aquaculture production of molluscs, and specifically Pacific oysters accounted for 84.2% of the world oyster production in 1991 (by weight) (FAO, 1993).

The wholesale value of cultured edible oysters in Australia was worth \$34.6 million in 1989-1990 (Treadwell et al., 1991). While this represented 18% of Australia's aquaculture sales (Treadwell et al., 1991), it was only about 1% in terms of world-wide oyster sales (Graham, 1991). In 1991, the Tasmanian Pacific oyster industry was worth A\$ 10.5 million (sold at the farm gate) (Stanley, 1993).

1.1.2 Taxonomy and distribution

The oyster *Crassostrea gigas* (Thunberg, 1793) has several common names including Pacific, Giant Pacific and Japanese oyster (Arakawa, 1990a). Its formal classification is as follows: Phylum Mollusca; Class Bivalvia; Sub-class Pteriomorpha; Order Ostreoida; Suborder Ostreina; Superfamily Ostreoidea; Family Ostreoidea; Sub-family Crassostreinae; Tribe Crassostreini; Genus *Crassostrea*; Species *gigas* (Vaught, 1989).

Varieties or types of Pacific oysters which are known in Japan include, in order of their north to south distribution, the Hokkaido, Miyagi, Hiroshima and Kumamoto (Imai and Sakai, 1961; Buroker et al., 1979; Arakawa, 1990a; Deupree, 1993). Types can usually be distinguished

based on shell size, shape and colour, and growth, condition index (meat weight either relative to shell cavity volume, or to shell weight) and survival of the oysters when cultured in water of differing temperature and other environmental conditions (Imai and Sakai, 1961; Arakawa, 1990a). The Kumamoto was found to have a low level of genetic similarity to other *C. gigas* types (Hiroshima and Miyagi), and was reclassified as a non-sibling species *C. sikamea* (Buroker et al., 1979; Arakawa, 1990a; Deupree, 1993).

The Pacific oyster is found from the low intertidal through to subtidal zone, in tropical to cool temperate climate, brackish waters (Harry, 1985). Pacific oysters are native to the Indo-West Pacific (Harry, 1985), Japan (Harry, 1985; Arakawa, 1990a), and along Asian coastlines, extending from Primorsky Kray, in Russia, through to the Korean Peninsula, China, south east Asia (Arakawa, 1990a), and Pakistan (Harry, 1985). They are also native to the Philippine Islands, Borneo, and Sumatra (Harry, 1985).

Introductions of the Pacific oyster to other parts of the world were aimed at establishing a new aquaculture industry. Pacific oysters have been successfully introduced into North America and Canada (Galtsoff, 1964), South America (Chew, 1990), Europe (Walne and Spencer, 1971; Chew, 1990), Africa (Chew, 1990), and Australia (Thomson, 1952; Chew, 1990; Dix, 1991). Pacific oysters were introduced from Japan into Tasmania, Australia, between the years 1947-1948 and 1951-1952 (Thomson, 1952; Dix, 1991). Thomson (1952) did not state the types introduced, however, based on the sites in Japan from which they were collected, those in Tasmania are likely to include Miyagi, Hiroshima and Kumamoto. However, a recent study by Deupree (1993), aimed at establishing whether the deeply cupped Tasmanian Pacific oyster was of the Kumamoto type, showed that the oysters, analysed via gel electrophoresis, were in fact genetically similar to the more common Miyagi type. It is therefore uncertain whether Tasmanian stocks contain the Kumamoto.

Pacific oysters were accidentally introduced into New Zealand, and were first accurately collected and reported in 1971 (Dinamani, 1991). The Pacific oyster is a prolific breeder and quickly colonised the North Island and parts of the South Island (Dinamani, 1991), and as early as 1978, New Zealand oyster farmers were culturing the Pacific oyster instead of the native rock oyster (*Saccostrea glomerata* = *Saccostrea commercialis*)

because similar market prices were obtained for both species, and because the Pacific oyster grows faster and could therefore be marketed in a shorter time (Holliday and Nell, 1987).

Similarly, the Pacific oyster was first recognised in the Pambula River, New South Wales (N.S.W.), Australia, in 1967 (Holliday and Nell, 1987). It quickly colonised most bays and estuaries in N.S.W., and southern Queensland, Australia (Holliday and Nell, 1987). In N.S.W., most of the farmers who culture the native Sydney rock oyster (*Saccostrea commercialis*), regard the Pacific oyster as a pest species. The Sydney rock oyster industry, Australia's largest edible oyster industry, is based on the collection of spat (juveniles) on tarred sticks, or plastic substrates (collectors), placed within bays or estuaries, and the subsequent culture to market size (grow-out) (Malcolm, 1987). The problem for these farmers has been that the Pacific oyster has been successfully out competing the Sydney rock oyster for collector space. However, the Pacific oyster is now cultured in Salamander Bay, N.S.W., on a commercial basis (Bird et al., 1991; Holliday et al., 1993b).

In most areas of Tasmania, feral populations of Pacific oysters have been limited, because the water temperatures have not usually been high enough to encourage the oysters to breed (C. Sumner, pers. comm., 1992). The Tamar river in northern Tasmania, however, was once used to collect Pacific oyster spat, over several years (Dix, 1991). Unreliable spat supplies prompted the development of commercial hatcheries (Dix, 1991). Currently four Tasmanian hatcheries provide spat to major Pacific oyster industries in Tasmania and South Australia (Dix, 1991), and a small industry in Victoria (O'Sullivan, 1990).

1.1.3 Single-seed

The spat from Tasmanian hatcheries are produced as 'single-seed' (also called 'unattached spat' or 'cultchless seed'). Here the larvae (free-swimming stage) are provided with crushed bivalve shells, of a similar size to that of the larvae, which the juveniles (spat), soon outgrow (Dix, 1991). Alternatively, spat (shell height = 4-8 mm) can be detached from plastic collectors by scraping, or flexing the plastic (R. Pugh, pers. comm., 1993). The oysters are then cultured to market size using single-seed

culture techniques; usually mesh enclosures are used to hold the spat (see below), and regular grading and density reductions are carried out.

In comparison, spat attached to hard surfaces for extended periods, for example tarred sticks until market size, tend to grow around the much larger collector surface (Galtsoff, 1964; Arakawa, 1990a), and often develop a poor shell shape (Galtsoff, 1964). Additionally, grading usually only occurs during 'culling' (removal of market-sized oysters from collectors), and the opportunities for density reductions are limited to adjusting the spacing between collectors (Malcolm, 1987). Clearly single-seed techniques enable better control of stocks.

It should be noted that since active cultivation of Pacific oysters in N.S.W. and New Zealand commenced, many farmers have turned to single-seed techniques (Holliday et al., 1988; Dinamani, 1991; Holliday et al., 1993b). Wild caught spat are detached from synthetic collectors (shell height ≥ 3 mm) and on-grown in mesh-covered sectionalised trays or cylinders (Holliday et al., 1988; Holliday et al., 1991b; Holliday et al., 1993a). Some N.S.W. farmers also use these techniques for Sydney rock oysters (Holliday et al., 1988). The single-seed farming strategies used to culture Pacific oysters in Australia have implications in terms of the quality of the marketable product, as will be discussed later.

Single-seed are protected by mesh enclosures until they have reached a size which does not allow predation, or losses due to wave action (Holliday et al., 1991b). Single-seed enclosures, or 'units', include trays, baskets, bags and cylinders suspended subtidally under rafts or longlines, or intertidally on racks or the seabed. Often farmers design and construct their own units and the type largely depends on the characteristics of the lease site (O'Meley, 1992). As the oysters are grown, they are transferred to enclosures with larger mesh sizes thereby increasing water flow and minimising fouling of the mesh (Holliday et al., 1991b; Holliday et al., 1993a). The mesh size should not be increased prematurely, however, since the oysters can grow into the mesh and become 'beak' shaped rather than the rounded shape required for the market (Holliday et al., 1991b).

Cultivation methods for Pacific oysters have been reviewed; in Japan (Korringa, 1976; Wisely et al., 1978; Kusuki, 1990), Europe (Korringa, 1976; Anderson, 1977; Héral and Deslous-Paoli, 1990), Canada (Quayle, 1988),

America (Korringa, 1976), New Zealand (Dinamani, 1991), and Australia (Dix, 1991).

1.1.4 Site selection

The Pacific oyster is cultured in a wide range of habitats ranging from clear cold-water, to turbid, warm-water sites (Walne and Spencer, 1971), and growth, meat condition and survival can vary widely (King, 1977; Agius et al., 1978; Wilson, 1987; Brown and Hartwick, 1988a).

Environmental factors which can affect shell growth in bivalves include; the food supply, water temperature (geographic, seasonal, daily), salinity, substratum, depth of the photic zone (Agius et al., 1978), turbidity, population density, and degree of exposure to high energy environments (Seed, 1980).

In particular, shell and meat growth of Pacific oysters at a particular site are affected by temperature, salinity, food levels, current velocity, wave action (Wilson, 1987; Brown and Hartwick, 1988a; Holliday et al., 1991a), culture methods (Spencer and Gough, 1978), and degree of aerial exposure employed (Spencer and Gough, 1978; Littlewood, 1988; Spencer, 1990). Pollutants (Agius et al., 1978; Spencer, 1990), disease organisms, predators, competitors and parasites can also affect growth and survival (Anderson, 1977; Briggs, 1978; Drinkwater and Howell, 1985; Littlewood, 1988; Quayle, 1988; Arakawa, 1990b; Spencer, 1990). Of these, the principal environmental factors affecting growth are water temperature and food abundance, both of which vary seasonally (Malouf and Breese, 1977; Brown and Hartwick, 1988a).

Brown and Hartwick (1988a) reported that Pacific oysters had best growth, in a temperate region, in sites with high spring and summer water temperatures, an abundance of phytoplankton, and non-stressful salinity levels. Adult Pacific oysters can tolerate salinities from 5-55‰ (Nell and Gibbs, 1986; Nell and Holliday, 1988), but somatic growth (body tissue growth excluding the germinal cells which give rise to gametes) only occurs between 16-31‰ (Bernard, 1983; Brown, 1988), and between 20-25‰ is considered to be optimum for growth (Bernard, 1983; Brown, 1988; Spencer, 1990). However, Pacific oysters have been successfully cultured in full strength seawater (35‰) (Maguire et al., 1994b), and in water of higher salinities (40-41‰) (King, 1977; Shpigel and Blaylock, 1991).

Pacific oyster larvae show fastest growth at salinities from 19-27‰, and survival is unaffected between 15-39‰ (Nell and Holliday, 1988). Small spat (1.1 mg) grow fastest between 15-30‰, but growth declines rapidly as salinity is increased from 30-45‰ (Nell and Holliday, 1988). For larger spat (0.68 g), salinities between 15-45‰ do not affect growth, and for both small and large spat, salinities between 15-45‰ do not affect their survival (Nell and Holliday, 1988).

In other studies conducted in temperate regions, low water temperatures in the winter cause slow or no growth in Pacific oysters, and growth is fastest during spring and summer (Imai and Sakai, 1961; Walne and Spencer, 1971; Askew, 1972; King, 1977; Malouf and Breese, 1977; Askew, 1978; Hall, 1984; Drinkwater and Howell, 1985; Brown, 1988; Spencer, 1990; Dinamani, 1991). Although Tasmania can also be considered as cool temperate (Maguire et al., 1994b), Pacific oysters cultured in Tasmania can also exhibit fast growth during autumn (Sumner, 1980a) and winter (Maguire et al., 1994b). In New Zealand, Dinamani (1991) similarly reported that growth of Pacific oysters can be fast in autumn.

Pacific oysters have been cultured in waters with temperatures ranging from -2°C (Askew, 1972) through to 34°C (Hughes-Games, 1977). The temperature at which no growth occurs is about 5.5°C (Spencer and Gough, 1978), while 10°C has been suggested as the minimum optimum temperature for growth (Askew, 1972); these may be influenced by food abundance, however (Brown and Hartwick, 1988b). Growth rates may not be enhanced in sexually mature adult oysters when temperatures are above 12°C, because energy is not only used for somatic growth but is also directed towards reproductive activity, or gametogenesis (Mann, 1979; Brown, 1988).

Oysters cultured intertidally, are also subject to air temperatures. ✓
Extremes can cause mortality depending upon the period of exposure. For example, high temperatures of 30-35°C (Kusuki, 1990), or freezing air temperatures (<0°C) (Spencer, 1990) will cause high mortalities. rock oysters cultured in N.S.W., and Queensland, suffer from a condition known as 'heat stress' and Hill, 1982). Mortalities are reduced by spraying the oysters with salt water or by covering them over with shade cloth (Sumner, 1980a; Potter and Hill, 1982).

comparison (Sumner, 1980a) so that usually these methods are not needed.

Oysters are filter feeders and in their natural environment they feed upon phytoplankton, and to a lesser extent, bacteria (Brown, 1988; Nell, 1993b), organic detritus (Brown, 1988; Crosby et al., 1989), and dissolved organic compounds (Fankboner and De Burgh, 1978; Nell et al., 1983; Nell and Gibbs, 1989; Nell, 1993b). While the nutritional quality of phytoplankton can vary widely (Brown et al., 1989; Nell, 1993b), and some algal blooms can be harmful (Shumway, 1990; Whyte et al., 1990; Hallegraeff, 1993), it is preferable that the oysters are exposed to the variety of species present in their natural environment, since it has been shown that mixed diets produce the fastest growth in oysters in laboratory situations (Epifanio, 1979; Brown et al., 1989).

In Tasmania, phytoplankton blooms typically occur twice yearly, during spring and autumn (Sumner, 1980a). High food availability in the spring combined with increasing water temperatures, usually results in high growth rates (Bayne and Newell, 1983; Brown, 1988). In the autumn, high food availability coincides with an increase in metabolic reserves prior to the winter months (Brown and Hartwick, 1988a), where low temperatures and food levels, in turn, coincide with reduced metabolic requirements in the oyster (Bernard, 1983; Brown, 1988).

Apart from selecting a suitable site, there is no control over phytoplankton species or their abundance in the oyster's environment. To an extent however, the culture methods used can increase food availability for single-seed oysters via density manipulation and increasing the mesh size of the enclosure to increase current flow to the oysters (O'Meley, 1992). Carrying capacity, or the amount of food within the water column of various sites, has become an increasing concern to aquaculturists (Héral and Deslous-Paoli, 1990; Kusuki, 1990). The concern is that, if established leases are expanded or new leases granted within an estuary, there may not be enough natural phytoplankton or other useable organic matter to support oyster growth. Recent economic models indicate that profits for Tasmanian farmers could drop by two-thirds if Pacific oysters took up to three years, rather than up to two years, to reach marketable size (Treadwell et al., 1991).

Water movement, or current flow, provides a continuous supply of food particles to the oysters (Westley, 1965). The current flow required to maintain oyster growth is inversely related to the amount of food particles in the water (Malouf and Breese, 1977; Brown and Hartwick, 1988a), and has been positively correlated to the feeding activity of Pacific oysters and other bivalves (Walne, 1970; Malouf and Breese, 1977). In addition, filter-feeding activity is positively related to temperature (Bernard, 1983), such that high flow rates are not beneficial at low temperatures, and weight loss can occur at high temperatures if the flow-rate is inadequate (Malouf and Breese, 1977). Optimum conditions for the growth of Pacific oysters are sheltered sites with tidal flows of up to 1-2 knots (0.50-1.0 m s⁻¹) (Spencer, 1990).

Excessive wave action can cause loss of oysters from their enclosures, and extreme tidal currents in conjunction with high wave action can cause damage to the culture equipment or to the oysters themselves (Spencer, 1990). Farmers take these factors into consideration when planning farm lay-out so that damage to culture equipment is minimised, whilst ensuring good water flow to the oysters. Tasmanian farmers may also increase the density of oysters per enclosure (R. Calvert, pers. comm., 1991), position the enclosures at different places on the farm, or place them subtidally.

In the United Kingdom (U.K.), annual mortality rates for juvenile and adult Pacific oysters held in sea-based trays are expected to be between 10-15% (Hall, 1984). Survival of Pacific oysters cultured in the U.K. is not, however, related to season (Walne and Davies, 1977), or water temperatures (Spencer and Gough, 1978). In Tasmania, low mortality rates are expected for Pacific oysters cultured in mesh enclosures; one study showed that Pacific oysters cultured for two years in mesh baskets can be <1% at favourable sites (Maguire et al., 1994b).

To prevent high mortalities the oysters need to be protected from predators; usually mesh enclosures are employed (Parsons, 1974; King, 1977; Spencer, 1990; Holliday et al., 1991b). For example, a study conducted in salt ponds (40‰) in South Australia showed that mortality of protected compared to unprotected Pacific oysters was 11 and 30%, respectively, after 7 months (King, 1977). Predators of Pacific oysters in Tasmania, include flatworms, and various fish, for example black bream (*Acanthopagrus* spp.) and greenback flounder (*Rhombosolea tapirina*),

Pacific gulls (*Larus pacificus*) and kelp gulls (*Larus dominicanus*), but these cause only minor stock losses (Dix, 1991). It should be noted, however, that the European shore crab (*Carcinus maenas*) which can cause high mortalities of Pacific oysters laid unprotected on the seabed (Parsons, 1974), has now colonised Tasmanian waters (Gardner, et al., 1994). Disease organisms are few in Tasmania (Dix, 1991), although they are present in very low numbers (Wilson, 1993).

1.1.5 Factors affecting marketability of Pacific oysters

Tasmanian Pacific oysters sold commercially are usually 65-75 mm in shell height (the longest shell dimension) (Dix, 1991), although there is some demand for larger oysters (C. Dyke, pers. comm., 1990). In some Australian states a market for smaller ('cocktail') oysters has developed, while Sydney rock oysters are usually sold at a smaller size than Pacific oysters (G. Maguire, pers. comm., 1995). The majority of Pacific oysters are sold live to retail fish shops, restaurants and hotels (Dix, 1991; Graham, 1991) where they are opened and presented in the half shell (Dix, 1991). Characteristics of marketable oysters for the half-shell trade are as follows. Before retail, the bivalves should be certified fit for human consumption (Graham, 1991). The shell should contain no shell blisters usually from spionid polychaetes (Skeel, 1979; Wilson, 1993), and should be cupped and rounded in shape. The meat should be flavoursome, without grit, and a high proportion of the shell cavity should be filled by the meat (as measured by a 'condition index' value). The meat should also be full and creamy in appearance. Finally, the oyster should have a shelf-life out of water of at least one week to allow for transport and storage, prior to sale (O'Meley, 1992).

Pacific oysters cultured in Tasmania are of a high quality, and usually meet the criteria of a marketable oyster because of the single-seed methods (use of mesh enclosures, density manipulations, and grading) used during grow-out. The meat condition, however, can be inadequate after spawning in summer, and oysters from different sites can vary greatly in meat condition (Maguire et al., 1994b).

Shell-boring mudworms (spionid polychaetes, for example *Polydora* spp.) can be a major problem because the blisters that they cause weaken the shell, making it difficult to 'shuck' (open) the live oysters, and disturbed

blisters can also render the product unfit for the half-shell trade (Littlewood, 1988; Dinamani, 1991). Additionally, because the oyster expends energy, in covering the blister with nacre, that would otherwise be devoted to growth, the condition of the oyster can be reduced and may even lead to death (Skeel, 1979). When the worms are not living inside oyster shells, they can also be found in the bottom sediments, and in the accumulated mud, faeces and pseudofaeces that build up around the oysters (Skeel, 1979).

In N.S.W., mudworm infection rates can be high. For this reason a N.S.W. farmer designed a rotating cylinder to help keep the oysters free from mud and silt (Holliday et al., 1993a). Tasmanian Pacific oysters rarely contain mudworm blisters (Dix, 1991; Wilson, 1993) partly because the oysters are cultured away from the bottom sediments, on intertidal racks (Dix, 1991; Nell, 1993a), the latter of which helps to desiccate the worms (Skeel, 1979), and because regular grading of the oysters helps to dislodge accumulated mud (R. Calvert, pers. comm., 1991). Mudworm can be a major problem on Pacific oyster farms in South Australia and New Zealand (G. Maguire, pers. comm., 1995).

A desirable characteristic of a marketable oyster, is that the meat should fill a high proportion of the shell cavity, quantified by calculating a static condition index. This is usually one of two indices; a ratio of the dry meat weight to shell cavity volume (CIvol), or the dry meat weight to dry shell weight ratio (CIshell). For convenience, each ratio is multiplied by a factor of 100 or 1000 (Brown and Hartwick, 1988b). Lucas and Beninger (1985) suggested that while CIshell is a health indicator, CIvol indicates product quality and is therefore an economic index. Although in general these definitions have been accepted, there is still much discussion within the scientific community about their relevance and meaning (see Appendix A).

Oysters with high condition index values, have high glycogen reserves or advanced gonad development (Gabbott, 1975; Mann, 1979) resulting in full, creamy meats (Maguire et al., 1994b), while spawned-out oysters have a grey and transparent appearance (Graham, 1991). Glycogen is used by the oysters as an energy store which is utilised during gametogenesis in the spring (Gabbott, 1975; Mann, 1978). A decline in glycogen or carbohydrate levels in the meat is synchronous with an increase in ova lipid levels (Gabbott, 1975). While it has been suggested that reallocation

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of energy from somatic growth to gamete production can lead to reduced growth rates (Sumner, 1980a; Brown, 1988), the effect on somatic growth upon spawning is that a major energy reserve is lost to the environment (Gabbott, 1975).

In Tasmania, gametogenesis in Pacific oysters begins in the spring (October) and culminates in a major spawning event during late summer (February), or sporadically throughout the summer, depending upon maximum water temperatures reached (Sumner, 1980a; 1980b). If temperatures do not exceed 18-20°C Pacific oysters will not spawn (Mann, 1979). When water temperatures are too low to activate spawning, their condition index values remain high (Hughes-Games, 1977; King, 1977; Graham, 1991). In Tasmania, Pacific oysters often do not spawn to completion, and may recover quickly (Graham, 1991), and not all oysters on a lease or on different leases may spawn at the same time. This allows marketing for most of the year, from Tasmania (Graham, 1991). However, individual farms may not be able to market oysters for up to three months (summer - autumn) in Tasmania, and this period may even be longer in some South Australian inlets (G. Maguire, pers. comm., 1995).

Triploid Pacific oysters have several advantages over diploids. Triploid oysters contain three sets of chromosomes per cell rather than the usual two (Beaumont and Fairbrother, 1991). Because triploid Pacific oysters are capable of only limited gametogenesis they retain meat condition during the spawning season (Maguire et al., 1994b). Additionally, Maguire et al. (1994b) found no evidence of spawning in triploid Pacific oysters cultured in Tasmania. Allen and Downing (1991) reported that American consumers prefer triploid Pacific oysters over normal diploids. In Tasmania, however, there were few differences in the response of taste-test panellists to triploid and diploid Pacific oysters although no poor, recently spawned diploid oysters were used in the tests (Maguire et al., 1994a).

In Japan and Korea, the high intertidal zone is used to culture spat during their first growing season (Imai and Sakai, 1961; Quayle, 1988; Kusuki, 1990). This 'hardens' the spat, such that the shell thickness increases (Littlewood et al., 1992) and the adductor muscle is strengthened (Imai and Sakai, 1961). The shelf life, or survival in air, is thought to be improved by this (Imai and Sakai, 1961; Quayle, 1988), and so they are

better able to survive during long distance transport and, or storage prior to sale (O'Meley, 1992). The oysters also have better survival rates when transferred after a few months to subtidal culture units, but the effectiveness of the hardening treatment tends to decrease the longer the spat are held subtidally (Kusuki, 1990).

1.1.6 Effects of culture techniques on the performance of Pacific oysters

1.1.6.1 Stocking density

High stocking densities can cause reduced growth and survival rates (Drinkwater and Howell, 1985; Spencer, 1990; Holliday et al., 1991b), clumping where two or more oysters fuse together (Spencer, 1990), an irregular shape (R. Calvert, pers. comm., 1991), and the oysters may grow into the mesh of enclosures (Neudecker, 1981b; Holliday et al., 1991b). Alternatively, low stocking densities are uneconomic because of the increased lease space, culture equipment and labour required to service them (Askew, 1978; Spencer et al., 1985; Spencer, 1990), and the oysters may suffer excessive shell abrasion and hence reduced growth (Holliday et al., 1991b).

Optimum stocking densities depend upon a number of factors, including the carrying capacity of a particular site (Brown and Hartwick, 1988a), and the size range of oysters to be stocked. Drinkwater and Howell (1985) recommended stocking Pacific oyster spat at just below the level where oysters would be touching when spread out evenly, while for Sydney rock spat, Holliday et al. (1991b) suggested that they cover 50% of the container bottom. In practice, Tasmanian farmers use the latter method for Pacific oyster spat, while adults are stocked in a single or double layer (C. Sumner, pers. comm., 1989). To optimise production the densities should be periodically reduced as the oysters grow (Walne and Spencer, 1971; Holliday et al., 1991b; Holliday et al., 1993a).

1.1.6.2 Degree of aerial exposure

Oysters cultured subtidally are not exposed to the air (0% exposure d⁻¹) except during retrieval, grading and handling, while those cultured in the intertidal zone are exposed to the air, the degree to which is dependent upon their position (vertical height) relative to the amplitude of the tide (Littlewood, et al., 1992). Subtidal culture usually produces the fastest shell growth rates in Pacific oysters, followed in sequential order, by intertidal off-bottom, subtidal bottom, and intertidal bottom culture (Parsons, 1974; Quayle, 1988).

Growth rates of Pacific oysters decrease with increasing exposure to air (Pereya, 1961; Walne and Davies, 1977; Spencer et al., 1978; Drinkwater and Howell, 1985; Spencer, 1990), although average differences of 4-9% average daily exposure are necessary to reduce growth (Spencer et al., 1978). Between 0-10% exposure there are only small differences in the growth of Pacific oysters (Walne and Davies, 1977; Spencer et al., 1978). Marked reductions in growth occur between 10-30% average daily exposure (Spencer et al., 1978). Interestingly, Spencer (1990) stated that "growth stops when oysters in trays are exposed to air for more than 35% of the time". However, earlier studies, based on extrapolation to the point of no growth for Pacific oysters, indicate a critical exposure of 36-47% depending on site (Spencer et al., 1978). In Tasmania, spat have been cultured to market size at levels of 40% (Sumner, 1980a), and up to 59% without growth ceasing (Maguire et al., 1994b).

In comparison, it has been found, that American oysters (*Crassostrea virginica*) can grow faster at certain intertidal levels (20-30% exposure d⁻¹) than at subtidal ones (Gillmor, 1982), and similarly, mangrove oysters (*Crassostrea rhizophorae*) held at subtidal (0% exposure d⁻¹) and mid-intertidal levels (10-17% exposure d⁻¹) were found to grow faster than those held at lower levels (1-3% exposure d⁻¹) (Littlewood, 1988). Gillmor (1982) suggested that in "high-intertidal forms there may be a degree of optimality associated with periodic exposure, if not an obligate relationship". This is despite the traditionally accepted idea that subtidal bivalves grow faster due to longer immersion times and therefore feeding times, than intertidal animals (Littlewood, 1988).

Crenshaw (1980), and Wilbur and Saleuddin (1983) reviewed the processes of shell formation and dissolution in molluscs. During periods

of aerial exposure, intertidal bivalves experience oxygen deprivation whilst their shell valves are closed (Crenshaw, 1980). The energetic requirements of the animal are supplied by anaerobic glycolysis, and the acidic end products of this metabolism, for example, succinic, lactic and propionic acids, must be neutralised to maintain the constant pH required for normal function (Crenshaw, 1980; Wilbur and Saleuddin, 1983). For molluscs, the shell is an alkali reserve such that part of the shell is dissolved, especially recently deposited shell on the outer margins, during periods of anaerobic respiration (Crenshaw, 1980; Wilbur and Saleuddin, 1983). Periodic shell dissolution may therefore account for the slower growth of some intertidal bivalves (Crenshaw, 1980). Shell dissolution also occurs to a lesser extent in subtidal bivalves, since these periodically close their valves whilst submerged (Crenshaw, 1980). It should be noted that some bivalves, including Pacific oysters, can also respire aerobically in air (Crenshaw, 1980; Seaman, 1991), the degree to which depends on how far apart the valves are opened (Crenshaw, 1980).

Intertidal culture has the following advantages; there is convenient access to stock (Spencer et al., 1985; Spencer, 1990), shell growth rates can be controlled or temporarily stopped by moving the stock to different exposure levels (Spencer, 1990), the shelf life improves (Imai and Sakai, 1961; Quayle, 1988), and the stock are kept relatively free from biofouling and predators (Arakawa, 1990b; Littlewood et al., 1992). In addition, unless fouling and predation are controlled in subtidally-cultured oysters, survival rates are likely to be higher at intertidal sites (Littlewood, 1988; Littlewood et al., 1992).

Pacific oysters can grow to a large size of up to 300 mm in shell height (Quayle, 1988; Dinamani, 1991) and, if unchecked, the shell can 'outgrow' the meat (Maguire et al., 1994b). This will of course affect the condition index and hence, marketability. For this reason, the high intertidal zone is often used by Pacific oyster farmers in Tasmania (C. Dyke, pers. comm., 1990), and elsewhere, to slow down the shell growth of larger oysters (Spencer, 1990). Spencer et al. (1978) reported that while there are marked reductions in growth between 10-30%, the effect on shell and meat growth of Pacific oysters was similar, so that the condition index (CI_{shell}) remained at a constant level irrespective of tidal exposure.

The effect of intertidal height on shell shape is not well documented in the literature. However, Maguire and Kent (1991), in a summary written

for oyster farmers reported that Pacific oysters cultured at 25-66% average exposure d^{-1} (see Section 4.2) had a better shape than subtidal oysters. The shape index used - shell depth/shell height \times shell length - indicated the amount of 'cup' (G. Maguire, pers. comm., 1995).

1.1.6.3 Shell abrasion *

An advantage in growing single-seed oysters, is that the oysters can be graded into size groups as they grow (Holliday et al., 1991b). During grading, the fragile new extensions on the outer shell margins, or collectively 'shell frill', is broken off or removed so that the shell heights of the oysters are reduced in comparison to undisturbed oysters (Sparks and Chew, 1960; Spencer, 1990; Spencer et al., 1992). Other shell abrasion treatments, applied deliberately or otherwise, include; mixing and handling of Pacific oysters during experimental work (Thomson, 1952; Sparks and Chew, 1960; Hughes-Games, 1977; Smith 1981; Bolton, 1982; Spencer et al., 1992; Smith, 1994), cleaning Pacific oysters using high pressure water (Spencer et al., 1992), excessive flotation on rafts causing European flat oysters (*Ostrea edulis*) and Australian native flat oysters (*Ostrea angasi*) to rub against each other and their mesh enclosures (Wilson, 1987; O'Meley and Hickman, 1988), storm and wave action causing bottom-cultured American oysters to roll around on the seabed, and dredging of these (Loosanoff and Nomejko, 1955), and rotating cylinders (Robert et al., 1993).

Spencer (1990) recommended that Pacific oysters be graded regularly up until their second year of growth. From their second year on, Spencer (1990) recommended that the oysters be graded at three to six monthly intervals because "frequent and excessively rough-handling retards growth". Tasmanian Pacific oysters are graded on average 5-7 times (R. Calvert, pers. comm., 1991) during their 18 month to 3 year grow-out period on a lease (Maguire et al., 1994b; G. Maguire, pers. comm., 1995). To limit shell losses, small oysters (shell height <15-20 mm) are usually graded underwater, using hand-held or mechanised sieves (O'Meley, 1992). Larger oysters are graded in air using grading machines which operate by vibrating steel or plastic mesh screens of varying sizes, although some farmers still grade the oysters by hand (O'Meley, 1992).

Spencer et al. (1992) subjected Pacific oysters to 13 different 'rough-handling' treatments (see Table 3, Section 4.1). They reported that simulated grading for 2 min in air severely affected growth, especially when the oysters were kept out of water overnight prior to grading. For the other treatments, the effects on growth were linked to the severity of the rough-handling treatment.

Loosanoff and Nomejko (1955) studied the effect of removing the shell frill of American oysters, including recently-formed, thin and transparent shell, as well as the older and thicker portions, such that the shell height was reduced by 4-7 mm. They found that the shell height of damaged oysters increased faster to compensate for the shell loss compared to the controls, and then grew at the same rate as the controls. They suggested that the initially rapid growth occurred because the mantle edge could protrude further. Once the normal ratio of body size and shell dimensions were re-established, however, the height increments became the same as for undamaged oysters. Factors which could slow the process of shell repair include mantle injury (Loosanoff and Nomejko, 1955), the age and condition of the oysters (Loosanoff and Nomejko, 1955; Neudecker, 1981a), and season, where in temperate regions shell growth and repair is slow during winter (Wilson, 1987).

Unusual results were obtained by Jakob and Wang (1994) for American oysters. They found that oysters handled on a bi-weekly basis had grown faster than those that were not handled, after 7 months in land-based tanks. As discussed in Section 4.2, their experiment may have been poorly designed because I consider that both groups could have been subjected to a form of "rough-handling".

If shell abrasion is too severe, oysters can grow into unusual shapes. For example, Sydney rock oysters cultured at low stocking densities in trays exposed to wave action, in the intertidal zone, can become ball-shaped with thick shell walls (Holliday et al., 1991b). Similarly, American oysters that survived a severe storm did not resume normal growth, but became stunted with thick, irregular shells (Loosanoff and Nomejko, 1955). In Pacific oysters, internal shell blistering can occur on both shell valves, and this was presumed to have been caused by mechanical damage to the meat (Spencer et al., 1992).

While several authors reported that mortality was not affected by the shell abrasion treatments applied (Sparks and Chew, 1960; Pereya, 1961; Smith, 1981), Spencer et al. (1992) found that it depends upon the severity of the treatment. In cases where the shell is worn away to the extent that holes in the shell valves exposes the meat to predators, mortality can occur (Loosanoff and Nomejko, 1955; Drinkwater and Howell, 1985).

Some Tasmanian farmers (C. Dyke, P. Chew, R. Calvert, C. Sumner, pers. comm., 1989) believe that removing the shell frill of Pacific oysters (shell height > 20 mm) during machine-grading can improve their condition index and shell shape. Another technique used by these farmers to remove shell frill is to deliberately shake the mesh enclosures, in which the oysters are contained, whilst out on the lease. This latter method also redistributes the oysters within their enclosure. Similarly, farmers in France periodically crack the shell frill of Pacific oysters by hand, or by forceful agitation of the oysters in their enclosures, during seasons when the shell growth rates are fastest (Anderson, 1977).

Spencer et al. (1992) reported that the CIshell of Pacific oysters can be affected negatively by shell abrasion, depending on the severity of the treatment. Robert et al. (1993) found that while increase in shell height was repressed, the shape as well as the condition index (CIshell) of Pacific oysters cultured in rotational cylinders were improved compared to those in mesh bags. Smith (1981) observed that European flat oysters (*Ostrea edulis*) grown in trays were large and thin-shelled if not cleaned or graded regularly, whereas those that were either cleaned, using a fire pump and, or graded using a rotary grader up to once per week, developed thicker and more cup-shaped shells. Hughes-Games (1977) also found that manually agitating Pacific oysters in water twice per week can improve the shape, in that the oysters became heavier for a given shell height. It would appear therefore, that shell abrasion can affect the shell shape of oysters, but that the effect on their condition index is less certain.

It has been reported that the removal of shell frill can affect the rate of gametogenesis and the sex of oysters. Bahr and Hillman (1967) filed the shell margins of fed or starved American oysters on a weekly basis, or when active shell secretion warranted it. Within the fed groups, filed oysters showed slightly faster gonad maturation over unfilled oysters, but in the starved oysters, the opposite occurred. They suggested that the enhanced maturation of filed groups when food was not a limiting factor,

may have been the stress of filing, initiating a species survival mechanism leading to gonad maturation. In addition, there was a predominance of males in both starved and fed filed oysters. They hypothesised that limited energy reserves shared between shell repair and gametogenesis led to the production of sperm in favour of ova because a smaller energy expenditure is required to produce sperm. Robert et al. (1993) had results supportive of Bahr and Hillman's (1967). They reported that Pacific oysters cultured in rotational cylinders matured faster than those in stationary mesh bags (controls) (Robert et al., 1993).

1.2 Summary and aims of this study

The Tasmanian Pacific oyster industry differs from other major edible oyster industries in the southern hemisphere because it is not based upon the collection of natural spatfall and culture of attached oysters, but relies instead, on the hatchery production of unattached spat, or 'single-seed', for grow-out in mesh enclosures until market size (Dix, 1991). Single-seed culture methods offer farmers better control over shell growth rates and shell shape. Survival rates are usually higher because the oysters are better protected from predatory losses by the mesh enclosures employed (Holliday et al., 1988; Spencer, 1990) and "culling" (removal of oysters from collectors), which usually results in high losses, is not necessary (Holliday et al., 1988).

The Tasmanian industry can be extremely profitable, provided the product can be marketed (Treadwell et al., 1991). The natural cycle of gametogenesis and spawning, however, can result in oysters remaining unmarketable for several months post-spawning, since the condition indices (indicators of marketability) are low and the oysters appear unappetising to the eye (Graham, 1991; O'Meley, 1992). For this reason triploid oysters are gaining importance because gametogenesis and spawning are limited (Maguire et al., 1994b).

Techniques used in the Tasmanian industry to encourage diploid Pacific oysters back into marketable condition after spawning include one, or all, of the following;

- i) relaying oysters from sites with low food abundance to more productive sites (information from hatchery companies Shellfish Culture Pty. Ltd., Tasmania, and Marine Culture Pty. Ltd., Tasmania),
- ii) density manipulations (R. Calvert, pers. comm., 1991),
- iii) using different levels in the intertidal zone, so that the oysters are exposed to some degree of aerial exposure each day (C. Dyke, P. Chew, R. Calvert, C. Sumner, pers. comm., 1989),
- iv) "handling" or treatments including, machine-grading, shaking baskets of oysters whilst out on the lease, and even shovelling

oysters around on concrete (C. Dyke, P. Chew, R. Calvert, C. Sumner, pers. comm., 1989).

*

The aim of this study was to determine how shell abrasion and aerial exposure treatments affect the meat to shell growth, and the general performance, of Pacific oysters cultured in Tasmania, as measured by growth in whole weight, shell and meat weight, and linear shell dimensions, and by the use of condition and shape indices, glycogen content and gonad development.

2. Materials and methods

2.1 Duration of experiments, sites, culture equipment and experimental oysters

Experiment 1 started on May 12 and finished on August 1, 1990 (81 d). A commercial oyster lease located in Little Swanport estuary, on the east coast of Tasmania (Fig. 1), was the site chosen for the study. It has a sandy and, or mud bottom with abundant seagrasses and native flat oyster (*Ostrea angasi*) beds. The site is largely sheltered from prevailing westerly winds by the surrounding hills. Predators are few and are mainly limited to Pacific gulls (*Larus pacificus*), kelp gulls (*Larus dominicanus*), black bream (*Acanthopagrus* spp.) and greenback flounder (*Rhombosolea tapirina*) (C. Dyke, pers. comm., 1990). The average tidal range was 0.5-1.8 m during the experimental period (MBH, 1990).

Treated softwood racks with horizontal rails (length = 37 m) set at a vertical distance of 30 cm apart, were used (Fig. 2a). The upper rail had been used to "condition" or "finish" Pacific oysters for a period of 4-6 weeks prior to sale, while the lower rail was nailed into place, and approximated the height used to culture smaller oysters on the farm (C. Dyke, pers. comm., 1990). The oysters were held in enclosures consisting of 12 mm rigid plastic mesh (Nylex®), formed into the shape of a basket (length 58 cm x width 39 cm x height 15 cm). A "unit" consisted of two baskets held together by treated softwood sticks inserted through the mesh (Fig. 2a). The units were attached to the rails by rubber bands (Parsons, 1974), and were positioned so that they did not overhang each other.

Pacific oysters from an intertidal commercial lease in north western Tasmania (Fig. 1), were machine-graded using a 37 mm screen, and those retained on this mesh size were transferred by road to the Little Swanport site. The oysters were then placed into 12 mm mesh baskets, and were cultured intertidally for a period of six weeks. A total of 9750 oysters were used for the experiment. Their initial (day 0) mean shell height and whole weight were respectively, 65.1 ± 0.5 mm and 27.7 ± 0.4 g (means \pm s.e.; n=270). Unfortunately, most oysters did not have obvious new shell growth, or shell-frill extensions (Fig. 3a); their appearance was similar to the oyster shown in Fig. 3b, without shell-frill extensions.

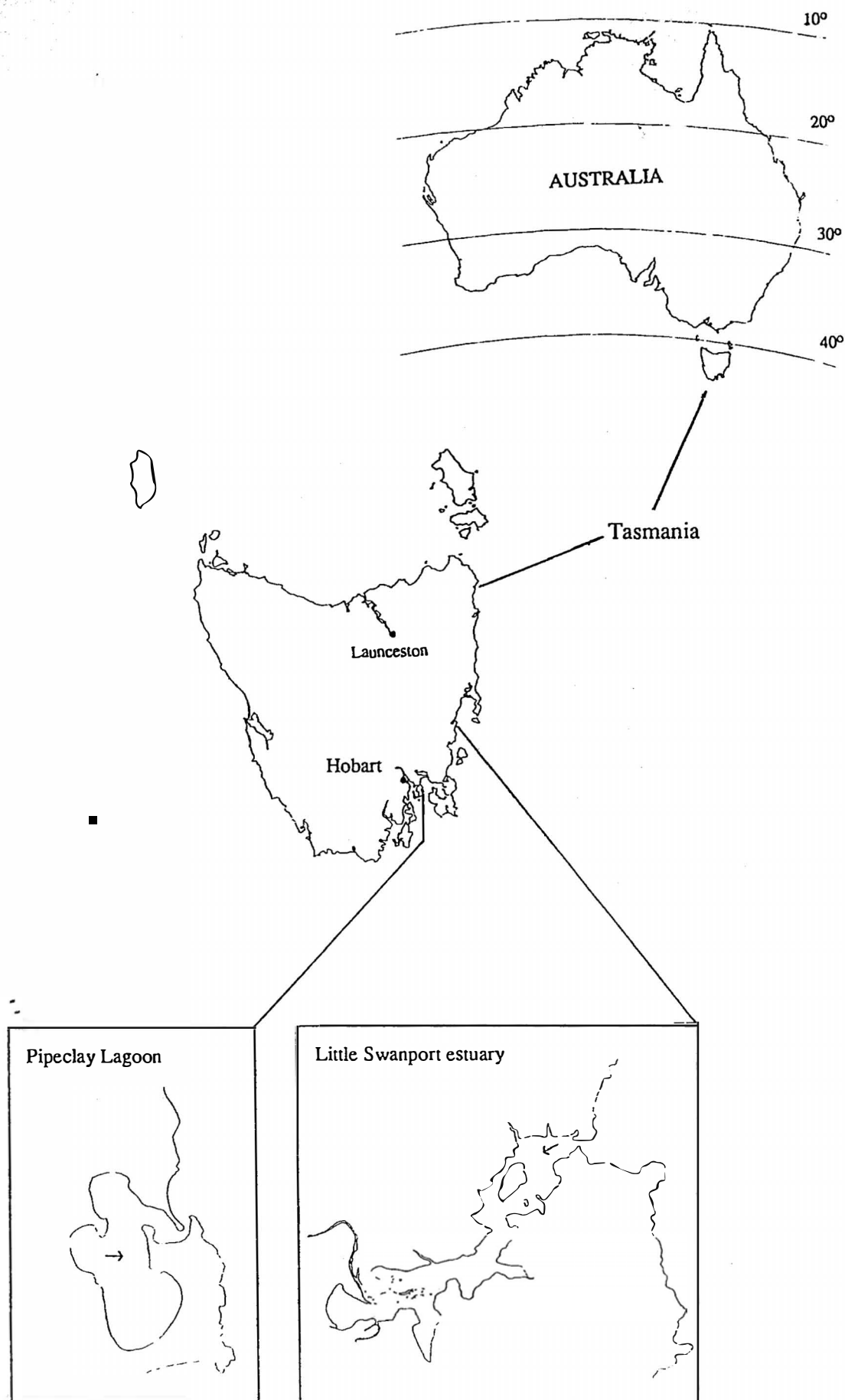
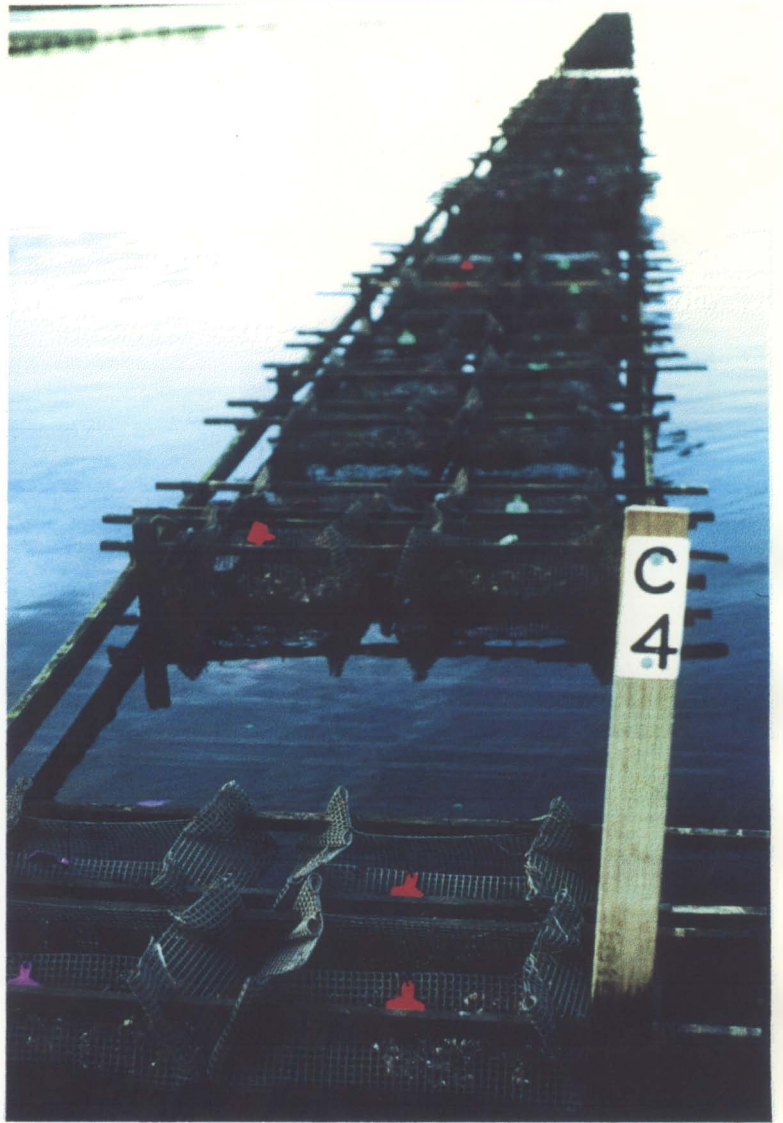


Fig. 1. Location of Experiment 1 and 2 study sites. Experiment 1 - Little Swanport estuary, Experiment 2 - Pipeclay Lagoon. Arrows show lease positions.

(a)



(b)



Fig. 2. Basket enclosures and racks used in Experiment 1 (a) at Little Swanport, and Experiment 2 (b) at Pipeclay Lagoon. In Experiment 1 the rails were set at a vertical distance of 30 cm apart, and in Experiment 2 the rails were 15 cm apart.

(a)



(b)



Fig. 3. Pacific oyster with (a) and without (b) shell-frill extensions.

Experiment 2 was conducted for 124 d, from 10 April until 12 August, 1991. A commercial oyster lease located in Pipeclay Lagoon, an estuary located on the south-east coast of Tasmania (Fig. 1) was the second study site chosen. It has a sandy bottom with little vegetation, and few predators; mainly Pacific gulls, flounder, and starfish (Woodward, 1985). The prevailing winds are mainly from the northwest, and due to the shallowness of the estuary, wave action can be quite severe (P. Chew, pers. comm., 1991). The average tidal range, over the experimental period, was 0.5-2.1 m (PAHBDL, 1991).

Due to the shallowness of the site, the rails (length = 50 m) were set at a vertical distance of 15 cm apart (Fig. 2b). The top rail had been used to "finish" oysters prior to market, while the lower rail, nailed into place, approximated the height used to culture smaller oysters. Units, similar to those used in Experiment 1, were used to hold the oysters.

Oysters for this experiment were from stocks held at the Pipeclay Lagoon lease. Three months prior to the experiment the oysters had been machine-graded over a 33 mm screen, but at initiation of Experiment 2 the oysters had grown substantial shell frill on their outer margins (Fig. 3a), and also had large 'flutes' (shell extensions on the left valve). The oysters had an initial (day 0) mean weight of 29.9 ± 0.6 g and mean shell height of 65.4 ± 0.7 mm (means \pm s.e.; $n=240$), and a total of 8640 oysters were used for this experiment.

2.2 Treatments

2.2.1 Shell abrasion procedures

Experiment 1 oysters were removed from the Little Swanport lease while in their baskets and transferred by punt to a land-based facility, where they were stored under tarpaulins overnight; the oysters were kept on land for a total of 27 h, before being replaced back on the lease. The next morning the baskets were overturned so that the oysters fell into plastic crates. These were randomly assigned into three treatment groups; oysters were to be machine-graded twice (MM), or only once (M), or be a control (C) group which were not machine-graded.

The treatments were carried out using a grading machine (Fig. 4) which had a tray (275 cm x 85 cm) with a 27.5 mm chicken-wire mesh base, set at an incline of 15°. An electric motor turned a pulley-belt which induced a reciprocating vertical lift of 6 mm at a frequency of 630 times per minute while another pulley-belt produced a horizontal displacement of 6 mm at a frequency of 700 times per minute. Randomly selected crates of oysters were overturned onto the highest point of the tray incline and collected at the other end using other crates into which the oysters fell a distance of up to 0.63 m. Oysters to be machine-graded twice (MM group) were subjected to a repeat treatment. Control oysters (C group) were left in their crates while the other two-thirds of the oysters were being machine-graded.

In Experiment 2, baskets of oysters were removed from the Pipeclay Lagoon lease and transferred by punt to a land-based facility. They were covered with a tarpaulin and left overnight on the punt; the oysters were kept on land for a total of 28 h, before being replaced back on the lease. The next day, the baskets of oysters were randomly assigned into two groups; those to be subjected to machine-grading once (M), or not machine-graded (C group).

Two thirds of the oysters were subjected to machine grading. The grading machine (Fig. 4) had a tray (92 cm x 28 cm) with a 30-mm steel mesh base and was set at an incline of 40°. An electric motor turned a pulley-belt which induced a reciprocating vertical lift of 4 mm at a frequency of 600 times per minute, while no horizontal displacement was produced (P. Chew, pers. comm., 1991). Crates of oysters were overturned onto the highest point of the tray incline into a large feeder bin and collected at the other end using crates into which the oysters fell a distance of up to 0.48 m. The control oysters (C group), however, were overturned out of their baskets gently onto grassed land to minimise shell breakage, prior to counting them into baskets.

After six weeks (day 38), half of the M group baskets were shaken vigorously in air for 30 sec, by two people holding the sticks supporting pairs of baskets. This new treatment group was designated as MB. These baskets were shaken again six weeks later (day 82).



Fig. 4. Grading machine used in Experiment 2.

2.2.2 Stocking densities and aerial exposure levels

The factorial design in Experiment 1 included; oysters to be held at a high growing height (H group) and those to be held at a low growing height (L group), such that there was a total of six combinations;

MMH	machine graded twice, high aerial exposure,
MML	machine graded twice, low aerial exposure,
MH	machine graded once, high aerial exposure,
ML	machine graded once, low aerial exposure,
CH	not machine graded, high aerial exposure,
CL	not machine-graded, low aerial exposure.

After the grading treatments were applied, groups of 80 oysters were counted into 25 baskets per combination (354 oysters m⁻² of floor area) and these were positioned randomly on the high and low rails of the experimental rack.

In Experiment 2, high (H group) and low (L group) growing heights were also used. The six combinations were;

MBH	machine graded once, baskets shaken at 6 weekly intervals, high aerial exposure,
MBL	machine graded once, baskets shaken at 6 weekly intervals, low aerial exposure,
MH	machine graded once, high aerial exposure,
ML	machine graded once, low aerial exposure,
CH	not machine-graded, high aerial exposure,
CL	not machine-graded, low aerial exposure.

Once the grading treatments had been applied, groups of 65 oysters were counted into 18 baskets per combination (288 oysters m⁻² of floor area). The baskets were then secured to the high and low rails of the experimental rack, in their randomly assigned positions.

2.3 Sampling regime

In Experiment 1, samples were taken weekly for the first four weeks; thereafter every three weeks until completion of the study (81 d). In

Experiment 2, samples were taken usually at two weekly intervals, except in weeks 8 and 14 which were not sampled (121 d).

The oysters themselves were treated as the replicates rather than the usual method of replicate containers (baskets) of animals. This overcame the problem of possible spatial heterogeneity on the lease because a few oysters from many baskets were sampled rather than intensive samples taken from a few replicate baskets. At each date, 3 or 4 oysters per basket were randomly sampled and transported by road out of water, in soft mesh bags within padded plastic boxes. At the laboratory, the shells were brushed clean in freshwater and fouling organisms were removed using a knife. The oysters in soft mesh bags were then placed into a recirculating system which contained 750 l of aerated and sand-filtered seawater, at ambient temperatures (10-19°C), for 1-3 d prior to analysis.

2.4 Abiotic measurements

2.4.1 Water temperature and salinity

Surface water temperatures were recorded ($\pm 0.5^\circ\text{C}$), usually on a daily basis, by the oyster farmers using calibrated thermometers. Water samples for salinity measurements, were collected from about 10 cm depth in clean, plastic containers which were tightly sealed to prevent evaporation. At the conclusion of each experiment these were analysed ($0-32 \pm 0.1\text{‰}$; $32-42 \pm 0.03\text{‰}$) using a Hamon Salinity-Temperature Bridge 602 Mk II® (Yeokal Pty. Ltd., Brookvale, Sydney, Australia).

2.4.2 Aerial exposure

Aerial exposure levels were not measured in Experiment 1. Maguire and Kent (1991) however, used the same racks in their work in the following year. They measured the exposure levels at each rail height at 15 min intervals, and the mean of these data, based on the same months, is reported in this study. Data presented relate to the floor of the oyster baskets rather than the rails that the baskets were suspended from.

In Experiment 2, aerial exposure levels were measured at 15 min intervals, at the position of oysters held in baskets, at each rail height. The components of the data logging system (Wesdata, Perth, Australia) included; a Wesdata exposure transducer[®], a Wesdata 390 data logger[®], a Wesdata hand-held field transfer unit[®] (150 K memory), and an IBM compatible computer for transfer of data to hard disk (Kent and Maguire, 1992). Due to installation problems and battery problems in the data logger, information was gained for only part of the experimental period (29 d; 15 July - 12 August, 1991).

2.5 Biotic measurements

Before removal from the recirculating seawater system, the bags containing the oysters were gently shaken underwater for at least 10 s. This was to ensure that the shell valves were tightly closed, thereby reducing loss of shell liquor (water), and hence whole weight. The oysters were then placed into labelled buckets containing ambient seawater while being processed. Sampling intensity (number of oysters per combination) is indicated in Section 3. ■

2.5.1 Survival

Survival was determined from the counts of live and dead oysters at the final and initial sample dates, taking into account the numbers of oysters sampled from the baskets.

2.5.2 Whole weight and shell growth

Individual oysters were removed from a labelled bucket, dried with paper towelling and the linear dimensions recorded to the nearest 0.5 mm using Vernier[®] callipers (Mitutoyo, Hiroshima, Japan). Height was measured as the maximum distance between the umbo and shell margin, length as the maximum dimension perpendicular to the height axis, and depth as the maximum distance between the left and right shell valves of the intact oyster (Fig. 5) (Galtsoff, 1964; King, 1977).

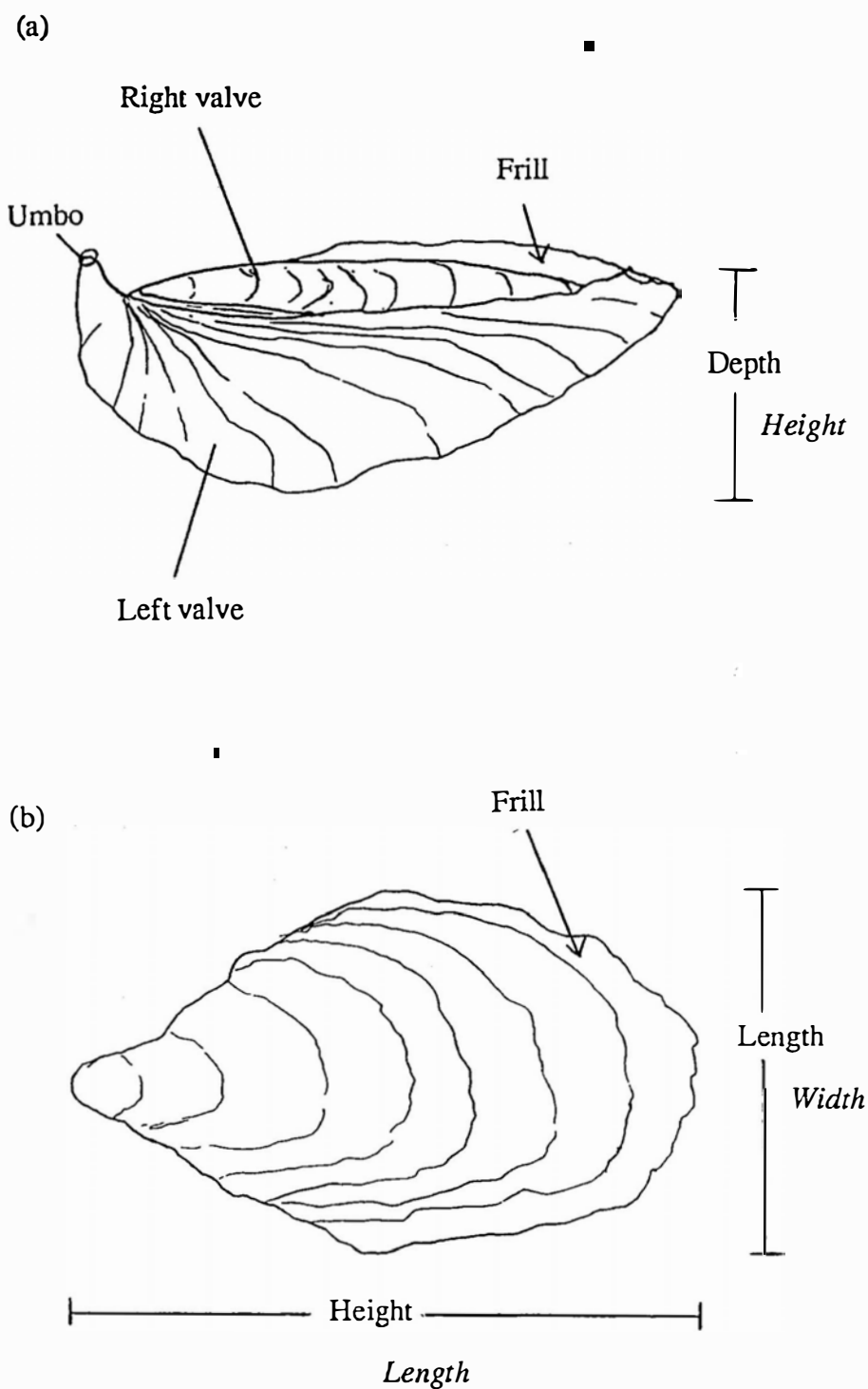


Fig. 5. External linear shell dimensions. Height, length, and depth, and their corresponding commonly used terms (*italics*). Shown also are the umbo, left (cupped) valve, right (flat) valve, and frill.

Each oyster was then weighed (± 0.01 g) to obtain the whole weight using a Mettler PM 4800 Delta Range® (Greifensee, Switzerland) balance. Oysters were opened by severing the ligament; the adductor muscle was then severed and detached from the shell valves using a flat-bladed knife. The insides of the shell valves were checked for the presence of mudworm (spionid polychaete) casts (Skeel, 1979; Wilson, 1993) and then these were blotted dry with paper towelling. These and any shell fragments were dried in air (18-22°C) for 24 h and then weighed again to obtain the dry shell weight (Brown and Hartwick, 1988a, b).

2.5.3 Meat growth

Both sides of the oyster meats were superficially dried on paper towelling for about 30 sec before being weighed to the nearest 0.1 g. These wet meats were then placed individually into snap-lock plastic bags and frozen. Later (up to four months), the meats were removed from the bags, by squeezing the meat and any liquid from the bag onto Pyrex® dishes. Individual dry meat weights were obtained by oven-drying at $80 \pm 1^\circ\text{C}$ to a constant weight (24-48 h) in a forced draft oven. The meats were placed into a desiccator, to prevent moisture absorption while cooling to room temperature. These were then weighed to the nearest 0.01g.

2.5.4 Condition indices

The volume condition index (CIvol) described by Lawrence and Scott (1982), and the dry shell condition index (CIshell) described by Brown and Hartwick (1988b) were used in this study.

$$\text{CIvol} = \frac{\text{dry meat weight (g)}}{\text{whole oyster weight (g) - dry shell weight (g)}} \times 1000$$

$$\text{CIshell} = \frac{\text{dry meat weight (g)}}{\text{dry shell weight (g)}} \times 1000$$

2.5.5 Shape indices

Two shape indexes, using linear dimensions of the intact whole oyster shell, were used. These were a "roundness" index, and a "cup" index;

$$\text{Roundness index} = \frac{\text{shell length (mm)}}{\text{shell height (mm)}}$$

$$\text{Cup index} = \frac{\text{shell depth (mm)}}{[\text{shell height (mm)} \times \text{shell length (mm)}]^{0.5}}$$

2.5.6 Glycogen content

In Experiment 1, the oysters used for glycogen analysis were shucked, and then superficially dried, wet meats were placed in individual plastic bags and frozen. Subsequently, the meats were thawed, and groups of five oyster meats were homogenised using a coffee grinder. The homogenate was then tested for glycogen content using the method of Keppler and Decker (1974). Results were expressed on a dry matter basis, using moisture content data obtained during condition index determinations.

In Experiment 2, groups of five dried oyster meats from condition index measurements were stored in plastic, airtight containers, for up to three months prior to analysis. These were analysed using a modified procedure of Keppler and Decker (1974) (Day and Maguire, unpublished data).

Analyses, for either experiment, were repeated when duplicate subsamples from the homogenate, based on five oysters, varied >15%.

2.5.7 Gametogenesis

For each combination, oyster meats were carefully removed from the shells, and stored in 10% formal calcium in seawater. After fixation, transverse sections of 3-5 mm were cut approximately 3 mm above the labial palps as recommended by Morales-Alamo and Mann (1989). For each oyster in Experiment 1, and every third oyster in Experiment 2, a transverse section was also cut at the position of the adductor muscle, in

order to obtain additional mantle tissue for assessment of possible damage due to the effects of shell abrasion (Loosanoff and Nomejko, 1955). The tissue was then processed using standard paraffin histology. Sections (4-7 μm) on glass slides were then stained with Mayer's haemotoxylin and eosin Y.

Gamete development was assessed using the staging system described by Dinamani (1974) for New Zealand rock oysters (*Saccostrea glomerata*). The stages were condensed into the following groups: 1/2, ripening; 3/4, ripe; 5/X, post-spawned; R, regressive stage.

Mantle tissue was assessed for possible damage at $\times 100$ magnification. Gonadal tissue sections also contained mantle tissue, and these were also assessed for possible damage following machine grading, on day 0, of each experiment; in Experiment 1, MM, M and C groups ($n=15$ group⁻¹), and M and C groups ($n=15$ group⁻¹) in Experiment 2 were assessed. In case tissue damage was not apparent soon after treatment, another 60 oysters from Experiment 1 were examined from the day 8 sample (MMH, MML, MH, ML, CH and CL groups; $n=10$ group⁻¹). The results are reported in Sections 3.2.1 and 3.4.1 (Survival).

2.5.8 Shelf life

Final sample (day 124) Experiment 2 oysters were used for the shelf life experiment. They were treated in the same manner as the other oysters, that is, prior to processing they were transported, cleaned, and placed in a recirculating seawater system (Section 2.3) where they were held for 3 d prior to processing; this was to allow them to recover from the likely stresses of handling and transport out of water. The oysters were removed from the water, they were randomly divided into 12 groups of 30 oysters each, and were then assigned randomly to plastic trays (0.57 m \times 0.34 m) (two trays per treatment combination; MBH, MBL, MH, ML, CH, CL). The 12 trays were then randomly assigned to three shelf levels of a wooden stand, situated in a room with an air temperature of 14°C and humidity of 94% for 55 days. Each morning, oysters which were gaping or dead were counted and removed. A gaping oyster had its shell valves apart (open). A live oyster was one which was closed tightly, or one which was gaping but which responded to gently pressing the valves closed; if the valves stayed closed it was considered to be alive. A dead

oyster did not respond to gently pressing the valves closed, and would continue to gape.

On the final sample date (55 d), the remaining oysters were placed into seawater for a period of 1 h, to determine whether they were still alive, or dead. Live oysters were those whose valves opened whilst in seawater, but which closed together again, and remained closed, after gentle pressing. Dead oysters were those that either did not open their valves in seawater, or else if they did, they continued to gape when the valves were gently pressed together; these six oysters were not excluded from the data set and their time of death was recorded as day 55. As the total number of oysters in the study was large ($n=360$), the effect of these six oysters on the results would have been quite minor. The results are reported as cumulative gape and cumulative mortality, every 5 d, except for an extra sample on day 7, which was when the first oysters had begun to gape.

2.6 Statistical analyses

In each experiment, and for each sample date, the data from eleven performance indices (whole weight, shell height, dry shell weight, dry meat weight, CIvol, CIshell, roundness index, cup index and glycogen content; and shell length and shell depth in Appendix D) were analysed using two-factor ANOVA including the shell abrasion X aerial exposure interaction based on fixed factors. The shelf life data from Experiment 2, were also analysed using two-factor ANOVA. An alpha value of 0.05 was used throughout. This represents a 1 in 20 chance of a Type 1 error ie, falsely rejecting a true null hypothesis. In this study, 189 interactions were assessed in two-factor ANOVAs and in only 12 cases was the null hypothesis rejected. This proportion (0.06) is consistent with the alpha value and suggests that these "significant interactions" may well be due to random variation rather than systematic (treatment) variation. When significant interactions occurred, the means for each combination of shell abrasion and aerial exposure were compared using Fisher's Least Significance Difference test (Fisher's LSD). When significant interactions were not found data were pooled for either shell abrasion or degree of aerial exposure and treatment levels within each of these two treatments were compared using Fisher's LSD. Homogeneity of variance was assessed using Cochran's test (Sokal and Rohlf, 1981). Variability is indicated by standard error (s.e.) values unless specified otherwise.

Normality of sample data for the eleven performance indices was assessed using the Shapiro-Wilk W test (Tietjen, 1986) (Appendix B). In very few cases were data found to be non-normal and none of the variables (for example whole weight or dry meat weight) were consistently non-normal (Appendix B). In the absence of a consistently large deviation from normality, parametric techniques were adopted throughout. Effects of treatments on gonad development or sex ratio were analysed using Chi-square tests (based on counts not percentage frequency data). Correlation analyses were also used (Appendix C). Data presented in Appendices E and F were analysed using one-factor ANOVA, and homogeneity of variance was assessed using Cochran's test (Sokal and Rohlf, 1981). The computer software packages used for data analysis were Statview 4.0 (Abacus Concepts, U.S.A.) and JMP 2.0 (SAS Institute, U.S.A.). Graphical figures were drawn using Cricket Graph III (Computer Associates, U.S.A.).

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1. Introduction

1.1 Review

This review aims to introduce the reader to the literature covering the taxonomy, distribution, marketing, site selection and cultivation methods for Pacific oysters (*Crassostrea gigas*). Where possible, specific studies which may be relevant to the effects of shell abrasion and aerial exposure on oysters are emphasised.

1.1.1 Production and value of Pacific oysters

Oysters are an important aquaculture product. In 1991, oysters accounted for 31% by weight (t) of the world aquaculture production of molluscs, and specifically Pacific oysters accounted for 84.2% of the world oyster production in 1991 (by weight) (FAO, 1993).

The wholesale value of cultured edible oysters in Australia was worth \$34.6 million in 1989-1990 (Treadwell et al., 1991). While this represented 18% of Australia's aquaculture sales (Treadwell et al., 1991), it was only about 1% in terms of world-wide oyster sales (Graham, 1991). In 1991, the Tasmanian Pacific oyster industry was worth A\$ 10.5 million (sold at the farm gate) (Stanley, 1993).

1.1.2 Taxonomy and distribution

The oyster *Crassostrea gigas* (Thunberg, 1793) has several common names including Pacific, Giant Pacific and Japanese oyster (Arakawa, 1990a). Its formal classification is as follows: Phylum Mollusca; Class Bivalvia; Sub-class Pteriomorpha; Order Ostreoida; Suborder Ostreina; Superfamily Ostreoidea; Family Ostreoidea; Sub-family Crassostreinae; Tribe Crassostreini; Genus *Crassostrea*; Species *gigas* (Vaught, 1989).

Varieties or types of Pacific oysters which are known in Japan include, in order of their north to south distribution, the Hokkaido, Miyagi, Hiroshima and Kumamoto (Imai and Sakai, 1961; Buroker et al., 1979; Arakawa, 1990a; Deupree, 1993). Types can usually be distinguished

based on shell size, shape and colour, and growth, condition index (meat weight either relative to shell cavity volume, or to shell weight) and survival of the oysters when cultured in water of differing temperature and other environmental conditions (Imai and Sakai, 1961; Arakawa, 1990a). The Kumamoto was found to have a low level of genetic similarity to other *C. gigas* types (Hiroshima and Miyagi), and was reclassified as a non-sibling species *C. sikamea* (Buroker et al., 1979; Arakawa, 1990a; Deupree, 1993).

The Pacific oyster is found from the low intertidal through to subtidal zone, in tropical to cool temperate climate, brackish waters (Harry, 1985). Pacific oysters are native to the Indo-West Pacific (Harry, 1985), Japan (Harry, 1985; Arakawa, 1990a), and along Asian coastlines, extending from Primorsky Kray, in Russia, through to the Korean Peninsula, China, south east Asia (Arakawa, 1990a), and Pakistan (Harry, 1985). They are also native to the Philippine Islands, Borneo, and Sumatra (Harry, 1985).

Introductions of the Pacific oyster to other parts of the world were aimed at establishing a new aquaculture industry. Pacific oysters have been successfully introduced into North America and Canada (Galtsoff, 1964), South America (Chew, 1990), Europe (Walne and Spencer, 1971; Chew, 1990), Africa (Chew, 1990), and Australia (Thomson, 1952; Chew, 1990; Dix, 1991). Pacific oysters were introduced from Japan into Tasmania, Australia, between the years 1947-1948 and 1951-1952 (Thomson, 1952; Dix, 1991). Thomson (1952) did not state the types introduced, however, based on the sites in Japan from which they were collected, those in Tasmania are likely to include Miyagi, Hiroshima and Kumamoto. However, a recent study by Deupree (1993), aimed at establishing whether the deeply cupped Tasmanian Pacific oyster was of the Kumamoto type, showed that the oysters, analysed via gel electrophoresis, were in fact genetically similar to the more common Miyagi type. It is therefore uncertain whether Tasmanian stocks contain the Kumamoto.

Pacific oysters were accidentally introduced into New Zealand, and were first accurately collected and reported in 1971 (Dinamani, 1991). The Pacific oyster is a prolific breeder and quickly colonised the North Island and parts of the South Island (Dinamani, 1991), and as early as 1978, New Zealand oyster farmers were culturing the Pacific oyster instead of the native rock oyster (*Saccostrea glomerata* = *Saccostrea commercialis*)

because similar market prices were obtained for both species, and because the Pacific oyster grows faster and could therefore be marketed in a shorter time (Holliday and Nell, 1987).

Similarly, the Pacific oyster was first recognised in the Pambula River, New South Wales (N.S.W.), Australia, in 1967 (Holliday and Nell, 1987). It quickly colonised most bays and estuaries in N.S.W., and southern Queensland, Australia (Holliday and Nell, 1987). In N.S.W., most of the farmers who culture the native Sydney rock oyster (*Saccostrea commercialis*), regard the Pacific oyster as a pest species. The Sydney rock oyster industry, Australia's largest edible oyster industry, is based on the collection of spat (juveniles) on tarred sticks, or plastic substrates (collectors), placed within bays or estuaries, and the subsequent culture to market size (grow-out) (Malcolm, 1987). The problem for these farmers has been that the Pacific oyster has been successfully out competing the Sydney rock oyster for collector space. However, the Pacific oyster is now cultured in Salamander Bay, N.S.W., on a commercial basis (Bird et al., 1991; Holliday et al., 1993b).

In most areas of Tasmania, feral populations of Pacific oysters have been limited, because the water temperatures have not usually been high enough to encourage the oysters to breed (C. Sumner, pers. comm., 1992). The Tamar river in northern Tasmania, however, was once used to collect Pacific oyster spat, over several years (Dix, 1991). Unreliable spat supplies prompted the development of commercial hatcheries (Dix, 1991). Currently four Tasmanian hatcheries provide spat to major Pacific oyster industries in Tasmania and South Australia (Dix, 1991), and a small industry in Victoria (O'Sullivan, 1990).

1.1.3 Single-seed

The spat from Tasmanian hatcheries are produced as 'single-seed' (also called 'unattached spat' or 'cultchless seed'). Here the larvae (free-swimming stage) are provided with crushed bivalve shells, of a similar size to that of the larvae, which the juveniles (spat), soon outgrow (Dix, 1991). Alternatively, spat (shell height = 4-8 mm) can be detached from plastic collectors by scraping, or flexing the plastic (R. Pugh, pers. comm., 1993). The oysters are then cultured to market size using single-seed

culture techniques; usually mesh enclosures are used to hold the spat (see below), and regular grading and density reductions are carried out.

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In comparison, spat attached to hard surfaces for extended periods, for example tarred sticks until market size, tend to grow around the much larger collector surface (Galtsoff, 1964; Arakawa, 1990a), and often develop a poor shell shape (Galtsoff, 1964). Additionally, grading usually only occurs during 'culling' (removal of market-sized oysters from collectors), and the opportunities for density reductions are limited to adjusting the spacing between collectors (Malcolm, 1987). Clearly single-seed techniques enable better control of stocks.

It should be noted that since active cultivation of Pacific oysters in N.S.W. and New Zealand commenced, many farmers have turned to single-seed techniques (Holliday et al., 1988; Dinamani, 1991; Holliday et al., 1993b). Wild caught spat are detached from synthetic collectors (shell height ≥ 3 mm) and on-grown in mesh-covered sectionalised trays or cylinders (Holliday et al., 1988; Holliday et al., 1991b; Holliday et al., 1993a). Some N.S.W. farmers also use these techniques for Sydney rock oysters (Holliday et al., 1988). The single-seed farming strategies used to culture Pacific oysters in Australia have implications in terms of the quality of the marketable product, as will be discussed later.

Single-seed are protected by mesh enclosures until they have reached a size which does not allow predation, or losses due to wave action (Holliday et al., 1991b). Single-seed enclosures, or 'units', include trays, baskets, bags and cylinders suspended subtidally under rafts or longlines, or intertidally on racks or the seabed. Often farmers design and construct their own units and the type largely depends on the characteristics of the lease site (O'Meley, 1992). As the oysters are grown, they are transferred to enclosures with larger mesh sizes thereby increasing water flow and minimising fouling of the mesh (Holliday et al., 1991b; Holliday et al., 1993a). The mesh size should not be increased prematurely, however, since the oysters can grow into the mesh and become 'beak' shaped rather than the rounded shape required for the market (Holliday et al., 1991b).

Cultivation methods for Pacific oysters have been reviewed; in Japan (Korringa, 1976; Wisely et al., 1978; Kusuki, 1990), Europe (Korringa, 1976; Anderson, 1977; Héral and Deslous-Paoli, 1990), Canada (Quayle, 1988),

North America (Korringa, 1976), New Zealand (Dinamani, 1991), and Australia (Dix, 1991).

1.1.4 Site selection

The Pacific oyster is cultured in a wide range of habitats ranging from clear cold-water, to turbid, warm-water sites (Walne and Spencer, 1971), and growth, meat condition and survival can vary widely (King, 1977; Agius et al., 1978; Wilson, 1987; Brown and Hartwick, 1988a).

Environmental factors which can affect shell growth in bivalves include; the food supply, water temperature (geographic, seasonal, daily), salinity, substratum, depth of the photic zone (Agius et al., 1978), turbidity, population density, and degree of exposure to high energy environments (Seed, 1980).

In particular, shell and meat growth of Pacific oysters at a particular site are affected by temperature, salinity, food levels, current velocity, wave action (Wilson, 1987; Brown and Hartwick, 1988a; Holliday et al., 1991a), culture methods (Spencer and Gough, 1978), and degree of aerial exposure employed (Spencer and Gough, 1978; Littlewood, 1988; Spencer, 1990). Pollutants (Agius et al., 1978; Spencer, 1990), disease organisms, predators, competitors and parasites can also affect growth and survival (Anderson, 1977; Briggs, 1978; Drinkwater and Howell, 1985; Littlewood, 1988; Quayle, 1988; Arakawa, 1990b; Spencer, 1990). Of these, the principal environmental factors affecting growth are water temperature and food abundance, both of which vary seasonally (Malouf and Breese, 1977; Brown and Hartwick, 1988a).

Brown and Hartwick (1988a) reported that Pacific oysters had best growth, in a temperate region, in sites with high spring and summer water temperatures, an abundance of phytoplankton, and non-stressful salinity levels. Adult Pacific oysters can tolerate salinities from 5-55‰ (Nell and Gibbs, 1986; Nell and Holliday, 1988), but somatic growth (body tissue growth excluding the germinal cells which give rise to gametes) only occurs between 16-31‰ (Bernard, 1983; Brown, 1988), and between 20-25‰ is considered to be optimum for growth (Bernard, 1983; Brown, 1988; Spencer, 1990). However, Pacific oysters have been successfully cultured in full strength seawater (35‰) (Maguire et al., 1994b), and in water of higher salinities (40-41‰) (King, 1977; Shpigel and Blaylock, 1991).

Pacific oyster larvae show fastest growth at salinities from 19-27‰, and survival is unaffected between 15-39‰ (Nell and Holliday, 1988). Small spat (1.1 mg) grow fastest between 15-30‰, but growth declines rapidly as salinity is increased from 30-45‰ (Nell and Holliday, 1988). For larger spat (0.68 g), salinities between 15-45‰ do not affect growth, and for both small and large spat, salinities between 15-45‰ do not affect their survival (Nell and Holliday, 1988).

In other studies conducted in temperate regions, low water temperatures in the winter cause slow or no growth in Pacific oysters, and growth is fastest during spring and summer (Imai and Sakai, 1961; Walne and Spencer, 1971; Askew, 1972; King, 1977; Malouf and Breese, 1977; Askew, 1978; Hall, 1984; Drinkwater and Howell, 1985; Brown, 1988; Spencer, 1990; Dinamani, 1991). Although Tasmania can also be considered as cool temperate (Maguire et al., 1994b), Pacific oysters cultured in Tasmania can also exhibit fast growth during autumn (Sumner, 1980a) and winter (Maguire et al., 1994b). In New Zealand, Dinamani (1991) similarly reported that growth of Pacific oysters can be fast in autumn.

Pacific oysters have been cultured in waters with temperatures ranging from -2°C (Askew, 1972) through to 34°C (Hughes-Games, 1977). The temperature at which no growth occurs is about 5.5°C (Spencer and Gough, 1978), while 10°C has been suggested as the minimum optimum temperature for growth (Askew, 1972); these may be influenced by food abundance, however (Brown and Hartwick, 1988b). Growth rates may not be enhanced in sexually mature adult oysters when temperatures are above 12°C, because energy is not only used for somatic growth but is also directed towards reproductive activity, or gametogenesis (Mann, 1979; Brown, 1988).

Oysters cultured intertidally, are also subject to air temperatures. Extremes can cause mortality depending upon the period of exposure. For example, high temperatures of 30-35°C (Kusuki, 1990), or freezing air temperatures (<0°C) (Spencer, 1990) will cause high mortalities. Sydney rock oysters cultured in N.S.W., and Queensland, suffer from a condition known as 'heat stress' during the summer months (Sumner, 1980a; Potter and Hill, 1982). Mortalities are reduced by spraying the oysters with salt water or by covering them over with shade cloth (Sumner, 1980a; Potter and Hill, 1982). In Tasmania, however, air temperatures are moderate by

comparison (Sumner, 1980a) so that usually these methods are not needed.

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Oysters are filter feeders and in their natural environment they feed upon phytoplankton, and to a lesser extent, bacteria (Brown, 1988; Nell, 1993b), organic detritus (Brown, 1988; Crosby et al., 1989), and dissolved organic compounds (Fankboner and De Burgh, 1978; Nell et al., 1983; Nell and Gibbs, 1989; Nell, 1993b). While the nutritional quality of phytoplankton can vary widely (Brown et al., 1989; Nell, 1993b), and some algal blooms can be harmful (Shumway, 1990; Whyte et al., 1990; Hallegraeff, 1993), it is preferable that the oysters are exposed to the variety of species present in their natural environment, since it has been shown that mixed diets produce the fastest growth in oysters in laboratory situations (Epifanio, 1979; Brown et al., 1989).

In Tasmania, phytoplankton blooms typically occur twice yearly, during spring and autumn (Sumner, 1980a). High food availability in the spring combined with increasing water temperatures, usually results in high growth rates (Bayne and Newell, 1983; Brown, 1988). In the autumn, high food availability coincides with an increase in metabolic reserves prior to the winter months (Brown and Hartwick, 1988a), where low temperatures and food levels, in turn, coincide with reduced metabolic requirements in the oyster (Bernard, 1983; Brown, 1988).

Apart from selecting a suitable site, there is no control over phytoplankton species or their abundance in the oyster's environment. To an extent however, the culture methods used can increase food availability for single-seed oysters via density manipulation and increasing the mesh size of the enclosure to increase current flow to the oysters (O'Meley, 1992). Carrying capacity, or the amount of food within the water column of various sites, has become an increasing concern to aquaculturists (Héral and Deslous-Paoli, 1990; Kusuki, 1990). The concern is that, if established leases are expanded or new leases granted within an estuary, there may not be enough natural phytoplankton or other useable organic matter to support oyster growth. Recent economic models indicate that profits for Tasmanian farmers could drop by two-thirds if Pacific oysters took up to three years, rather than up to two years, to reach marketable size (Treadwell et al., 1991).

Water movement, or current flow, provides a continuous supply of food particles to the oysters (Westley, 1965). The current flow required to maintain oyster growth is inversely related to the amount of food particles in the water (Malouf and Breese, 1977; Brown and Hartwick, 1988a), and has been positively correlated to the feeding activity of Pacific oysters and other bivalves (Walne, 1970; Malouf and Breese, 1977). In addition, filter-feeding activity is positively related to temperature (Bernard, 1983), such that high flow rates are not beneficial at low temperatures, and weight loss can occur at high temperatures if the flow-rate is inadequate (Malouf and Breese, 1977). Optimum conditions for the growth of Pacific oysters are sheltered sites with tidal flows of up to 1-2 knots ($0.50\text{-}1.0\text{ m s}^{-1}$) (Spencer, 1990).

Excessive wave action can cause loss of oysters from their enclosures, and extreme tidal currents in conjunction with high wave action can cause damage to the culture equipment or to the oysters themselves (Spencer, 1990). Farmers take these factors into consideration when planning farm lay-out so that damage to culture equipment is minimised, whilst ensuring good water flow to the oysters. Tasmanian farmers may also increase the density of oysters per enclosure (R. Calvert, pers. comm., 1991), position the enclosures at different places on the farm, or place them subtidally.

In the United Kingdom (U.K.), annual mortality rates for juvenile and adult Pacific oysters held in sea-based trays are expected to be between 10-15% (Hall, 1984). Survival of Pacific oysters cultured in the U.K. is not, however, related to season (Walne and Davies, 1977), or water temperatures (Spencer and Gough, 1978). In Tasmania, low mortality rates are expected for Pacific oysters cultured in mesh enclosures; one study showed that Pacific oysters cultured for two years in mesh baskets can be <1% at favourable sites (Maguire et al., 1994b).

To prevent high mortalities the oysters need to be protected from predators; usually mesh enclosures are employed (Parsons, 1974; King, 1977; Spencer, 1990; Holliday et al., 1991b). For example, a study conducted in salt ponds (40‰) in South Australia showed that mortality of protected compared to unprotected Pacific oysters was 11 and 30%, respectively, after 7 months (King, 1977). Predators of Pacific oysters in Tasmania, include flatworms, and various fish, for example black bream (*Acanthopagrus* spp.) and greenback flounder (*Rhombosolea tapirina*),

Pacific gulls (*Larus pacificus*) and kelp gulls (*Larus dominicanus*), but these cause only minor stock losses (Dix, 1991). It should be noted, however, that the European shore crab (*Carcinus maenas*) which can cause high mortalities of Pacific oysters laid unprotected on the seabed (Parsons, 1974), has now colonised Tasmanian waters (Gardner, et al., 1994). Disease organisms are few in Tasmania (Dix, 1991), although they are present in very low numbers (Wilson, 1993).

1.1.5 Factors affecting marketability of Pacific oysters

Tasmanian Pacific oysters sold commercially are usually 65-75 mm in shell height (the longest shell dimension) (Dix, 1991), although there is some demand for larger oysters (C. Dyke, pers. comm., 1990). In some Australian states a market for smaller ('cocktail') oysters has developed, while Sydney rock oysters are usually sold at a smaller size than Pacific oysters (G. Maguire, pers. comm., 1995). The majority of Pacific oysters are sold live to retail fish shops, restaurants and hotels (Dix, 1991; Graham, 1991) where they are opened and presented in the half shell (Dix, 1991). Characteristics of marketable oysters for the half-shell trade are as follows. Before retail, the bivalves should be certified fit for human consumption (Graham, 1991). The shell should contain no shell blisters usually from spionid polychaetes (Skeel, 1979; Wilson, 1993), and should be cupped and rounded in shape. The meat should be flavoursome, without grit, and a high proportion of the shell cavity should be filled by the meat (as measured by a 'condition index' value). The meat should also be full and creamy in appearance. Finally, the oyster should have a shelf-life out of water of at least one week to allow for transport and storage, prior to sale (O'Meley, 1992).

Pacific oysters cultured in Tasmania are of a high quality, and usually meet the criteria of a marketable oyster because of the single-seed methods (use of mesh enclosures, density manipulations, and grading) used during grow-out. The meat condition, however, can be inadequate after spawning in summer, and oysters from different sites can vary greatly in meat condition (Maguire et al., 1994b).

Shell-boring mudworms (spionid polychaetes, for example *Polydora* spp.) can be a major problem because the blisters that they cause weaken the shell, making it difficult to 'shuck' (open) the live oysters, and disturbed

blisters can also render the product unfit for the half-shell trade (Littlewood, 1988; Dinamani, 1991). Additionally, because the oyster expends energy, in covering the blister with nacre, that would otherwise be devoted to growth, the condition of the oyster can be reduced and may even lead to death (Skeel, 1979). When the worms are not living inside oyster shells, they can also be found in the bottom sediments, and in the accumulated mud, faeces and pseudofaeces that build up around the oysters (Skeel, 1979).

In N.S.W., mudworm infection rates can be high. For this reason a N.S.W. farmer designed a rotating cylinder to help keep the oysters free from mud and silt (Holliday et al., 1993a). Tasmanian Pacific oysters rarely contain mudworm blisters (Dix, 1991; Wilson, 1993) partly because the oysters are cultured away from the bottom sediments, on intertidal racks (Dix, 1991; Nell, 1993a), the latter of which helps to desiccate the worms (Skeel, 1979), and because regular grading of the oysters helps to dislodge accumulated mud (R. Calvert, pers. comm., 1991). Mudworm can be a major problem on Pacific oyster farms in South Australia and New Zealand (G. Maguire, pers. comm., 1995).

A desirable characteristic of a marketable oyster, is that the meat should fill a high proportion of the shell cavity, quantified by calculating a static condition index. This is usually one of two indices; a ratio of the dry meat weight to shell cavity volume (CIvol), or the dry meat weight to dry shell weight ratio (CIshell). For convenience, each ratio is multiplied by a factor of 100 or 1000 (Brown and Hartwick, 1988b). Lucas and Beninger (1985) suggested that while CIshell is a health indicator, CIvol indicates product quality and is therefore an economic index. Although in general these definitions have been accepted, there is still much discussion within the scientific community about their relevance and meaning (see Appendix A).

Oysters with high condition index values, have high glycogen reserves or advanced gonad development (Gabbott, 1975; Mann, 1979) resulting in full, creamy meats (Maguire et al., 1994b), while spawned-out oysters have a grey and transparent appearance (Graham, 1991). Glycogen is used by the oysters as an energy store which is utilised during gametogenesis in the spring (Gabbott, 1975; Mann, 1978). A decline in glycogen or carbohydrate levels in the meat is synchronous with an increase in ova lipid levels (Gabbott, 1975). While it has been suggested that reallocation

of energy from somatic growth to gamete production can lead to reduced growth rates (Sumner, 1980a; Brown, 1988), the effect on somatic growth upon spawning is that a major energy reserve is lost to the environment (Gabbott, 1975).

In Tasmania, gametogenesis in Pacific oysters begins in the spring (October) and culminates in a major spawning event during late summer (February), or sporadically throughout the summer, depending upon maximum water temperatures reached (Sumner, 1980a; 1980b). If temperatures do not exceed 18-20°C Pacific oysters will not spawn (Mann, 1979). When water temperatures are too low to activate spawning, their condition index values remain high (Hughes-Games, 1977; King, 1977; Graham, 1991). In Tasmania, Pacific oysters often do not spawn to completion, and may recover quickly (Graham, 1991), and not all oysters on a lease or on different leases may spawn at the same time. This allows marketing for most of the year, from Tasmania (Graham, 1991). However, individual farms may not be able to market oysters for up to three months (summer - autumn) in Tasmania, and this period may even be longer in some South Australian inlets (G. Maguire, pers. comm., 1995).

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Triploid Pacific oysters have several advantages over diploids. Triploid oysters contain three sets of chromosomes per cell rather than the usual two (Beaumont and Fairbrother, 1991). Because triploid Pacific oysters are capable of only limited gametogenesis they retain meat condition during the spawning season (Maguire et al., 1994b). Additionally, Maguire et al. (1994b) found no evidence of spawning in triploid Pacific oysters cultured in Tasmania. Allen and Downing (1991) reported that American consumers prefer triploid Pacific oysters over normal diploids. In Tasmania, however, there were few differences in the response of taste-test panellists to triploid and diploid Pacific oysters although no poor, recently spawned diploid oysters were used in the tests (Maguire et al., 1994a).

In Japan and Korea, the high intertidal zone is used to culture spat during their first growing season (Imai and Sakai, 1961; Quayle, 1988; Kusuki, 1990). This 'hardens' the spat, such that the shell thickness increases (Littlewood et al., 1992) and the adductor muscle is strengthened (Imai and Sakai, 1961). The shelf life, or survival in air, is thought to be improved by this (Imai and Sakai, 1961; Quayle, 1988), and so they are

better able to survive during long distance transport and, or storage prior to sale (O'Meley, 1992). The oysters also have better survival rates when transferred after a few months to subtidal culture units, but the effectiveness of the hardening treatment tends to decrease the longer the spat are held subtidally (Kusuki, 1990).

1.1.6 Effects of culture techniques on the performance of Pacific oysters

1.1.6.1 Stocking density

High stocking densities can cause reduced growth and survival rates (Drinkwater and Howell, 1985; Spencer, 1990; Holliday et al., 1991b), clumping where two or more oysters fuse together (Spencer, 1990), an irregular shape (R. Calvert, pers. comm., 1991), and the oysters may grow into the mesh of enclosures (Neudecker, 1981b; Holliday et al., 1991b). Alternatively, low stocking densities are uneconomic because of the increased lease space, culture equipment and labour required to service them (Askew, 1978; Spencer et al., 1985; Spencer, 1990), and the oysters may suffer excessive shell abrasion and hence reduced growth (Holliday et al., 1991b).

Optimum stocking densities depend upon a number of factors, including the carrying capacity of a particular site (Brown and Hartwick, 1988a), and the size range of oysters to be stocked. Drinkwater and Howell (1985) recommended stocking Pacific oyster spat at just below the level where oysters would be touching when spread out evenly, while for Sydney rock spat, Holliday et al. (1991b) suggested that they cover 50% of the container bottom. In practice, Tasmanian farmers use the latter method for Pacific oyster spat, while adults are stocked in a single or double layer (C. Sumner, pers. comm., 1989). To optimise production the densities should be periodically reduced as the oysters grow (Walne and Spencer, 1971; Holliday et al., 1991b; Holliday et al., 1993a).

1.1.6.2 Degree of aerial exposure

Oysters cultured subtidally are not exposed to the air (0% exposure d^{-1}) except during retrieval, grading and handling, while those cultured in the intertidal zone are exposed to the air, the degree to which is dependent upon their position (vertical height) relative to the amplitude of the tide (Littlewood, et al., 1992). Subtidal culture usually produces the fastest shell growth rates in Pacific oysters, followed in sequential order, by intertidal off-bottom, subtidal bottom, and intertidal bottom culture (Parsons, 1974; Quayle, 1988).

Growth rates of Pacific oysters decrease with increasing exposure to air (Pereya, 1961; Walne and Davies, 1977; Spencer et al., 1978; Drinkwater and Howell, 1985; Spencer, 1990), although average differences of 4-9% average daily exposure are necessary to reduce growth (Spencer et al., 1978). Between 0-10% exposure there are only small differences in the growth of Pacific oysters (Walne and Davies, 1977; Spencer et al., 1978). Marked reductions in growth occur between 10-30% average daily exposure (Spencer et al., 1978). Interestingly, Spencer (1990) stated that "growth stops when oysters in trays are exposed to air for more than 35% of the time". However, earlier studies, based on extrapolation to the point of no growth for Pacific oysters, indicate a critical exposure of 36-47% depending on site (Spencer et al., 1978). In Tasmania, spat have been cultured to market size at levels of 40% (Sumner, 1980a), and up to 59% without growth ceasing (Maguire et al., 1994b).

In comparison, it has been found, that American oysters (*Crassostrea virginica*) can grow faster at certain intertidal levels (20-30% exposure d^{-1}) than at subtidal ones (Gillmor, 1982), and similarly, mangrove oysters (*Crassostrea rhizophorae*) held at subtidal (0% exposure d^{-1}) and mid-intertidal levels (10-17% exposure d^{-1}) were found to grow faster than those held at lower levels (1-3% exposure d^{-1}) (Littlewood, 1988). Gillmor (1982) suggested that in "high-intertidal forms there may be a degree of optimality associated with periodic exposure, if not an obligate relationship". This is despite the traditionally accepted idea that subtidal bivalves grow faster due to longer immersion times and therefore feeding times, than intertidal animals (Littlewood, 1988).

Crenshaw (1980), and Wilbur and Saleuddin (1983) reviewed the processes of shell formation and dissolution in molluscs. During periods

of aerial exposure, intertidal bivalves experience oxygen deprivation whilst their shell valves are closed (Crenshaw, 1980). The energetic requirements of the animal are supplied by anaerobic glycolysis, and the acidic end products of this metabolism, for example, succinic, lactic and propionic acids, must be neutralised to maintain the constant pH required for normal function (Crenshaw, 1980; Wilbur and Saleuddin, 1983). For molluscs, the shell is an alkali reserve such that part of the shell is dissolved, especially recently deposited shell on the outer margins, during periods of anaerobic respiration (Crenshaw, 1980; Wilbur and Saleuddin, 1983). Periodic shell dissolution may therefore account for the slower growth of some intertidal bivalves (Crenshaw, 1980). Shell dissolution also occurs to a lesser extent in subtidal bivalves, since these periodically close their valves whilst submerged (Crenshaw, 1980). It should be noted that some bivalves, including Pacific oysters, can also respire aerobically in air (Crenshaw, 1980; Seaman, 1991), the degree to which depends on how far apart the valves are opened (Crenshaw, 1980).

Intertidal culture has the following advantages; there is convenient access to stock (Spencer et al., 1985; Spencer, 1990), shell growth rates can be controlled or temporarily stopped by moving the stock to different exposure levels (Spencer, 1990), the shelf life improves (Imai and Sakai, 1961; Quayle, 1988), and the stock are kept relatively free from biofouling and predators (Arakawa, 1990b; Littlewood et al., 1992). In addition, unless fouling and predation are controlled in subtidally-cultured oysters, survival rates are likely to be higher at intertidal sites (Littlewood, 1988; Littlewood et al., 1992).

Pacific oysters can grow to a large size of up to 300 mm in shell height (Quayle, 1988; Dinamani, 1991) and, if unchecked, the shell can 'outgrow' the meat (Maguire et al., 1994b). This will of course affect the condition index and hence, marketability. For this reason, the high intertidal zone is often used by Pacific oyster farmers in Tasmania (C. Dyke, pers. comm., 1990), and elsewhere, to slow down the shell growth of larger oysters (Spencer, 1990). Spencer et al. (1978) reported that while there are marked reductions in growth between 10-30%, the effect on shell and meat growth of Pacific oysters was similar, so that the condition index (CI_{shell}) remained at a constant level irrespective of tidal exposure.

The effect of intertidal height on shell shape is not well documented in the literature. However, Maguire and Kent (1991), in a summary written

for oyster farmers reported that Pacific oysters cultured at 25-66% average exposure d^{-1} (see Section 4.2) had a better shape than subtidal oysters. The shape index used - shell depth/shell height x shell length - indicated the amount of 'cup' (G. Maguire, pers. comm., 1995).

1.1.6.3 Shell abrasion

An advantage in growing single-seed oysters, is that the oysters can be graded into size groups as they grow (Holliday et al., 1991b). During grading, the fragile new extensions on the outer shell margins, or collectively 'shell frill', is broken off or removed so that the shell heights of the oysters are reduced in comparison to undisturbed oysters (Sparks and Chew, 1960; Spencer, 1990; Spencer et al., 1992). Other shell abrasion treatments, applied deliberately or otherwise, include; mixing and handling of Pacific oysters during experimental work (Thomson, 1952; Sparks and Chew, 1960; Hughes-Games, 1977; Smith 1981; Bolton, 1982; Spencer et al., 1992; Smith, 1994), cleaning Pacific oysters using high pressure water (Spencer et al., 1992), excessive flotation on rafts causing European flat oysters (*Ostrea edulis*) and Australian native flat oysters (*Ostrea angasi*) to rub against each other and their mesh enclosures (Wilson, 1987; O'Meley and Hickman, 1988), storm and wave action causing bottom-cultured American oysters to roll around on the seabed, and dredging of these (Loosanoff and Nomejko, 1955), and rotating cylinders (Robert et al., 1993).

Spencer (1990) recommended that Pacific oysters be graded regularly up until their second year of growth. From their second year on, Spencer (1990) recommended that the oysters be graded at three to six monthly intervals because "frequent and excessively rough-handling retards growth". Tasmanian Pacific oysters are graded on average 5-7 times (R. Calvert, pers. comm., 1991) during their 18 month to 3 year grow-out period on a lease (Maguire et al., 1994b; G. Maguire, pers. comm., 1995). To limit shell losses, small oysters (shell height <15-20 mm) are usually graded underwater, using hand-held or mechanised sieves (O'Meley, 1992). Larger oysters are graded in air using grading machines which operate by vibrating steel or plastic mesh screens of varying sizes, although some farmers still grade the oysters by hand (O'Meley, 1992).

Spencer et al. (1992) subjected Pacific oysters to 13 different 'rough-handling' treatments (see Table 3, Section 4.1). They reported that simulated grading for 2 min in air severely affected growth, especially when the oysters were kept out of water overnight prior to grading. For the other treatments, the effects on growth were linked to the severity of the rough-handling treatment.

Loosanoff and Nomejko (1955) studied the effect of removing the shell frill of American oysters, including recently-formed, thin and transparent shell, as well as the older and thicker portions, such that the shell height was reduced by 4-7 mm. They found that the shell height of damaged oysters increased faster to compensate for the shell loss compared to the controls, and then grew at the same rate as the controls. They suggested that the initially rapid growth occurred because the mantle edge could protrude further. Once the normal ratio of body size and shell dimensions were re-established, however, the height increments became the same as for undamaged oysters. Factors which could slow the process of shell repair include mantle injury (Loosanoff and Nomejko, 1955), the age and condition of the oysters (Loosanoff and Nomejko, 1955; Neudecker, 1981a), and season, where in temperate regions shell growth and repair is slow during winter (Wilson, 1987).

Unusual results were obtained by Jakob and Wang (1994) for American oysters. They found that oysters handled on a bi-weekly basis had grown faster than those that were not handled, after 7 months in land-based tanks. As discussed in Section 4.2, their experiment may have been poorly designed because I consider that both groups could have been subjected to a form of "rough-handling".

If shell abrasion is too severe, oysters can grow into unusual shapes. For example, Sydney rock oysters cultured at low stocking densities in trays exposed to wave action, in the intertidal zone, can become ball-shaped with thick shell walls (Holliday et al., 1991b). Similarly, American oysters that survived a severe storm did not resume normal growth, but became stunted with thick, irregular shells (Loosanoff and Nomejko, 1955). In Pacific oysters, internal shell blistering can occur on both shell valves, and this was presumed to have been caused by mechanical damage to the meat (Spencer et al., 1992).

While several authors reported that mortality was not affected by the shell abrasion treatments applied (Sparks and Chew, 1960; Pereya, 1961; Smith, 1981), Spencer et al. (1992) found that it depends upon the severity of the treatment. In cases where the shell is worn away to the extent that holes in the shell valves exposes the meat to predators, mortality can occur (Loosanoff and Nomejko, 1955; Drinkwater and Howell, 1985).

Some Tasmanian farmers (C. Dyke, P. Chew, R. Calvert, C. Sumner, pers. comm., 1989) believe that removing the shell frill of Pacific oysters (shell height > 20 mm) during machine-grading can improve their condition index and shell shape. Another technique used by these farmers to remove shell frill is to deliberately shake the mesh enclosures, in which the oysters are contained, whilst out on the lease. This latter method also redistributes the oysters within their enclosure. Similarly, farmers in France periodically crack the shell frill of Pacific oysters by hand, or by forceful agitation of the oysters in their enclosures, during seasons when the shell growth rates are fastest (Anderson, 1977).

Spencer et al. (1992) reported that the CIshell of Pacific oysters can be affected negatively by shell abrasion, depending on the severity of the treatment. Robert et al. (1993) found that while increase in shell height was repressed, the shape as well as the condition index (CIshell) of Pacific oysters cultured in rotational cylinders were improved compared to those in mesh bags. Smith (1981) observed that European flat oysters (*Ostrea edulis*) grown in trays were large and thin-shelled if not cleaned or graded regularly, whereas those that were either cleaned, using a fire pump and, or graded using a rotary grader up to once per week, developed thicker and more cup-shaped shells. Hughes-Games (1977) also found that manually agitating Pacific oysters in water twice per week can improve the shape, in that the oysters became heavier for a given shell height. It would appear therefore, that shell abrasion can affect the shell shape of oysters, but that the effect on their condition index is less certain.

It has been reported that the removal of shell frill can affect the rate of gametogenesis and the sex of oysters. Bahr and Hillman (1967) filed the shell margins of fed or starved American oysters on a weekly basis, or when active shell secretion warranted it. Within the fed groups, filed oysters showed slightly faster gonad maturation over unfilled oysters, but in the starved oysters, the opposite occurred. They suggested that the enhanced maturation of filed groups when food was not a limiting factor,

may have been the stress of filing, initiating a species survival mechanism leading to gonad maturation. In addition, there was a predominance of males in both starved and fed filed oysters. They hypothesised that limited energy reserves shared between shell repair and gametogenesis led to the production of sperm in favour of ova because a smaller energy expenditure is required to produce sperm. Robert et al. (1993) had results supportive of Bahr and Hillman's (1967). They reported that Pacific oysters cultured in rotational cylinders matured faster than those in stationary mesh bags (controls) (Robert et al., 1993).

1.2 Summary and aims of this study

The Tasmanian Pacific oyster industry differs from other major edible oyster industries in the southern hemisphere because it is not based upon the collection of natural spatfall and culture of attached oysters, but relies instead, on the hatchery production of unattached spat, or 'single-seed', for grow-out in mesh enclosures until market size (Dix, 1991). Single-seed culture methods offer farmers better control over shell growth rates and shell shape. Survival rates are usually higher because the oysters are better protected from predatory losses by the mesh enclosures employed (Holliday et al., 1988; Spencer, 1990) and "culling" (removal of oysters from collectors), which usually results in high losses, is not necessary (Holliday et al., 1988).

The Tasmanian industry can be extremely profitable, provided the product can be marketed (Treadwell et al., 1991). The natural cycle of gametogenesis and spawning, however, can result in oysters remaining unmarketable for several months post-spawning, since the condition indices (indicators of marketability) are low and the oysters appear unappetising to the eye (Graham, 1991; O'Meley, 1992). For this reason triploid oysters are gaining importance because gametogenesis and spawning are limited (Maguire et al., 1994b).

Techniques used in the Tasmanian industry to encourage diploid Pacific oysters back into marketable condition after spawning include one, or all, of the following;

- i) relaying oysters from sites with low food abundance to more productive sites (information from hatchery companies Shellfish Culture Pty. Ltd., Tasmania, and Marine Culture Pty. Ltd., Tasmania),
- ii) density manipulations (R. Calvert, pers. comm., 1991),
- iii) using different levels in the intertidal zone, so that the oysters are exposed to some degree of aerial exposure each day (C. Dyke, P. Chew, R. Calvert, C. Sumner, pers. comm., 1989),
- iv) "handling" or treatments including, machine-grading, shaking baskets of oysters whilst out on the lease, and even shovelling

oysters around on concrete (C. Dyke, P. Chew, R. Calvert, C. Sumner, pers. comm., 1989).

The aim of this study was to determine how shell abrasion and aerial exposure treatments affect the meat to shell growth, and the general performance, of Pacific oysters cultured in Tasmania, as measured by growth in whole weight, shell and meat weight, and linear shell dimensions, and by the use of condition and shape indices, glycogen content and gonad development.

Results

Experiment 1

3.1 Abiotic measurements

3.1.1 Water temperature and salinity

The average daily, surface water temperature in Experiment 1 was 10.7°C (n=49), while minimum and maximum temperatures were 6.5°C (day 53) and 14°C (day 5) (Fig. 6a), respectively.

Until day 48, the average daily salinity remained stable at 35.8‰ (n=35). It then dropped to a minimum of 3.2‰ near day 53, but recovered quickly (Figs. 6b, 6c). The maximum recorded salinity was 36.3‰ (day 44), while the average reading overall was 34.0‰ (n=52).

3.1.2 Aerial exposure

Oysters held at the low growing height (L group) were subtidal (0% exposure d⁻¹), while those held at the high growing height (H group) received, on average, 26% exposure d⁻¹.

3.2 Biotic measurements

Interactions between shell abrasion and aerial exposure treatments were not consistent (one interaction shown in each of Figs. 7a, 8a, 9a, 15a).

3.2.1 Survival

Estimated survival was high at 98.1%, and ranged from 97.2-99.2% for individual baskets. No treatment related trends were evident in survival data. Out of a total of 9750 oysters sampled, only five oyster shells contained mudworm (spionid polychaete) blisters. None of the oysters in the day 0 sample (n=45) showed signs of mantle tissue damage, and in the

day 8 sample, only one oyster from the MH group (n= 60 oysters) showed unusual tissue structure such that, some brown granulated cells, some eosinophilic granular cells, and many haemocytes were present.

3.2.2 Growth

There was a general trend from mid-May until the beginning of August, of increasing whole weight (4.0 g month^{-1}), shell height, dry shell weight and dry meat weight in Experiment 1 Pacific oysters (Figs. 7-10). While no treatment related trends were evident due to shell abrasion, Pacific oysters held at the low growing height (L group; $0\% \text{ exposure d}^{-1}$) generally grew faster than those at the high growing height (H group; $26\% \text{ exposure d}^{-1}$).

3.2.2.1 Whole weight and shell growth

The average whole weight increased from $27.7 \pm 0.4 \text{ g}$ (n=270) to $37.9 \pm 0.4 \text{ g}$ (n=540) (Fig. 7a). After the initial machine-grading treatments, on day 0, the MM group had a significantly smaller ($P<0.05$) mean whole weight compared to the M group (the MM group were 8% smaller), but not when compared to the C group ($P>0.05$), the latter two of which had similar values ($P>0.05$) (Fig. 7b). Apart from this, shell abrasion did not affect ($P>0.05$) whole weight on any sample (Fig. 7b). Aerial exposure was significant ($P<0.05$) on day 8, such that $H>L$, but after this the L group grew much faster than the H group, after day 13 ($P<0.05$, days 64 and 81) (Fig. 7c).

Shell height increased from a mean of $65.1 \pm 0.5 \text{ mm}$ (n=270) to $70.4 \pm 0.4 \text{ mm}$ (n=540) (Fig. 8a); length and depth increased from $32.6 \pm 0.2 \text{ mm}$ (n=180) and $21.5 \pm 0.2 \text{ mm}$ (n=180) to $40.1 \pm 0.3 \text{ mm}$ (n=360) and $23.8 \pm 0.2 \text{ mm}$ (n=360), respectively (Appendix D, Figs. D-i, -iv). Shell abrasion did not significantly affect shell height ($P>0.05$) for any sample (Fig. 8b). Aerial exposure was more influential; after day 21, the L group grew much faster than the H group ($P<0.05$, days 42, 64 and 81) (Fig. 8c).

The mean dry shell weight increased from $15.9 \pm 0.4 \text{ g}$ (n=90) to $23.3 \pm 0.3 \text{ g}$ (n=360) (Fig. 9a). Shell abrasion was significant ($P<0.05$) on days 0 ($M>MM$) and 81 ($MM, C>M$), only (Fig. 9b). Aerial exposure affected shell

weight; the L group grew much faster than the H group after day 21 ($P<0.05$, days 64 and 81) (Fig. 9c).

3.2.2.2 Meat growth

The average dry meat weight increased from 0.60 ± 0.02 g ($n=90$) to 1.28 ± 0.02 g ($n=360$) during the study (Fig. 10a). Shell abrasion did not significantly affect ($P>0.05$) dry meat weight growth (Fig. 10b). The meat growth of the L group was much faster than the H group after day 21 ($P<0.05$), but was no different by the final sample (day 81) ($P>0.05$) (Fig. 10c).

3.2.3 Condition indices

The condition indices (CIvol, CIshell) of Experiment 1 Pacific oysters improved over the study (Figs. 11, 12). Shell abrasion did not affect the condition indices. Pacific oysters held at the high growing height (H group) had higher condition indices than those held at the lower growing height (L group), by the end of the study.

3.2.3.1 Volume condition index

The volume condition index (CIvol) increased from 56.1 ± 1.4 ($n=90$) to 95.3 ± 0.7 ($n=360$) (Fig. 11a). Except for day 8 (MM, C > M; $P<0.05$), shell abrasion did not cause significant effects on the CIvol ($P>0.05$) (Fig. 11b). Aerial exposure was significant ($P<0.05$) on day 21 where L>H, but by day 81 the trends had reversed such that H>L ($P<0.05$) (Fig. 11c).

3.2.3.2 Shell condition index

The shell condition index (CIshell) increased from an initial mean of 37.6 ± 0.8 ($n=90$) to 55.0 ± 0.4 ($n=360$) (Fig. 12a). Shell abrasion was a significant factor ($P<0.05$) on day 8 only (MM, C > M) (Fig. 12b). The effect of aerial exposure was significant ($P<0.05$) on days 21 and 42 when the L group had higher values compared to the H group, but as for CIvol, the H group had a higher CIshell than the L group by the last sample (H > L, $P<0.05$) (Fig. 12c).

3.2.4 Shape indices

For the majority of oysters, the roundness index improved and the cup index declined and, or remained relatively constant, over the study (Figs. 13, 14). Shell abrasion did not affect these indices. Pacific oysters held on the high rack (H group) had a much higher cup index, but a lower roundness index than those held on the low rack (L group), by the end of the study.

3.2.4.1 Roundness index

The roundness index increased from 0.51 ± 0.04 (n=360) to 0.58 ± 0.005 (n=360) (Fig. 13a). By the end of the study there was no significant effect of shell abrasion on the roundness index ($P>0.05$); significant differences ($P<0.05$) were evident on two occasions (days 21 and 64), but the trends were not consistent (Fig. 13b). Aerial exposure was significant ($P<0.05$) for the last three samples (days 42-81) when the roundness of the L group increased in comparison to the H group, whose values remained relatively constant (Fig. 13c).

3.2.4.2 Cup index

The cup index decreased from 0.47 ± 0.04 (n=360) to 0.45 ± 0.005 (n=360) (Fig. 14a). Shell abrasion was not a significant factor ($P>0.05$) (Fig. 14b). Aerial exposure caused significant effects ($P<0.05$) on cup index towards the end of the study (H>L; days 64 and 81), such that the mean cup index of the L group declined while that of the H group remained relatively constant (Fig. 14c).

3.2.5 Glycogen content

Glycogen content (g per 100 g dry oyster meat) increased from a mean of 7.1 ± 0.9 (n=18) to 9.4 ± 1.3 (n=36) by day 42, but by day 81 the glycogen content had dropped to 5.8 ± 0.4 (n=36) (Fig. 15a). Shell abrasion was only significant ($P<0.05$) on days 8 (MM>M, C) and 81 (MM, C>M) (Fig. 15b). Aerial exposure was not significant ($P>0.05$) for any sample; however, the H group generally had a higher glycogen content than the L group (Fig. 15c).

3.2.6 Gametogenesis

Sex ratio (male: female: indeterminate) was not significantly different ($P>0.05$) amongst treatment groups, from May (day 0) through to the last sample in August (day 81) [Fig. 16a(i)]. There were, however, more females in June (day 42) (55%; $n=60$) and August (68%; $n=59$), compared to males or regressive (R; sex group indeterminate) stages [Fig. 16a(i)]. Gonad staging showed that most oysters (80%; $n=45$) were in post-spawned (5/X) and regressive stages in May. By June, most oysters (63%; $n=60$) were ripening (1/2), and some of these (15%; $n=59$) had entered a more advanced ripening stage (3/4) by August [Fig. 16a(ii)].

Shell abrasion did not significantly ($P>0.05$) affect sex ratio [Fig. 16b(i)], and except for the June sample, nor did it affect gonad development [Fig. 16b(ii)]. The significant difference ($P<0.05$) in June was most likely caused by the M group having representatives (3%) in a ripe stage, which were not present in the MM or C groups [Fig. 16b(ii)].

Aerial exposure did not affect sex group ratios [(Fig. 16c(i)], or gonad development [Fig. 16c(ii)].

Chi-square analysis of gonad stage versus sex was significant on day 81 (Table 1) because a disproportionate number of ripening stage oysters were female [Fig. 16a(i)].

TABLE 1

Summary of Chi-square analysis of gonad stage versus sex¹ of Pacific oysters (*C. gigas*) in Experiment 1. All treatment groups (MMH, MML, MH, ML, CH, CL) were included in the analysis.

Day(s)	Month(s)	Number of oysters analysed (n)	Chi-square analysis of gonad stage vs sex ¹
42	June	56	NS
81	August	59	**
42 + 81	June and August	115	**

¹ R stage (sex group is indeterminate) individuals removed from analysis. MM, oysters machine-graded twice; M, oysters machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number. NS, the null hypothesis of independence is retained ($P>0.05$); ** = $P<0.01$.

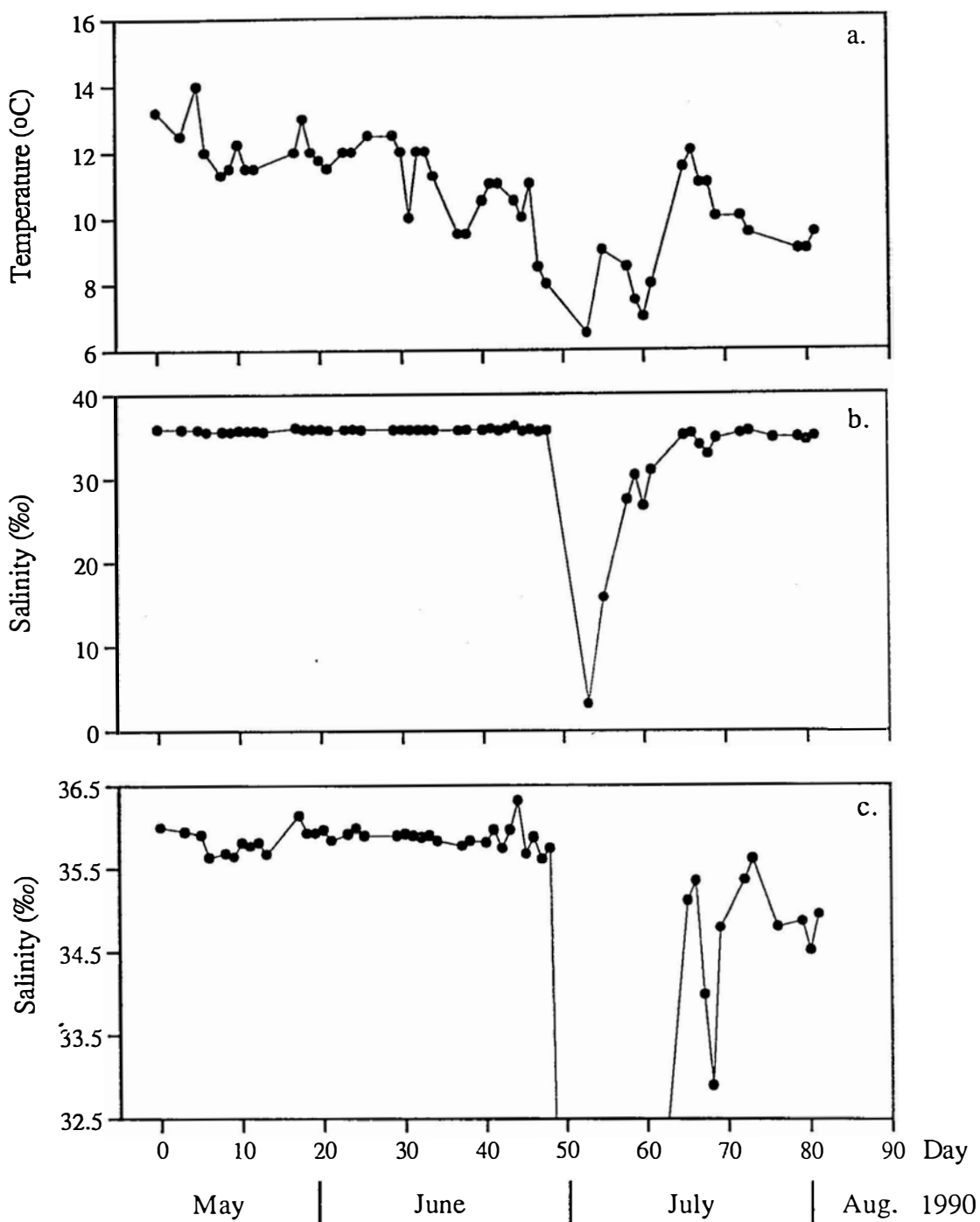


Fig. 6. Surface water temperature (a) and salinity (b) and (c) [(c) is an enlargement of (b)] at Little Swanport in Experiment 1.

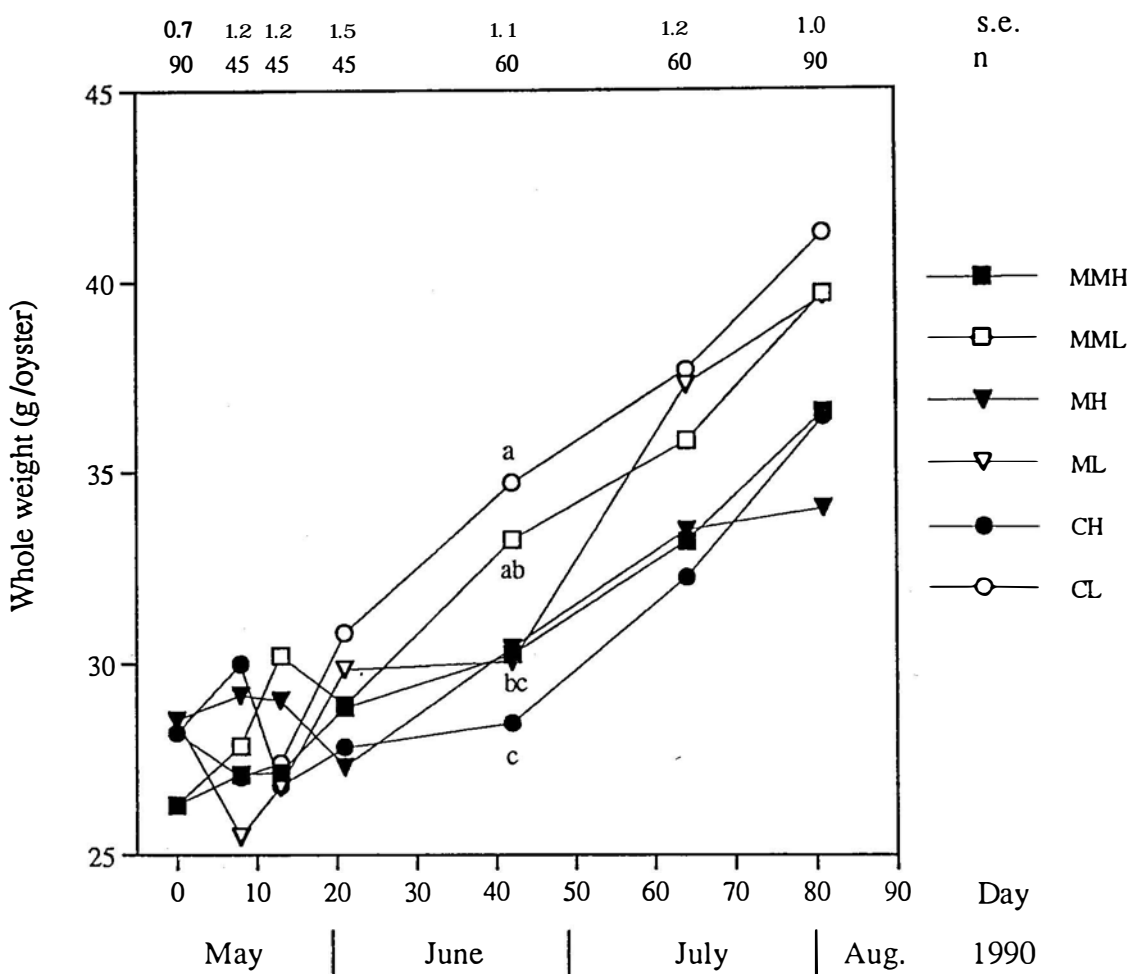
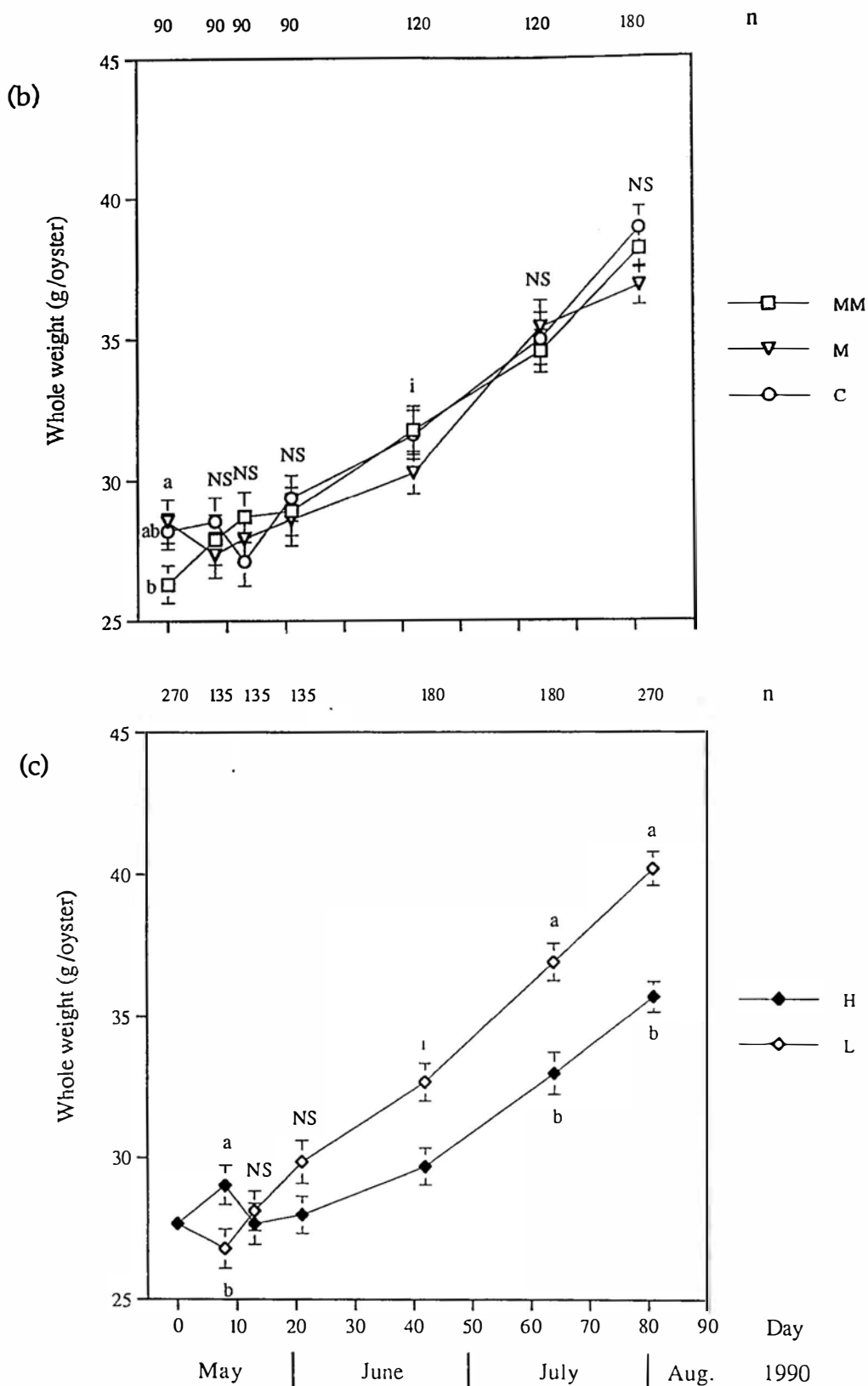


Fig. 7a. Effects of shell abrasion and aerial exposure on the mean whole weight of Pacific oysters (*C. gigas*) in Experiment 1. There was a significant interaction ($P < 0.05$) on day 42, and pairwise comparisons (Fisher's LSD) are shown [means which share common letters do not differ significantly ($P > 0.05$)]. MM, machine-graded twice; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; s.e., pooled standard error; n, sample number.



Figs. 7b-c. Effects of shell abrasion (b) and aerial exposure (c) on the mean whole weight of Pacific oysters (*C. gigas*) in Experiment 1 (means \pm s.e.). NS, for the same sample, means do not differ significantly ($P>0.05$); the letters a, b indicate that means differ significantly ($P<0.05$); i, for this sample a significant interaction (Fig. 7a) prevented statistical comparisons of means based on pooling. MM, machine-graded twice; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number.

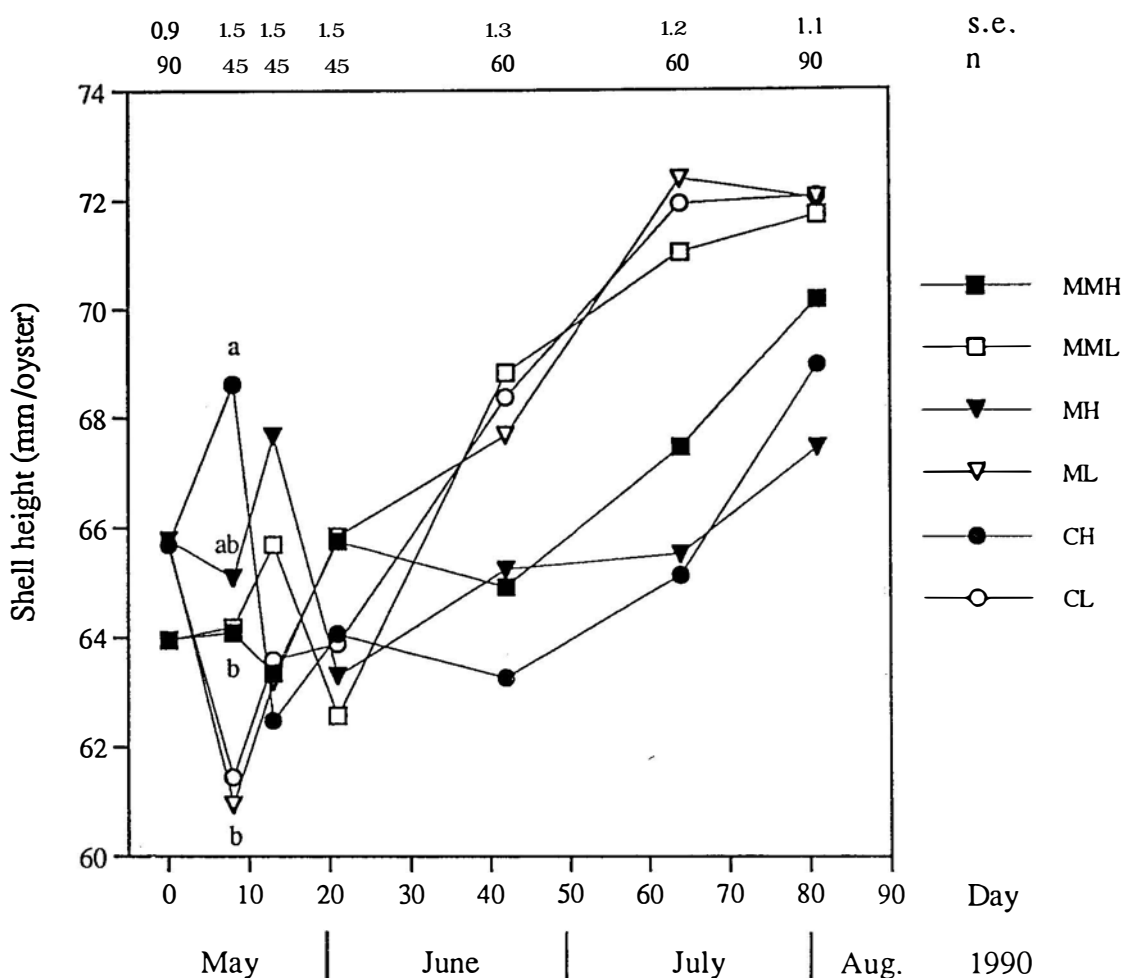
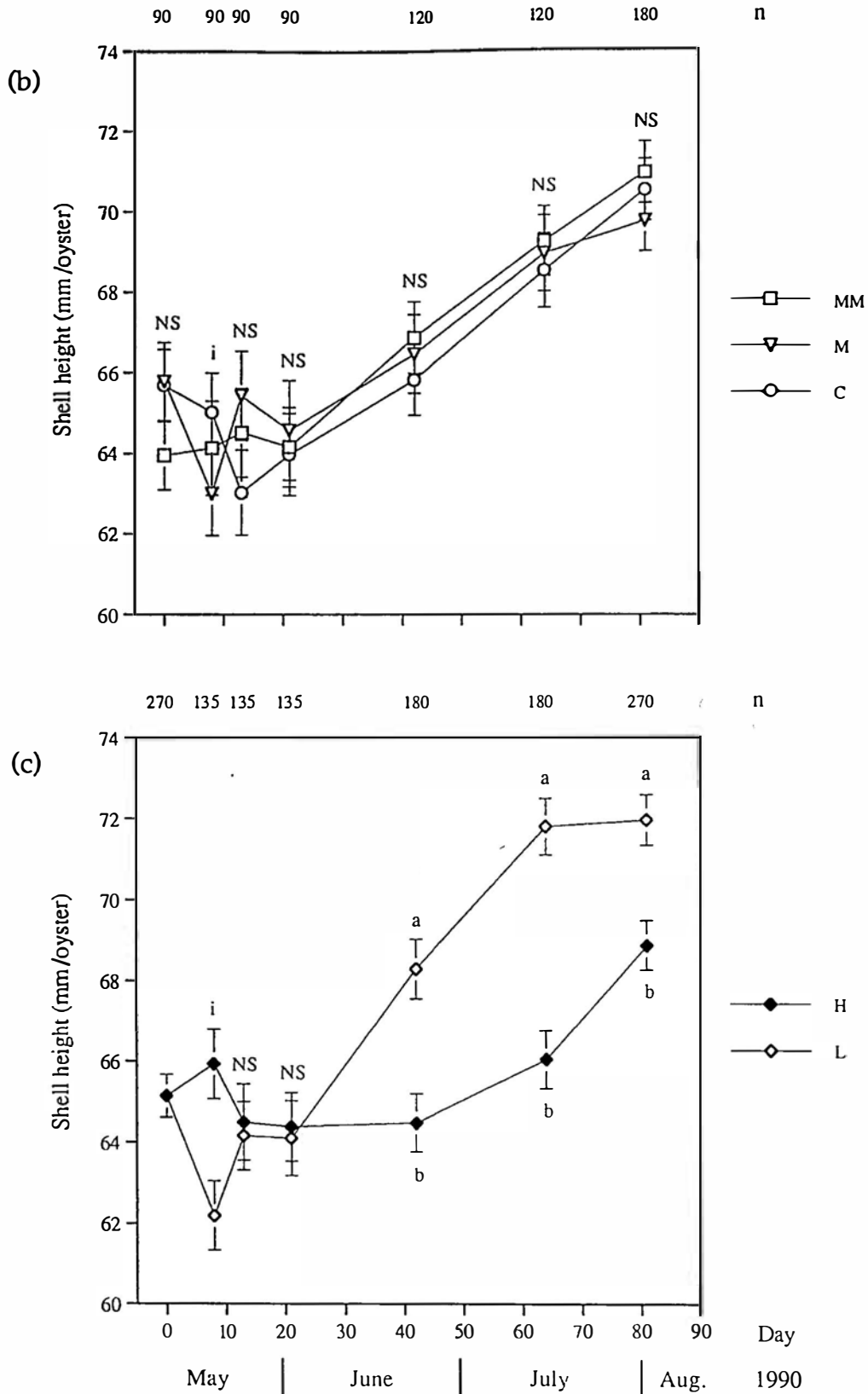


Fig. 8a. Effects of shell abrasion and aerial exposure on the mean shell height of Pacific oysters (*C. gigas*) in Experiment 1. There was a significant interaction ($P < 0.05$) on day 8, and pairwise comparisons (Fisher's LSD) are shown [means which share common letters do not differ significantly ($P > 0.05$)]. MM, machine-graded twice; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; s.e., pooled standard error; n, sample number.



Figs. 8b-c. Effects of shell abrasion (b) and aerial exposure (c) on the mean shell height of Pacific oysters (*C. gigas*) in Experiment 1 (means \pm s.e.). NS, for the same sample, means do not differ significantly ($P > 0.05$); the letters a, b indicate that means differ significantly ($P < 0.05$); i, for this sample a significant interaction (Fig. 8a) prevented statistical comparisons of means based on pooling. MM, machine-graded twice; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number.

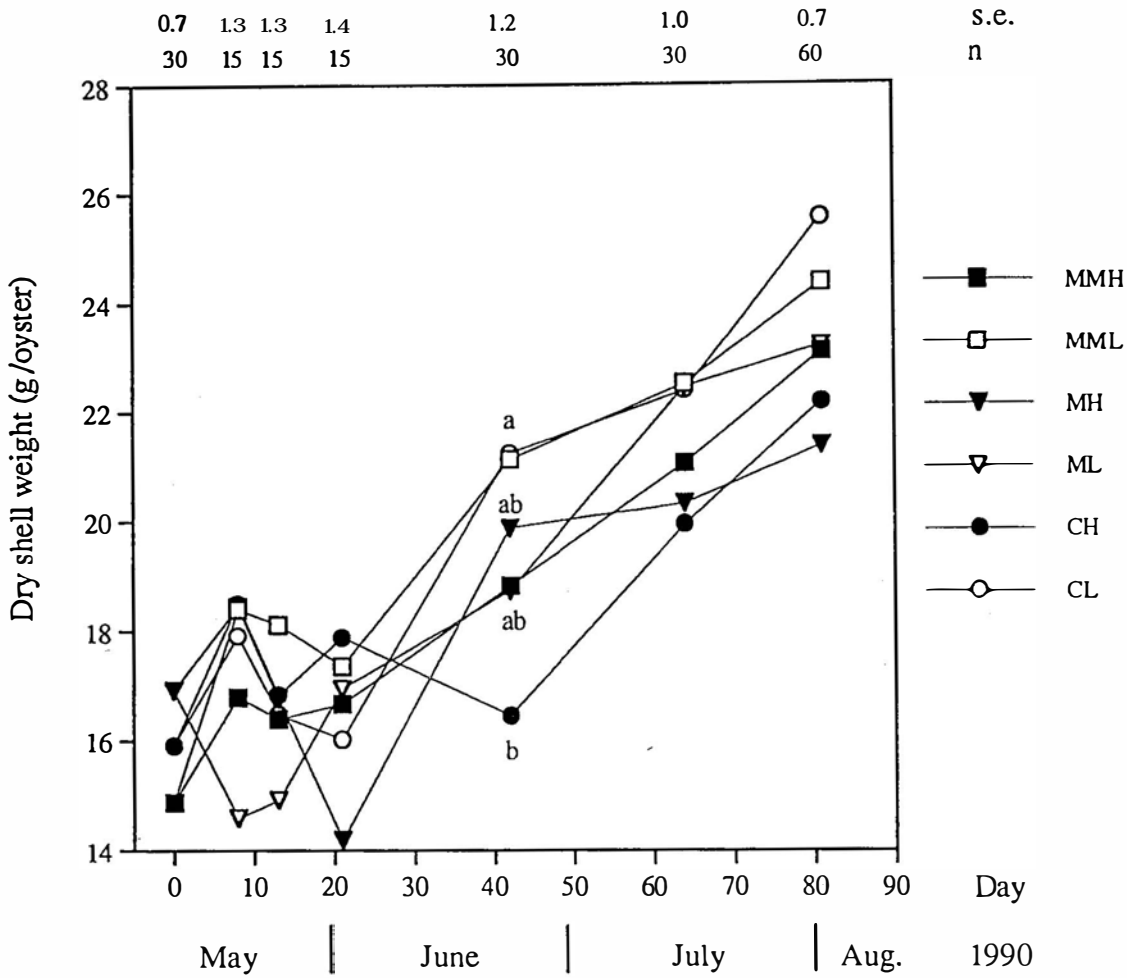
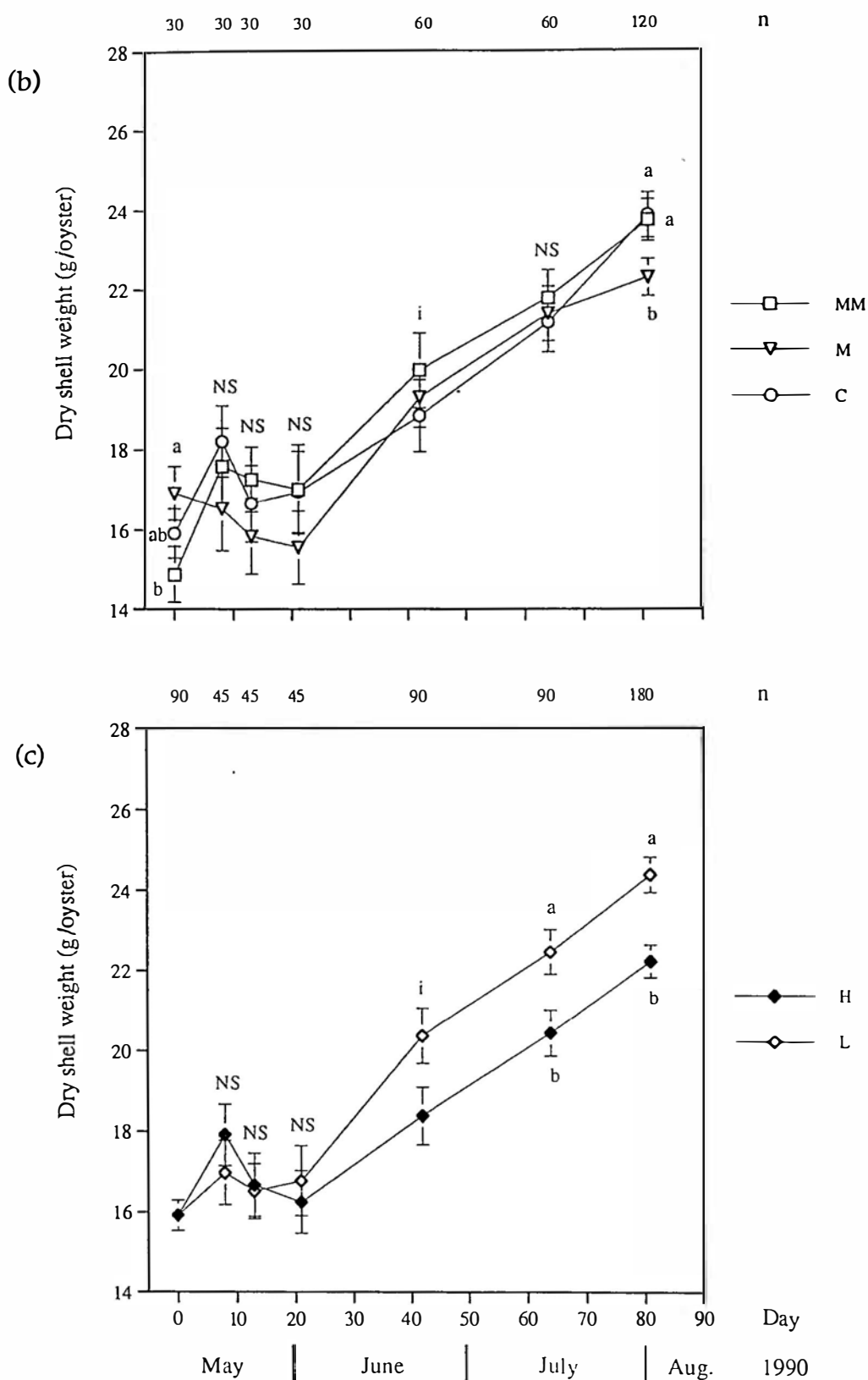


Fig. 9a. Effects of shell abrasion and aerial exposure on the mean dry shell weight of Pacific oysters (*C. gigas*) in Experiment 1. There was a significant interaction ($P < 0.05$) on day 42, and pairwise comparisons (Fisher's LSD) are shown [means which share common letters do not differ significantly ($P > 0.05$)]. MM, machine-graded twice; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; s.e., pooled standard error; n, sample number.



Figs. 9b-c. Effects of shell abrasion (b) and aerial exposure (c) on the mean dry shell weight of Pacific oysters (*C. gigas*) in Experiment 1 (means \pm s.e.). NS, for the same sample, means do not differ significantly ($P>0.05$); the letters a, b indicate that means differ significantly ($P<0.05$); i, for this sample a significant interaction (Fig. 9a) prevented statistical comparisons of means based on pooling. MM, machine-graded twice; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number.

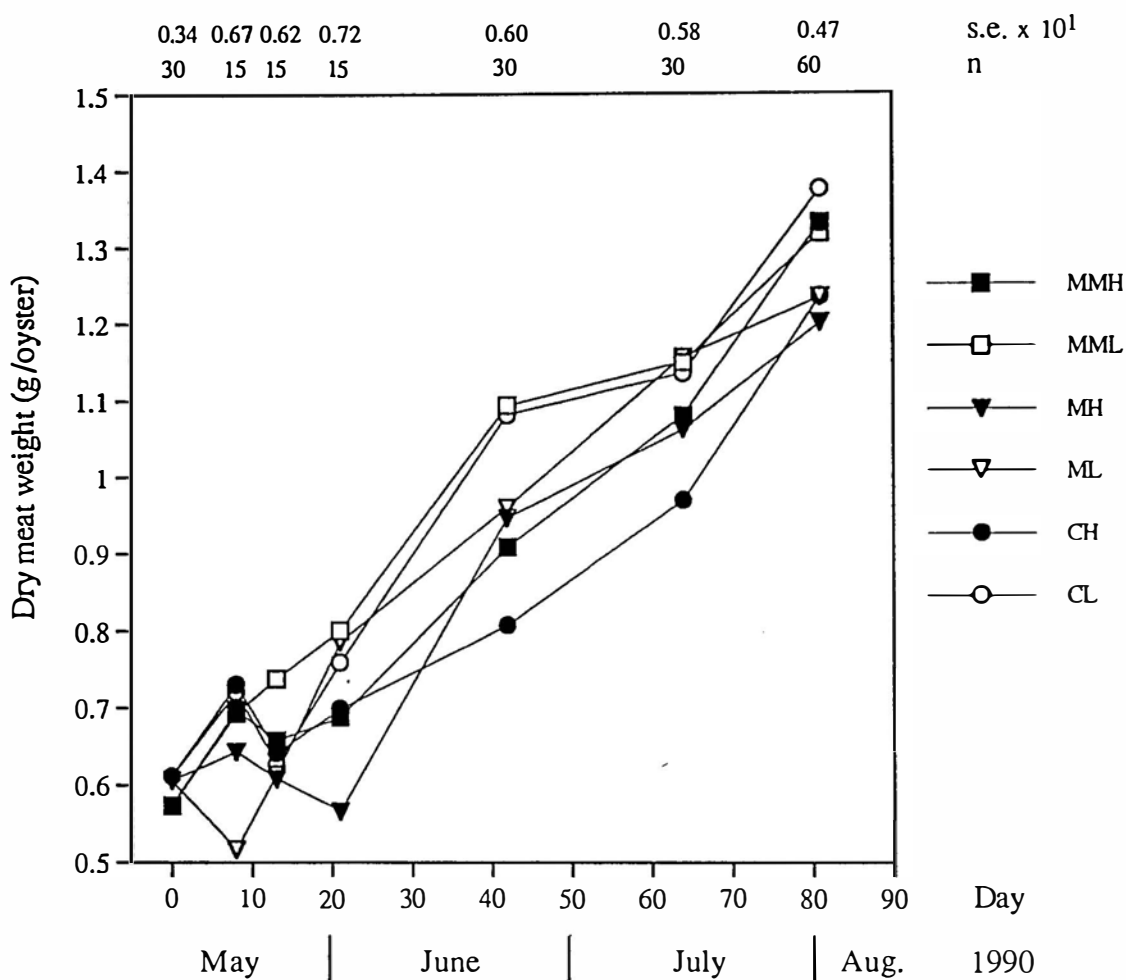
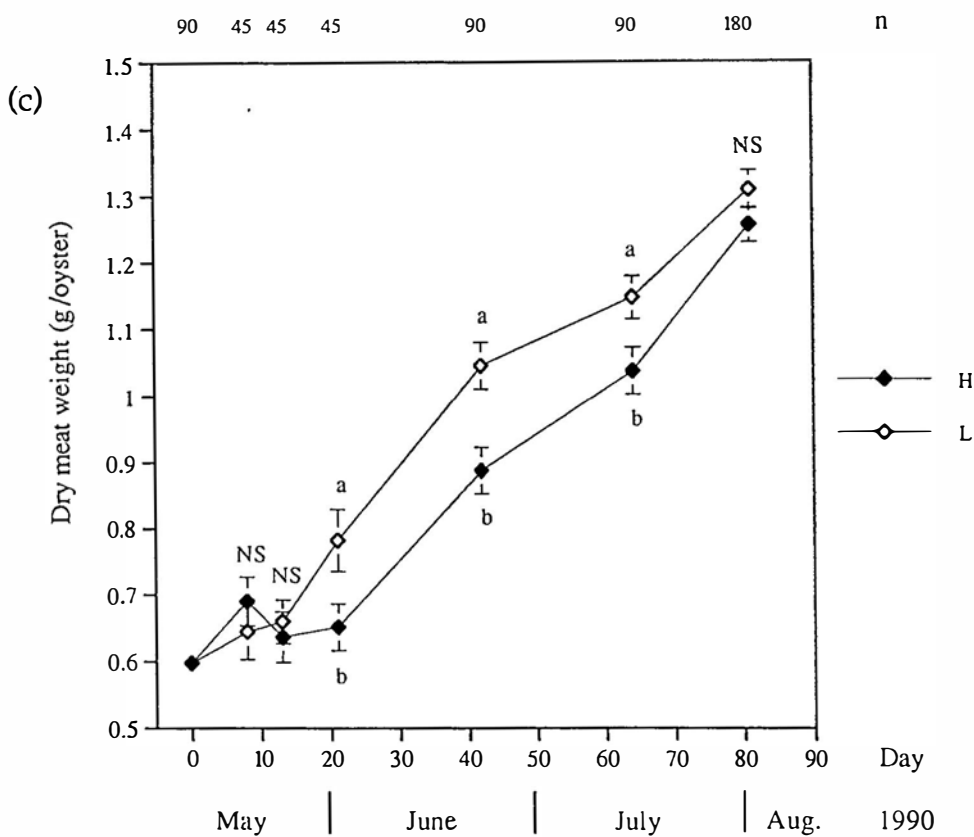
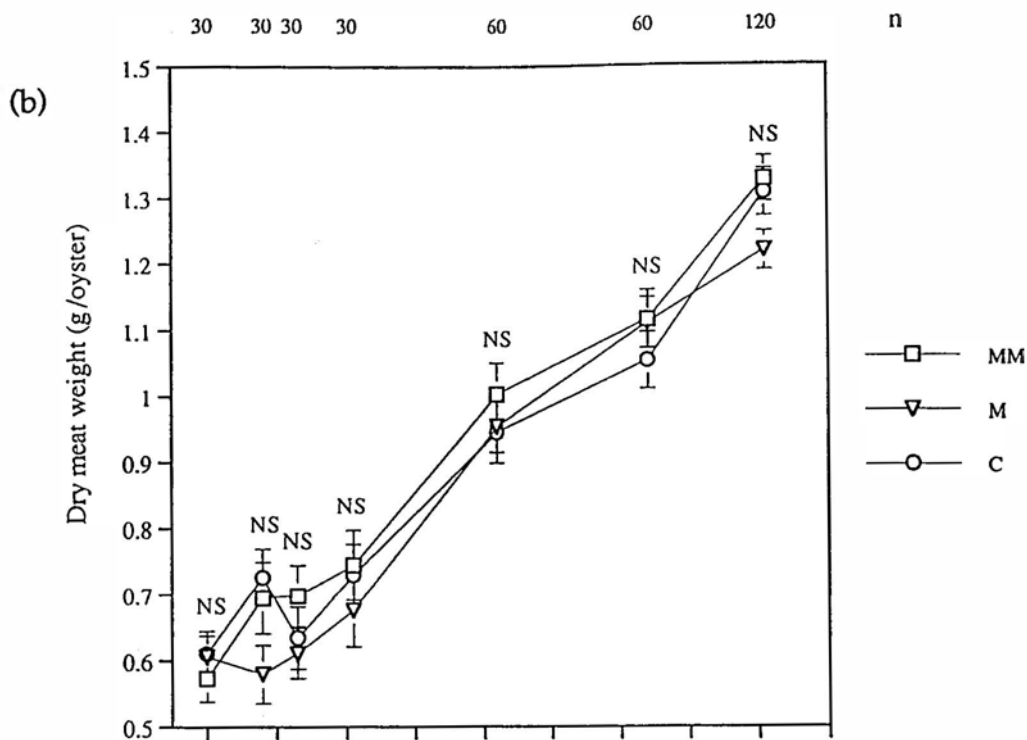


Fig. 10a. Effects of shell abrasion and aerial exposure on the mean dry meat weight of Pacific oysters (*C. gigas*) in Experiment 1. MM, machine-graded twice; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; s.e., pooled standard error; n, sample number.



Figs. 10b-c. Effects of shell abrasion (b) and aerial exposure (c) on the mean dry meat weight of Pacific oysters (*C. gigas*) in Experiment 1 (means \pm s.e.). NS, for the same sample, means do not differ significantly ($P > 0.05$); the letters a, b indicate that means differ significantly ($P < 0.05$). MM, machine-graded twice; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number.

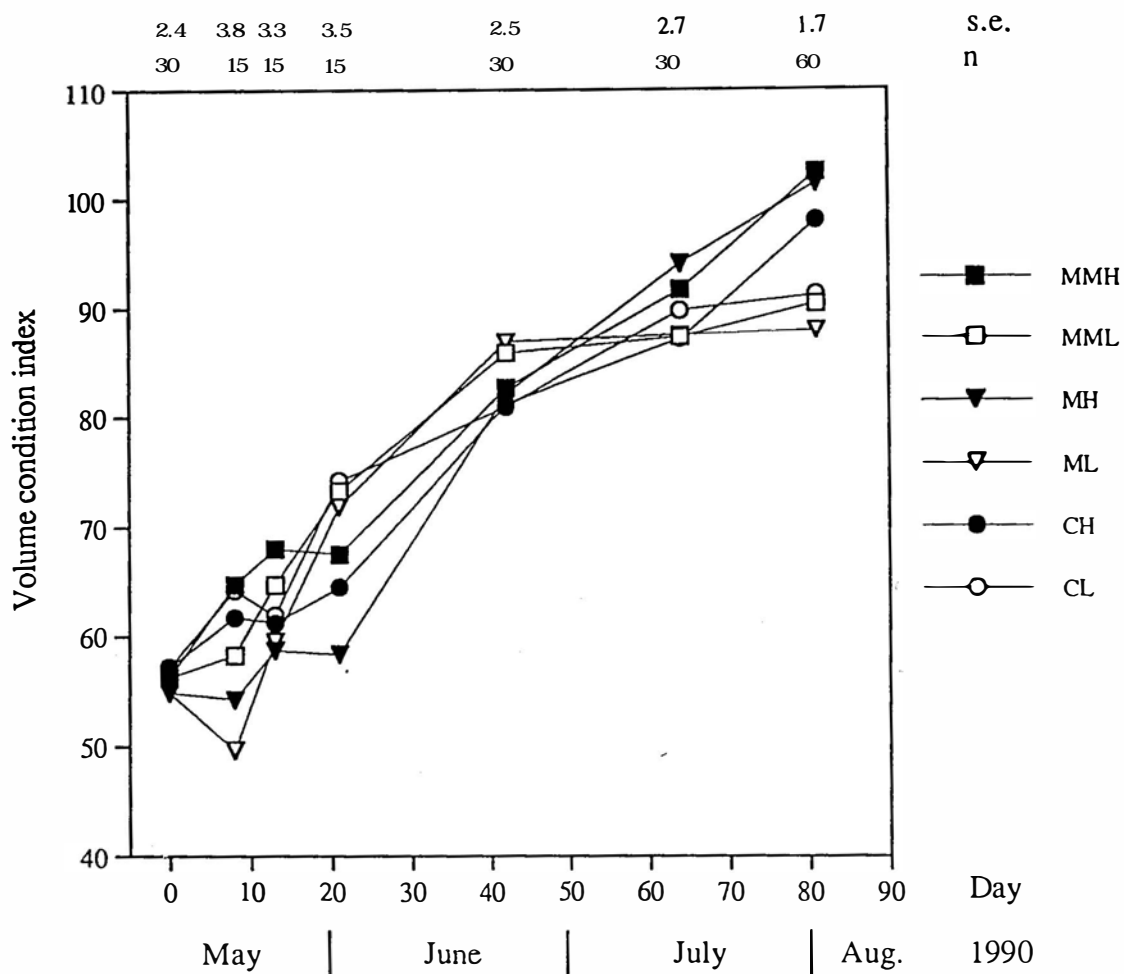


Fig. 11a. Effects of shell abrasion and aerial exposure on the mean volume condition index (CIvol) of Pacific oysters (*C. gigas*) in Experiment 1. MM, machine-graded twice; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; s.e., pooled standard error; n, sample number.

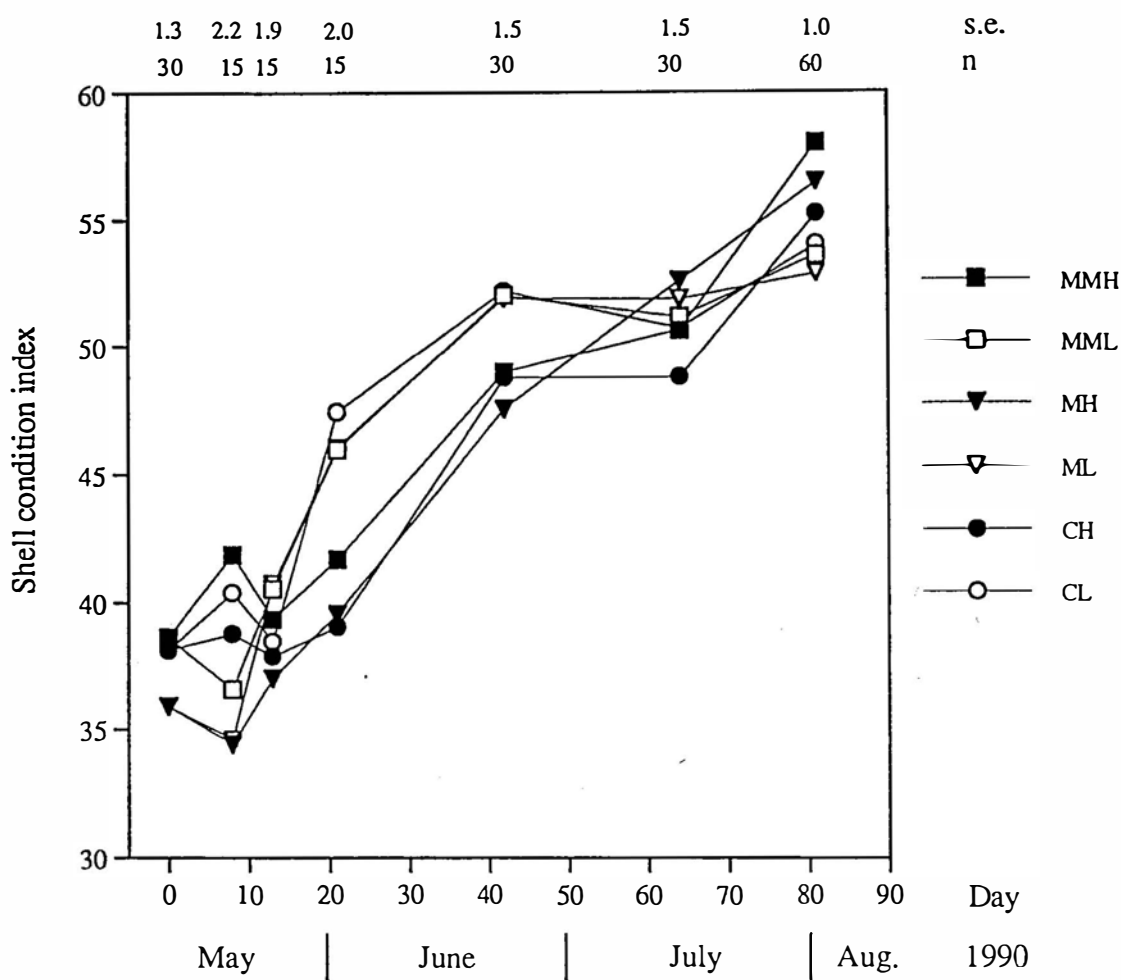


Fig. 12a. Effects of shell abrasion and aerial exposure on the mean shell condition index (CI_{shell}) of Pacific oysters (*C. gigas*) in Experiment 1. MM, machine-graded twice; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; s.e., pooled standard error; n, sample number.

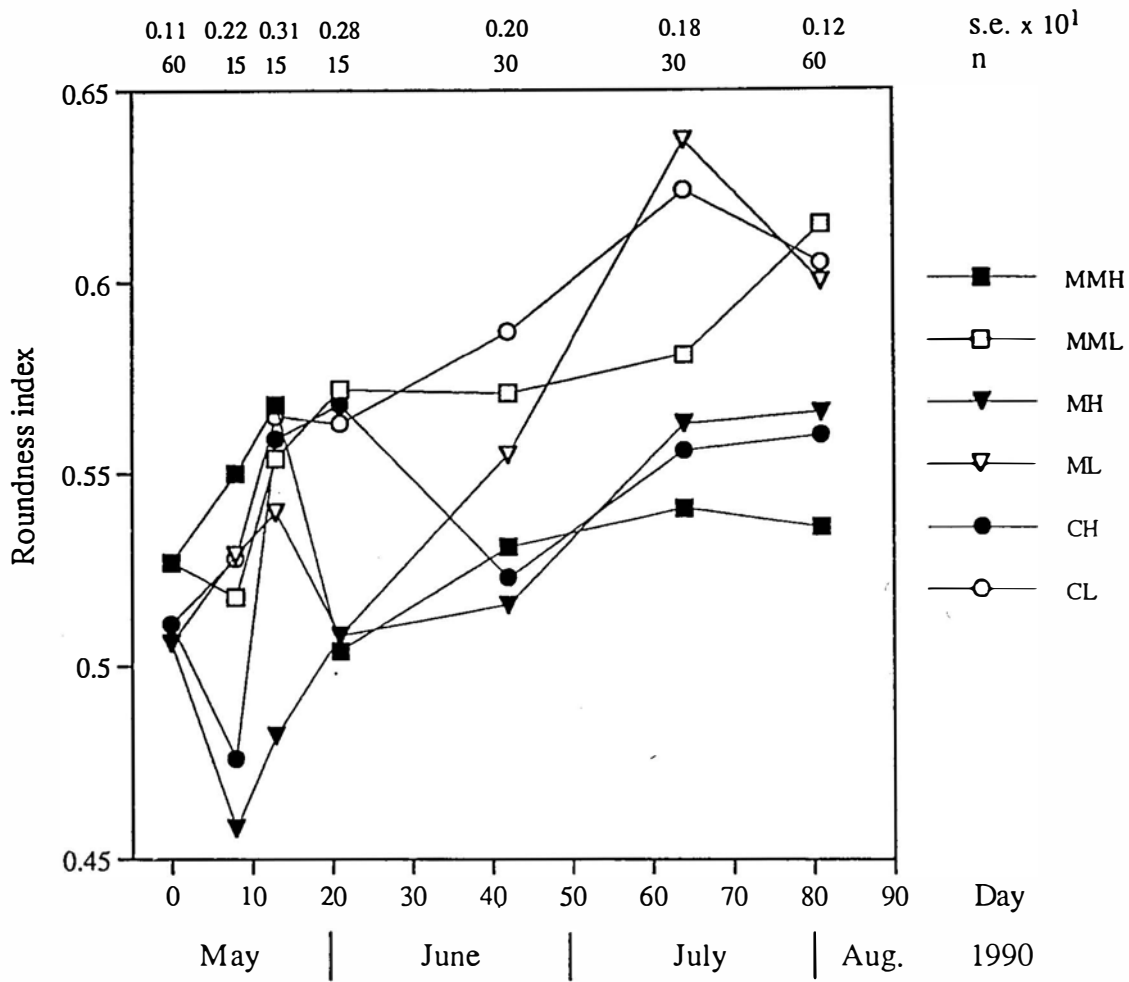
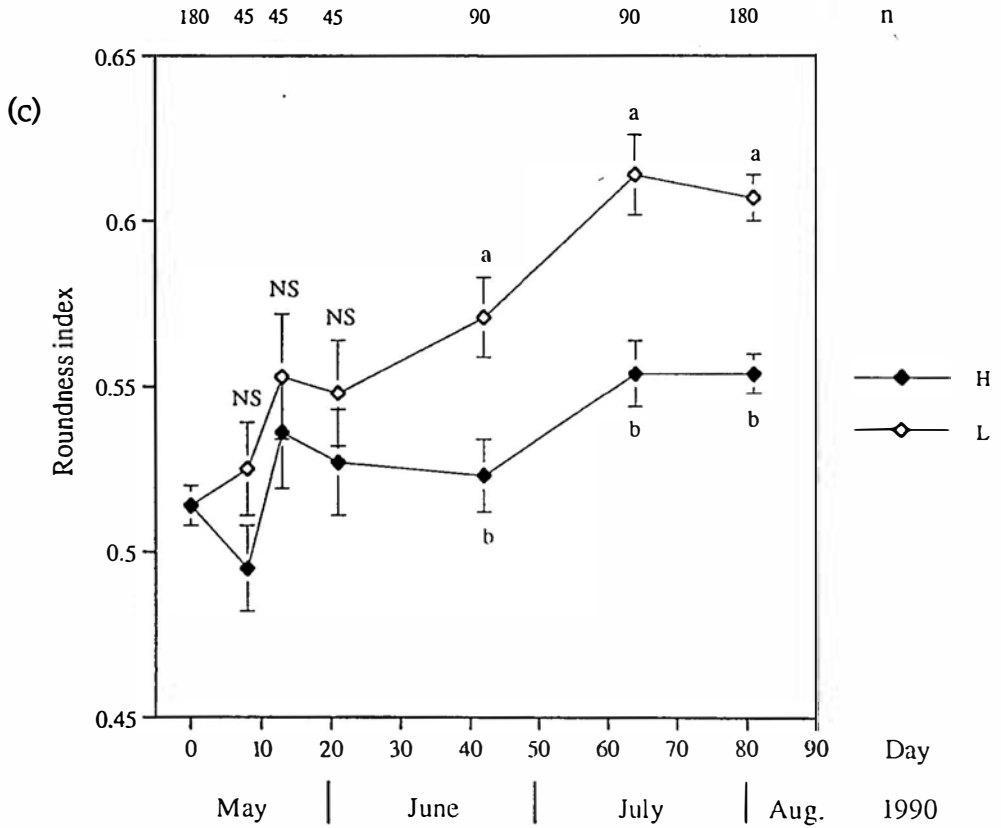
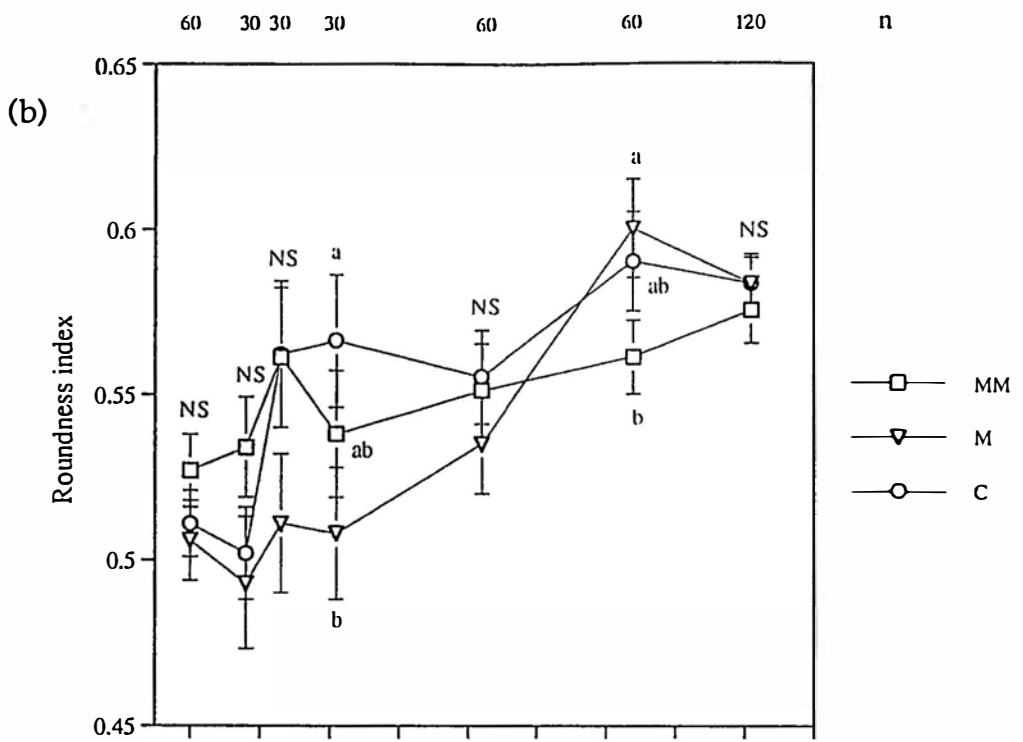


Fig. 13a. Effects of shell abrasion and aerial exposure on the mean roundness index of Pacific oysters (*C. gigas*) in Experiment 1. MM, machine-graded twice; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; s.e., pooled standard error; n, sample number.



Figs. 13b-c. Effects of shell abrasion (b) and aerial exposure (c) on the mean roundness index of Pacific oysters (*C. gigas*) in Experiment 1 (means \pm s.e.). NS, for the same sample, means do not differ significantly ($P>0.05$); the letters a, b indicate that means differ significantly ($P<0.05$). MM, machine-graded twice; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number.

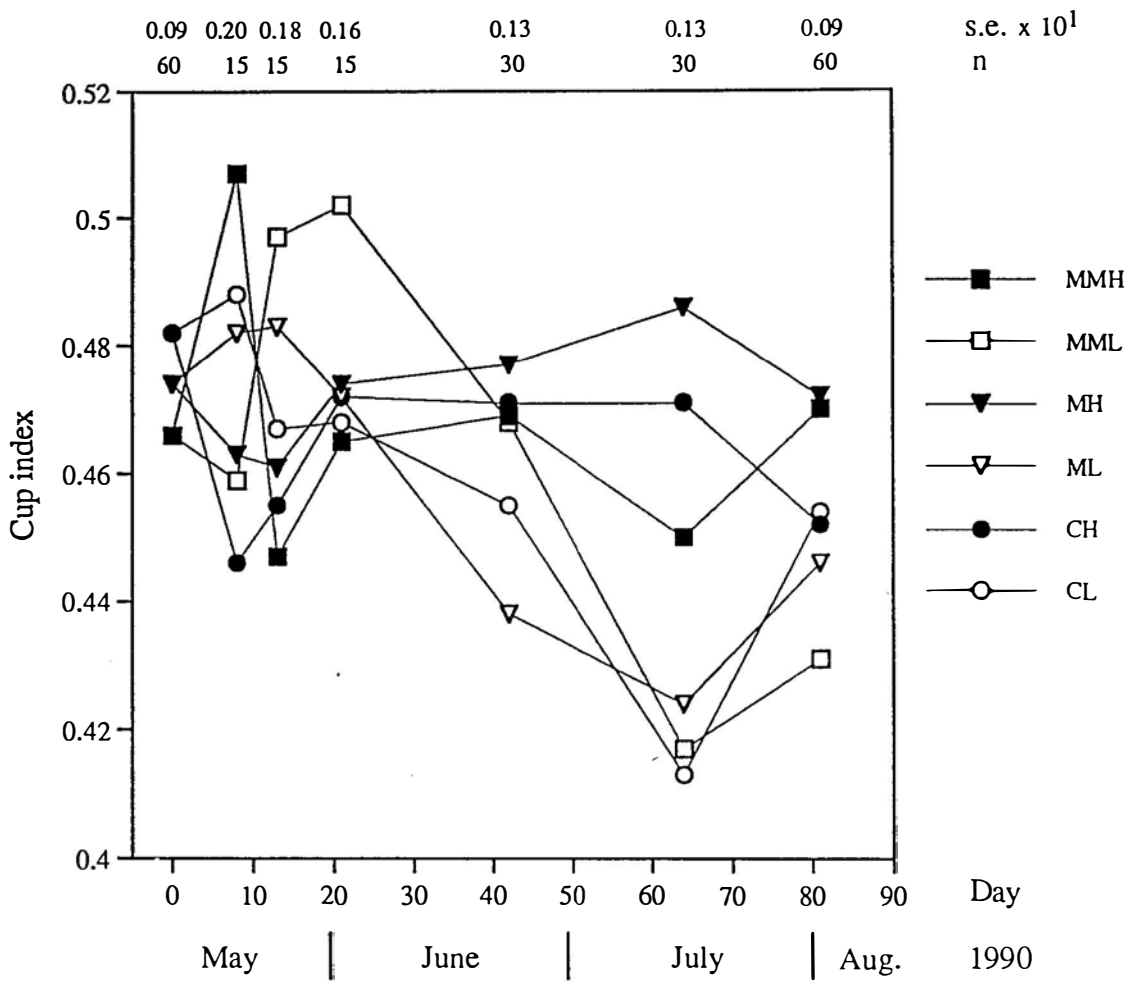
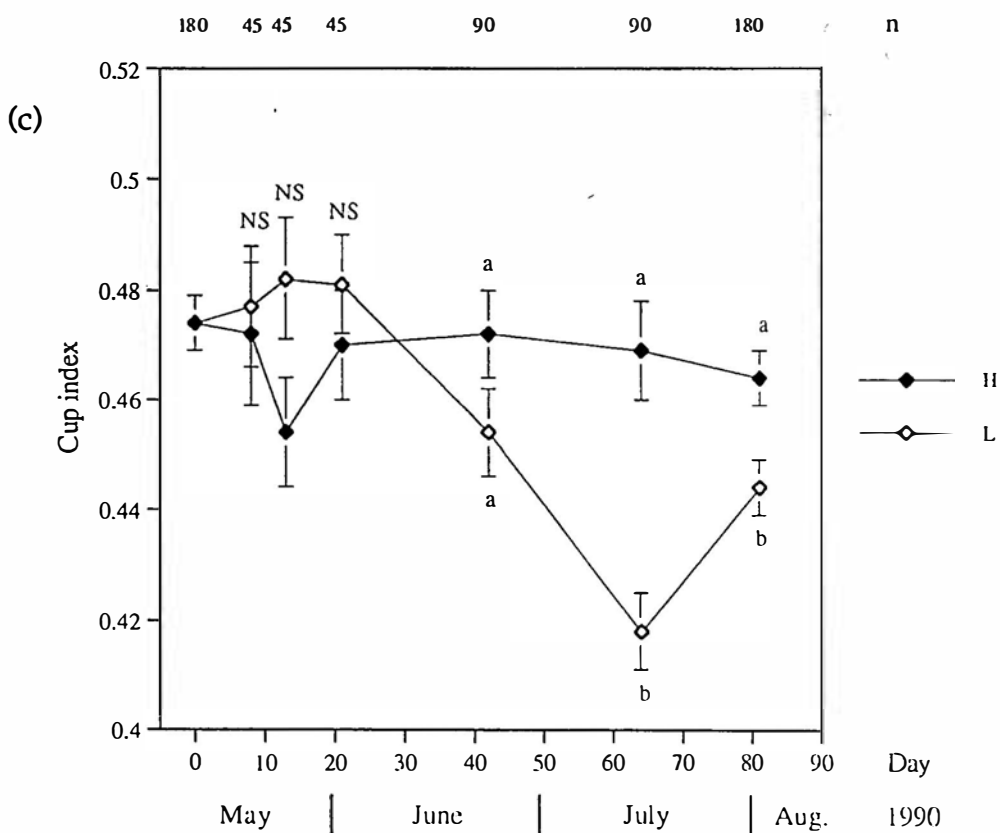
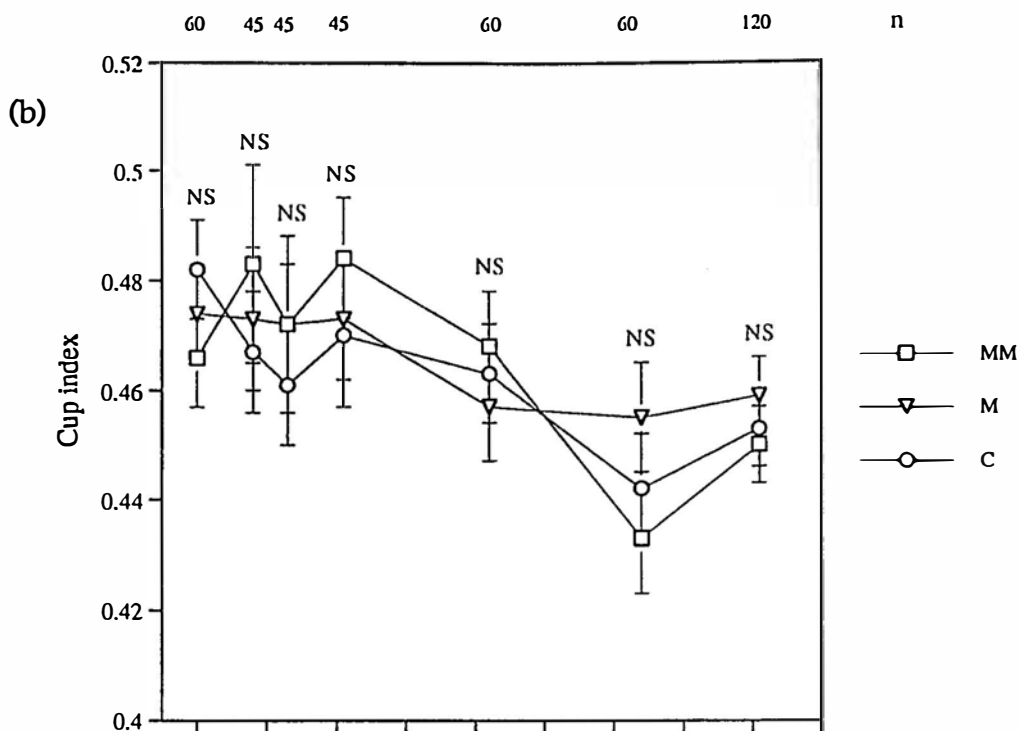


Fig. 14a. Effects of shell abrasion and aerial exposure on the mean cup index of Pacific oysters (*C. gigas*) in Experiment 1. MM, machine-graded twice; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; s.e., pooled standard error; n, sample number.



Figs. 14b-c. Effects of shell abrasion (b) and aerial exposure (c) on the mean cup index of Pacific oysters (*C. gigas*) in Experiment 1 (means \pm s.e.). NS, for the same sample, means do not differ significantly ($P > 0.05$); the letters a, b indicate that means differ significantly ($P < 0.05$). MM, machine-graded twice; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number.

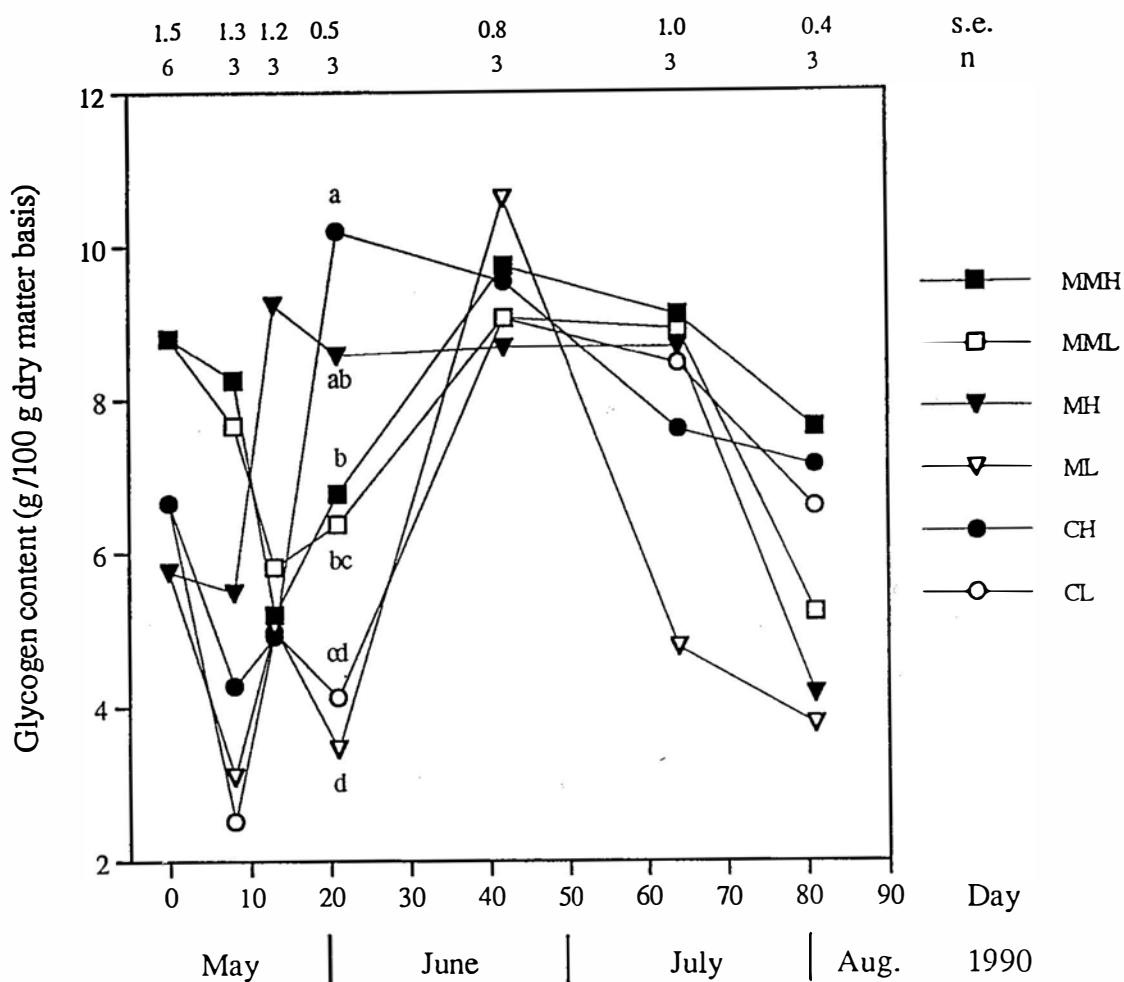
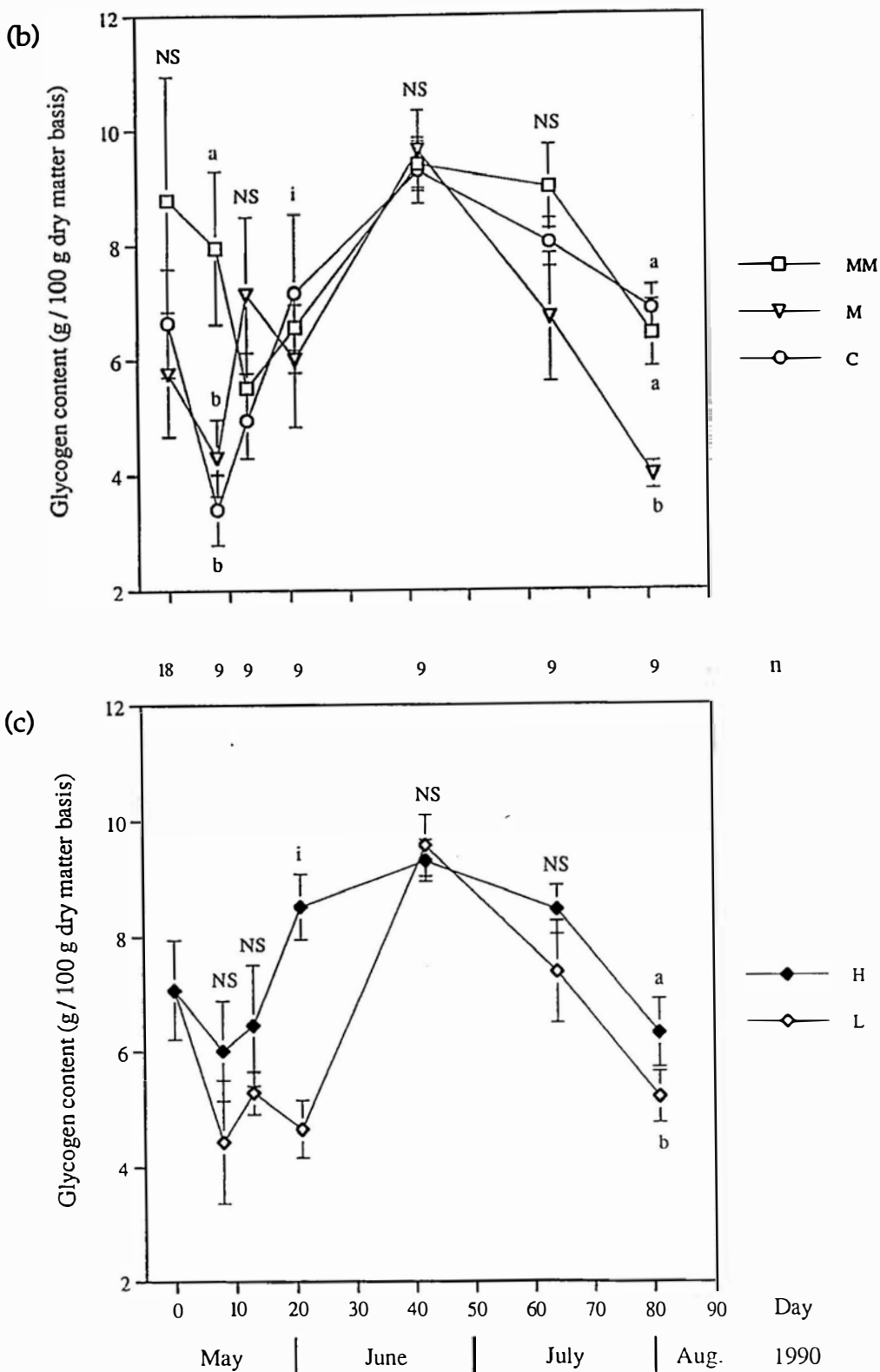


Fig. 15a. Effects of shell abrasion and aerial exposure on the mean glycogen content of Pacific oysters (*C. gigas*) in Experiment 1. There was a significant interaction ($P < 0.05$) on day 21, and pairwise comparisons (Fisher's LSD) are shown [means which share common letters do not differ significantly ($P > 0.05$)]. MM, machine-graded twice; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; s.e., pooled standard error; n, sample number.



Figs. 15b-c. Effects of shell abrasion (b) and aerial exposure (c) on the mean glycogen content of Pacific oysters (*C. gigas*) in Experiment 1 (means \pm s.e.). NS, for the same sample, means do not differ significantly ($P>0.05$); the letters a, b indicate that means differ significantly ($P<0.05$); i, for this sample a significant interaction (Fig. 15a) prevented statistical comparisons of means based on pooling. MM, machine-graded twice; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number.

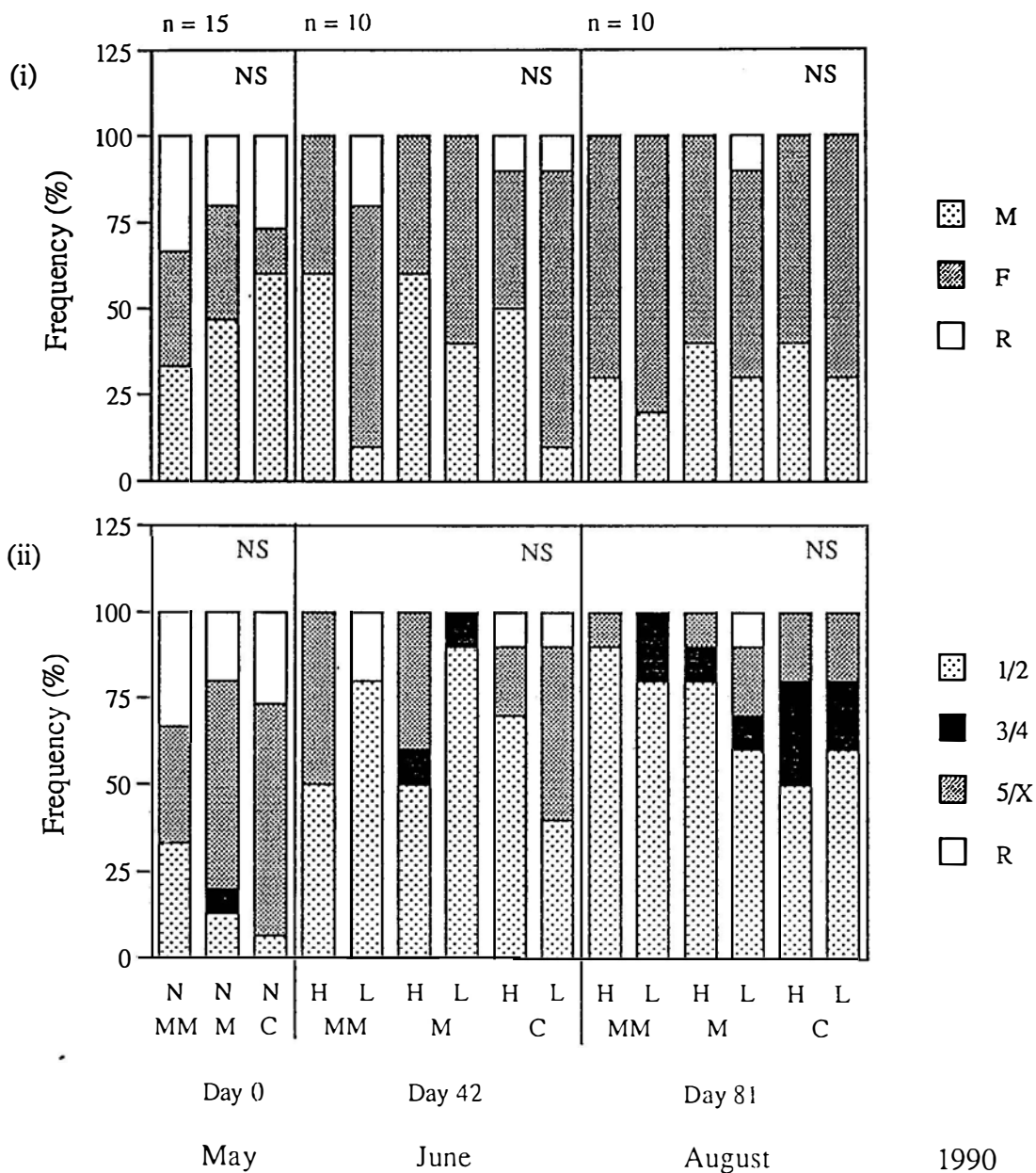


Fig. 16a. Effects of shell abrasion and aerial exposure on the sex group (i) and gonad stage (ii) of Pacific oysters (*C. gigas*) in Experiment 1. (i) M, male; F, female; R, regressed (sex group is indeterminate). (ii): 1/2, ripening; 3/4, ripe; 5/X, post-spawned; R, regressed. MM, machine-graded twice; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number. NS, the null hypothesis of independence is retained ($P > 0.05$).

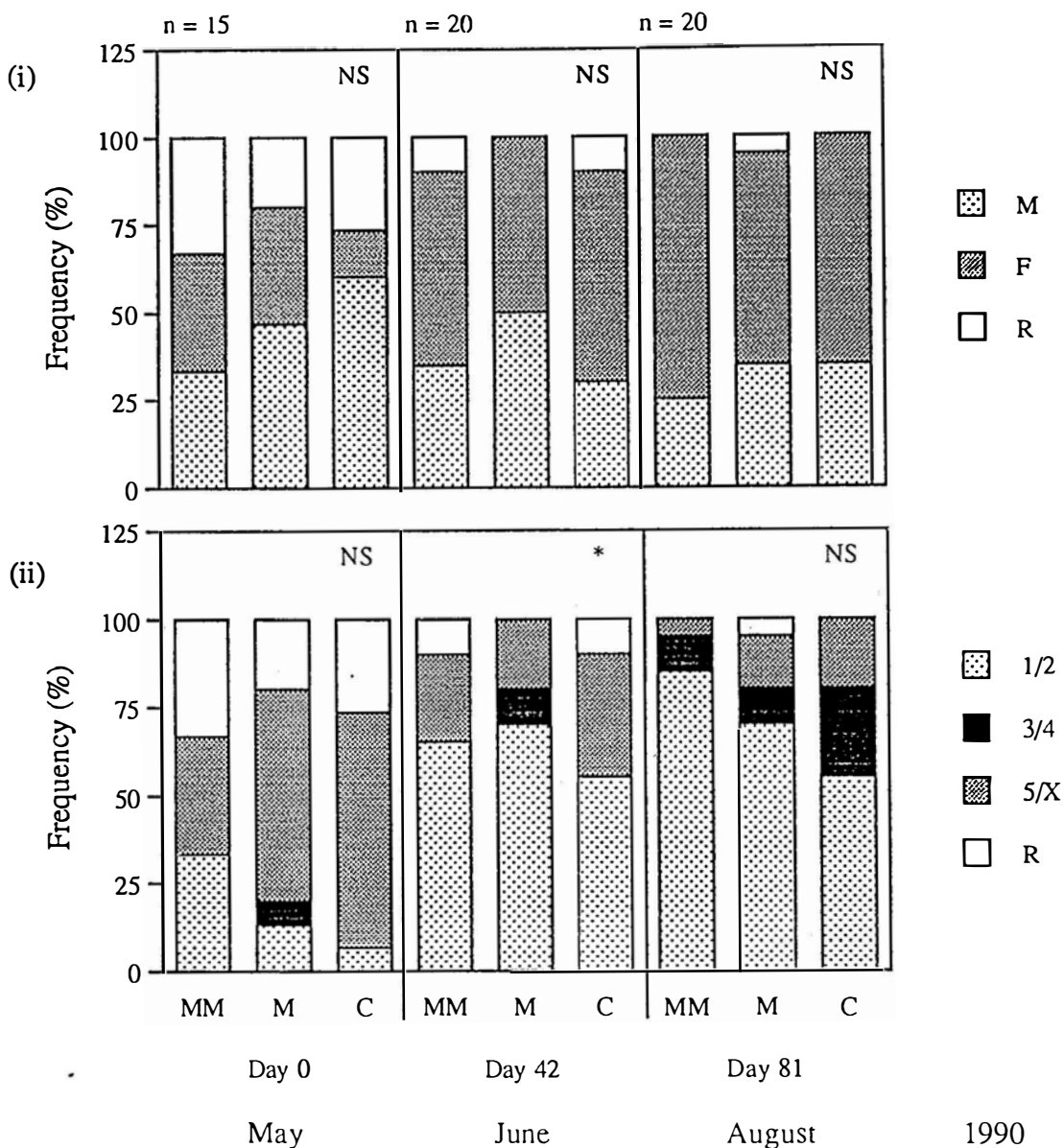


Fig. 16b. Effects of shell abrasion on the sex group (i) and gonad stage (ii) of Pacific oysters (*C. gigas*) in Experiment 1. (i) M, male; F, female; R, regressed (sex group is indeterminate). (ii): 1/2, ripening; 3/4, ripe; 5/X, post-spawned; R, regressed. MM, machine-graded twice; M, machine-graded once; C, control; n, sample number. NS, the null hypothesis of independence is retained ($P > 0.05$); * = $P < 0.05$.

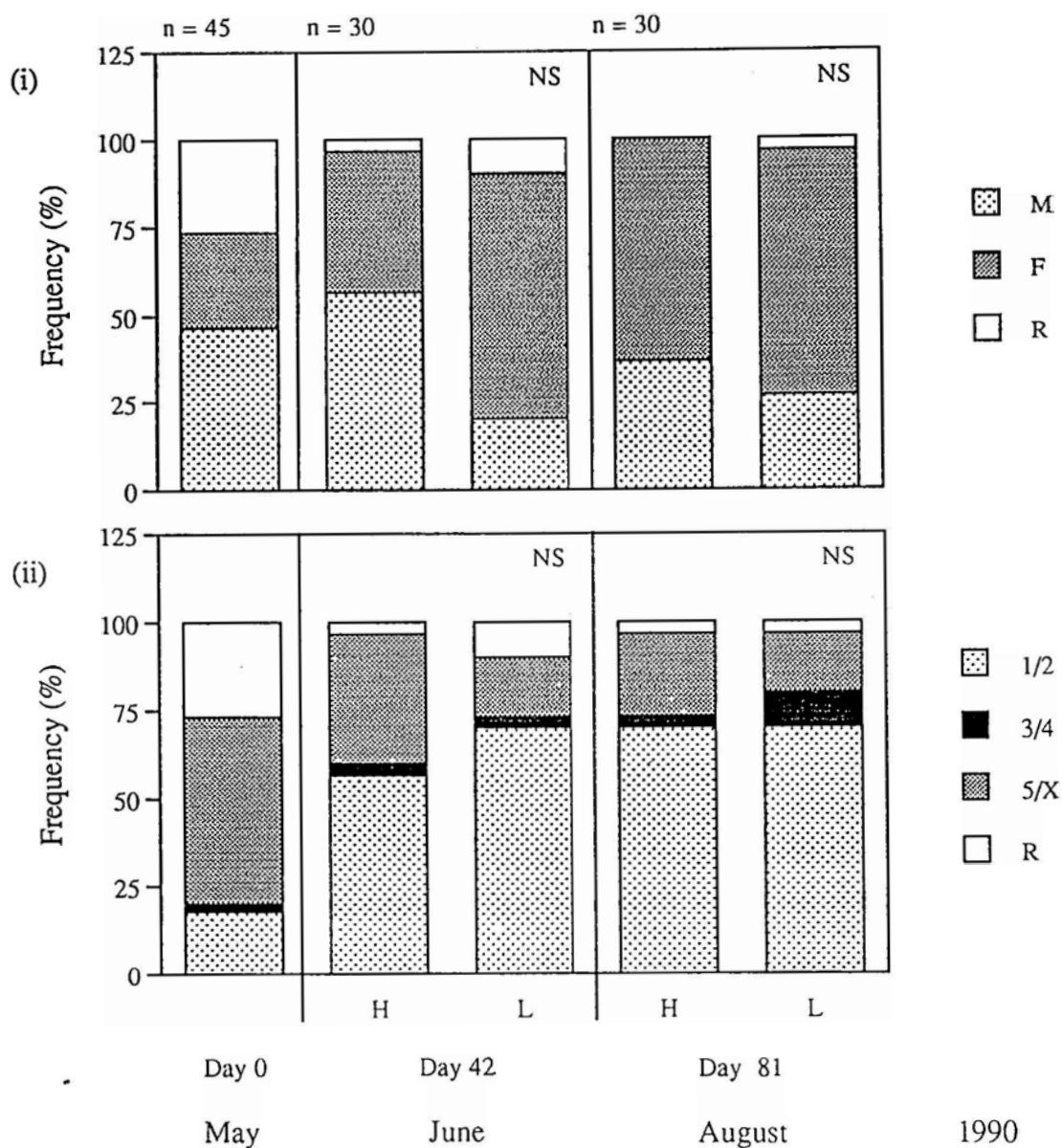


Fig. 16c. Effects of aerial exposure on the sex group (i) and gonad stage (ii) of Pacific oysters (*C. gigas*) in Experiment 1. (i) M, male; F, female; R, regressed (sex group is indeterminate). (ii): 1/2, ripening; 3/4, ripe; 5/X, post-spawned; R, regressed. H, high aerial exposure; L, low aerial exposure; n, sample number. NS, the null hypothesis of independence is retained ($P>0.05$).

Experiment 2

3.3 Abiotic measurements

3.3.1 Water temperature and salinity

The average daily water temperature at Pipeclay Lagoon was 11.2°C (n=69). Minimum and maximum temperatures were 6.0°C (day 105) and 16.5°C (day 15), respectively (Fig. 17a).

The average daily salinity was 34.2‰ (n=68), and ranged from a minimum of 33.4‰ (day 86) to a maximum of 35.0‰ (day 10) (Fig. 17b).

3.3.2 Aerial exposure

The average daily exposure was 0% exposure d⁻¹ for oysters held at the low growing height (L group) and 7% exposure d⁻¹ for oysters held at the high growing height (H group).

3.4 Biotic measurements

Interactions between shell abrasion and aerial exposure treatments were not consistent (one interaction shown in each of Figs. 18a, 23a, 24a, 26a, D-vii, D-x, and three interactions shown in Fig. 28a).

3.4.1 Survival

Overall survival was estimated to be 99.0%, and ranged from 98.5-99.8% for individual baskets. No treatment related trends were evident. Out of the total number of oysters sampled (n=8640), only nine oyster shells contained spionid polychaete blisters. No abnormal mantle tissue was found in oysters in the day 0 sample (n=30).

3.4.2 Growth

Ignoring treatment effects, best growth in whole weight (7.3 g month^{-1}), shell height, dry shell weight and dry meat weight in Experiment 2 Pacific oysters occurred from the beginning of the experiment, in mid-April, until mid-May. This was followed by slower growth (whole weight = 1.6 g month^{-1}) until the end of the experiment in mid-August (Figs. 18-21).

By the final sample, pooled data for shell abrasion treatments showed that the C group had performed better in terms of their mean whole weight, shell height, and dry shell and dry meat weights, than MB and M groups. The values for the M group were mostly intermediate. Aerial exposure ($0\text{-}7\% \text{ exposure d}^{-1}$) had no effect on growth.

3.4.2.1 Whole weight and shell growth

The average whole weight increased from $30.4 \pm 0.6 \text{ g}$ ($n=240$) to $44.2 \pm 0.7 \text{ g}$ ($n=360$) (Fig. 18a). After the initial machine-grading, the M group were significantly ($P<0.05$) smaller in mean whole weight compared to controls (approximately 1% smaller) (Fig. 18b). For the last four samples (days 51-124), the mean whole weight of the C group was higher than the M group, which in turn was higher than the MM group, but data were only significantly different ($P<0.05$) on days 51 ($C>MB$) and 124 ($C>M$, MB) (Fig. 18b). Aerial exposure did not affect ($P>0.05$) whole weight growth of L ($0\% \text{ exposure d}^{-1}$), compared to H group ($7\% \text{ exposure d}^{-1}$) oysters (Fig. 18c).

Shell height increased from a mean of $65.4 \pm 0.7 \text{ mm}$ ($n=240$) to $77.0 \pm 0.6 \text{ mm}$ ($n=360$) (Fig. 19a). Shell length and shell depth increased from means of $39.1 \pm 0.5 \text{ mm}$ ($n=120$) and $22.8 \pm 0.3 \text{ mm}$ ($n=120$) to $44.5 \pm 0.4 \text{ mm}$ ($n=360$) and $25.0 \pm 0.2 \text{ mm}$ ($n=360$), respectively (Appendix D, Figs. D-vii, -x).

Measurements at the lease showed that shell abrasion treatments removed substantial shell frill. After the initial machine grading, on day 0, the M group oysters were $3.3 \pm 0.4 \text{ mm}$ ($P>0.05$) and $5.9 \pm 0.4 \text{ mm}$ smaller ($P>0.05$) ($n=13$) in their mean shell height and shell length dimensions, respectively, compared to their size prior to treatment (Appendix E). These results are reflected in Fig. 19b and Fig. D-viii (Appendix D), where a comparison of the C group (similar to the M

group prior to their being machine-graded) and M groups (measured after grading) shows $C > M$ ($P < 0.05$) on day 0. Subsequent samples on days 10 and 23, for mean shell height and shell length of the C and M groups were no longer different ($P > 0.05$), however (Figs. 19b, D-viii).

On day 38 (week 6), half of the M group were shaken in their baskets creating the MB group. This treatment caused the MB group to become significantly smaller ($P < 0.05$) in mean shell height and length dimensions, compared to the M group (Fig. 19b, D-viii). Meanwhile, C and M groups still had very similar dimensions, such that $C, M > MB$ ($P < 0.05$) (Fig. 19b, D-viii). Measurements of the MB group showed reductions in shell height and shell length to be respectively, 3.4 ± 0.5 mm ($P > 0.05$) and 2.5 ± 0.4 mm ($P < 0.05$) ($n=29$) (Appendix E). Additional shell frill was removed from the MB group on day 82 (week 12); reductions in shell height and shell length were 4.5 ± 0.6 mm ($P > 0.05$) and 2.9 ± 0.7 mm ($P > 0.05$) ($n=29$), respectively (Appendix E). However, this change is not reflected in the mean values for the groups of 90 oysters sampled on days 84 and 96 (Fig. 19b). The outcome, by the final sample, was $C > M > MB$ ($P < 0.05$) for shell height (Fig. 19b), and $C, M > MB$ ($P < 0.05$) for shell length (Fig. D-viii).

Aerial exposure did not affect the shell height growth of H and L groups ($P > 0.05$) (Fig. 19c), whilst for shell length, the significant differences ($P < 0.05$) on days 96 and 124 did not show consistent trends (Fig. D-ix).

The mean dry shell weight increased from 16.9 ± 0.4 g ($n=120$) to 28.6 ± 0.6 g ($n=180$) (Fig. 20a). Shell abrasion did not cause consistent trends in dry shell weight growth even though significant differences ($P < 0.05$) did occur on days 0 ($C > M$), 51 ($M > MB$) and 124 ($C > M, MB$) (Fig. 20b). Aerial exposure did not affect dry shell weight ($P > 0.05$) (Fig. 20c).

3.4.2.2 Meat growth

The mean dry meat weight increased from 0.58 ± 0.02 g ($n=120$) to 1.04 ± 0.05 g ($n=180$) (Fig. 21a). Shell abrasion was significant ($P < 0.05$) for dry meat weight on day 124 ($C > M$), only (Fig. 21b). Aerial exposure was not a significant factor ($P > 0.05$) (Fig. 21c).

3.4.3 Condition indices

Generally the condition indices (CIvol, CIshell) of Experiment 2 Pacific oysters increased until mid-May, declined until mid-July, and then increased again until the end of the experiment (Figs. 22, 23). The CIvol showed much clearer trends for the effects of shell abrasion than did CIshell; the MB group had a higher CIvol than M or C groups, and usually the M group had a higher CIvol than the C group. Aerial exposure had some effect on the condition indices such that the H group generally had higher, but usually not significantly higher, values compared to the L group.

3.4.3.1 Volume condition index

The CIvol increased from a mean of 47.4 ± 1.1 (n=120) to 58.0 ± 0.7 (n=180) (Fig. 22a). Trends due to shell abrasion appeared after day 38; the MB group had a higher CIvol than M or C groups, and the CIvol of the M group was usually higher than that of the C group [$P < 0.05$, days 38 (MB, $M > C$), 51 (MB $> C$), 82 (MB, $M > C$), 96 (MB $> M > C$) and 124 (MB $> M$, C)] (Fig. 22b). After day 51, the H group had a consistently higher CIvol than the L group, but the treatment effect was only significant ($P < 0.05$) on day 96 (Fig. 22c).

3.4.3.2 Shell condition index

The CIshell increased from a mean of 34.1 ± 0.7 (n=120) to 36.2 ± 0.4 (n=180) (Fig. 23a). Shell abrasion had caused significant effects ($P < 0.05$) on CIshell on several occasions [days 38 (MB, $M > C$), 82 ($M > C$), and 96 (MB $> M$, C)], but differences were not significant by the last sample (Fig. 23b). The H group had a consistently higher CIshell than the L group after day 23, but the treatment effect was only significantly different ($P < 0.05$) on day 96 (Fig. 23c).

3.4.4 Shape indices

Generally, the roundness index values declined and then became relatively constant and, or increased depending on treatment effects (Fig. 24). Similarly, cup index values increased or decreased depending on treatment (Fig. 25). For the latter part of the study, the MB group had a

lower mean roundness index but higher cup index compared to M and C groups. Aerial exposure did not affect the roundness index; the cup index of the H group, however, was generally higher than that of the L group.

3.4.4.1 Roundness index

The average roundness index decreased from a mean of 0.61 ± 0.06 (n=240) to 0.58 ± 0.005 (n=360) (Fig. 24a). Shell abrasion was significant ($P < 0.05$) on days 0 (C>M) CK, 51 (M>MB, C), 82 and 96 (M, C>MB), and 124 (M>C>MB), such that after day 82, C and M groups had a rounder shape compared to the MB group (Fig. 24b). Aerial exposure was not a significant factor ($P > 0.05$) for any sample (Fig. 24c).

3.4.4.2 Cup index

The average cup index decreased from a mean of 0.46 ± 0.04 (n=240) to 0.43 ± 0.003 (n=360) (Fig. 25a). Shell abrasion was significant ($P < 0.05$) on day 0 (M>C), but the major trend was that the cup index values of the MB group were usually much higher than either the M or C groups [MB>M, C ($P < 0.05$) days 38, 51, 82, 96, 124] (Fig. 25b). Aerial exposure was significant ($P < 0.05$) on days 51, 82, and 96, such that the H group had a higher mean cup index compared to the L group; however, these differences had subsided by the last sample (Fig. 25c).

3.4.5 Glycogen content

Glycogen content (g per 100 g dry meat weight) increased from a mean of 5.5 ± 0.33 (n=24) on day 0, to 13.5 ± 0.40 (n=36) (Fig. 26a). Shell abrasion did not cause significant effects ($P > 0.05$) (Fig. 26b). Aerial exposure was significant ($P < 0.05$) on day 124 only (H>L); generally however, the H group attained higher glycogen levels than the L group (Fig. 26c).

3.4.6 Gametogenesis

Sex ratios from April (day 0) through to August (day 124), had a lower frequency of males in comparison to either female or regressive stage (R) oysters [Fig. 27a(i)]. Gonad staging in May (day 38) showed that most

oysters (74%; n=90) were in post-spawned (5/X) and regressive stages, but by July (day 82), and August, 36% (n=60) and 48% (n=59), respectively, had entered a ripening stage (1/2) of development [Fig. 27a(ii)]. Notable, in comparison to Experiment 1, was that few individuals had reached a ripe (3/4) stage by August [Figs. 16a(ii), 27a(ii)]. In May, the significant difference ($P<0.05$) was most likely caused by the MH and CH groups having more individuals in post-spawning and regressive stages, respectively. The significant difference ($P<0.01$) in July, was due to the fact that while most groups had representatives from ripening, post-spawning and regressive stages, the MBH and MH groups lacked one of these (MBH lacked post-spawning stage; MH lacked regressive stage) [Fig. 27a(ii)].

Sex ratio was not affected ($P>0.05$) by shell abrasion [Fig. 27b(i)]. Gonad development stages were significantly different ($P<0.05$) in July and August [Fig. 27c(ii)]. In July, the M group had a higher frequency of oysters in ripening and post-spawned stages than either the MB or C groups; counteracting this, however, was that by August, the M group had the highest frequency of regressive stage individuals [Fig. 27c(ii)]. Aerial exposure was not significant for either sex ratio [Fig. 27c(i)], or gonad stage [Fig. 27c(ii)].

Chi-square analysis of gonad stage versus sex was significant on day 38 (Table 2, next page) because a disproportionate number of post-spawned (5/X) oysters were female [Fig. 27a(i)]. The significant result on day 82 (Table 2) was because most of the ripening (1/2) stage oysters were also female [Fig. 27a(i)].

3.4.7 Shelf life

Oysters usually gaped before they died (Figs. 28a, 29a); by the final sample (55 d), six oysters were in fact dead when presumed to be alive. No trends were evident, in the cumulative gape or cumulative mortality curves, either due to shell abrasion (Figs. 28b, 29b), or aerial exposure (Figs. 28c, 29c).

TABLE 2

Summary of Chi-square analysis of gonad stage versus sex¹ of Pacific oysters (*C. gigas*) in Experiment 2. All treatments (MBH, MBL, MH, ML, CH, CL) were included in the analysis.

Day(s)	Month(s)	Number of oysters analysed (n)	Chi-square analysis of gonad stage vs sex ¹
38	May	59	*
82	July	59	*
124	August	68	NS
38 + 82 + 124	May, July and August	186	**

¹ R stage (sex group is indeterminate) individuals removed from analysis. MB, oysters machine-graded once and baskets were shaken on days 38 and 82; M, oysters machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number. NS, the null hypothesis of independence is retained ($P > 0.05$); * = $P < 0.05$; ** = $P < 0.01$.

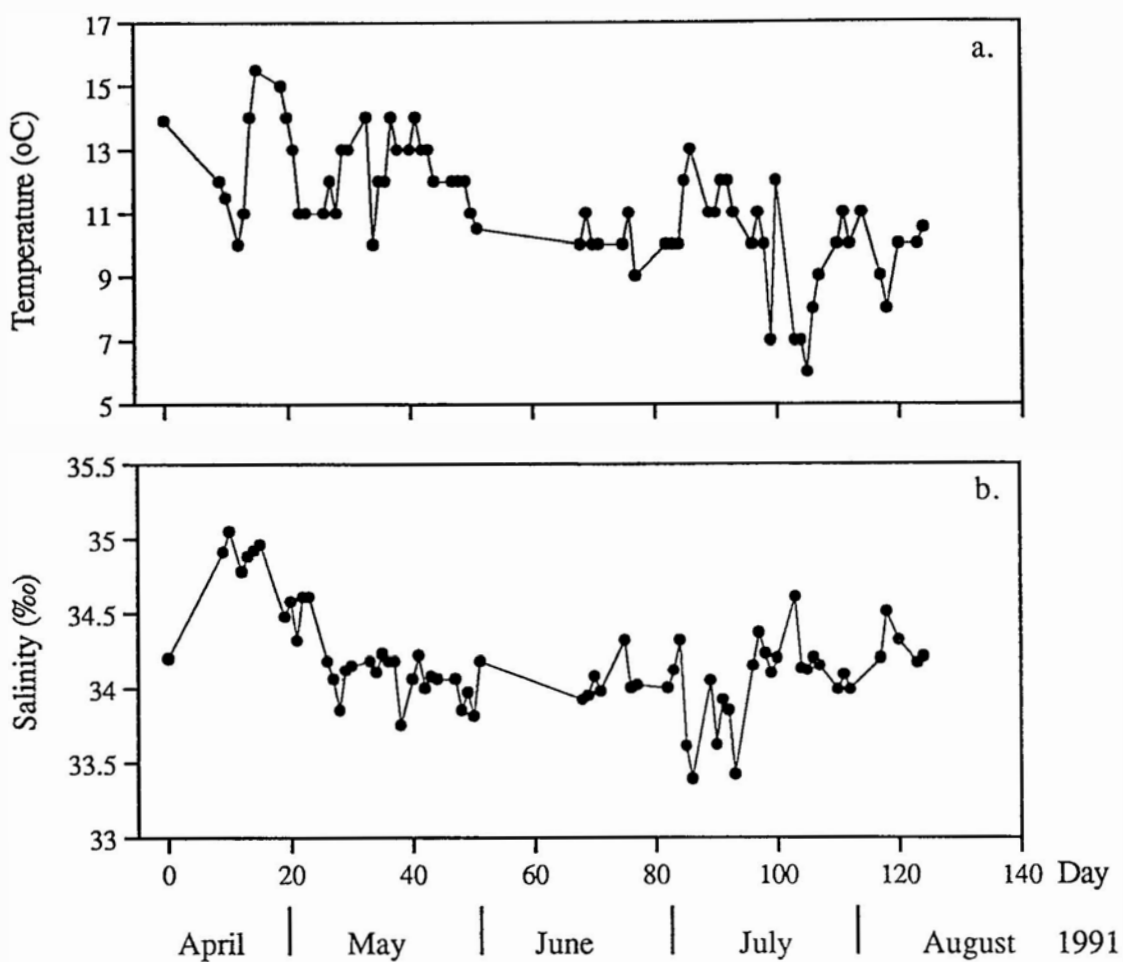


Fig. 17. Surface water temperature (a) and salinity (b) at Pipeclay Lagoon in Experiment 2.

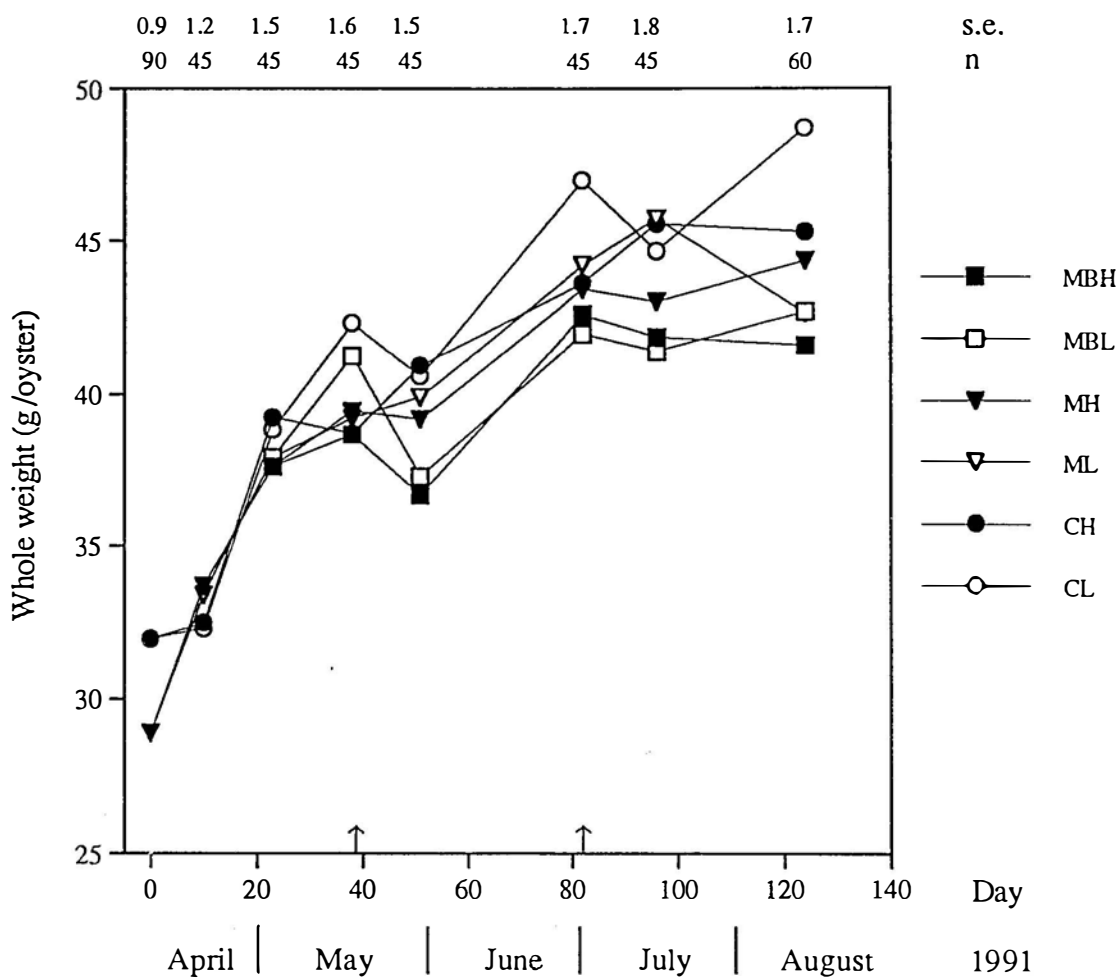
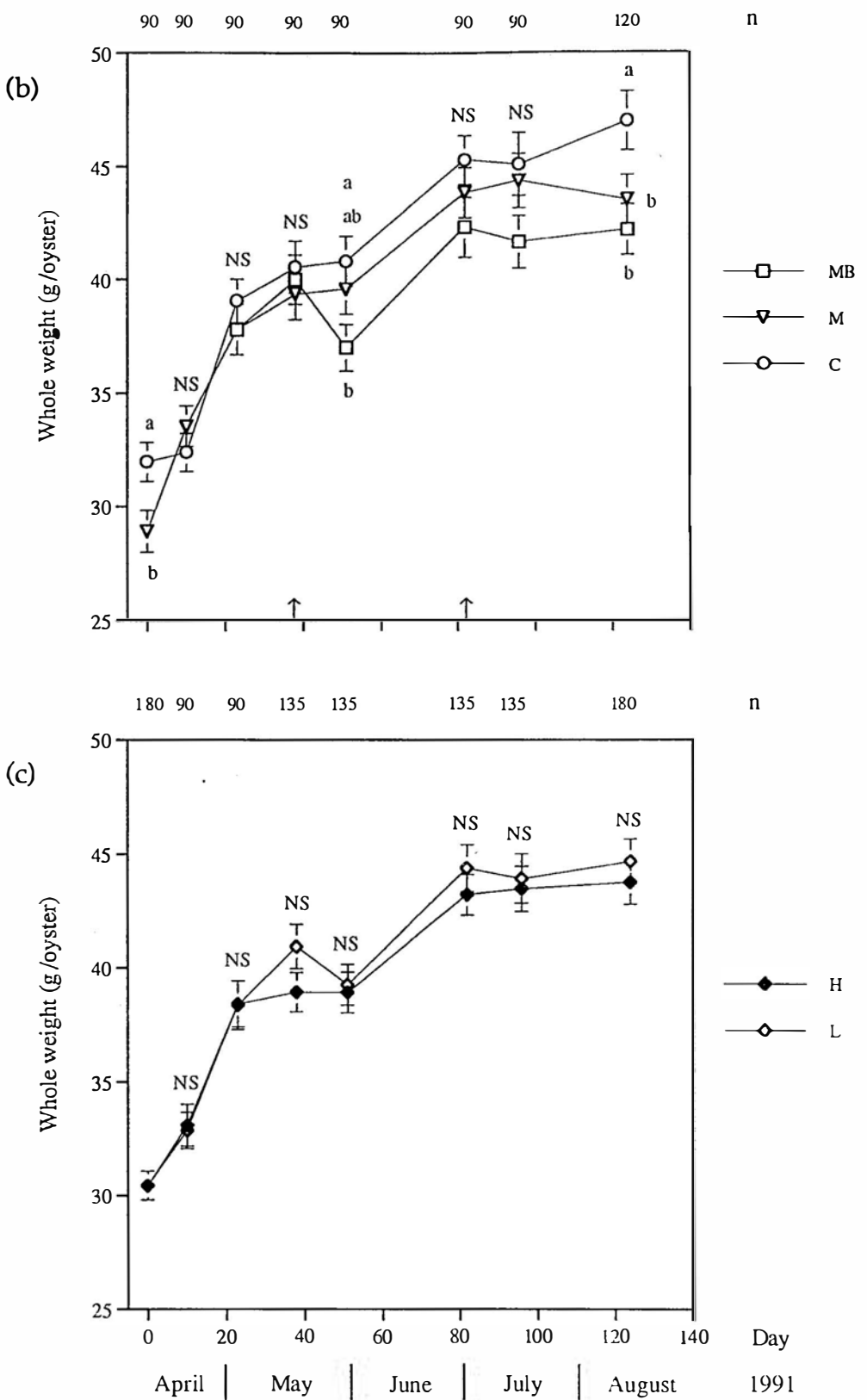


Fig. 18a. Effects of shell abrasion and aerial exposure on the mean whole weight of Pacific oysters (*C. gigas*) in Experiment 2. MB, machine-graded once and baskets were shaken on days 38 and 82 (shown by arrows); M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; s.e., pooled standard error; n, sample number.



Figs. 18b-c. Effects of shell abrasion (b) and aerial exposure (c) on the mean whole weight of Pacific oysters (*C. gigas*) in Experiment 2 (means \pm s.e.). NS, for the same sample, means do not differ significantly ($P>0.05$); the letters a, b indicate that means differ significantly ($P<0.05$). MB, machine-graded once and baskets shaken twice on days 38 and 82 (shown by arrows); M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number.

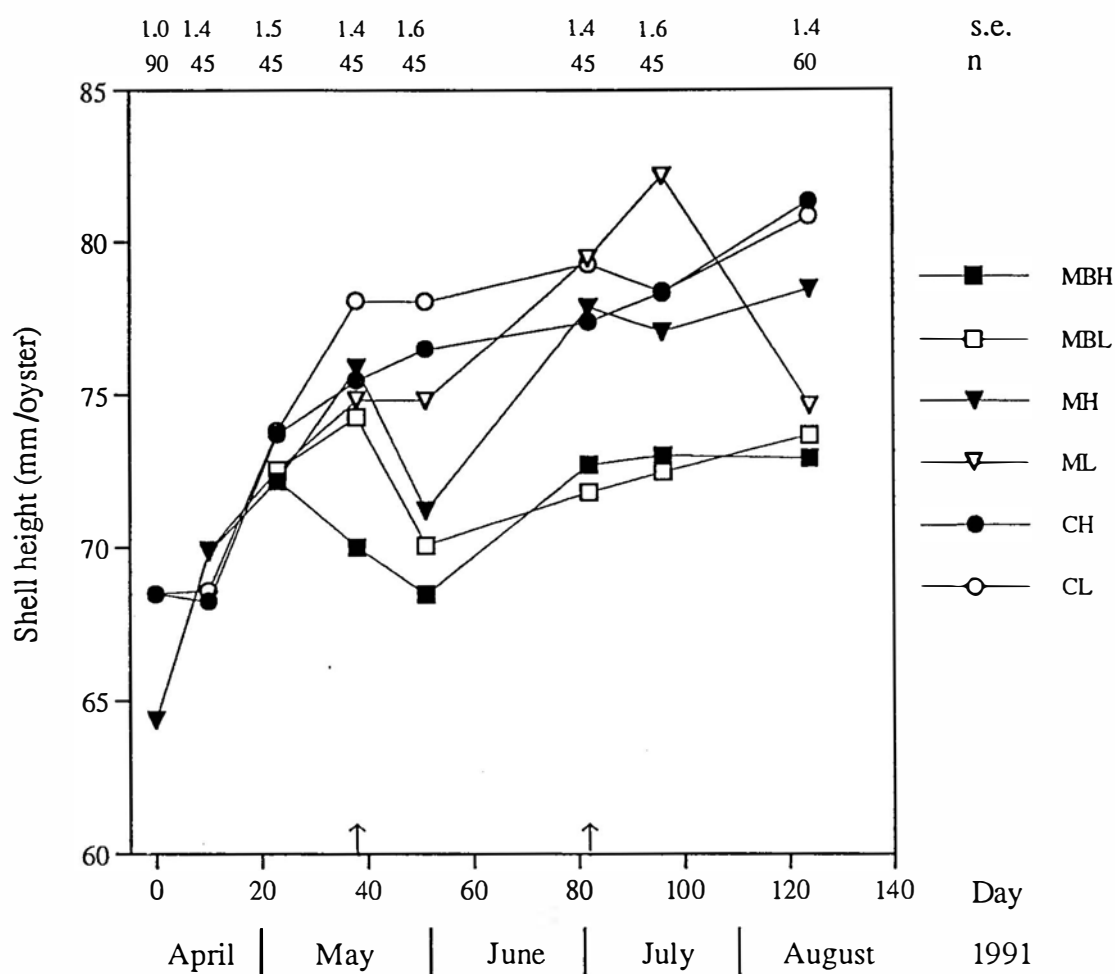
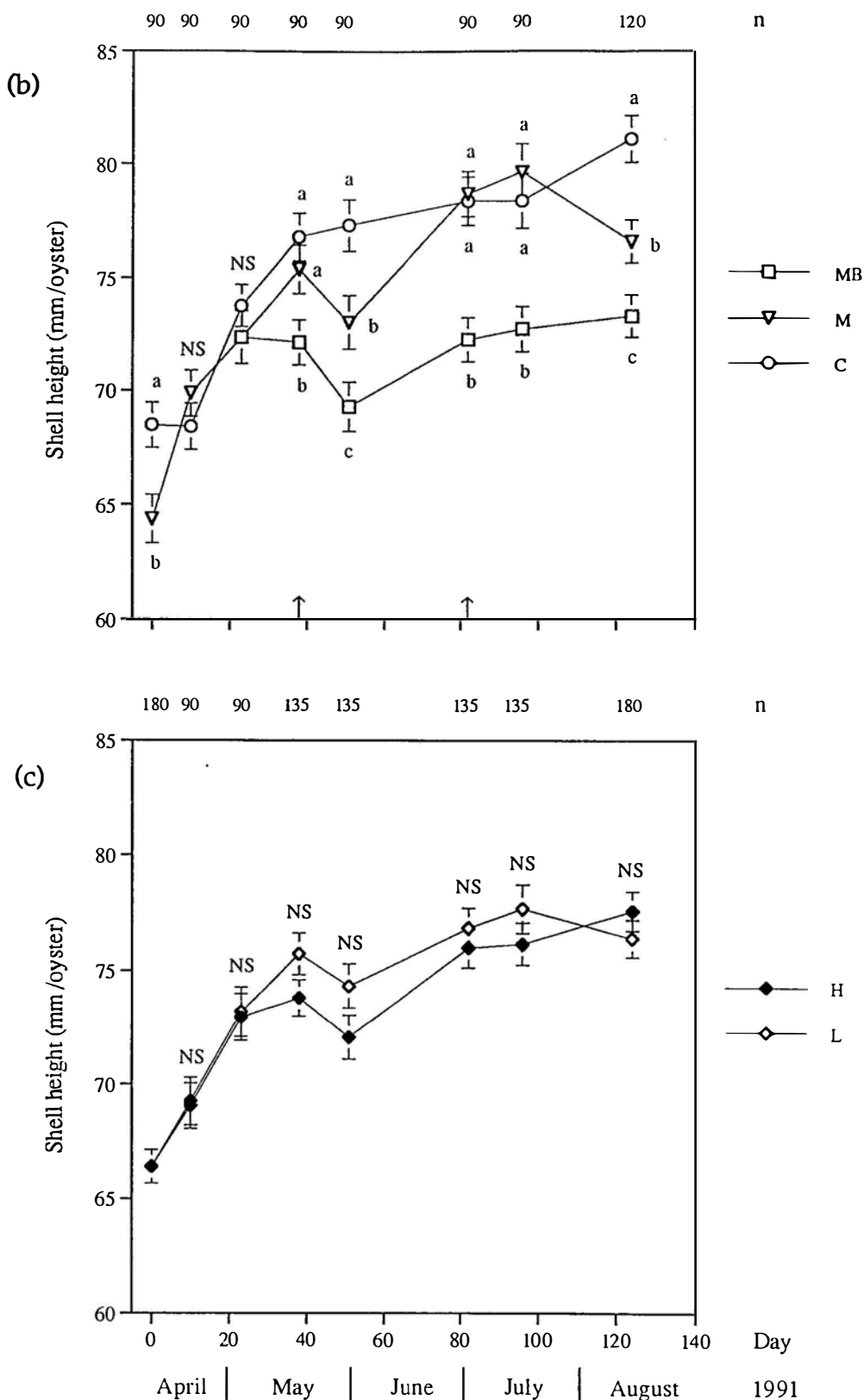


Fig. 19a. Effects of shell abrasion and aerial exposure on the mean shell height of Pacific oysters (*C. gigas*) in Experiment 2. MB, machine-graded once and baskets were shaken on days 38 and 82 (shown by arrows); M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; s.e., pooled standard error; n, sample number.



Figs. 19b-c. Effects of shell abrasion (b) and aerial exposure (c) on the mean shell height of Pacific oysters (*C. gigas*) in Experiment 2 (means \pm s.e.). NS, for the same sample, means do not differ significantly ($P>0.05$); the letters a, b, c indicate that means differ significantly ($P<0.05$). MB, machine-graded once and baskets shaken twice on days 38 and 82 (shown by arrows); M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number.

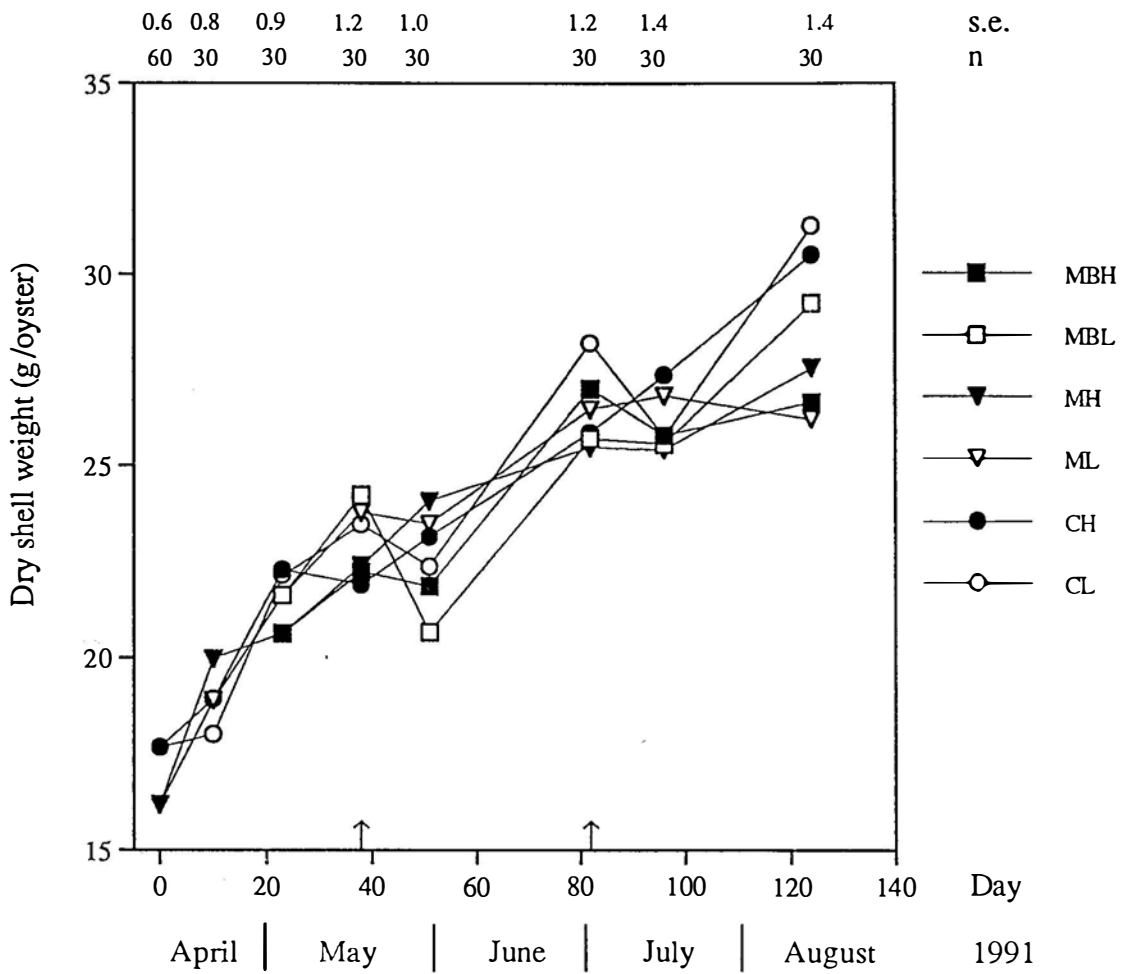
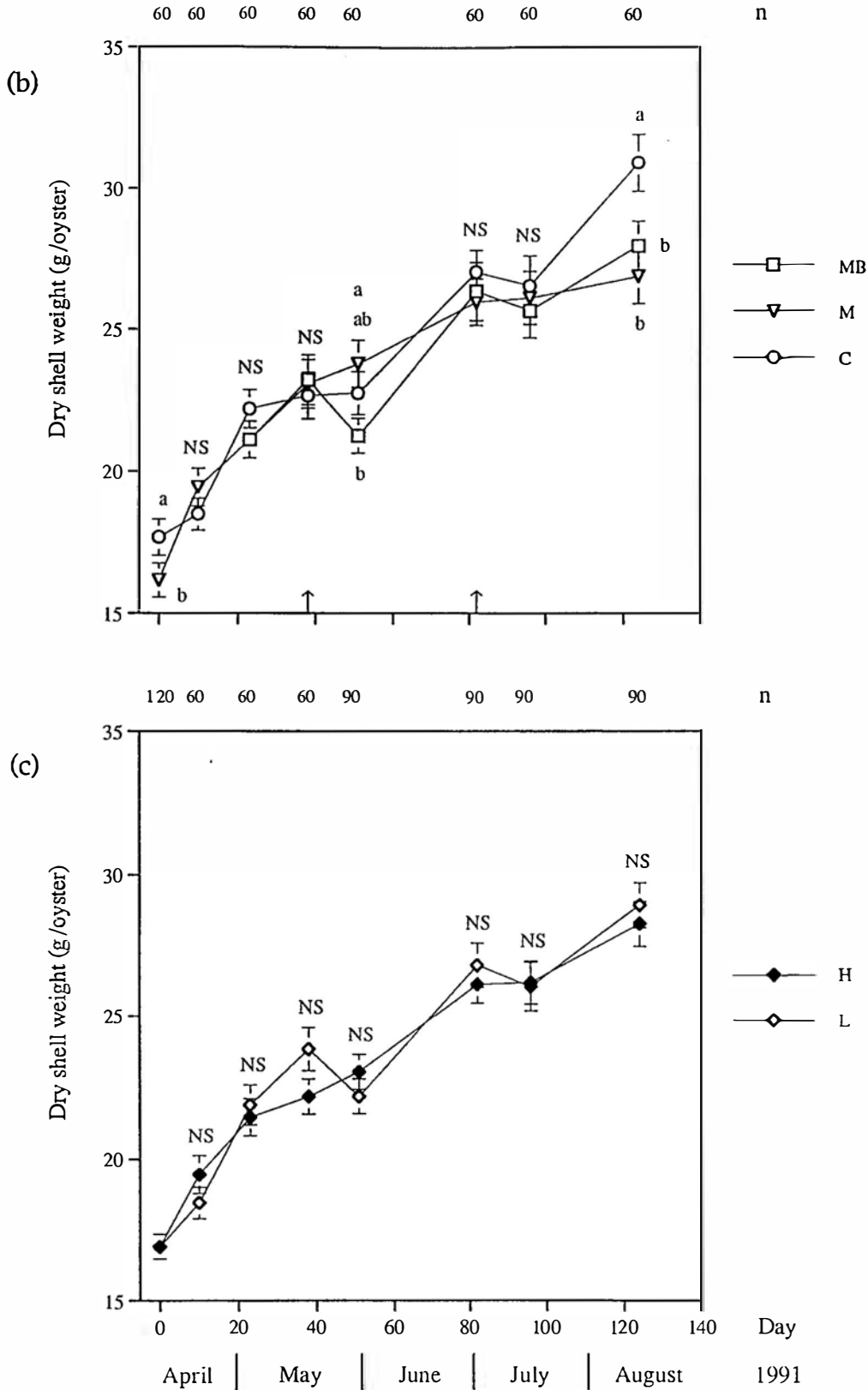


Fig. 20a. Effects of shell abrasion and aerial exposure on the mean dry shell weight of Pacific oysters (*C. gigas*) in Experiment 2. MB, machine-graded once and baskets were shaken on days 38 and 82 (shown by arrows); M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; s.e., pooled standard error; n, sample number.



Figs. 20b-c. Effects of shell abrasion (b) and aerial exposure (c) on the mean dry shell weight of Pacific oysters (*C. gigas*) in Experiment 2 (means \pm s.e.). NS, for the same sample, means do not differ significantly ($P>0.05$); the letters a, b indicate that means differ significantly ($P<0.05$). MB, machine-graded once and baskets shaken twice on days 38 and 82 (shown by arrows); M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number.

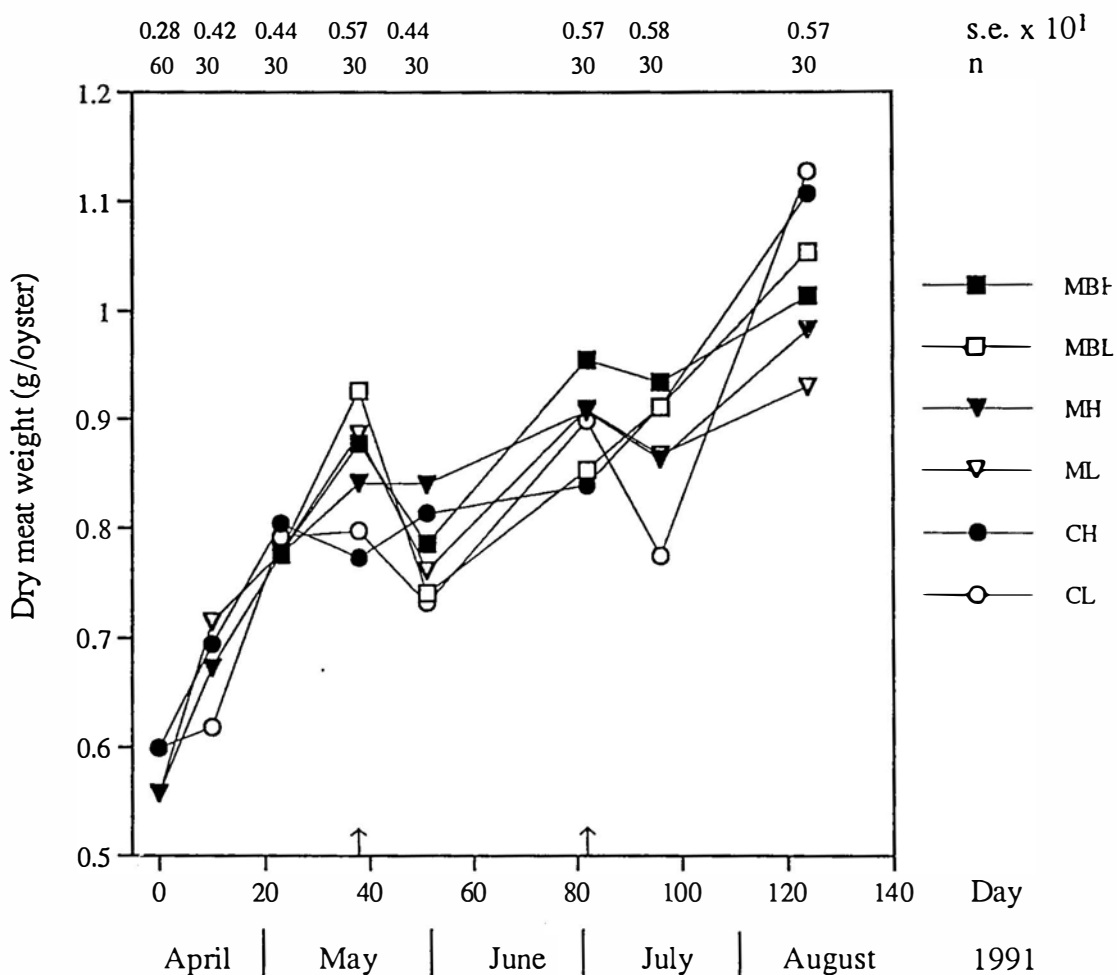
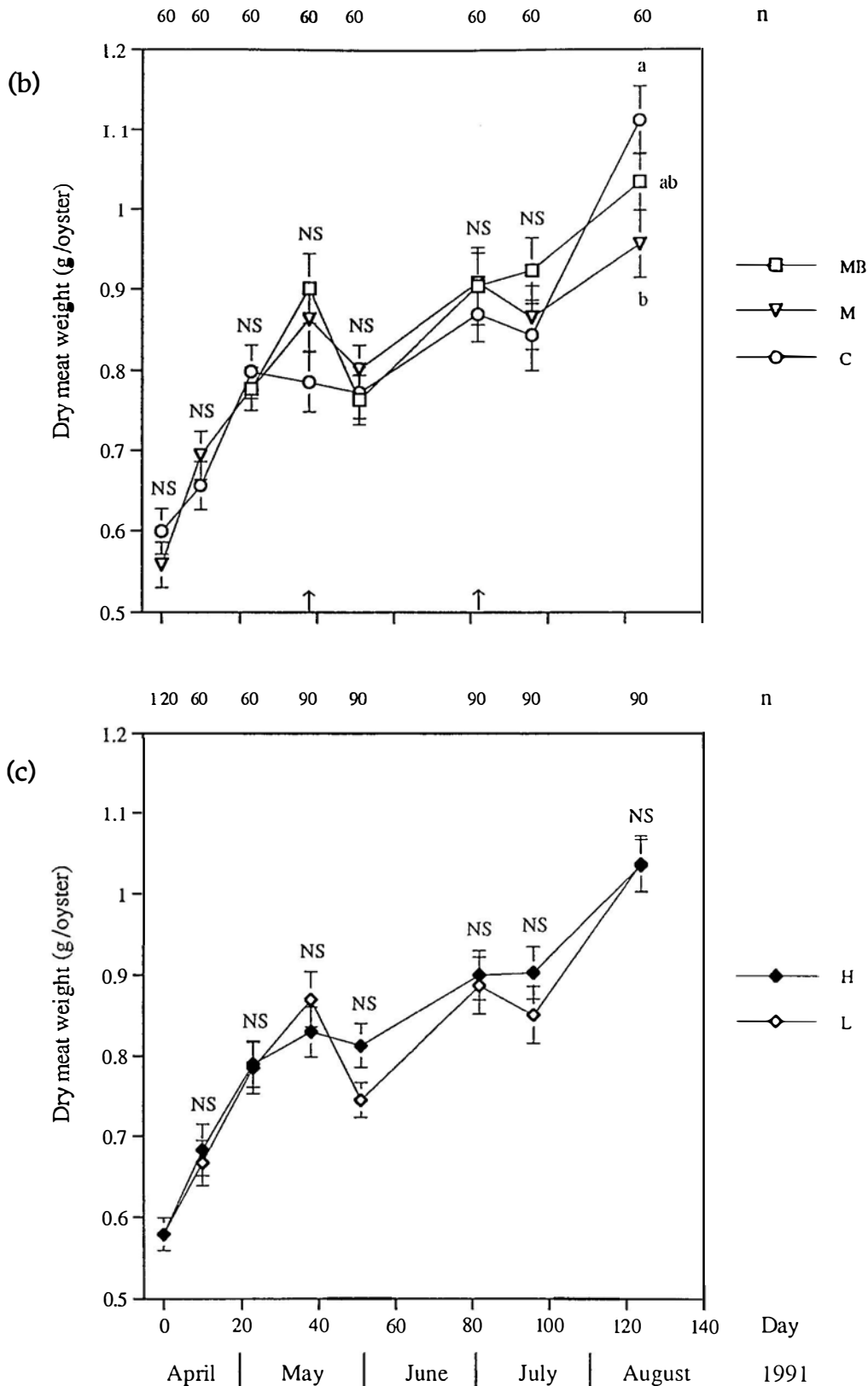


Fig. 21a. Effects of shell abrasion and aerial exposure on the mean dry meat weight of Pacific oysters (*C. gigas*) in Experiment 2. MB, machine-graded once and baskets were shaken on days 38 and 82 (shown by arrows); M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; s.e., pooled standard error; n, sample number.



Figs. 21b-c. Effects of shell abrasion (b) and aerial exposure (c) on the mean dry meat weight of Pacific oysters (*C. gigas*) in Experiment 2 (means \pm s.e.). NS, for the same sample, means do not differ significantly ($P>0.05$); the letters a, b indicate that means differ significantly ($P<0.05$). MB, machine-graded once and baskets shaken twice on days 38 and 82 (shown by arrows); M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number.

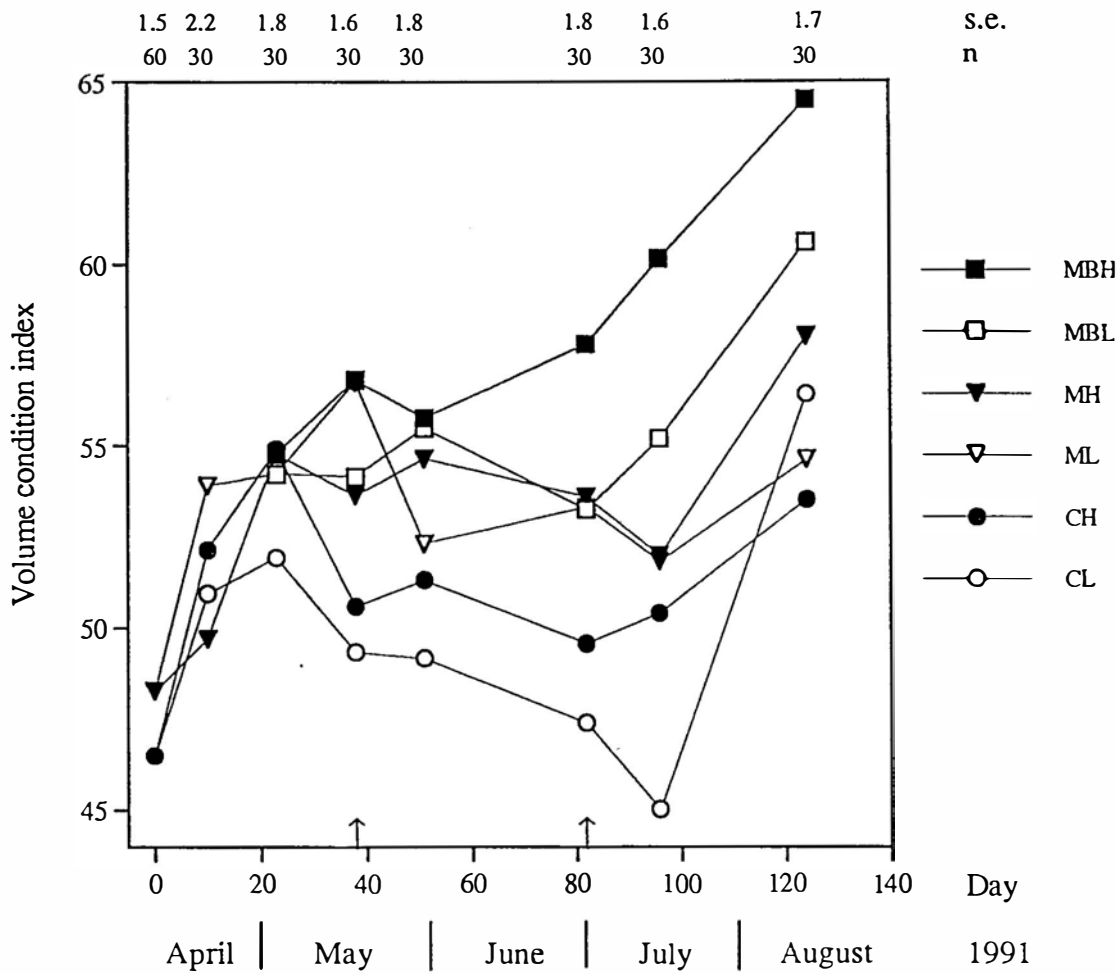
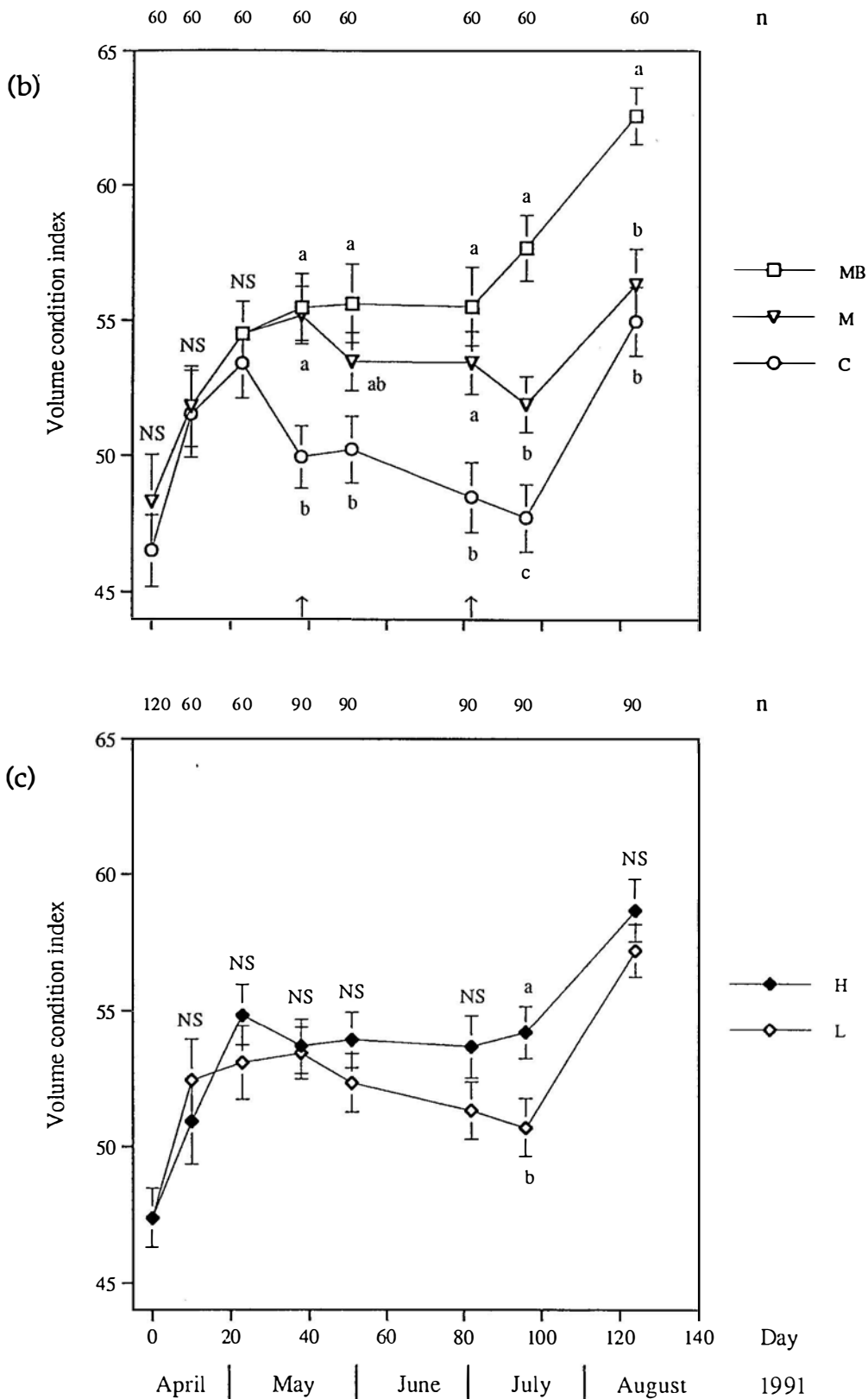


Fig. 22a. Effects of shell abrasion and aerial exposure on the mean volume condition index (CIvol) of Pacific oysters (*C. gigas*) in Experiment 2. MB, machine-graded once and baskets were shaken on days 38 and 82 (shown by arrows); M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; s.e., pooled standard error; n, sample number.



Figs. 22b-c. Effects of shell abrasion (b) and aerial exposure (c) on the mean volume condition index (CIvol) of Pacific oysters (*C. gigas*) in Experiment 2 (means \pm s.e.). NS, for the same sample, means do not differ significantly ($P > 0.05$); the letters a, b, c indicate that means differ significantly ($P < 0.05$). MB, machine-graded once and baskets shaken twice on days 38 and 82 (shown by arrows); M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number.

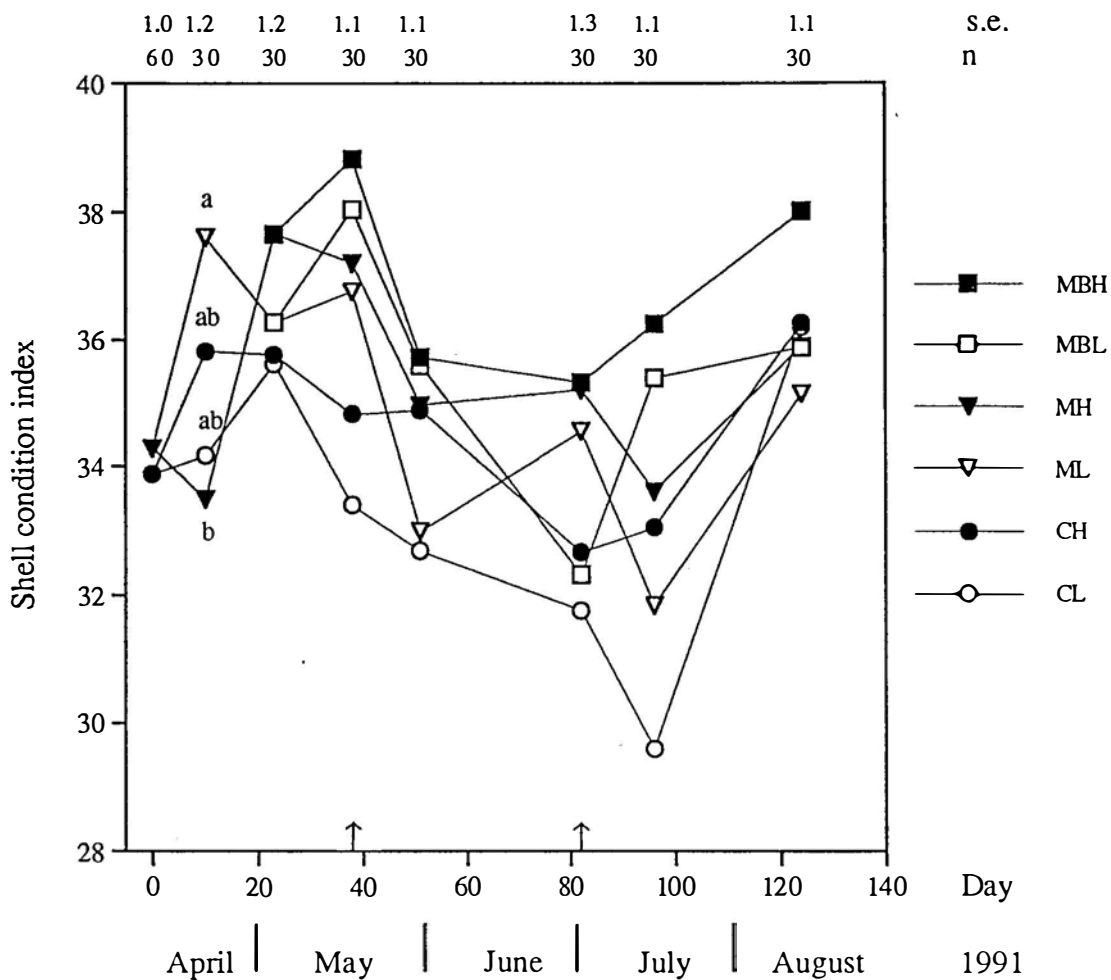
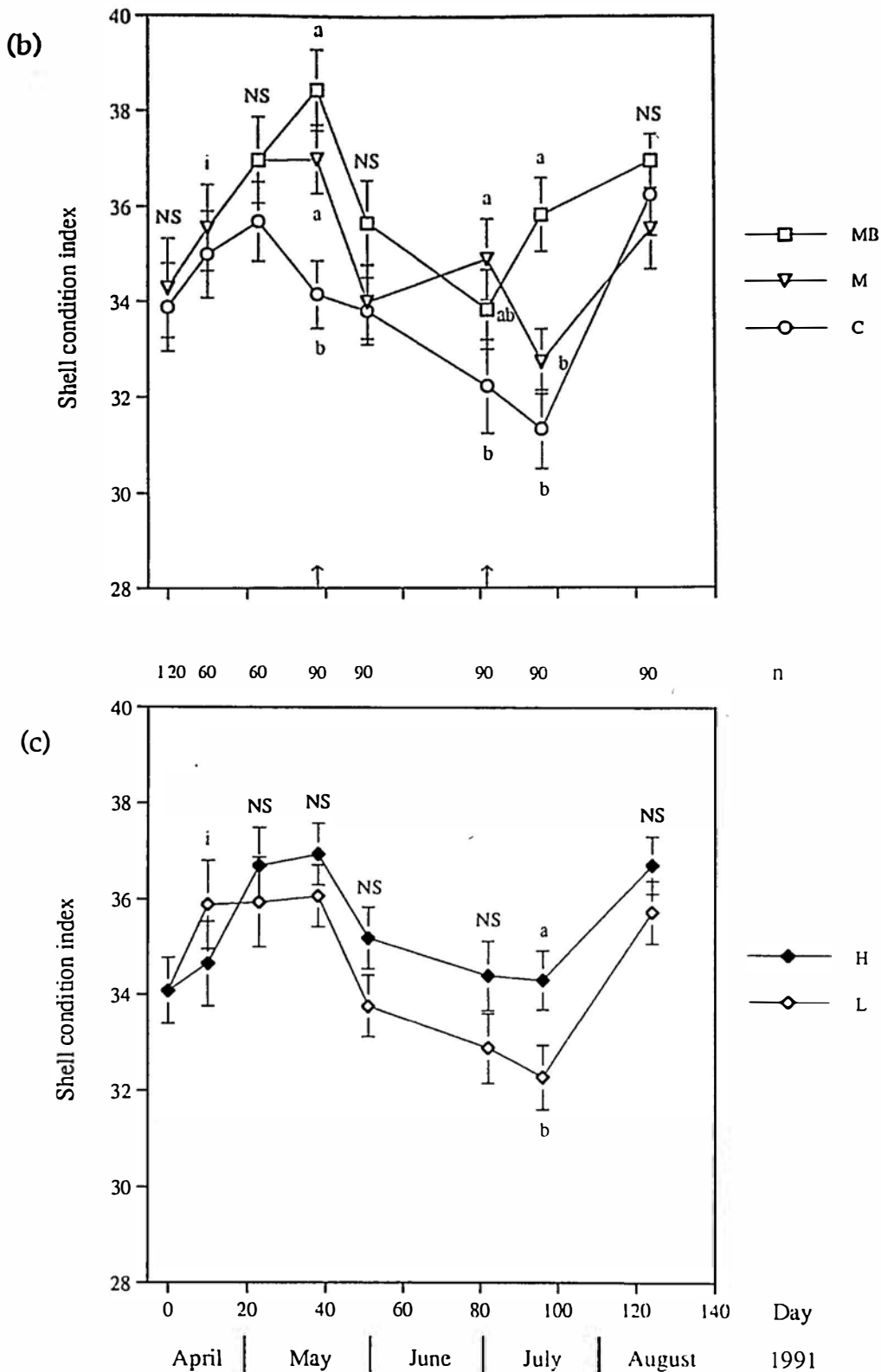


Fig. 23a. Effects of shell abrasion and aerial exposure on the mean shell condition index (CI_{shell}) of Pacific oysters (*C. gigas*) in Experiment 2. There was a significant interaction ($P < 0.05$) on day 10, and pairwise comparisons (Fisher's LSD) are shown [means which share common letters do not differ significantly ($P > 0.05$)]. MB, machine-graded once and baskets were shaken on days 38 and 82 (shown by arrows); M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; s.e., pooled standard error; n, sample number.



Figs. 23b-c. Effects of shell abrasion (b) and aerial exposure (c) on the mean shell condition index (CI_{shell}) of Pacific oysters (*C. gigas*) in Experiment 2 (means \pm s.e.). NS, for the same sample, means do not differ significantly ($P > 0.05$); the letters a, b indicate that means differ significantly ($P < 0.05$); i, for this sample a significant interaction (Fig. 23a) prevented statistical comparisons of means based on pooling. MB, machine-graded once and baskets shaken on days 38 and 82 (shown by arrows); M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number.

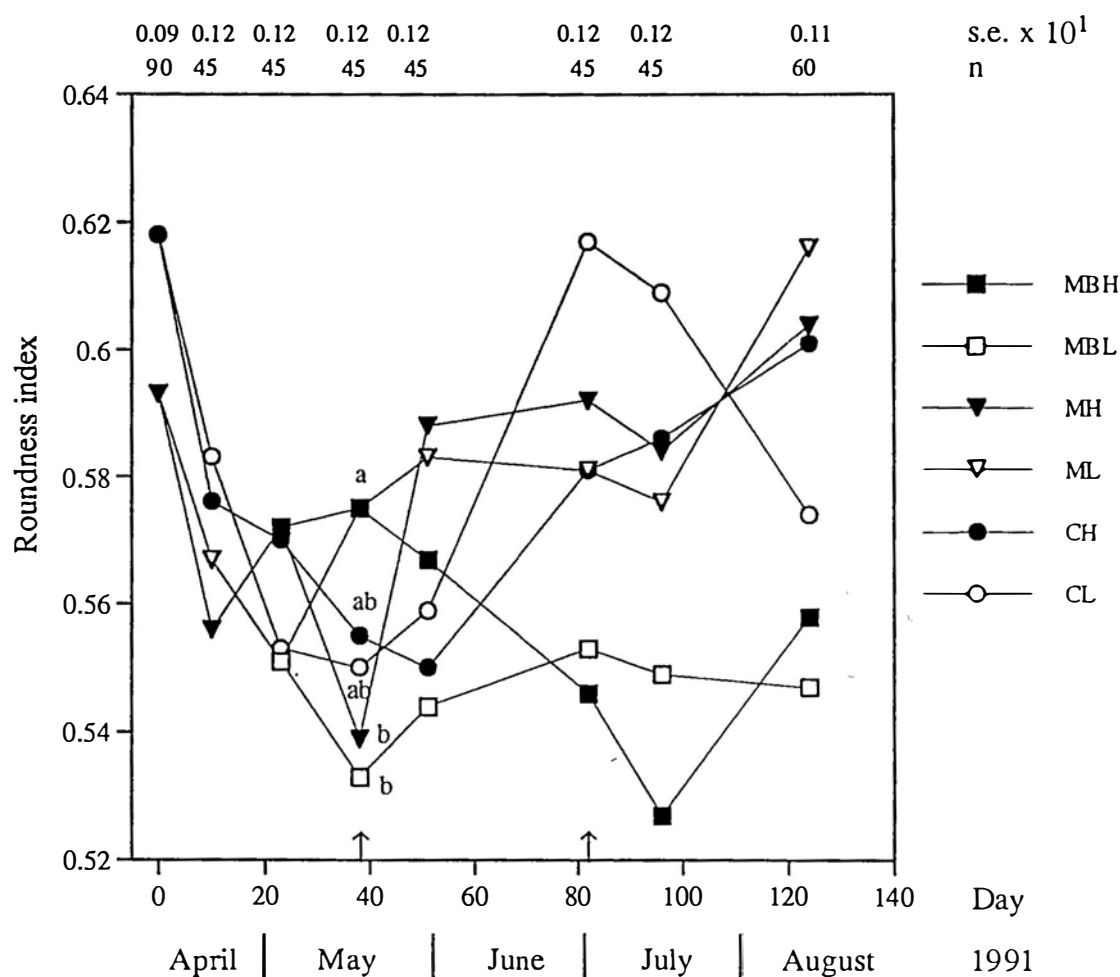
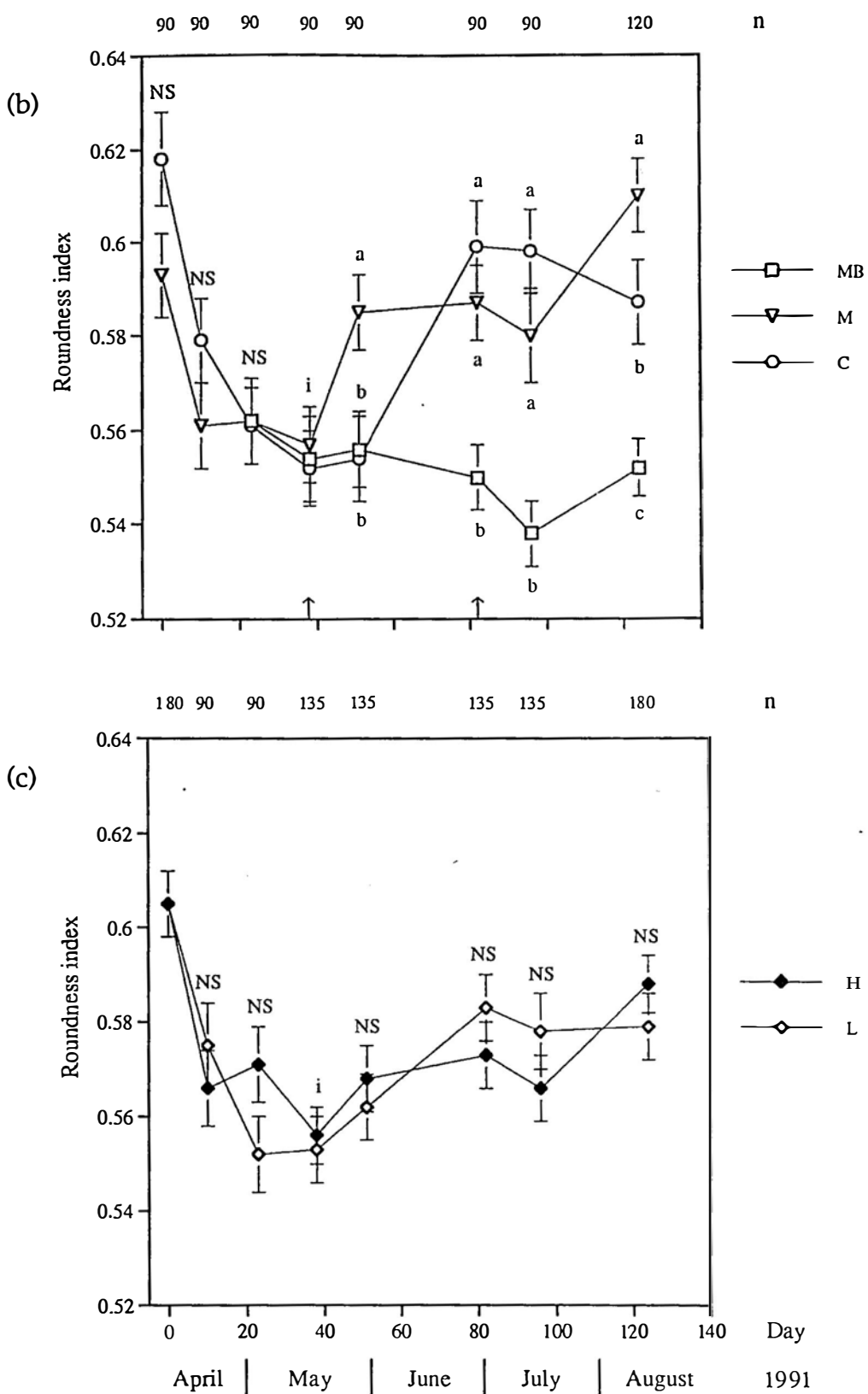


Fig. 24a. Effects of shell abrasion and aerial exposure on the mean roundness index (CIshell) of Pacific oysters (*C. gigas*) in Experiment 2. There was a significant interaction ($P < 0.05$) on day 38, and pairwise comparisons (Fisher's LSD) are shown [means which share common letters do not differ significantly ($P > 0.05$)]. MB, machine-graded once and baskets were shaken on days 38 and 82 (shown by arrows); M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; s.e., pooled standard error; n, sample number.



Figs. 24b-c. Effects of shell abrasion (b) and aerial exposure (c) on the mean roundness index (CIshell) of Pacific oysters (*C. gigas*) in Experiment 2 (means \pm s.e.). NS, for the same sample, means do not differ significantly ($P > 0.05$); the letters a, b, c indicate that means differ significantly ($P < 0.05$); i, for this sample a significant interaction (Fig. 24a) prevented statistical comparisons of means based on pooling. MB, machine-graded once and baskets shaken on days 38 and 82 (shown by arrows); M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number.

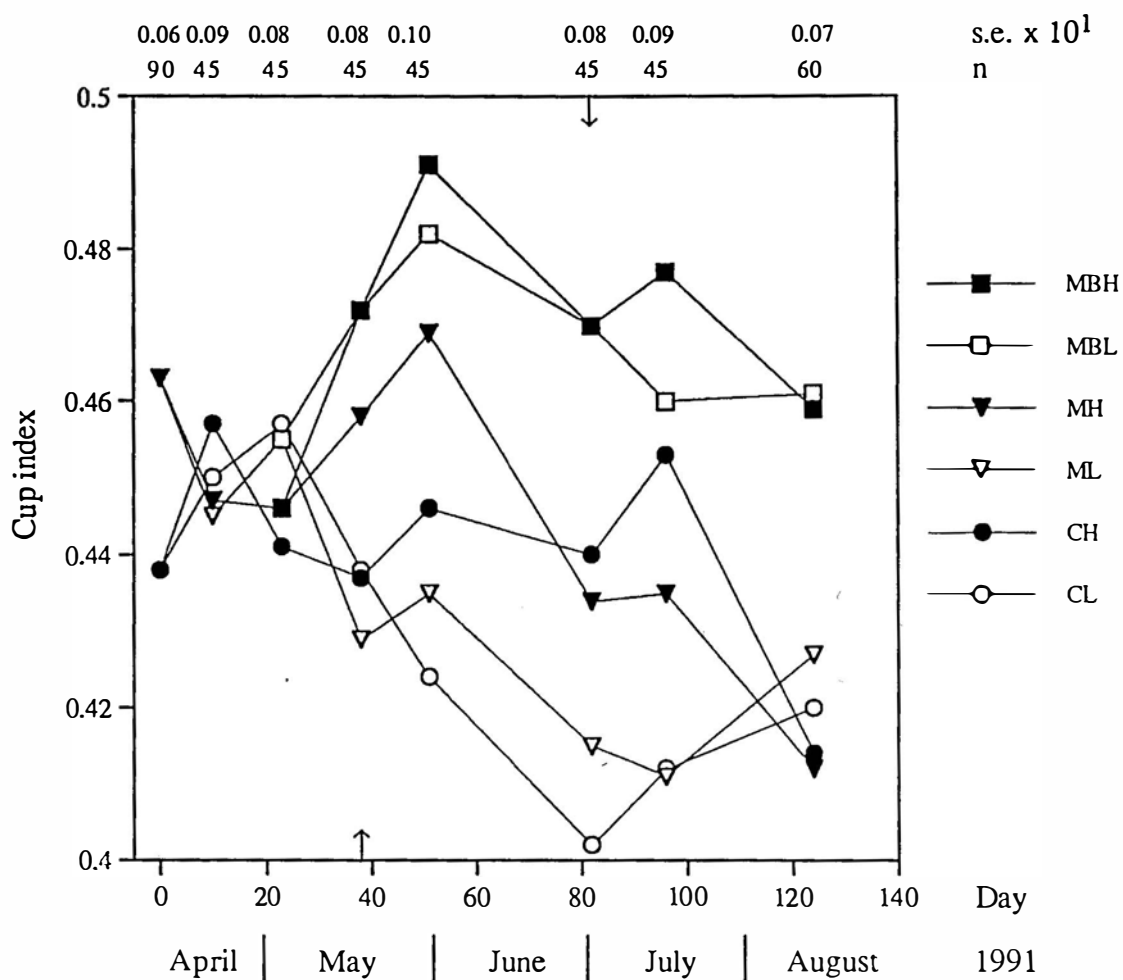
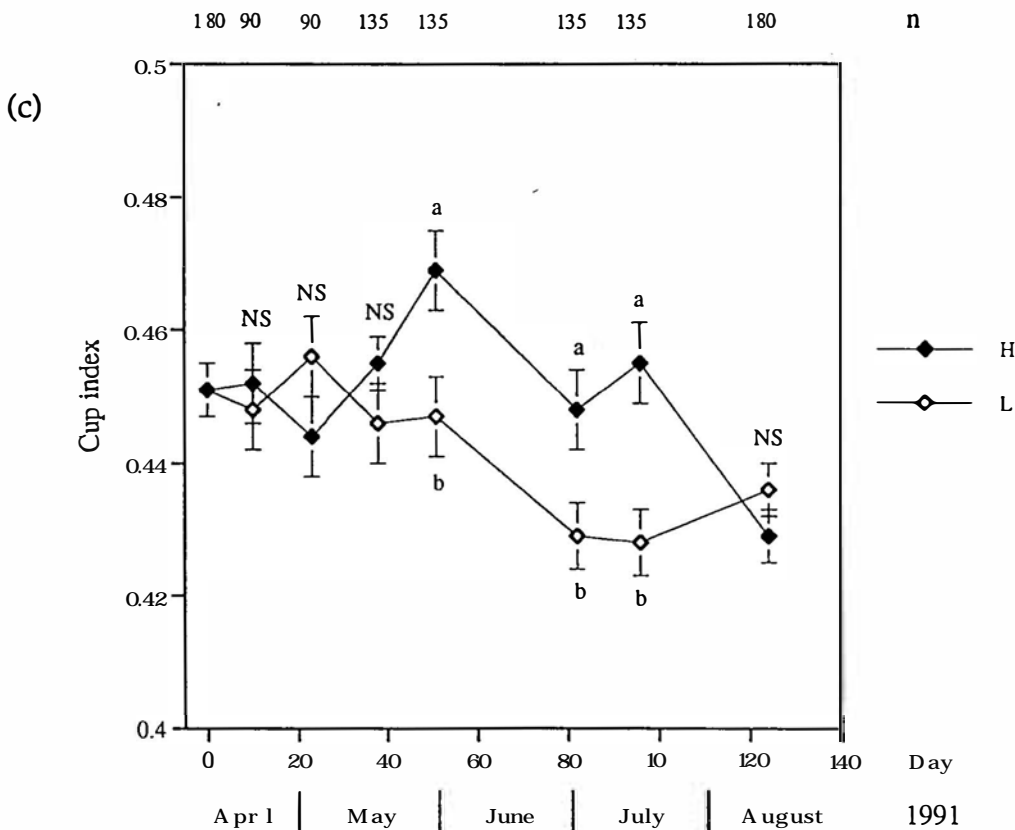
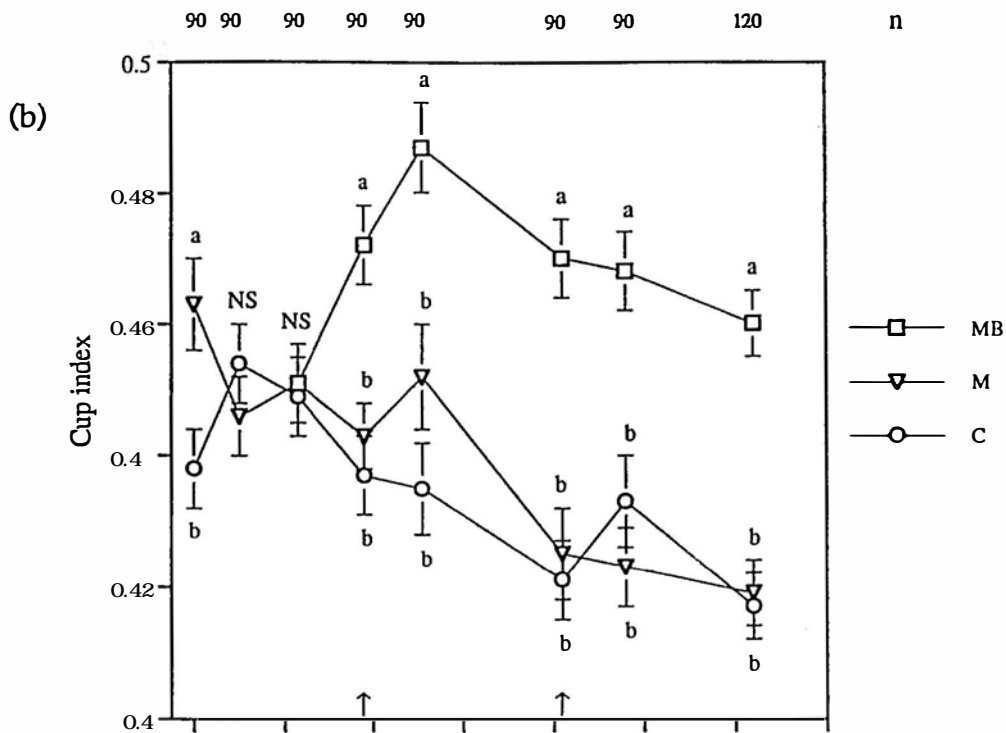


Fig. 25a. Effects of shell abrasion and aerial exposure on the mean cup index of Pacific oysters (*C. gigas*) in Experiment 2. MB, machine-graded once and baskets were shaken on days 38 and 82 (shown by arrows); M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; s.e., pooled standard error; n, sample number.



Figs. 25b-c. Effects of shell abrasion (b) and aerial exposure (c) on the mean cup index of Pacific oysters (*C. gigas*) in Experiment 2 (means \pm s.e.). NS, for the same sample date, means do not differ significantly ($P > 0.05$); the letters a, b indicate that means differ significantly ($P < 0.05$). MB, machine-graded once and baskets shaken twice on days 38 and 82 (shown by arrows); M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number.

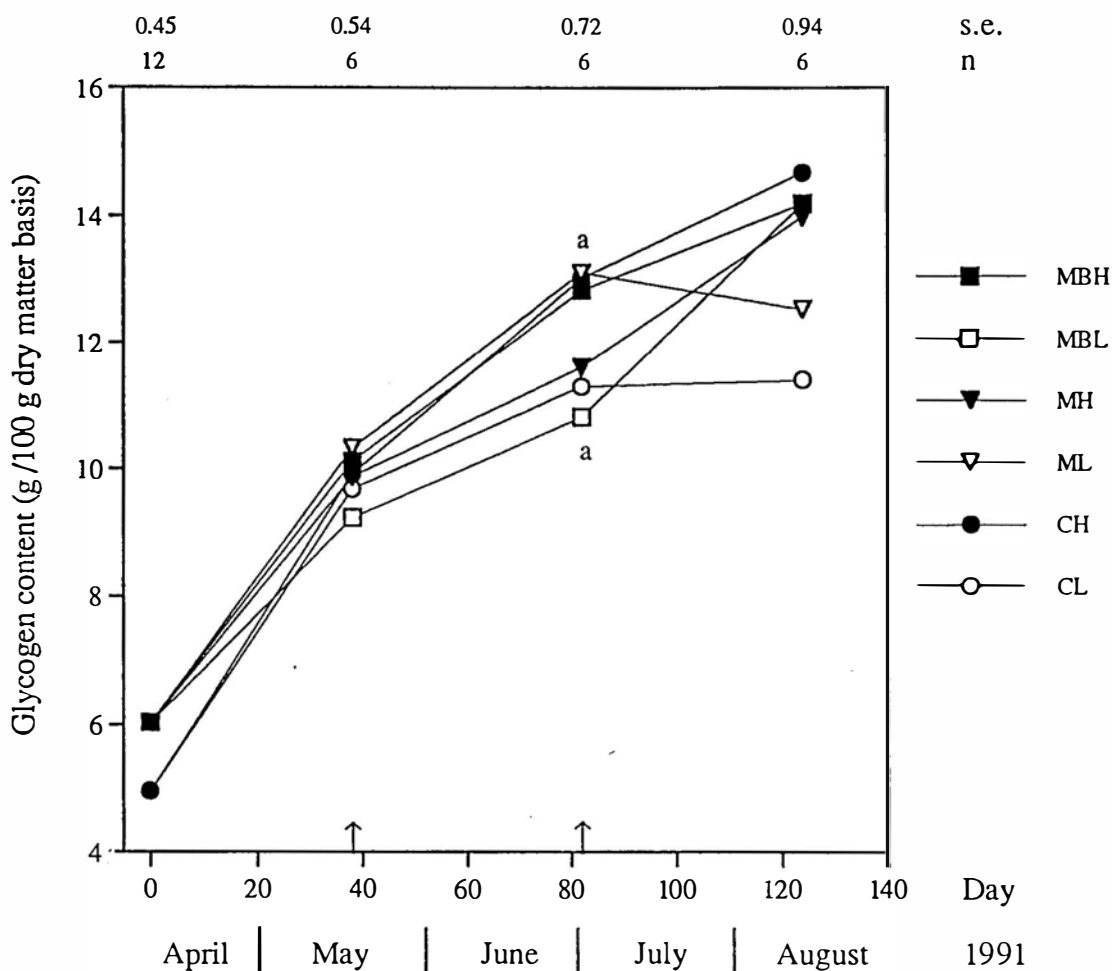
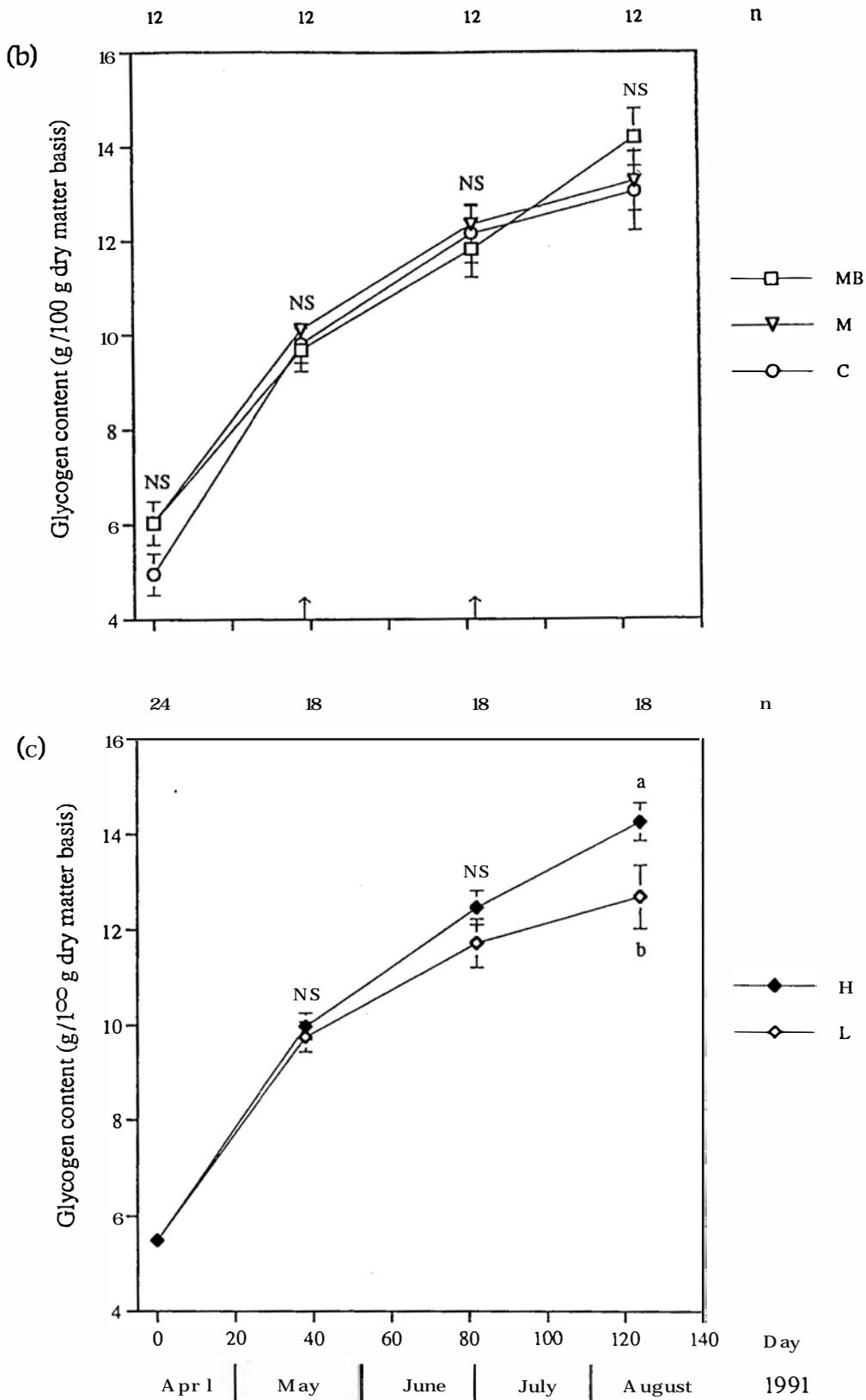


Fig. 26a. Effects of shell abrasion and aerial exposure on the mean glycogen content of Pacific oysters (*C. gigas*) in Experiment 2. There was a significant interaction ($P < 0.05$) on day 82, and pairwise comparisons (Fisher's LSD) are shown [means which share common letters do not differ significantly ($P > 0.05$)]. MB, machine-graded once and baskets were shaken on days 38 and 82 (shown by arrows); M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; s.e., pooled standard error; n, sample number.



Figs. 26b-c. Effects of shell abrasion (b) and aerial exposure (c) on the mean glycogen content of Pacific oysters (*C. gigas*) in Experiment 2 (means \pm s.e.). NS, for the same sample, means do not differ significantly ($P>0.05$); the letters a, b indicate that means differ significantly ($P<0.05$); i, for this sample a significant interaction (Fig. 26a) prevented statistical comparisons of means based on pooling. MB, machine-graded once and baskets shaken on days 38 and 82 (shown by arrows); M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number.

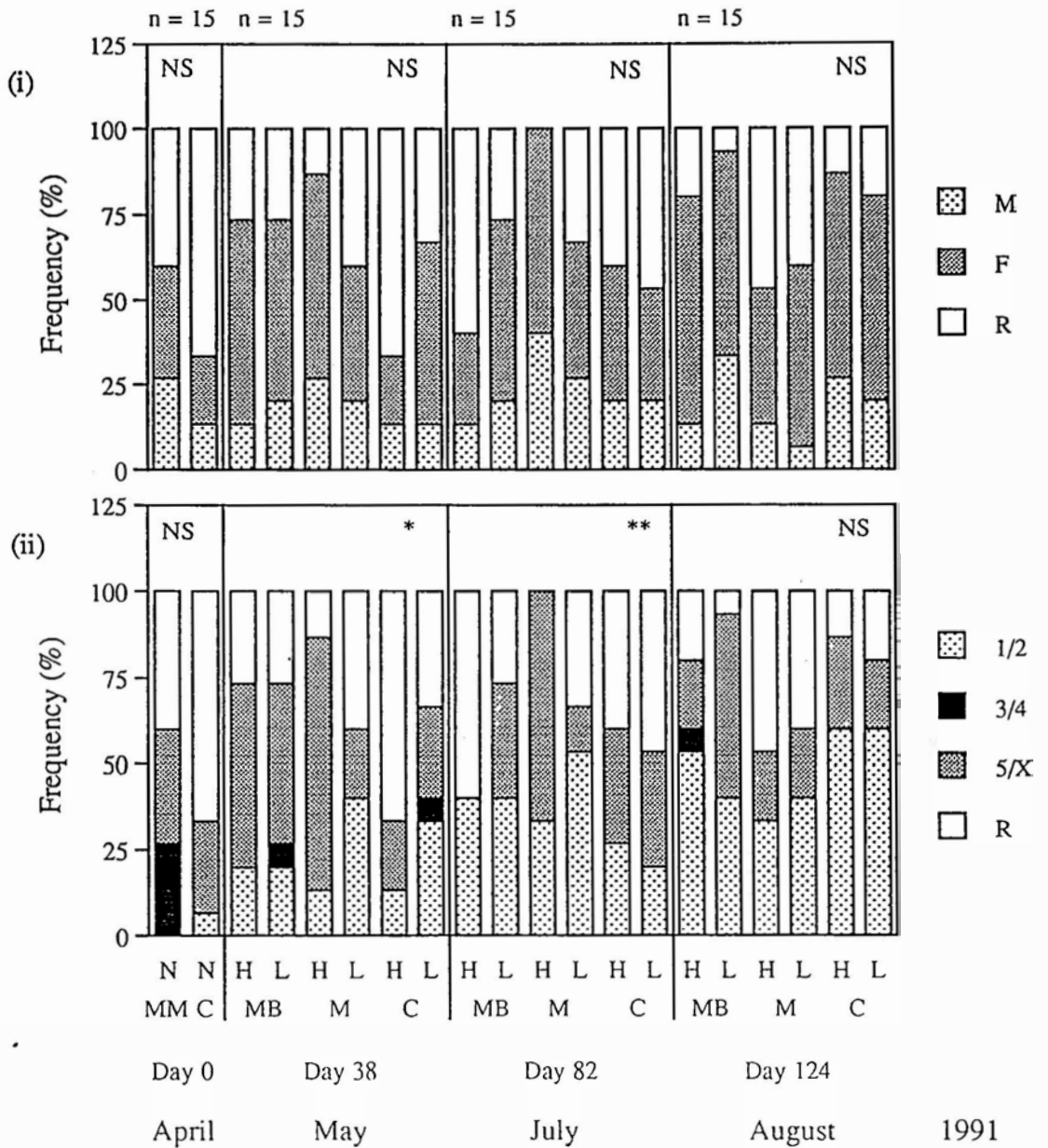


Fig. 27a. Effects of shell abrasion and aerial exposure on the sex group (i) and gonad stage (ii) of Pacific oysters (*C. gigas*) in Experiment 2. (i) M, male; F, female; R, regressed (sex group is indeterminate). (ii) 1/2, ripening; 3/4, ripe; 5/X, post-spawned; R, regressed. MB, machine-graded once and baskets were shaken on days 38 and 82; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number. NS, the null hypothesis of independence is retained ($P > 0.05$); * = $P < 0.05$; ** = $P < 0.01$.

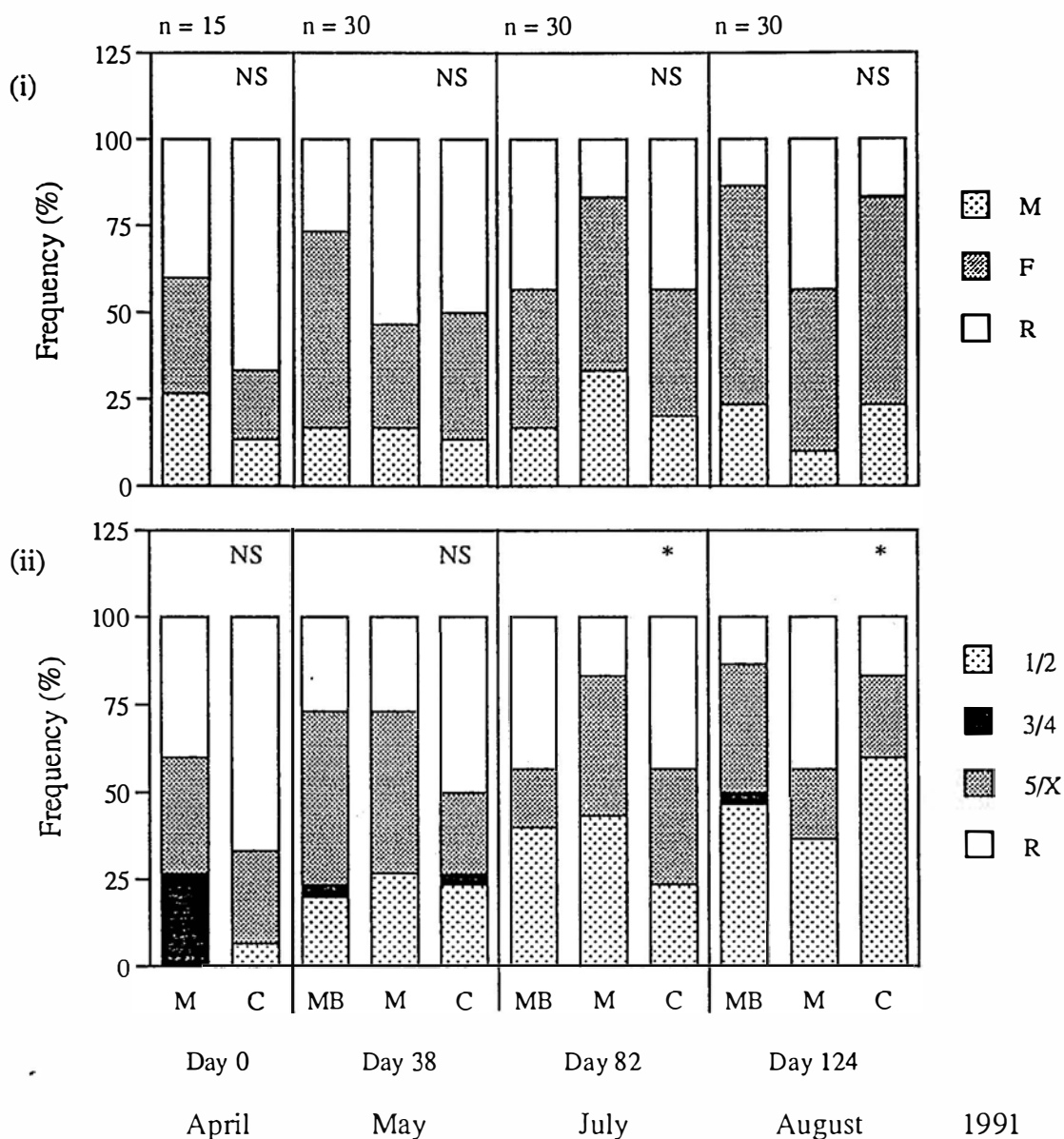


Fig. 27b. Effects of shell abrasion on the sex group (i) and gonad stage (ii) of Pacific oysters (*C. gigas*) in Experiment 2. (i) M, male; F, female; R, regressed (sex group is indeterminate). (ii) 1/2, ripening; 3/4, ripe; 5/X, post-spawned; R, regressed. MB, machine-graded once and baskets were shaken on days 38 and 82; M, machine-graded once; C, control; n, sample number. NS, the null hypothesis of independence is retained ($P>0.05$); * = $P<0.05$.

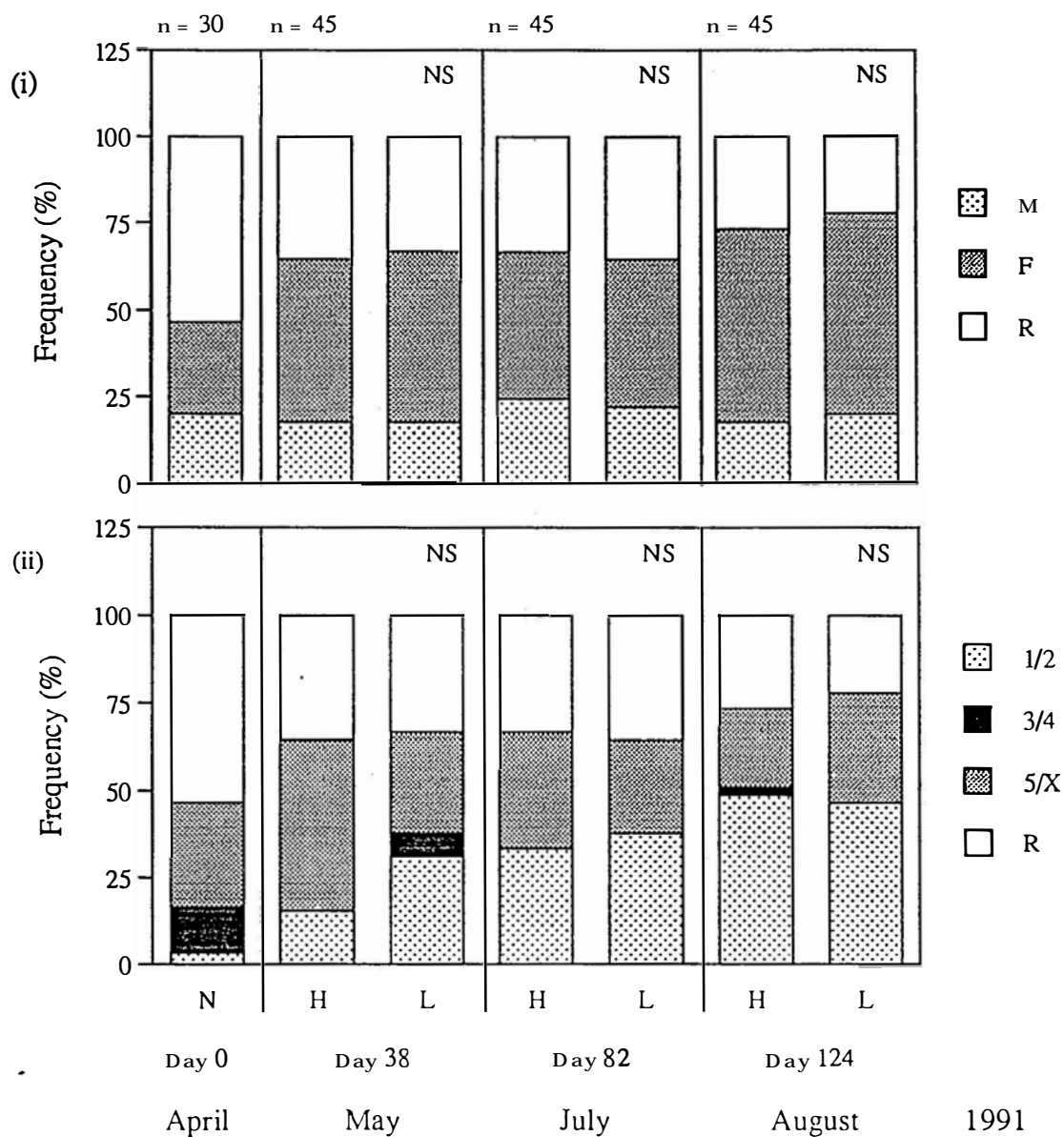


Fig. 27c. Effects of aerial exposure on the sex group (i) and gonad stage (ii) of Pacific oysters (*C. gigas*) in Experiment 2. (i) M, male; F, female; R, regressed (sex group is indeterminate). (ii): 1/2, ripening; 3/4, ripe; 5/X, post-spawned; R, regressed. H, high aerial exposure; L, low aerial exposure; n, sample number. NS, the null hypothesis of independence is retained ($P > 0.05$).

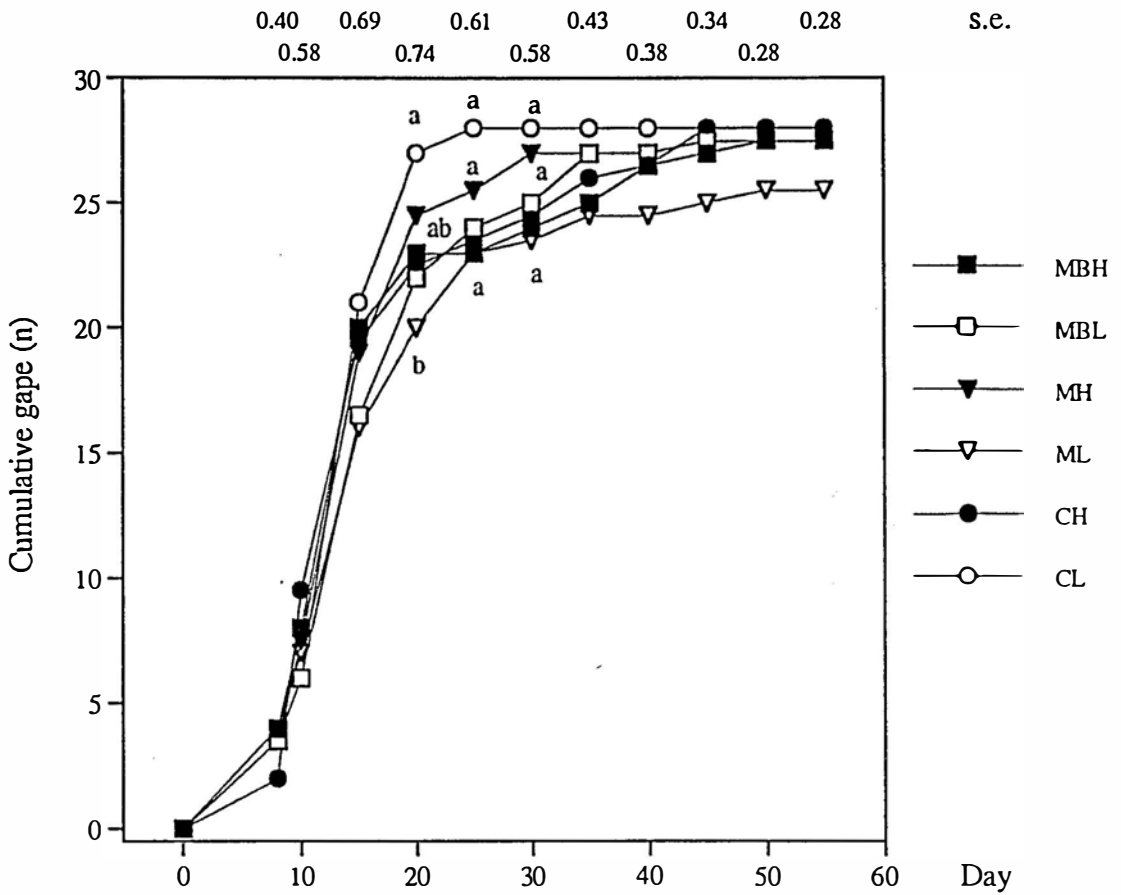
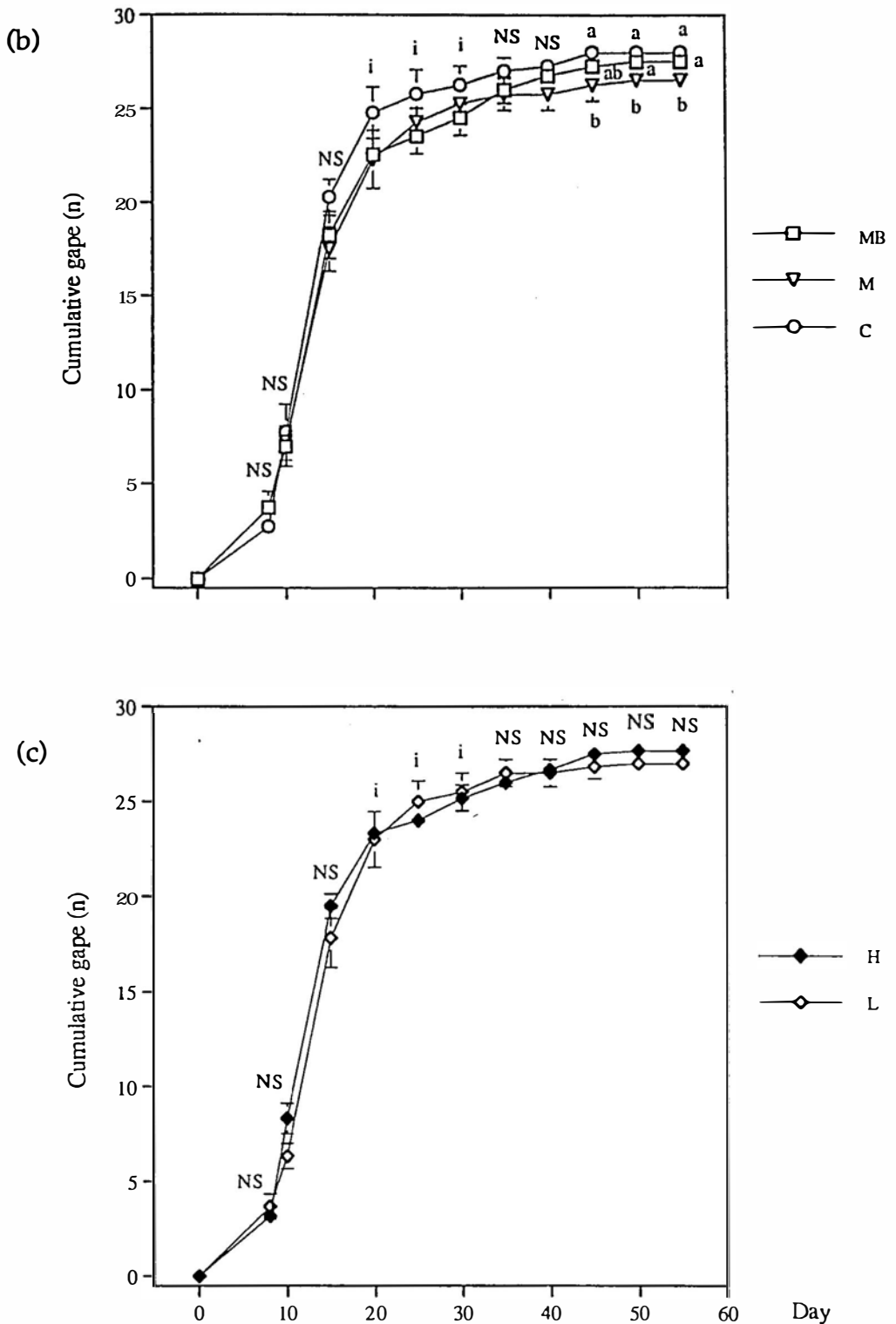


Fig. 28a. Effects of shell abrasion and aerial exposure on the mean cumulative gape of groups of 30 Pacific oysters (*C. gigas*) from Experiment 2, held in air (14°C, 94% humidity). There were significant interactions ($P < 0.05$) on days 20, 25 and 30, and pairwise comparisons (Fisher's LSD) are shown [means which share common letters do not differ significantly ($P > 0.05$)]. MB, machine-graded once and baskets were shaken on days 38 and 82; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; s.e., pooled standard error; n, sample number.



Figs. 28b-c. Effects of shell abrasion (b) and aerial exposure (c) on the mean cumulative gape of groups of 30 Pacific oysters (*C. gigas*) from Experiment 2, held in air (14°C, 94% humidity) (means \pm s.e.). NS, for the same sample, means do not differ significantly ($P>0.05$); the letters a, b indicate that means differ significantly ($P<0.05$); i, for these samples a significant interaction (Fig. 28a) prevented statistical comparisons of means based on pooling. MB, machine-graded once and baskets shaken on days 38 and 82; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number.

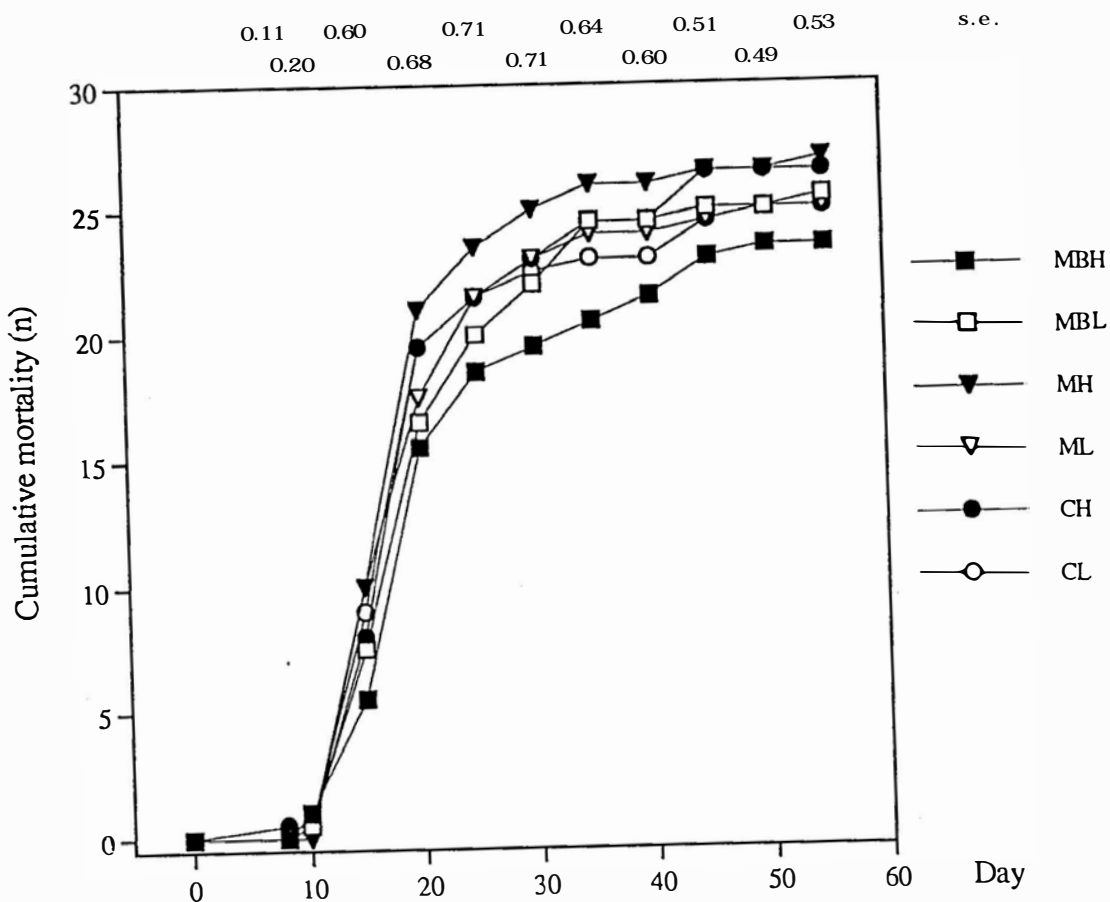
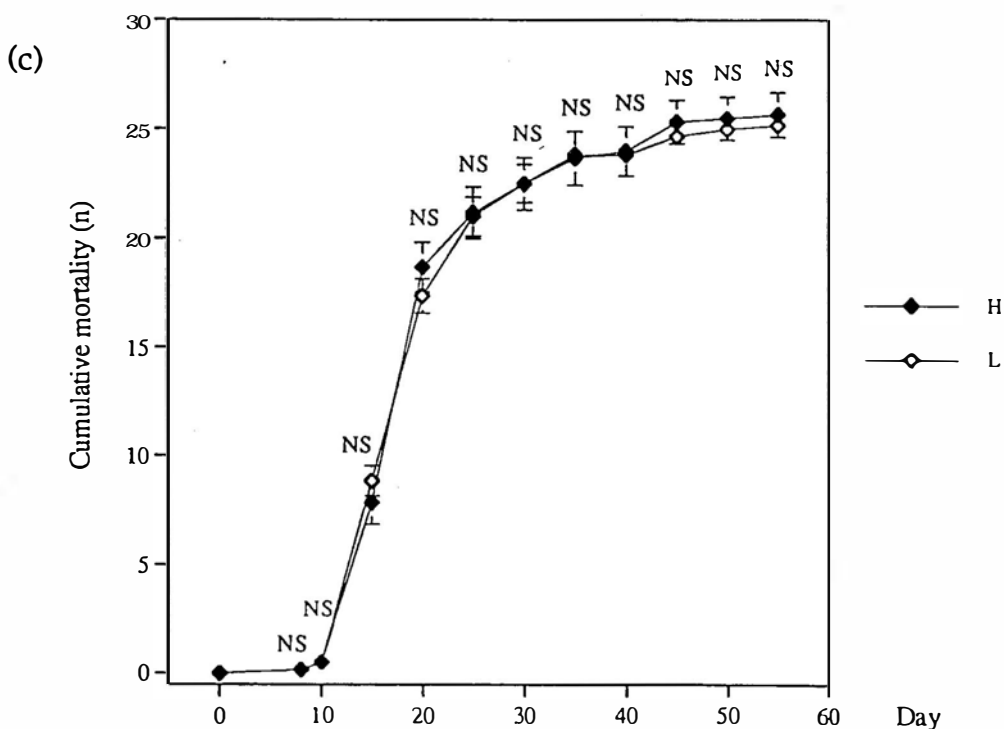
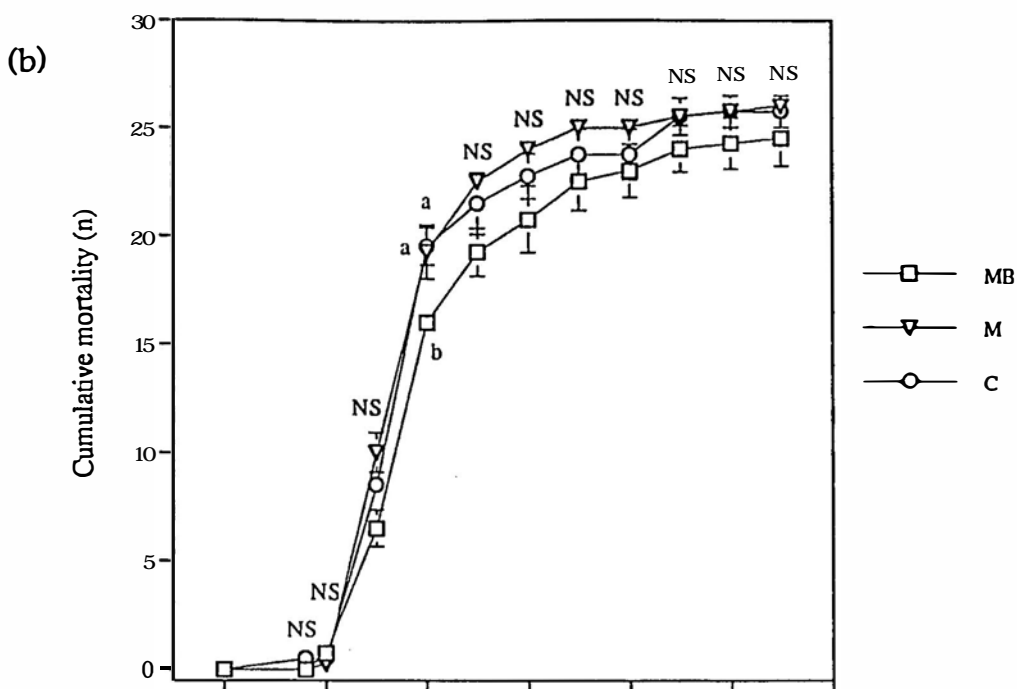


Fig. 29a. Effects of shell abrasion and aerial exposure on the mean cumulative mortality groups of 30 Pacific oysters (*C. gigas*) from Experiment 2, held in air (14°C, 94% humidity). MB, machine-graded once and baskets were shaken on days 38 and 82; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; s.e., pooled standard error; n, sample number.



Figs. 29b-c. Effects of shell abrasion (b) and aerial exposure (c) on the mean cumulative mortality of groups of 30 Pacific oysters (*C. gigas*) from Experiment 2, held in air (14°C, 94% humidity) (means \pm s.e.). NS, for the same sample, means do not differ significantly ($P > 0.05$); the letters a, b indicate that means differ significantly ($P < 0.05$). MB, machine-graded once and baskets shaken on days 38 and 82; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number.

4. Discussion

4.1 Survival

The high survival of >97% shown in Experiments 1 and 2 compares well to a study by Maguire et al. (1994b), who found that diploid and triploid Pacific oysters cultured in favourable sites in Tasmania experience negligible mortality (<1%) over a 2 year period. Even at a poor site, the mortalities were still only found to be 0.3 and 1.0% per month for diploids and triploids, respectively (Maguire et al., 1994b). The low incidence of mudworm (spionid polychaetes) (Skeel, 1979) and the use of mesh enclosures, which provide predator protection, are likely to have contributed to the high survival (King, 1977; Spencer, 1990).

The high survival rates of Pacific oysters cultured in Tasmania have been shown to be a key factor in the profitability of this industry (Treadwell et al., 1991). In contrast, in the other major Australian oyster industry based on Sydney rock oysters (*S. commercialis*), high mortalities occur often. In one study, the percentage mortality of Sydney rock oysters cultured in Salamander Bay, N.S.W., was reported to be 21.5% over a 2.5 year period (Nell et al., 1994).

Pacific oysters cultured in sea-based trays in the U.K. can be expected to have annual mortality rates of between 10-15% (Hall, 1984). However, the market size in the U.K. is larger (75 g/oyster; Spencer, 1990; Spencer et al., 1992) than those sold in Tasmania (>60 g/oyster; Maguire et al., 1994b), and it takes a longer time to reach market size in the U.K. (≤ 4 years) (Spencer et al., 1992), compared to 18 months to 3 years in Tasmania (Maguire et al., 1994b; G. Maguire, pers. comm., 1995). Thus these annual mortality rates can mean great losses overall in the U.K. For instance, Spencer et al. (1992) reported that the survival of Pacific oysters cultured to market size in intertidal trays (about 5% exposure d^{-1}), which took about 3.3 years, was 49%.

Survival was not affected by the shell abrasion treatments used in this study. In contrast, Spencer et al. (1992) found that for Pacific oysters, mortality could range from 0-100% (read from Fig. 4), depending on the harshness of the treatment applied. The trials carried out by Spencer et al. (1992) were extensive, and included 13 'rough-handling' treatments

performed at about monthly intervals, during two growing seasons in the Northern hemisphere (Table 3). The oysters were kept at an exposure level of about 5% exposure d⁻¹ (Spencer et al., 1992). The treatments were applied to duplicate batches of 50 Pacific oysters as they grew from an initial mean size of 0.2 g (mean shell height = 12.5 mm) through to a final size of 38-92 g. Additionally, they also tested the effect of applying these treatments within 2 or 26 h after collection.

TABLE 3

Rough-handling treatments used on Pacific oysters (*C. gigas*) by Spencer et al. (1992). Treatments were applied on five occasions between May and November, 1988, and on nine occasions between March and December, 1989.

- Agitation ¹ in air, for 1 or 2 min;
- Agitation¹ in water, for 1 or 2 min;
- Pressure hosing at 60 kg cm⁻² from 0.5 m above, for 1 or 2 min;
- Pressure hosing at 120 kg cm⁻² from 0.5 m above, for 1 or 2 min;
- Dropping oysters onto concrete from 0.5 or 1.0 m above;
- Dropping oysters onto other oysters from 0.5 or 1.0 m above ; and
- No treatment (control).

¹ Simulated grading was accomplished by placing the oysters in a tray (44 x 33 x 5 cm deep), with a rigid, 6 mm plastic mesh base and top. An electric motor-driven shaking device induced a reciprocating vertical lift of 2-3 cm at a frequency of 360 times per minute.

The results of Spencer et al. (1992) are discussed in detail for two reasons; one is that this is the most comprehensive study carried out in respect to the effects of shell abrasion ('rough-handling') of Pacific oysters, and the other is that some of their results, contrast strongly with this study. It is assumed that the rough-handling trials that they carried out did cause shell abrasion, but this cannot be confirmed because they did not report the immediate changes in shell dimensions, induced by the treatments. They did indicate that agitation in air for 1 or 2 min caused average losses in whole weight of 5 and 7%, respectively, for 4-8 g oysters; however, Spencer et al. (1992) noted that the losses could include surface moisture, shell and cavity fluid.

By the final sample (20 months), Spencer et al. (1992) found that survival of the Pacific oysters ranged between 60-100% for most treatments, except where pressure-hosing was applied incorrectly. In this case, the distance between the nozzle end and the oysters was less than the experimental

between the nozzle end and the oysters was less than the experimental treatment distance of 0.5 m, and survival was as low as 0% (Spencer et al., 1992). Excluding the pressure-hosing treatments, oysters agitated in air for 1 or 2 min, and oysters dropped onto concrete from 0.5 or 1 m, had the next lowest percentage survival compared to controls (read from Fig. 4 in Spencer et al., 1992). Table 4 shows the Spencer et al. (1992) results for several treatments, including agitation in water. It is obvious that the survival of oysters (9-19%), left out of water overnight (for up to 26 h), and then agitated in air for 2 min, was extremely low compared to the other treatments. Spencer et al. (1992) did not, however, attempt to explain the contrasting results between the relatively high survival (70-75%) of oysters agitated in air for 1 min compared to those agitated for 2 min, within 26 h after collection. Many Tasmanian farmers regularly leave Pacific oysters on land overnight before grading them the next day, as was done in this study (for 27-28 h), and survival appears not to be affected (C. Dyke, pers. comm., 1990). In the absence of statistical analysis of survival data by Spencer et al. (1992), the only conclusion that can be drawn with confidence is that agitation in air for 2 min, within 26 h after collection of oysters, severely depressed survival.

TABLE 4

Percentage survival after 20 months, of Pacific oysters (*C. gigas*) subjected to agitation¹ in air or water, for 1 or 2 min, dropped onto concrete from 0.5 or 1 m above, and no treatment (control), in the Spencer et al. (1992) study. Treatments were applied within either 2 or 26 h after collection. The figures are approximate and were read from Fig. 4 in Spencer et al. (1992).

Treatment	Within 2 h after collection	Within 26 h after collection
Agitation in air for 1 min	70-88	70-75
Agitation in air for 2 min	68-77	9-19
Agitation in water for 1 min	85-92	90-95
Agitation in water for 2 min	85-95	85-100
Dropping onto concrete from 0.5 m above	75-90	93-95
Dropping onto concrete from 1.0 m above	60-95	97-100
No treatment (control)	90-95	83-98

¹ Simulated grading was accomplished by placing the oysters in a tray (44 x 33 x 5 cm deep), with a rigid, 6 mm plastic mesh base and top. An electric motor-driven shaking device induced a reciprocating vertical lift of 2-3 cm at a frequency of 360 times per minute.

Intuitively, it might be expected that small oysters would be more prone to mortality when subjected to shell abrasion treatments. For instance, to help limit shell damage in Pacific oyster spat (<20 mm), Tasmanian farmers usually grade them in water (O'Meley, 1992). The Spencer et al. (1992) study showed, however, that survival (Fig. 7) of small oysters (<17g; read from Fig. 6) subjected to five agitation in air treatments, for 2 min, between May - November 1988, was largely unaffected. Mortality increased dramatically as oysters reached a larger size and were subjected to a total of nine treatments during May - November 1989. In May 1989, survival was 88% (mean whole weight = 22 g; read from Fig. 6), but by November 1989, only 22% were left (mean whole weight = 51 g; read from Fig. 6)*.

Spencer et al. (1992) did not attempt to explain the disparity in survival of small, compared to large oysters. However, it appears that small oysters were subjected to shell abrasion treatments, on average every 36 days. In comparison, larger oysters were subjected to abrasion treatments on average every 20 days. Despite the fact that shell losses are repaired quickly (Loosanoff and Nomejko, 1955; Bahr and Hillman, 1967; Smith, 1994), it may be that the large oysters were not given the chance to fully repair their shell, before more was removed. For instance, Smith (1994) considered that 1 month was an adequate time period for there to be a measurable difference (during summer) in shell growth of Pacific oysters, after shell frill removal (8 mm). Since these oysters were continually repairing shell, this must have had some, if not a large, metabolic cost. For instance it is known that shell growth accounts for about one third of the total energy expenditure of growth (Dame, 1972; Wilbur and Saleuddin, 1983; Brown and Hartwick, 1988b). Additionally, in the northern hemisphere the months May - November, correspond to the summer and autumn spawning seasons of Pacific oysters (Quayle, 1988; Sumner, 1980a, b). In the second year of Spencer et al. (1992) study, the oysters should have reached maturity, and the subsequent costs of gametogenesis, spawning, and recovery (Gabbott, 1975; Mann, 1978; Quayle, 1988), may also have affected survival (Quayle, 1988). The Pacific oysters in the present study had also reached maturity by the start of the experiments (see Sections 3.2.6, 3.4.6), and were quite large; on

*It should be noted, however, that in using these data, that survival percentages taken from Fig. 7 in Spencer et al. (1992) were related to treatments carried out 26 h of collection, whereas mean whole weights read from Fig. 6, were for treatments carried out 2 h after collection.

average 30 and 28 g, in Experiments 1 and 2, respectively. While the effects of agitation on oyster survival in the Spencer et al. (1992) study have been related to oyster size, it also should be noted that adverse effects could be accumulative and not just related to the sensitivity of different size oysters.

Robert et al. (1993) compared the growth and survival of Pacific oysters cultured in rotational cylinders to those in stationary mesh bags (controls), over a 14 month period. The cylinders caused shell abrasion, and therefore reduced shell height growth in comparison to controls (Robert et al., 1993; also see Section 4.2). They did not compare survival of the oysters in cylinders to those in bags, but stated that mortality was low (<10% and <5% in oysters with respective initial mean whole weights of 3 and 20 g) (Robert et al., 1993). Holliday et al. (1993a) also used rotational cylinders, to compare the effect of stocking densities (0.5-6.0 oysters cylinder⁻¹) on the growth and survival of Sydney rock oysters. Mortality after 3 months was reported to be 11.7 and 22.5%, respectively, for oysters with initial whole weights of 0.2 and 0.4 g (Holliday et al., 1993a). However, in a summary report written for N.S.W. farmers, Holliday et al. (1990) had earlier reported that survival of Sydney rock oyster spat in cylinders, was only 43.4% after 102 d, but even lower survival was reported for the spat enclosed in trays (24.5%). Clearly, the appropriateness of rotating cylinders may depend on site characteristics. In another report, Holliday et al. (1991b) found that it was unfavourable to stock Sydney rock oyster spat (mean whole weight = 0.09-1.56 g) at a very low density (1200 spat m⁻²) in sectionalised trays; wave action caused the oysters to move excessively in their sparsely stocked tray sections, to the extent that shell abrasion caused the spat to become ball-shaped in appearance with thick shell walls, but survival, after 12 months, was not affected by stocking density ($P>0.05$), however, and was very high (97.5%) (Holliday et al., 1991b).

This study and published results (Holliday et al., 1990, 1991b, 1993a; Robert et al., 1993) suggest that oysters are tolerant of shell abrasion. Spencer et al. (1992) showed, however, that high mortalities can result for abrasion treatments that are particularly harsh, that is, agitation in air for 2 min, within 26 h of collection of oysters. Spencer et al. (1992) noted that the shell structure of the oysters agitated in air had been affected with the outer layers becoming detached from the shell periodically during the trial. They also found that by the end of the study, a proportion (10%)

showed internal blistering of both valves, "presumably as a reaction to mechanical damage to flesh" (Spencer et al., 1992). Loosanoff and Nomejko (1955) suggested that mantle injury could slow the process of shell repair. In this study, only one out of 135 oysters had mantle tissue which was damaged. Also, Munday (pers. comm., 1995) found no evidence of significant damage to living tissues in a limited study of Tasmanian Pacific oysters which had been "rumbled". Thus it can be said that the shell abrasion treatments used in this study, and those typically used by Tasmanian farmers, are not, in general, harmful to Pacific oysters.

Survival was also not affected by the average daily aerial exposures (0-26%) tested in this study. Other author's have also shown that survival is largely unaffected in Pacific oysters held subtidally compared to 5% exposure (Spencer and Gough, 1978; Spencer et al., 1985), or at 10% compared to 40% (Pereya, 1961). However, it is known that extreme air temperatures can cause mortality in intertidal Pacific oysters (Kusuki, 1990; Spencer, 1990). For instance in South Australia, mortality of Pacific oysters was found to be dependent on growing height during hot weather in January and February 1993 (G. & S. Tonkin, pers. comm., 1995). By comparison, air temperatures in Tasmania are moderate (Sumner, 1980a) and are not likely to cause mortality.

4.2 Whole weight and shell growth

In Experiment 1, whole weight and dry shell weight growth, were slow initially before increasing linearly, after early June. In contrast, the growth of Experiment 2 oysters slowed after mid-May (Figs. 18, 20), suggesting a seasonal growth pattern. Sumner (1980a, b) reported seasonal growth patterns of Pacific oysters cultured at two Tasmanian sites, over 1.5-2 year periods. Maguire et al. (1994b) reported linear growth patterns over a 2 year period at two Tasmanian sites, while at a poor site, the growth patterns were seasonal, over a 3 year period. An explanation of the differences in growth patterns is beyond the scope of this study, however, since data from a wide range of environmental variables, at numerous sites, are needed to establish causal relationships (Brown and Hartwick, 1988a). Clearly the differences in temperature and salinity (Figs. 6, 17) between the two experiments, were not sufficient to

explain the occurrence of relatively linear growth in Experiment 1 and very fast initial growth followed by slow growth in Experiment 2.

Brown and Hartwick (1988a) established that the three major environmental variables affecting the growth of Pacific oysters, cultured subtidally, to be water temperature, food abundance and salinity. In this study, food abundance was not measured, but the oysters were sampled along the entire length of rack used to hold the basket enclosures, such that food availability should not have confounded the outcome of these experiments. The densities used reflected commercial practices (C. Dyke, pers. comm., 1990), and the glycogen levels in Experiment 2 oysters increased linearly (Fig. 26a), suggesting that food abundance was not always limiting upon growth. It has also been shown that Pacific oysters can have rapid shell and meat growth during periods of glycogen accumulation (Maguire et al., 1994b). For whatever reason(s), the poor growth during Experiment 2 coincided with poor growth in commercial stocks in Pipeclay Lagoon in 1991 compared to previous years (P. Chew, pers. comm., 1992).

Data in this study, and those read from Figs. 3 and 4 in Maguire et al. (1994b) for their Little Swanport and Pittwater sites, the latter of which is the closest to Pipeclay Lagoon, are compared in Table 5. These show that within the same time frames, the oysters attained similar sizes, in terms of their whole weight, shell height and dry shell weight (Table 5). Comparisons with other Tasmanian studies (Thomson, 1952; Sumner, 1980a, b) are complicated since attached rather than unattached oysters were used (Maguire et al., 1994b). Maguire et al. (1994b) reported, however, that the growth of Pacific oysters in Pittwater and in Pipeclay Lagoon, the latter of which was used to culture attached oysters in Sumner's (1980b) study, were similar.

The shell abrasion treatments applied on day 0 of Experiment 1 appeared to cause the MM group to become significantly smaller ($P < 0.05$) in whole weight and dry shell weight compared to the M group, but not when compared to the C group ($P > 0.05$) (Figs. 7b, 9b). Shell height results on day 0 were similar ($P > 0.05$) (Fig. 8b). Considering that few oysters had noticeable shell frill extensions prior to shell abrasion treatments being applied, and that the M group did not differ to that of the C group on the initial sample suggests that these results are most likely due to random variation rather than treatment effects. Overall, the abrasion treatments

TABLE 5

Growth rates of Pacific oysters (*C. gigas*) in this study compared to those cultured by Maguire et al. (1994b). [Mean comparisons are based upon the time it would have taken for the Pacific oysters in the Maguire et al. (1994b) study to reach the final mean whole weight, shell height, dry shell weight and dry meat weight of Pacific oysters in this study].

Site	Whole weight (g oyster ⁻¹)			Shell height (mm oyster ⁻¹)			Dry shell weight (g oyster ⁻¹)			Dry meat weight (g oyster ⁻¹)		
	Initial size (g)	g month ⁻¹	Time (months)	Initial size (mm)	mm month ⁻¹	Time (months)	Initial size (g)	g month ⁻¹	Time (months)	Initial size (g)	g month ⁻¹	Time (months)
Little Swanport ¹	27.7	4.0	2.5	65.1	2.1	2.5	15.9	2.9	2.5	0.60	0.26	2.5
Little Swanport ²	4.0		2.5		2.3	2.3		2.9	2.5		0.18	3.8
Pipeclay Lagoon ¹	30.4	3.4	4.0	65.4	2.9	4.0	16.9	2.9	4.0	0.58	0.11	4.0
Pittwater ²	3.8		3.6		2.6	4.5		2.7	4.4		0.15	3.1

¹ this study.

² data read from Figs. 3 and 4 in Maguire et al. (1994b).

³ Maguire et al. (1994b) did not oven dry the shells but superficially dried them at ambient temperature.

used in Experiment 1 did not affect ($P>0.05$) whole weight (Fig. 7b) or shell height (Fig. 8b) indices in later samples, and for most samples (five out of seven), the treatments did not affect ($P>0.05$) the dry shell weight (Fig. 9b) either.

In Experiment 2, despite the fact that there were few differences ($P>0.05$, most cases) in whole weight and dry shell weight due to shell abrasion, the general trend was $C \geq M \geq MB$ for the last five out of eight samples (Figs. 18b, 20b), while for shell height the trend was clearly $C, M > MB$ (Fig. 19b). This shows that shell abrasion can retard shell growth. The major differences between the control oysters in each experiment were the relatively large shell frills and flutes (shell extensions on the left valve) of Experiment 2 oysters, at the beginning of that trial. For example, marked M group oysters measured at the lease site, before and after grading, lost a mean of 3.3 ± 0.4 mm in shell height and 5.9 ± 1.0 mm in shell length ($n=13$) (Appendix E). In relation to the C group, the M group were 4.0 mm smaller ($P<0.05$) in shell height ($n=90$) (Fig. 19b), and the initial machine-grading also caused this group to be smaller than controls ($P<0.05$) for both whole and dry shell weights (Figs. 18b, 20b).

By day 10, however, the mean whole weights, and dry shell weights, of M and C groups were no longer significantly different ($P>0.05$) (Figs. 18b, 20b). Spencer et al. (1992) suggested that reductions in whole weight can be due to actual shell loss, water adhering to the shell, and loss of shell cavity fluids. After collection, all oysters in the present study were resuspended in seawater for at least 24 h before measurements took place, allowing them time to recover their shell cavity fluids. Additionally, a separate experiment showed that shell loss due to abrasion causes only small reductions ($P>0.05$) in whole weight (Appendix F). Therefore, the initial differences in whole weight between C and M groups, may have been due to water adhering under the shell frill and flutes of the ungraded C group oysters.

When half of the M group baskets were shaken in air on day 38, creating the MB group, neither the mean whole weight, or the dry shell weight of the oysters changed significantly ($P>0.05$) (Figs. 18b, 20b). Similarly, on day 82, shaking baskets did not significantly ($P>0.05$) change their mean whole weight, or dry shell weight in comparison to M and C groups (Figs. 18b, 20b). Appendix F supports these results because, and as noted above, Pacific oysters (initial whole weight = 76.5 ± 1.1 g, initial shell height =

93.2 \pm 0.9 mm, n=120) shaken in mesh baskets in air for 1 min, only lost 2.6% ($P>0.05$) of their whole weight. By the final sample, however, MB and M groups had smaller ($P<0.05$) whole weights than the C group (Figs. 18b), showing that adverse effects of grading on shell growth extend beyond initial loss.

Measurements of marked oysters showed that substantial shell frill was removed during shaking of baskets. On day 38, actual reductions in shell height and shell length were respectively 3.5 \pm 0.5 mm ($P>0.05$) and 2.5 \pm 0.4 mm ($P<0.05$) (n=29) (Appendix E). These reductions in shell height compare well to the results for the majority of oysters, on day 38. That is, the newly created MB group had become significantly smaller ($P<0.05$) in shell height (approximately 3.2 mm smaller) and length (approximately 2.1 mm smaller) (n=90) dimensions, compared to the M group, its predecessor (Figs. 19b, D-viii). Additional shell frill was removed from the MB group on day 82; reductions in shell height and shell length were 4.8 \pm 0.6 mm ($P>0.05$) and 3.2 \pm 0.5 mm ($P>0.05$) (n=29), respectively (Appendix E).

Clearly, the effect of shaking baskets on day 38 caused slower growth of the MB group compared to the M and C groups, and growth of the MB group was further retarded when the baskets were shaken again on day 82 (Figs. 19b, D-viii). It is interesting that the initial machine-grading of the M group did not restrict their growth in comparison to the C group (Fig. 19b). This suggests that shell abrasion treatments need to be applied regularly, for example every six weeks (MB group) during winter, and probably more often during the warmer months, if it is wished to hold back the shell growth of Pacific oysters cultured in Tasmania, using similar abrasion techniques to those used in these experiments.

In the Spencer et al. (1992) study, the weight losses measured immediately after rough-handling treatments were applied to small oysters (4-8 g mean whole weight), were reported to be small (1-2% for a range of treatments), but the agitation in air for 1 or 2 min treatment (using a simulated grader) caused mean weight losses of 5 and 7%, respectively (Spencer et al., 1992). When the oysters were larger (19-24 g mean whole weight) the weight losses were higher, and averaged 10 and 14% for oysters agitated in air for 1 or 2 min, respectively (Spencer et al., 1992). In comparison, this study has shown that machine-grading (in air) can cause whole weight losses of between 1-8%, in Pacific oysters, with

initial mean whole weights of 27-30 g (Figs. 7b, 18b). It may be that the higher weight losses in the Spencer et al. (1992) study, for similar sized oysters, were caused by the use of a simulated grader rather than a commercial grader, and perhaps longer treatment times (1 and 2 min) than used in the present study (approximately 0.5 min for oysters to come off the grader).

In the Spencer et al. (1992) study, the rough-handling treatments which caused Pacific oysters to have a significantly smaller ($P < 0.05$) mean whole weight compared to controls, after 20 months of culture, were agitation in air for 1 or 2 min (within 2 h or 26 h of collection), pressure hosing (120 kg cm^{-2}) applied incorrectly at less than 0.5 m (within 2 h of collection), and dropping oysters onto concrete from 1.0 m above (within 2 h of collection); however, in the agitation in air for 1 min treatment, and the latter two treatments listed, one out of the two replicates did not differ significantly ($P > 0.05$) from the controls (read from Fig. 3 in Spencer et al., 1992).

Of particular interest to this study, was that by the final sample in the Spencer et al. (1992) study, the mean whole weight of oysters agitated in air (simulated grading) for 1 min were 15% (within 2h) and 21% (within 26h) smaller, and oysters agitated in air for 2 min were 40% (within 2h) and 46% (within 26 h) smaller, than controls (mean whole weight = 80-86 g) (calculated from data read from Fig. 3 in Spencer et al., 1992). The MB group in this study were only 11% smaller compared to controls, by the final sample (Fig. 18b). The growth rate advantage of the control oysters in the Spencer et al. (1992) study, compared to those agitated in air for 1 or 2 min, 2 or 26 h within collection (shown in brackets), was 18% (1 min; 2h), 27% (1 min; 26h), 65% (2 min; 2 h) and 86% (2 min; 26h) (calculated from data read from Fig. 3 in Spencer et al., 1992). In comparison, Experiment 2 control oysters had only a 13% growth rate advantage, in terms of their whole weight, compared to the MB group (Fig. 18b).

Robert et al. (1993) compared the growth of Pacific oysters cultured in rotational cylinders fixed to intertidal horizontal metal frames, to those cultured in mesh bags (1m long x 0.5 m wide) held on 30 cm high trestles. Care was taken with respect to immersion time, such that the cylinders and bags were set at similar bathymetric levels, in the Bay of Arcachon, France (Robert et al., 1993). Two size groups of Pacific oysters ['spat', initial whole weight = 3 g (6-8 months old), and 'small oysters', initial

whole weight = 20g (18 months old)] were cultured for a period of 14 months (Robert et al., 1993). Additionally they carried out a fattening experiment, using 'large' Pacific oysters [initial whole weight = 65 g (24 months old)] cultured at densities of 150, 200 and 250 oysters cylinder⁻¹ compared to 150 oysters bag⁻¹, over a three month period during autumn (Robert et al., 1993). They reported that the whole weight growth of spat in bags was higher during their first year, but was not statistically significant by the final sample (Robert et al., 1993). Small oysters in cylinders exhibited slower whole weight growth rates, which by the final sample were statistically significant ($P=0.001$), while in the fattening experiment, which used larger oysters, few or no differences were seen in whole weight, between batches (Robert et al., 1993). In short Robert et al. (1993) found that cylinders can retard whole weight growth of small oysters, but that these have little or no effect on larger oysters.

Holliday et al. (1990), in a report written for N.S.W. farmers, compared the growth of Sydney rock oyster spat in rotational cylinders and sectionalised trays, and those attached to plastic discs. They reported that growth was significantly higher in trays than in cylinders, but that retention and survival of spat in cylinders was significantly higher than in trays (Holliday et al., 1990). It should be noted that the cylinder was constructed from 0.5 mm stainless steel mesh, rather than from plastic mesh; it is likely to be even more abrasive than plastic mesh. However, site characteristics could also have been influential.

For similar sized oysters (say 20-30 g), the shell abrasion treatments used in Experiment 2 of this study, had only a minor effect on whole weight growth (Fig. 18b), when compared to the Spencer et al. (1992) and Robert et al. (1993) results. This is most likely because there were fewer repetitive treatments i.e., the oysters were only handled 1-3 times, over a shorter time frame, in this study. For instance, Spencer et al. (1992) handled their oysters repeatedly, i.e., on 14 occasions over 19 months, while in the Robert et al. (1993) study, "the spat and oysters had been vigorously tumbled in cylinders resulting in severe shoot damage". It is certain, however, that the agitation in air for 2 min treatments used by Spencer et al. (1992) were far too harsh, since whole weight growth was severely retarded in those oysters.

For most samples in Experiment 2, there was no difference in the mean dry shell weight of shell-abraded oysters, but by the final sample, both MB

and M groups were significantly smaller ($P<0.05$) compared to the C group (Fig. 20b). Because the M group became 'suddenly' smaller than the C group, these differences were most likely due to random variation rather than treatment effects (Fig. 20b), and therefore, it can be said that shell abrasion in this study did not affect dry shell weight growth.

Robert et al. (1993) reported that 'spat' had similar dry shell weight growth patterns, whether in cylinders or bags. For 'small' oysters in cylinders, the lower whole weight was "partially explained by differences in dry shell weight but not in dry meat weight" (Robert et al., 1993). The results of their fattening experiment are difficult to interpret because Robert et al. (1993) did not present all their data. Robert et al. (1993) wrote, however, that 'large oysters' in cylinders at a density of 150 oysters cylinder⁻¹ exhibited a higher mean dry shell weight after 3 months of culture, but did not state whether this was in comparison to 200 oysters cylinder⁻¹, or 150 oysters bag⁻¹ (250 oysters cylinder⁻¹ were excluded from the discussion because they did not rotate normally).

Spencer et al. (1992) did not report final mean dry shell weights (or shell heights). Smith (1994), in New Zealand, cultured large Pacific oysters (initial mean shell height = 78.2 ± 5.3 mm s.d., $n=300$) in rotational and fixed, 'standard height' cylinders for a period of four months (as well as fixed lower cylinders set 30 cm above the substrate), and could find no consistent trends in their dry shell weight. It should be noted, that the oysters in rotational cylinders were exposed to air only during Extreme Low Water Neap (E.L.W.N.) tides, whereas those in standard cylinders, which will be used as the comparison for the present discussion, were at a standard rack height (1 m above the substrate), used to culture Pacific oysters on commercial leases (exposure levels were not measured) (Smith, 1994). Thus treatment effects in Smith's (1994) study could be due to differences in both aerial exposure and shell abrasion.

In Experiment 2, the general trend in mean shell height growth was $C, M > MB$, but by the final sample, MB and M groups were 9 and 6% smaller ($P<0.05$) compared to the C group (final mean shell height = 81 mm) (Fig. 19b). Smith (1994) reported that large Pacific oysters in rotational cylinders were significantly smaller ($P<0.0001$) in shell height, by the final sample (8% smaller; calculated from an average of two values read from Fig. 5.5a), compared to those in fixed, standard cylinders. In contrast, Robert et al. (1993) showed that the final mean shell height of

'spat' and 'small' Pacific oysters in rotational cylinders was significantly smaller ($P=0.001$) compared to the controls. In fact, the 'spat' in cylinders were 37% smaller (calculated from data read from Fig. 3a) compared to the controls (final mean shell height = 77 mm), by the final sample. Robert et al. (1993) did not report the final mean shell heights of 'large' oysters in their fattening experiment.

The unusual results obtained by Jakob and Wang (1994) for American oysters, where 'handled' oysters - counted and weighed while still attached to flexible plastic strips - on a bi-weekly basis, grew faster than those that were 'not handled' requires discussion. The handled and unhandled groups were kept in separate but unreplicated tanks, and hence the design was pseudoreplicated (Underwood, 1981). On a weekly basis, both tanks were drained and then the plastic strips to which all the oysters (0.2 g initial weight) were attached, were washed by hosing with fresh water. After 7 months in these tanks, the final mean whole weight of handled compared to unhandled oysters were respectively, 34.8 ± 2.2 g and 28.7 ± 2.7 g (mean \pm s.d., n not stated). Mortality was "fairly high" at 22% for oysters that were handled and 30% for the unhandled oysters. These results, however, are difficult to interpret for several reasons. I suggest that because both groups were regularly hosed with fresh water, that in fact both groups were handled, and that not only would the duration and intensity of hosing with freshwater (not reported) remove shell frill but the strips were flexible, thereby increasing the intensity of the treatment. Taking the work of Spencer et al. (1992) into account, the researchers, therefore, without having a prescribed time period, and water pressure, could have influenced the results.

Spencer et al. (1978) reported that differences of 4-9% aerial exposure are necessary to produce significant differences in the growth of Pacific oysters, depending on sampling intensity. In Experiment 2, the exposure levels (0 compared to 7% exposure d^{-1}) did not produce significantly different ($P>0.05$) mean whole weights, shell heights or shell weights, on any sample (Figs. 18c, 19c, 20c). Similarly, Walne and Davies (1977), and Spencer et al. (1978) found that between 0-10% exposure there are only small differences in the whole weight, shell weight and meat weight of Pacific oysters. In Experiment 1, however, levels of 0 compared to 26% exposure d^{-1} , caused the L group to grow much faster ($P<0.05$) than the H group, after day 42 (Figs. 7c, 8c, 9c). The growth rate advantages of the

L group compared to the H group, were for whole weight, shell height, and dry shell weight, 56%, 82% and 42%, respectively (Figs. 7c, 8c, 9c).

An interesting assertion not tested in this study, was that Spencer and Gough (1978) suggested that the point of no growth in Pacific oysters, in the U.K., occurs between 36-47% exposure. This level was later modified by Spencer (1990) to be at 35% exposure. Pereya (1961) reported that shell growth of Pacific oysters grown at 40% exposure in Puget Sound was reduced by 56% in comparison to those grown subtidally. In contrast, Maguire et al. (1994b) reported that Pacific oysters cultured at levels of up to 59% exposure, at one of the sites used in this study (Little Swanport), still grew rapidly.

In a summary prepared for oyster farmers Maguire and Kent (1991) reported, however, that the mean whole weight of Pacific oysters held subtidally (0% aerial exposure d^{-1}) was 62% faster compared to those at the high growing height (summer exposure range 45-66%; autumn exposure range 25-45%; G. Kent, pers. comm., 1992), after 5 months (summer and autumn) of culture in Little Swanport. Shell weight patterns were similar to whole weight patterns (Maguire and Kent, 1991). It is interesting to note that despite the higher exposure levels in their study, compared to Experiment 1 of this study (average of 26% exposure d^{-1}), that subtidal oysters in each, had a similar growth rate advantage of 62% (Maguire and Kent, 1991) and 56% (Fig. 8b), respectively.

In New Zealand, Pacific oysters were cultured experimentally at three exposure levels, corresponding to high-, mid-, and low-intertidal heights, at 0.5 m apart; the mid-intertidal height (approximately 1.0 m above the substrate) had been used to culture Pacific oysters on a commercial farm (Visser, 1993). Visser (1993) found that the oysters at the low- and mid-intertidal heights had, after 2-3 months, higher mean shell 'lengths' (shell height in this study) and dry shell weights, than those at the high-intertidal height. This is to be expected. Further comparisons with the present study are not warranted, however, because average exposure times were not quantified in Visser's (1993) study.

This study, and others (Spencer et al., 1992; Smith, 1994) have shown that shell abrasion treatments, applied on a regular basis, to Pacific oysters with large shell frill extensions, will retard their shell growth in terms of their whole weight, shell height and, or dry shell weight growth.

Increased levels of aerial exposure will also reduce shell growth in Pacific oysters (this study; Visser, 1993; Maguire et al., 1994b).

4.3 Meat growth

The meat growth of Experiment 1 oysters was rapid (Figs. 10a, b, c). This is confirmed against Maguire et al. (1994b) data for Pacific oysters cultured at the same site, where in comparison, a similar increase from 0.6-1.3 g was estimated to have taken 3.8 months compared to 2.5 months in this study (Table 5). In Experiment 2, however, the dry meat growth slowed after day 21 (Figs. 20 a, b, c), and followed a similar pattern to that of the whole weight, shell height and shell weight growth at this site (Figs. 18-20). In comparison to the data shown in Maguire et al. (1994b) for their Pittwater site, the meat growth in Experiment 2 was slower (Table 5).

Shell abrasion, in this study, did not improve the meat growth in comparison to the controls in either experiment (Figs. 10b, 21b). Spencer et al. (1992) did not report the dry meat growth of Pacific oysters subjected to rough-handling trials. They stated, however, that there was a close correlation between the dry meat and shell weights, to that of the live weights, suggesting therefore, that these were smaller in oysters subjected to extreme rough-handling treatments (1 or 2 min agitation in air).

Robert et al. (1993) found that continual rumbling of Pacific oyster 'spat' in cylinders, over a 14 month period, caused the dry meat weight of these to be 30% higher ($P=0.001$) than those in bags (controls; final mean dry meat weight = 1.12 g) (calculated from data read from Fig. 4c).

Alternatively, for 'small oysters' there was no statistical difference in dry meat weights by the final sample (Robert et al., 1993). Robert et al. (1993) reported, however, that for similar interval volume values (ml) [similar to shell cavity volume (g) in this study], higher dry meat weight values were recorded in cylinders (for both 'spat' and 'small oysters'). In the fattening experiment, a higher dry meat weight ($P=0.01$) was found in the oysters stocked at a density of 150 oysters cylinder⁻¹ (Robert et al., 1993), but as noted earlier, they did not state whether this was in comparison to 200 oysters cylinder⁻¹ or 150 oysters bag⁻¹.

Smith (1994) reported that Pacific oysters (initial mean shell height = 78.2 ± 5.3 mm s.d., $n=300$) subjected to abrasion in rotational cylinders had a

significantly higher mean dry meat weight (48% higher; calculated from an average of two values read from Fig. 5.8a), by the final sample (4 months), compared to standard height, fixed cylinders used as controls (final average mean dry meat weight = 1.85 g). However, as noted earlier, this comparison is confounded by differences in aerial exposure. These authors results do suggest, however, that shell abrasion can improve the dry meat weight growth compared to controls. Since similar effects were not seen in this study, it suggests that abrasion treatments would need to be applied regularly, over an extended time period, for there to be an effect.

Exposures (0-7% exposure d⁻¹) in Experiment 2 caused no differences in the dry meat weight growth ($P>0.05$) (Fig. 10c). In Experiment 1, however, oysters maintained at 0% exposure d⁻¹ (L group) had a higher mean dry meat weight compared to those at 26% exposure d⁻¹ (H group) from days 21-63 ($P<0.05$) (on day 42 the L group were 18% larger), but by day 81 these were similar ($P>0.05$; L group only 4% larger) (Fig. 10c). That the meat growth pattern between days 21-63 was similar to that of the whole weight, and dry shell weight growth (Figs. 7c, 9c), is to be expected (Spencer et al., 1978). The fact that between days 63-81, the H group appeared to grow faster, but the mean dry meat weight growth of the L group appeared to slow, suggests that other factors were operating. This increase in dry meat weight cannot, however, be attributed to a higher glycogen content either, since high levels recorded earlier in the study did not lead to better dry meat weights in comparison to the L group (Figs. 10c, 15c). In the study summarised by Maguire and Kent (1991), the response of Pacific oysters, in terms of meat growth, to a difference in aerial exposure depended on stocking density and hence faster meat growth only occurred in subtidal oysters at low stocking density. In Experiment 1 of this study, however, the biomass within each basket increased only modestly (about 5%), so that density should not have been a factor.

Visser (1993) reported that low-, mid-, and high- intertidal heights (0.5 m apart, mid-intertidal height = 1.0 m above substrate; exposure levels were not measured) did not significantly affect ($P>0.05$) the mean dry meat weight of Pacific oysters. While Visser (1993) found that there was a significant (two batches; $P<0.05$, $P<0.001$) trend of dry meat weight decreasing as the density was increased (40, 80 and 160 oysters per basket enclosure, 0.45m² in size), similar to Maguire and Kent (1991), she found,

in one of two experimental batches, a significant result for an analysis of dry meat weight in the rack height \times density interaction ($P < 0.05$), and that "a significant result in this interaction suggests that height has a modifying effect on the factor density".

Spencer et al. (1978) reported that both meat and shell growth of Pacific oysters was reduced, at exposures greater than 10%. In contrast to Spencer et al. (1978), however, the meat growth results of Pacific oysters in this study are consistent with the results of Maguire and Kent (1991) and Visser (1993) in that the effect of a large difference in degree of aerial exposure is much greater for shell growth than meat growth.

4.4 Condition index

Condition indices, such as CIvol and CIshell, can be used to indicate the physiological state of a bivalve (Rainer and Mann, 1992) (Appendix A), and whether it can be marketed. The results for both these indices are presented in this thesis for two reasons; first to evaluate possible difference between them (Appendix A), and two, because it is how well the meat fills the shell cavity that helps determine whether the oysters should be marketed, best shown by CIvol. Generally, Tasmanian Pacific oysters with a CIvol of ≥ 70 are acceptable to the markets, although a minimum of 80 is preferable (Maguire et al., 1994b). In Experiment 1, the mean CIvol of all treatment groups was acceptable (CIvol ≥ 70), just after early June (day 21), and reached about 95 by August (day 81) (Fig. 11a), showing that these oysters could be marketed from June until they spawned, most likely in the next summer (Sumner, 1980a, b; Maguire et al., 1994b). The mean CIvol of Experiment 2 oysters, however, remained lower than acceptable (CIvol ≤ 70) throughout, but showed some improvement after mid-July (Fig. 22a). By August, one treatment (MB group) had almost reached a CIvol of 65, which may be acceptable for some markets (Maguire et al., 1994b).

Shell abrasion did not affect either the CIvol or the CIshell indices ($P > 0.05$) in Experiment 1 oysters (Figs. 11b, 12b). This is to be expected (Maguire et al., 1994b) because the components which affect these, ie., the whole weight, dry shell and dry meat weights, and oyster shape were, in 31 out of 35 cases, not significantly different ($P > 0.05$) between shell abrasion treatments (Figs. 7b, 8b, 9b).

In Experiment 2, there was a clear trend, after day 51, of MB and M groups having a higher CIvol than the C group (Fig. 22b). By the final sample, however, the MB group still had a higher CIvol ($P<0.05$), but the CIvol of M and C groups were similar ($P>0.05$) (Fig. 22b). The CIshell did not follow the pattern of the CIvol index well, but generally the MB and M groups also had higher CIshell indices compared to the C group (Fig. 23b). Cup index was related to CIvol and CIshell indices, such that the more cupped the oyster, the higher the index (Appendix C). For example, after day 21, the trend for cup index was MB>M, C ($P<0.05$) (Fig. 25b), which is similar to the trend shown for CIvol (Fig. 22b).

The other component which could indirectly affect the CIvol and CIshell is the whole weight; larger oysters (C group) had larger shell cavity volumes, but similar sized meats as smaller oysters (MB, M groups) ($P>0.05$ for most samples) (Figs. 18b, 21b). For example, cavity volumes on a weight basis for MB, M and C groups were respectively, 17.5g, 18.0g, 21.3g ($n=60$), by the final sample (day 124). It could be argued that the condition index values, especially the CIvol, were higher in the MB and M groups because their meats more effectively filled their shells, than in the C group. It should, however, be noted that the final dry meat weight of the C group was greater than for the MB ($P>0.05$) and M ($P<0.05$) groups (Fig. 21b). Furthermore correlation analyses indicate that CIvol and CIshell are independent ($P>0.01$) of whole weight (Appendix C).

In Experiment 2, a comparison of MB and C groups indicated that shell abrasion treatments, repeated on a regular basis, can favourably improve the CIvol of Pacific oysters by about 14%, after 4 months of culture (Fig. 22b). This may be enough to influence marketability. Alternatively, if the abrasion treatments are carried out less frequently (M group), an improved CIvol may be lost after a period of time, on the lease, which in this experiment was after 4 months (Fig. 22b). Since this study was carried out, other workers (Robert et al., 1993; Smith, 1994) have also shown that if the shell abrasion treatments are not too severe, the condition index of Pacific oysters subjected to these, is also improved, compared to controls.

Robert et al. (1993) showed that Pacific oyster 'spat' (initial mean whole weight = 3 g), cultured for 14 months in rotational cylinders, had a significantly higher CIvol ($P=0.001$) compared to controls (mean CIvol=59), in mesh bags (45% higher; calculated from data read from Fig.

5a). Similar results ($P=0.001$) were obtained for 'small oysters' (initial mean whole weight = 20 g), over the same time period (Robert et al., 1993). However, while the figures in Robert et al. (1993) for 'spat' show positive increases for the first 8 months, in whole weight, dry shell and dry meat weight (Figs. 4a, b, c), Fig. 5a shows that the mean CIvol value declined, sharply, in cylinder oysters after 6 months. This may be an inconsistent result in the Robert et al. (1993) study, since for there to be a decline in condition index, one would expect a decline in dry meat weight values also.

Although not directly stated by Robert et al. (1993), the higher CIvol ($P=0.01$) of cylinder oysters (150 oysters cylinder⁻¹) were probably due to the fact that they had higher dry meat weights, for similar intervalve volumes, compared to controls (see Section 4.3). This is an opposite case to the hypothesis presented earlier, where shell abrasion appeared to prevent large increases in shell cavity volume, but did not affect the dry meat weight of Experiment 2 oysters.

Smith (1994) found that large Pacific oysters in rotational cylinders had significantly higher CIshell values (about 45% higher) than oysters in standard cylinders, after 4 months of culture. Because the dry shell weights did not differ between treatments, the higher CIshell values were a reflection of the higher meat weights of oysters in rotational cylinders (Smith, 1994). However, as noted earlier, Smith's results are confounded by exposure differences. Earlier in his study, Smith (1994) reported that the condition index values of Pacific oysters (mean shell heights 43.3-64.5 mm) periodically stirred in their baskets, every 10 days over a 3 month period, were significantly greater than controls (not stirred). In this case, however, Smith (1994) suggested that this was most likely due to the lower dry shell weights of oysters in the stirred baskets.

Spencer et al. (1992) reported that Pacific oysters subjected to most rough-handling treatments, had similar CIshell values, ranging between 35-47. Oysters agitated in air for 2 min within 2 h of collection, had a significantly poorer ($P<0.05$) CIshell (Spencer et al., 1992). It should be noted, that in the Spencer et al. (1992) study, their treatment levels correspond to an individual replicate rather than a mean of replicates. Added to this was that for some of the treatments, survival was too low to give reliable estimates of CIshell (or for that matter, mean whole weights).

Interesting trends occurred in the CIvol and CIshell results for Experiment 1 in relation to aerial exposure. By day 21 the L group (0% exposure d⁻¹) had better mean indices than the H group (26% exposure d⁻¹) ($P < 0.05$), but by the final sample the H group had the higher means ($P < 0.05$) (Figs. 11c, 12c). This reversal in trends can be explained. The L group had higher CI values compared to the H group, by day 21 (Figs. 11c, 12c), because although both groups had similar whole and dry shell weights ($P > 0.05$) (Figs. 7c, 9c), the mean dry meat weight of the L group was 20% higher ($P < 0.05$) (Fig. 10c). Further, and larger increases in both the whole and dry shell weights of the L group (Figs. 7c, 9c), however, but similar mean dry meat weights ($P > 0.05$; day 81) (Fig. 10c), caused the L group to have smaller ($P < 0.05$) CI values than the H group, by the final sample (Figs. 11c, 12c). The cup index (Fig. 14c) of the L group was also much lower ($P < 0.05$), and the cavity volume 15% larger than that of the H group. Thus the shell of the L group had 'outgrown' the meat, leading to the better CI of the H group by the final sample.

For the latter part of Experiment 2, the H group (7% exposure d⁻¹) generally had higher CIvol and CIshell values than the L group, although these differences were not significant ($P > 0.05$) except for one sample (Figs. 22c, 23c). It was notable that this advantage in CI values was most evident on the days when the cup index for the H group was significantly higher than for the L group ($P < 0.05$) (Figs. 22c, 23c, 25c) and whole weight, shell weight and dry meat weight were not significantly affected by aerial exposure ($P > 0.05$) (Figs. 18c, 20c, 21c).

Spencer et al. (1978) reported that exposures over the range 10-30% did not affect the CIshell values of Pacific oysters, cultured in trays. The CIshell was unaffected, they said, because reductions in dry shell and meat weights with increased exposures between 10-30%, were similar (Spencer et al., 1978). In contrast, Maguire and Kent (1991) reported that the mean CIvol of Pacific oysters cultured subtidally (0% exposure d⁻¹) was much lower (difference of 35 units), after 5 months on the lease, compared to those held at 25-66% exposure. This was because the shells of subtidal oysters grew much faster (62% faster) than those held at 25-66%, and because the subtidal oysters had only an 11% higher mean dry meat weight by the final sample (Maguire and Kent, 1991; also see Section 4.2). Visser (1993) also found, that due to suppression of shell growth, the CIshell values of oysters held at a high-intertidal height were higher (two

batches; $P < 0.001$, $P > 0.05$) than those held at low and mid-intertidal heights.

Therefore, in contrast to the Spencer et al. (1978) study, there is strong evidence to show that Pacific oysters cultured at low intertidal levels will grow larger amounts of shell, relative to meat. For this reason the CIvol and CIshell indices of these can become poorer, over time, in comparison to those cultured at higher levels. Overall the experiments in this study indicate that both regular shell abrasion and a high degree of aerial exposure can improve condition index largely through repression of shell growth.

4.5 Shape index

From a marketing perspective, long, narrow oysters are undesirable (Graham, 1991), as are relatively slender oysters in relation to shell depth. Shape indices devised in this study to determine marketability of Pacific oysters, were the roundness index (shell length/shell height) and the cup index [shell depth/(shell height x shell length)^{0.5}]; each multiplied by a factor of 100. Mean roundness values ranged from 0.46-0.64 in Experiment 1 (Fig. 13a), and from 0.53-0.62 in Experiment 2 (Fig. 19a). The closer to 1, the rounder the oyster; these oysters were therefore relatively narrow, since the shell length was about half that of the height. The cup index values ranged from 0.41-0.51 in Experiment 1 (Fig. 14a), and from 0.40-0.49 in Experiment 2 (Fig. 25a), with most values well below 0.5 at both sites. If the values had reached close to 1 the oysters would have been 'ball shaped', or conical in appearance.

Shell abrasion in Experiment 1 did not significantly affect ($P > 0.05$) either the roundness or the cup indices of any sample (Figs. 13b, 14b). In theory, shell abrasion could affect roundness because of greater losses in shell length compared to shell height (Appendix E, Figs. E-iv, -v). Shell growth on the outer margins can occur on two sides of the length axis, but only one for the height axis (Galtsoff, 1964), thereby allowing greater losses along the length axis.

By the last three samples in Experiment 2, M and C groups had a significantly higher ($P < 0.05$) mean roundness index compared to the MB group (Fig. 24b). This was because the MB group oysters had effectively

been prevented from growing substantial shell frill (Fig. 19b; Appendix D, Fig. D-viii; Appendix E, Figs. E-i, ii, iv).

Provided shell depth is unaffected, retarding shell height and length through shell abrasion could, in theory, lead to higher cup index values. The cup index of the M group was significantly higher ($P < 0.05$) compared to the C group, on day 0 of Experiment 2 (Fig. 25b). Shaking baskets also substantially improved ($P < 0.05$) the cup index of the MB group in comparison to M and C groups (Fig. 25b). The cup index of the M and C groups declined over time, because while the three groups had a similar mean shell depth (Appendix D, Fig. D-xi), growth in height (Fig. 19b) and length (Appendix D, Fig. D-viii) were less restricted. By the end of the trial, the MB group had a higher ($P < 0.05$) mean cup index (mean cup index = 0.46) compared to both M and C groups (mean cup indices = 0.42 for both) (Fig. 25b).

Neither Spencer et al. (1992), nor Smith (1994), investigated the effect of shell abrasion on shell shape. Robert et al. (1993) used the ratio of shell depth to shell height (shell 'width' to shell height in their study), and reported that this index was much better in Pacific oysters cultured in rotational cylinders compared to those in mesh bags (controls). This result is consistent with the present study, since when the shell height and length are retarded the shell depth would be a large factor in either Robert's index or the cup index used in this study.

Both Robert et al. (1993) and Smith (1994) presented shell height, length and depth results. For comparisons with this study, I calculated the final mean roundness and cup indices from the results presented in Fig. 3 in Robert et al. (1993) (for 'spat'), and in Figs. 4.4, 4.5, 5.5, 5.6 in Smith (1994), for shell-abraded Pacific oysters compared to controls (Table 6). Similar to this study, the cup index of oysters subjected to regular abrasion (those stirred in their baskets, those in rotational cylinders, or those subjected to machine-grading and basket shaking each six weeks - MB group), had higher cup indices compared to controls (Table 6). Unlike this study, the rotational cylinders, in both Robert et al. (1993) and Smith's (1994) studies, produced higher roundness indices compared to controls (Table 6). For this reason, it is still not certain how different intensity and frequency of abrasion will affect the roundness of Pacific oysters.

TABLE 6

Comparison of final shell shape indices of Pacific oysters (*C. gigas*) subjected to shell abrasion treatments in this study, to shape indices calculated from data in Robert et al. (1993) and Smith (1994). Group means of shell height, shell length, and shell depth in Robert et al. (1993) and Smith (1994) were used for the calculations rather than individual data.

	Shell abrasion treatment	Time (months)	Initial shell height (means \pm s.d.) (mm)	Final roundness index	Final cup index
Robert et al. (1993)	Rotational cylinders	14	20 ¹	0.62	0.56
	Control (bags)			0.52	0.36
Smith (1994)	Stirred baskets ²	3	43.3 \pm 4.8	0.57	0.49
	Control (not stirred)			0.59	0.45
	Stirred baskets ²	3	62.5 \pm 4.8	0.57	0.46
	Control (not stirred)			0.56	0.43
	Rotational cylinders	4	78.2 \pm 5.3	0.56	0.55
	Control (fixed cylinders)			0.44	0.40
O'Meley ³	MB	4	-	0.55	0.46
	M	"	64.4 \pm 9.9	0.61	0.42
	C	"	68.4 \pm 9.4	0.59	0.42

¹ Standard deviation was not reported in Robert et al. (1993). The range in shell heights was estimated to be 20-23 mm and was read from Fig. 3 in Robert et al. (1993).

² Baskets were stirred approximately every 10 days for the duration of the experiment (Smith, 1994).

³ this study. MB, oysters machine-graded and baskets were shaken for 0.5 min on days 38 and 82; M, oysters machine-graded; C, control.

Too much abrasion can cause oysters to become ball-shaped in appearance (Loosanoff and Nomejko, 1955; Holliday et al., 1991b), so that the oyster will not sit upright on a plate (R. Calvert, pers. comm., 1991). It is obvious that the treatments used in this study, however, did not cause such an extreme effect.

The deeply-cupped Kumamoto (*C. sikamea*) oyster may no longer exist in Japan as a pure stock (Deupree, 1993). It was thought, however, that Tasmanian stocks contained these, due to the fact that many of the oysters on farms were deeply cupped (Deupree, 1993). Deupree (1993) analysed the genetic characteristics of selected oysters sent to him by a Tasmanian hatchery (Shellfish Culture Pty. Ltd.) and found that these

oysters were not of the Kumamoto type. Whether or not the Kumamoto type exists in Tasmanian stocks, it is apparent that the shell shape of single-seed oysters, especially Pacific oysters, are superior to those cultured as attached spat (Holliday et al., 1988; Graham, 1991).

In Experiment 1, the roundness index of the L group (0% exposure d⁻¹) showed a steady increase, while that of the H group (26% exposure d⁻¹) increased only modestly by comparison; by the last sample, the L group had a much rounder shape ($P<0.05$) (Fig. 13c). This was because L group oysters grew more shell frill along the shell height and length axes than did the H group (Fig. 8c; Appendix D, Fig. D-iii). The cup index of the H group, however, was higher than the L group after day 42 ($P<0.05$, days 64 and 81) (Fig. 14c), showing greater growth in height and length dimensions in relation to depth, of the L group compared to the H group (Fig. 8c; Appendix D, Figs. D-iii, -vi).

In Experiment 2, the exposure levels tested (0 vs 7% exposure d⁻¹) did not affect ($P>0.05$) the roundness index (Fig. 25c). The cup index, however, was significantly higher ($P<0.05$) in the H group compared to the L group between days 51-96, but not by the final sample ($P>0.05$) (day 124) (Fig. 25c).

Maguire and Kent (1991) reported that Pacific oysters cultured at 25-66% average exposure (see Section 4.2) had a better (cup) shape than subtidal oysters, when a similar cup index to the present study (shell depth/shell height x shell length) was used (G. Maguire, pers. comm, 1995).

It should be noted that while shell abrasion did not cause changes in shell depth, that of aerial exposure did; the depth value for the L group was usually larger ($P<0.05$, days 42 and 81) than that of the H group (Appendix D, Fig. D-vi), and similar, but less pronounced, trends were evident in Experiment 2 (Appendix D, Fig. D-xii).

As indicated in Section 4.4, the cup index can markedly affect the value of the CI_{vol} and CI_{shell} indices. Generally, the CI indices follow that of the cup index, as a comparison of the relevant figures (Figs. 11c, 12c, 14c of Experiment 1, and Figs. 22c, 23c, 25c of Experiment 2), and correlations (Appendix C), show.

While aerial exposure (Experiment 1) and shell abrasion (Experiment 2) significantly affected cup index, the size of those effects was relatively small (maximum of 0.05 units). Similarly, treatment effects on the roundness index were relatively small (maximum of 0.06 units).

4.6 Glycogen content

Variation amongst replicates was much higher in Experiment 1 (Figs. 15b, c) than in Experiment 2 (Fig. 27b, c). This may be a result of the methods of analysis used in Experiment 1, since the glycogen content was determined from homogenised wet meats, rather than uniformly powdered dry meats as used in Experiment 2. It was difficult to obtain a representative homogenate from a more coarse wet meat sample when using a domestic blender (S. Hindrum, pers. comm., 1990).

The glycogen content in Experiment 1 oysters increased from a mean of 7.1 ± 0.9 (n=18) to 9.4 ± 1.3 (n=36) before declining after day 42, to a minimum of 5.8 ± 0.4 (n=36) (Fig. 15a). In Experiment 2, however, the glycogen content increased from a mean of 5.5 ± 0.3 (n=24) to 13.5 ± 0.4 (n=36) throughout the study (Fig. 16a).

The different trends shown cannot be explained by a positive correlation between glycogen content and dry meat growth, since the dry meats of Experiment 1 oysters exhibited a steady growth (Fig. 10a), while those in Experiment 2 grew more slowly after day 38 (Fig. 21a). Differences in gonad development were the most probable cause, since gamete production and maturation, deplete glycogen reserves (Gabbott, 1975; Mann, 1978). In Experiment 1, 63% of the oysters were in a ripening (1/2) stage in June (day 42), and by August (day 81), 15% were ripe (3/4) (Fig. 16a). In contrast, in Experiment 2, 36% and 48% of the oysters were in a ripening (1/2) stage in July (day 82) and August (day 124), respectively, but only 2% were ripe (3/4) by August (Fig. 27a). It is suggested, therefore, that Experiment 1 oysters put more energy into gamete production and maturation than did Experiment 2 oysters, and therefore used more of the glycogen reserves.

Shell abrasion treatments did not affect the glycogen content of oysters in either experiment (Figs. 15b and 26b). In contrast, Robert et al. (1993) found that 'small' Pacific oysters held in rotational cylinders had a higher

carbohydrate content compared to bag-cultured oysters. In their study glycogen content represented 85-95% of the total carbohydrates. In contrast few differences in the carbohydrate content of 'spat' cultured in cylinders or bags were evident (Robert et al. 1993), probably because oyster spat do not accumulate large amounts of glycogen (Gabbott, 1975). Large oysters stocked at either 150 or 200 oysters cylinder⁻¹, had higher carbohydrate contents than those in bags (150 oysters bag⁻¹) (Robert et al., 1993).

It would appear therefore, that the shell abrasion treatments used in this study were not severe enough, or of a sufficient duration, to influence the glycogen content of Pacific oysters cultured in Tasmania. Certainly, the treatments used in this study cannot, as hoped by some Tasmanian farmers, improve the glycogen levels in market size oysters during autumn and winter seasons.

In both experiments, the glycogen content of the H group was generally higher than that of the L group (Figs. 15c, 25c). This is in contrast to Spencer and Gough (1978), who found that carbohydrate levels in Pacific oysters cultured at aerial exposure levels of 0-30% were not changed. However, the final mean live weight of the oysters ranged from 3.3-27.1 g, suggesting that the oysters were not as mature as those used in this study, and therefore were less likely to accumulate large glycogen reserves (Gabbott, 1975).

For sexually mature Pacific oysters cultured in Tasmania, however, there is a definite advantage in terms of glycogen content, when the oysters are cultured intertidally rather than subtidally, during late autumn and winter seasons. The importance of glycogen is debatable, however. Allen and Downing (1991) suggested that American consumers prefer triploid Pacific oysters due to their high glycogen content, and reduced gonad development, over diploid Pacific oysters. Taste panels conducted by Maguire et al. (1994a), however, showed that glycogen, which is largely tasteless, is not necessarily a good predictor of Australian consumer response, in Pacific oysters with acceptable condition (≥ 70). They did suggest, however, that glycogen content could influence the texture of oysters, which they showed was strongly correlated (0.78; $P < 0.001$) to overall acceptability (Maguire et al., 1994a).

4.7 Gametogenesis

This study was restricted to autumn and winter months which provided only a small window from which to interpret the gametogenic activity of the oysters. This was in accordance with the wishes of some Tasmanian farmers, since it is during these months that marketing of Pacific oysters is limited, due to the long recovery period after spawning, in summer (C. Sumner, pers. comm., 1989). These farmers wished to know whether shell abrasion and, or aerial exposure would prompt an early recovery of glycogen levels, and subsequent gametogenic activity.

Other studies on Pacific oysters in temperate regions have shown, that the: gonads ripen during spring; gonads are ripe during spring-summer; oysters are capable of spawning during summer-early autumn; resorption of unused gametes occurs during autumn; and, a quiescent period occurs during winter while energy reserves, particularly glycogen, are built up again (Walne and Mann, 1975; Sumner, 1980a, b; Dinamani, 1987; Quayle, 1988; Maguire et al., 1994b). These activities are all, however, dependent on water temperature, salinity, and food (Quayle, 1988). In particular it is known, that a high percentage of Tasmanian Pacific oysters are ripe during summer and early autumn months (December-March) (Gardner et al., 1994).

In Experiment 1, most oysters (80%; $n=45$) were in post-spawned (5/X) and regressive (R) stages in May (day 0, late autumn), by June (mid-winter), 63% ($n=60$) had entered a ripening stage (1/2), and by August (day 81, late-winter), 15% ($n=59$) of these were ripe (3/4) [Fig. 16a(ii)]. These oysters were therefore following the normal sequence of reproductive stages, leading to spawning in summer and autumn (Gardner et al., 1994).

In April (day 0, mid-autumn) of Experiment 2, 27% ($n=30$) of the M group were ripe, but by May (day 38, late autumn), the unused gametes were either being resorbed (stages 5/X, R) (Dinamani, 1974; Mann, 1978), or the oysters had spawned [Fig. 27a(ii)]. The former hypothesis is more likely, because the condition indices of all treatment groups increased, rather than decreased, during this period (Figs. 22a, 23a). Gonad staging in May (day 38) showed that most treatments (74%; $n=90$), including the MH and ML groups were, in fact, in post-spawned and regressive stages [Fig. 27a(ii)]. By July (day 82, mid-winter), and August (day 82, late-winter), 36% ($n=60$) and 48% ($n=59$) of the oysters, respectively, had entered a

ripening stage of development [(Fig. 27a(ii))]. Compared to Experiment 1, however, few Experiment 2 oysters had reached a ripe stage (2%, n=59) by August (Fig. 27a(ii)). Once again, however, it is unlikely that food limitations were responsible for the slower development of Experiment 2 oysters. Quayle (1988) stated that in areas of low food abundance, males can out-number females, but in both experiments, females outnumbered males by August, in each year [Figs. 16a(ii), 27a(i)].

Bahr and Hillman (1967) indicated that repeated shell damage (removal of shell frill) could increase gametogenic activity in the American oyster. They filed the edges of fed and starved oysters, as outlined by Loosanoff and Nomejko (1955), on a weekly basis. Within the fed groups, oysters with filed shell edges showed a "slightly higher degree of development of mature gonads" compared to unfiled oysters. The opposite case occurred for unfed oysters, where unfiled oysters showed a slightly better maturation than filed oysters (Bahr and Hillman, 1967). They suggested that the enhanced gonad maturation of filed oysters, when food was not a factor, may have been due to a stress factor which initiated a species survival mechanism leading to gonad maturation.

This hypothesis is supported by results of Robert et al. (1993), who found that Pacific oyster spat (initial whole weight = 3 g) cultured in rotational cylinders, for a period of 14 months, reached maturity faster than those cultured in stationary mesh bags. In this case, the rotational cylinders removed shell frill ("shoot breakage") on a regular basis (Robert et al. (1993). They did not assess the reproductive activity of 'small' or 'large' oysters, however.

In a study of intertidal gastropods (*Nucella emarginata*), Geller (1990) removed approximately 3 mm from their shells, by grinding. He found that damaged females developed more egg capsules than control females, indicating an increase in reproductive effort, although total production of embryos per female did not differ between treatments (Geller, 1990). Geller (1990) suggested that these results were consistent with a life-history model "which predicts that reproductive effort should increase when adult mortality rises relative to juvenile mortality".

The paper by Bahr and Hillman (1967) was of interest to some Tasmanian farmers (C. Dyke, P. Chew, R. Calvert, C. Sumner, pers. comm., 1989), since increased gonadal activity would, it was thought, lead to fatter

oysters in a shorter time period following spawning. The results from this study, however, do not lend support to any of the above, since in this work, shell-abraded oysters did not show increased gonadal development and maturation compared to controls [Figs. 16b(ii), 27b(ii)].

Bahr and Hillman (1967) also found, that of the filed oysters, in both fed and starved groups, that there was a predominance of males. They hypothesised that this was due to limited energy reserves shared between shell repair and gametogenesis leading to the production of sperm in favour of eggs, since the male gonad "probably requires a smaller energy expenditure". Quayle (1988) supported this hypothesis by saying that food supplies can influence the ratio of females to males (see above). In each case, some type of stress factor, shell abrasion or lack of food, was suggested to be the cause of a change in the female to male ratio.

In both Experiments 1 and 2, there was a predominance of females throughout the study periods, but no effect on the female to male ratio due to the shell abrasion treatments applied. Therefore, the results of Bahr and Hillman (1967) could not be verified.

No published literature was found dealing with the effects of aerial exposure on gonadal development, or the female to male ratio, in Pacific oysters. In this study, aerial exposure did not affect ($P>0.05$) either the sex ratio [Figs. 16c(i), 27c(i)], or gonad stage [Figs. 16c (ii), 27c(ii)].

To assess the effects of shell abrasion and aerial exposure more comprehensively, trials in spring would be necessary.

4.8 Shelf life

The shelf life of aquaculture products is of the utmost importance during the processing, distribution, and marketing stages, prior to, and after sale (Graham, 1991). In particular, live oysters must remain that way, before they are opened and presented in the half-shell (Graham, 1991). Graham (1991) reported that the shelf life of live oysters depends on variables including origin, method of culture, storage temperature and purification (depuration) method. The shelf life of Tasmanian Pacific oysters is of considerable interest to Tasmanian farmers, who sell to N.S.W. and other markets where Sydney rock oysters are also marketed (Graham, 1991).

This additional experiment (Section 3.4.7), was aimed at assessing how the culture methods, shell abrasion and aerial exposure, might affect the shelf life and survival of Pacific oysters.

Shelf life was assessed by how long, in days, it would take for final sample Experiment 2 oysters held in air at a temperature of 14°C, and a humidity of 94%, to open ('gape'). Gaping oysters are not marketable (Graham, 1991), because for instance, the meats could become contaminated during transport, or storage (Bird et al., 1991). The results representing shelf-life are presented as cumulative gape, for each five day period, and include day 7, which was plotted because this was when the first oysters had begun to gape. Additionally, mortality rates were of interest - did the gape and mortality curves follow similar patterns?

Similar trends were evident in the shelf life and mortality curves (Figs. 28a, 29a). This shows, that once Pacific oysters have gaped, in addition to exposing the meat to potential contamination (Bird et al., 1991), the oysters will not survive for much longer. Examination of the meats of gaping oysters showed that these were emaciated, and in some cases there was a strong smell (hydrogen sulphide-like) emanating from inside the shell. Clearly gaping oysters should not be marketed.

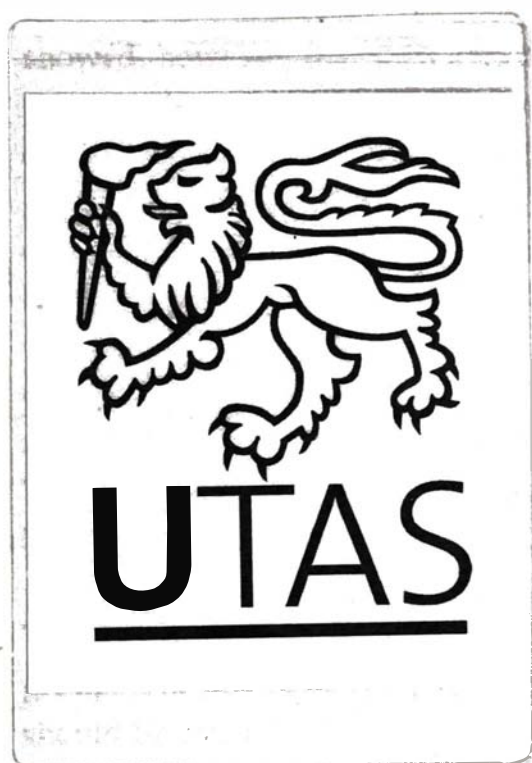
By day 7 of the experiment, 11% of the oysters had gaped, and 62% had gaped by day 15 (Fig. 28a). Bird et al. (1991) found that purified Pacific oysters (whole weight range = 44-94 g, mean = 66 g) stored at room temperature (21-26°C, mean 23°C) were gaping or dead, from day 4, and that more than 50% were gaping or dead by day 8. Those stored under refrigeration (1-10°C, mean 5°C), however, lasted longer, such that only 14% were found to be gaping or dead by day 11, with 75% similarly affected by day 14 (Bird et al., 1991). It is interesting that despite the much higher air temperature used in this (14°C), compared to the Bird et al. (1991) study (mean = 5°C), that only 62% had gaped compared to 75%, respectively, by days 14-15. Bird et al. (1991) reported, however, that some of the oysters were gaping prior to commencement of purification; they had been held in air at 30°C for 31 h prior to purification (for 36 h), and that there was noticeable mortality after completion of purification. They concluded that Pacific oysters in sound condition which are harvested and prepared for purification in cool temperatures and purified immediately are likely to have a longer shelf life (Bird et al., 1991).

Seaman (1991) stored Pacific oysters in air for 20 weeks, at 0 and 7°C, and found that survival was improved in oysters which were sprinkled with water (irrigated) compared to those that were not. Oysters kept without irrigation experienced total mortality in less than 20 weeks, whilst in the irrigated oysters, survival was 27% of the adults and 8% of the juveniles at 0°C, and 52% of the adults and 80% of the juveniles at 7°C (Seaman, 1991). Seaman (1991) wrote that this confirms that "5-7°C is best for a few weeks air storage of *C. gigas* seed", and it would seem that this range is also better for air storage of adults. Although irrigated (aerobic) oysters survived for much longer than those kept dry, Seaman (1991) suggested that, in theory, better survival should be attained by oysters forced to remain anaerobic, because this metabolism uses less energy. Anaerobic metabolism will occur in oysters whose shell valves are tightly closed (Crenshaw, 1980).

Mantzaris et al. (1991) did several shelf life trials with Australian native flat oysters (*O. angasi*). They identified three key factors which would allow flat oysters to have a shelf life of 2-3 weeks; continuous chilling, a moist environment, and applying pressure to prevent oysters from gaping (Mantzaris et al. 1991). Mantzaris et al. (1991) wrote that the moist environment, and ensuring that the shell valves were closed would prevent the meat from drying out. It was not discussed by these authors, but anaerobic metabolism was also likely to have occurred in oysters treated in this manner; this may also have extended their shelf life (Seaman, 1991). The oysters in the present study were allowed to open or close at will.

Neither shell abrasion, or the aerial exposure levels used in Experiment 2 affected shelf life (Figs. 28b, 28c), or survival (Figs. 29b, 29c). No published reports were found in the literature dealing with the effects of shell abrasion on the shelf life of oysters. In relation to exposure, however, Imai and Sakai (1961), and Arakawa (1990a), wrote that oysters cultured intertidally would have a better shelf-life than those cultured subtidally. This extension of Experiment 2 has shown that this was not the case, when the difference in exposure levels are only 0 compared to 7% exposure d⁻¹. Graham (1991) in reporting unpublished data from Maguire and Kent (1991) wrote that Pacific oysters cultured at 25-66% exposure d⁻¹ and then stored in air at 15°C and 94% humidity, survived longer (mean = 20.7 d) than subtidal oysters (15.8 d). Therefore it is likely that the exposure levels need to be greater than those tested, to improve

both the shelf life and survival of Pacific oysters held in air over extended periods.



5. Conclusions

In both experiments one treatment was relatively innocuous (little shell frill removed in Experiment 1 and little difference in aerial exposure in Experiment 2). Hence the interaction between these treatments cannot be considered to have been assessed adequately. However, both shell abrasion and aerial exposure can, as believed by Tasmanian farmers, affect the condition index of Pacific oysters.

Due to the fact that Experiment 1 oysters did not have large shell frill extensions, the shell abrasion treatments used did not change the components (whole weight, dry shell weight, dry meat weight, or cup index), which can affect condition index (CI_{vol} or CI_{shell}). Experiment 2 showed, however, that shell abrasion treatments applied to Pacific oysters with large shell frills, will affect these components, to a greater or smaller extent. In this case, the oysters subjected to shell abrasion (MB and M groups) had a higher CI_{vol} compared to the controls (C group), for most of the study. The CI_{shell} of shell-abraded oysters showed similar trends, but because the dry meat and shell weights were similar, the differences were not as pronounced as for CI_{vol}. Correlations of cup index with condition index (CI_{vol} or CI_{shell}) showed that these are positively related, such that the more cupped the oyster, the higher the index. Therefore, shell-abraded oysters (MB and M groups) usually had both higher cup and condition indices than controls (C group).

These effects were more pronounced in the MB group than in the M group. For this reason, the frequency of the shell abrasion treatments should be considered; whilst shell abrasion repeated on a regular basis (every 6 weeks; MB group) was found to favourably improve the CI_{vol} of Pacific oysters in this study, compared to controls (C group), those that were treated only once at the beginning (M group), were not significantly different to controls by the end of Experiment 2 (4 months). Other workers have also shown (Robert, 1993; Smith, 1994) that some types of shell abrasion treatments, applied on a regular basis, had a more pronounced effect on the condition index, and the cup shape, of Pacific oysters than observed in this study.

The shell abrasion treatments used in this study did not impair survival. Spencer et al. (1992) suggested that internal shell blistering of Pacific oysters in their experiment, may have been caused by tissue damage

during extremely rough abrasion treatments. Assessment of the condition of the mantle tissue of many oysters in this study showed no evidence of damage, showing that the treatments commonly used by Tasmanian farmers are not likely to harm the oysters.

The large difference between aerial exposure treatment levels (H and L) in Experiment 1, had a much greater effect on the shell growth than meat growth, because by the final sample (2.7 months), the mean dry meat weights were similar for both H and L groups. While shell growth was retarded in the H group, the L group continued to grow rapidly. This led to a better CIvol and CIshell of the H group compared to the L group, by the final sample. The cup index of the H group was also better. This in contrast to Spencer et al. (1978), but similar to results from Maguire and Kent (1991) and Visser (1993).

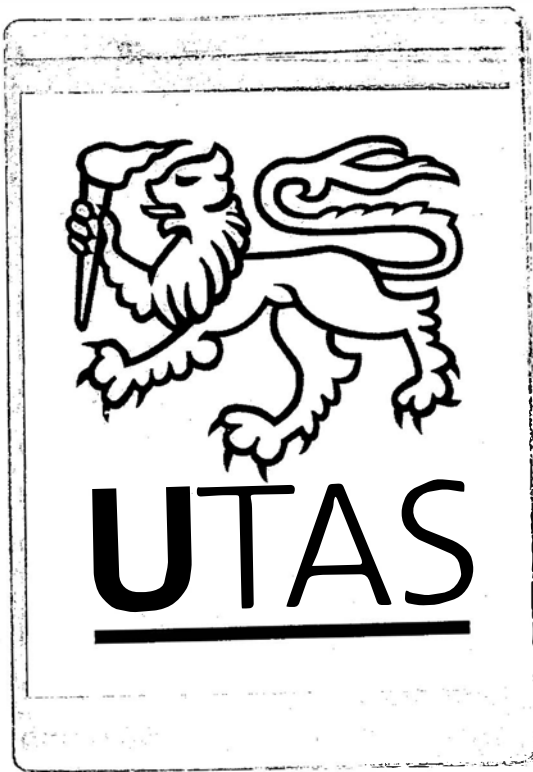
The idea that shell abrasion or aerial exposure treatments would have a dramatic effect on the meat growth of Pacific oysters, was not substantiated by this study. There was a strong correlation between dry shell and meat weight (Appendix C), but the relationship between the two can be influenced by management strategies. Similarly, these treatments can change the shape of the oyster, to either enhance or decrease the value of the cup index, which in turn may affect the CIvol and CIshell indices. The shell abrasion and aerial exposure treatments operated via the same mechanism, that is, intertidal or MB group Pacific oysters showed slower shell growth in relation to meat growth, compared to controls (subtidal, or oysters not subjected to shell abrasion), and therefore condition indices were enhanced.

Shell abrasion did not affect the glycogen content, but greater aerial exposure did enhance glycogen levels. Neither shell abrasion nor aerial exposure affected gonad development. Ideally, it would be good to investigate treatment effects on condition index in the warmer months of the year. However, such research is of limited commercial significance, unless spawning can be delayed.

It would have been interesting to include stocking density as a factor in these experiments and to have assessed the effect of aerial exposure on shelf life by using larger differences in aerial exposure. However, these topics were addressed in concurrent research by Maguire and Kent (1991). Similarly, these researchers are assessing the other major potential value

of grading, that is, containing size variation (G. Maguire, pers. comm., 1995).

Future directions of research into shell abrasion should consider the effects of repeated grading over longer periods of time, and determine the optimum time intervals between abrasion treatments. This would allow for assessment of the time oysters need to repair their shell frills in different seasons.



Appendix A

A comparative analysis of the volume condition index (CIvol) and the shell condition index (CIshell)

The use of bivalve condition indices has been reviewed by Mann (1978), Lucas and Beninger (1985), Crosby and Gale (1990), and Rainer and Mann (1992), and although Lawrence and Scott's (1982), and Brown and Hartwick's (1988b) articles were not reviews, they contain relevant information. In all of these, the main point of contention was the appropriate use of, and difference between the volume condition index (CIvol) and the shell condition index (CIshell). The aim of Appendix A is to compare these indices.

i. Bivalve condition indices and inherent measurement problems

According to Galtsoff (1964) and Mann (1978) the first bivalve condition index used to determine the marketable condition of oysters, was a ratio of the wet meat volume to shell cavity volume. Since this index is based upon an animal's wet meat weight, it can suffer from inaccuracies due to the amount of draining time (Lucas and Beninger, 1985; Lawrence and Scott, 1988), and osmoregulation in stressed organisms (Lawrence and Scott, 1988). Within the scientific community, a dry meat weight to shell cavity volume ratio was used next (Galtsoff, 1964; Mann, 1978). Since it incorporates losses in dry meat weight, and increases in water content due to spawning, this ratio is a better indicator of quality (Mann, 1978).

Condition indices based upon volumetric measurements of the internal shell cavity volume [where the shell cavity volume (ml) equals the difference in the volume of water displaced by the whole bivalve, minus the volume of the valves alone (Brown and Hartwick, 1988b)] suffer, however, from poor precision, due to the displacement methods used (Lucas and Beninger, 1985). Passive methods of water displacement may suffer from volumetric measuring errors due to surface tension around the exposed surface of the water moderating the flow of water (Rainer and Mann, 1992), and although active displacement methods give better accuracy (Rainer and Mann, 1992), other potential problems include water density changes and manipulative errors (Lawrence and Scott, 1982).

Lawrence and Scott (1982) used a gravimetric method for measuring shell cavity volume in American oysters (*Crassostrea virginica*), which is based

on the assumption, that the density of oyster meat is very similar to that of water (1 g cm^{-3}) (Lawrence and Scott, 1982; Lucas and Beninger, 1985). Hence "the difference between the weight in air of the intact, dried oyster minus the dried shell valves will yield the internal shell cavity volume (by weight)" (Lawrence and Scott, 1982). They showed that there was a significant correlation between volumetric and gravimetric methods used to determine volume condition index (CIvol), between the values of 15.6 and 141.19.

The gravimetric method for measuring CIvol [dry meat weight (g)/ shell cavity volume (g)] was chosen for this study, because it is accurate, simple, and time efficient (Lawrence and Scott, 1982), and the precision and reliability are good for oysters (Lucas and Beninger, 1985). The gravimetric method would not be applicable to all bivalves (Lucas and Beninger (1985), however, because of mantle water loss through the imperfect seal between the valves of some bivalves, for example scallops. Crosby and Gale (1990) also recommended the gravimetric method for measuring shell cavity volume in oysters as it resulted in a lower measuring error and coefficient of variation in their study, and because "it is easy and fast to use".

In the Lawrence and Scott (1982) method the whole oyster was dried in air for a period of 45-60 min, and only oysters remaining tightly closed were analysed. In this study, oysters were removed individually from a bucket containing ambient seawater, which was also periodically shaken to encourage the oysters to remain tightly closed, and then the whole oyster shell was superficially dried (Section 2.5.2). This method successfully prevented loss of shell cavity fluids due to oysters opening during measuring, but created another difficulty, that of superficially drying the shell of the intact oyster. The problem was pronounced, especially in those oysters which had large shell frills and flutes, because water can adhere under these extensions (Spencer et al., 1992). For this reason, Gardner (1994) recommended that after shucking, the shell valves be superficially dried also, prior to weighing. This is in contrast to the method used in this, and in Lawrence and Scott's (1982) study, since in these the valves were air-dried for a period of 24-30 h prior to weighing.

Gardner (1994) compared the shell cavity volumes of Pacific oysters (approximately 3 y of age, $n=60$) whose valves were superficially dried as

opposed to those that were then further dried for 24 h in air, prior to weighing, to cavity volumes obtained by displacement measurements. The displacement measurements were carried out using the method described by Rodhouse (1977). Gardner (1994) found that the cavity volumes obtained by weighing air dried valves were approximately 13% greater than those obtained by displacement measurements for the same oysters. Cavity volumes obtained by weighing superficially dried valves immediately after shucking were approximately 2% greater than those obtained by displacement measurements for the same oysters (Gardner, 1994).

Despite the inconsistency in estimates of cavity volume, however, both forms of the Lawrence and Scott (1982) method (wet valve and dry valve) correlated significantly ($P < 0.001$) with the Rodhouse (1977) method (Gardner, 1994). For this reason Gardner (1994) concluded that the Lawrence and Scott (1982) method of determining condition index accurately reflected the condition index data obtained with displacement estimates of cavity volume. He warned, however, that "comparison of actual condition index values obtained by the different methods should be undertaken cautiously" (Gardner, 1994). Clearly, the key point is to use a particular method in a consistent manner once the condition index method has been selected.

ii. Physiological significance of CIshell and CIvol

The scientific community has generally accepted the definitions suggested by Lucas and Beninger (1985); CIshell is an ecophysiological indicator used to characterise the health of a cultured stock, while CIvol is described as an economic index and indicates the quality of the product. However, while the CIshell index indicates environmental stress or sexual activity (Lucas and Beninger, 1985), the same could be argued about the CIvol index. For instance, Crosby and Gale (1990) suggest that CIvol is an indicator of nutritive status and stress, and that it is also more meaningful than CIshell. CIvol is a relative index, while CIshell, according to Crosby and Gale (1990) is an absolute index, which compares "metabolism directed towards calcification processes and metabolism focused towards somatic and gametic processes of glycogen storage, protein synthesis and vitellogenesis". Because it does not account for variations in shell cavity volume, due to shell shape or variability in shell thickness (Mann, 1978; Crosby and Gale, 1990), it cannot be an

indicator of nutritive or environmental stress, signifying recent catabolic or anabolic activity (Crosby and Gale, 1990).

Rainer and Mann (1992), however, disagreed with their conclusions, suggesting that either CIshell or CIvol may be used, since the requirement of any "static condition index ratio is to provide a stable denominator to compare with a sensitive numerator". They argued that either shell weight or shell cavity volume can be used as the denominator, since both will increase over time (or remain constant, Mann, 1978), and decreases are unlikely except from minor losses due to shell abrasion or shell boring organisms. The meat, however, will increase or decrease (Mann, 1978), or vary depending upon "sexual and metabolic activity of the organism" (Lucas and Beninger, 1985; Rainer and Mann, 1992).

Considering the above discussion, one would hope that the two indices would relate well. In this study, the CIvol and CIshell of Pacific oysters (whole weight range = 20-77 g; n=180) were not as closely related as might be anticipated (c.c. = 0.63, $P < 0.001$) (Appendix C). Similarly, Brown and Hartwick (1988b) who cultured Pacific oysters (two size classes; shell heights 21.6 ± 5.4 mm, n=158 and 45.2 ± 8.9 mm, n=160) in ten sites in British Columbia, Canada, for a period of 14 months, found that the correlation between the two indices was significant but very low ($r^2 = 0.18$, $P \leq 0.001$), for all sites combined. The present study has shown that condition index values can vary greatly due to the culture methods used. For this reason, the better correlation between CIvol and CIshell in this study, compared to that reported in Brown and Hartwick's (1988b) study, may have been due to the fact that only a single group of oysters were used for the analysis (one group of oysters from one site, and collected on only one sample date).

Rainer and Mann (1992) compared the CIvol-p (cavity volume measured by passive displacement) and CIvol-a (cavity volume measured by active displacement) to the CIshell of American oysters (size range 36-96 mm, n=125) from data collected over a one month period. They found that there was a modest predictive capability for the relationship between CIvol-p and CIshell ($r^2=0.21$, $P < 0.001$), but no relationship between CIvol-a and CIshell ($r^2=0.00$, $P > 0.05$).

These studies show that the relationships between the various condition indices used, on single groups of oysters, are at best modest. The conclusion of Rainer and Mann (1992), which is similar to that of Gardner's (1994), is worth noting here. They wrote; "condition indices clearly have value for comparisons within data sets that have been consistently collected; however, comparisons with quantitative data of other authors and/or historical data sets collected by other investigators or methods may be limited to discussion of temporal trends rather than absolute values".

iii. Correlations of CIshell and CIvol with environmental variables, and oyster size

In this study, the null hypothesis of independence for CIvol and whole weight, and CIshell and whole weight, of Pacific oysters (whole weight range = 20-77 g; n=270), was retained ($P>0.01$) (Appendix C).

Brown and Hartwick (1988b) used multiple regression equations to relate whole weight of Pacific oysters to environmental factors (water temperature, salinity, chlorophyll *a*), as independent variables on CIvol and CIshell (n=111). They found that CIvol was related to the whole weight ($r^2 = 0.39$, $P\leq 0.001$), and to temperature, salinity, and chlorophyll *a* concentrations, in decreasing order of importance. The CIshell was firstly related to water temperature ($r^2 = 0.41$, $P\leq 0.001$), then salinity, and chlorophyll *a* concentrations, but the null hypothesis of independence was retained ($P>0.05$) for whole weight (Brown and Hartwick, 1988b). For this reason, they stated that Pacific oysters of different size ranges could be compared using the CIshell index, provided salinity conditions are not limiting to oyster growth. The CIvol, it was suggested, however, warrants the use of a size correction factor, and for this reason would seriously limit the usefulness of this index in comparative work (Brown and Hartwick, 1988b).

Rainer and Mann (1992) used linear regressions to determine the relationships between oyster size (American oysters; shell height range = 36-96 mm; n=125) and CIshell, CIvol-p, or CIvol-p. Whole animal volume and shell height were used as measures of oyster size, which are "size descriptors not used in condition index calculation" (Rainer and Mann, 1992). In each case they found that the r^2 term was very low (highest $r^2 = 0.009$). They concluded that there was no relationship

between oyster size and CIshell, CIvol-p, or CIvol-a (Rainer and Mann, 1992). It should be noted that they did not refer to Brown and Hartwick's (1988b) study.

That these three studies gave such varying results in relation to whole weight versus CIvol or CIshell of Pacific oysters, and other cupped (*Crassostrea* spp.) oysters, also supports the conclusions of Rainer and Mann (1992) and Gardner (1994). This study has shown that shell shape will affect condition index; in particular, the cup index has been correlated to both the CIvol and CIshell (Appendix C). Since the culture conditions can affect shell shape (Section 4.5), it is suggested that this is another reason why comparative work using CIvol and CIshell would be limited.

iv. Effects of shell growth on the CIshell and CIvol

Littlewood et al. (1992) cultured single-seed American oysters at five different levels in the intertidal zone (28-60% aerial exposure), for a period of seven months. The oysters were initially 9 months old; by the final sample, their shell heights ranged from 55-72 mm (read from Fig. 3b in Littlewood et al., 1992). Their final sample results (n=50) showed that there was a trend towards decreased growth and condition (CIvol and CIshell) with increased exposure levels (Littlewood et al., 1992). However, the decline in CIshell values, with increased exposure levels, was much greater than that shown for CIvol (Littlewood et al., 1992). This, they said, was because increases in shell thickness, occurring at high exposure levels (Littlewood, 1988; Littlewood et al, 1992) markedly reduced the value of CIshell (Littlewood et al., 1992). Although a decrease in CIvol was statistically significant with increasing exposure also, the changes were not as amplified as for CIshell (Littlewood et al., 1992). They therefore recommended the use of CIvol rather than CIshell when comparing oysters subjected to differing levels of exposure.

Note, however, that this is in direct contrast to Spencer et al. (1978) who, for Pacific oysters, found that, though growth of meat and shell was reduced at high exposure levels (10-30%), the dry meat weight to shell weight ratio (CIshell) remained approximately constant.

Brown and Hartwick (1988b) suggested that CIvol may be inappropriate for assessing the physiological status of oysters in a particular

environment. This was because lower dry meat weight to shell ratios of oysters at their medium growth sites resulted in a reduction of internal volume and an increase in CIvol, because of increased shell thickness, compared to their high growth sites (Brown and Hartwick, 1988a, b). They hypothesised that shell thickening was partially related to food availability because phytoplankton abundance was lowest at their medium growth sites (Brown and Hartwick, 1988a). Their rationale was, that it may be energetically preferable for a nutritionally stressed oyster to increase shell deposition in preference to meat growth (Brown and Hartwick, 1988b).

In the present study, the estimated impact of different treatments on oyster condition depended on whether CIvol or CIshell values were used, since these showed different trends, depending on the treatments applied. For instance, shell abrasion affected the CIvol to a much greater extent than CIshell, in Experiment 2 (Figs. 22b vs 23b). Alternatively, the effects of aerial exposure on the CIvol and CIshell were similar in Experiments 1 and 2, but the differences in the CIshell values, when comparing H and L groups, were in most cases slightly larger than the CIvol values (Figs. 11b vs 12c, 22c vs 23c). As discussed earlier, Littlewood et al. (1992) also found that the American oyster showed smaller reductions in CIvol than in CIshell values, with increased exposure levels (28-60%).

In summary then, Brown and Hartwick (1988b) suggested that CIvol may show high values, due to shell thickening, when in fact the oysters may be nutritionally stressed. On the other hand, Littlewood et al. (1992) said that the effects of shell thickening at high levels of aerial exposure will give low values for the CIshell index. In effect therefore, due to the effects of shell thickening, both indices can suffer. As long as the researcher is aware that these factors come into play it is not necessarily a disadvantage.

vi. Conclusions

It has been suggested that either the CIvol or CIshell may be used to indicate the physiology of a bivalve (Rainer and Mann, 1992). Brown and Hartwick (1988b), however, found that the CIvol is influenced largely by the size of the animal, so that comparative work may be limited in this respect. I recommend the use of CIvol because it incorporates three-

rather than two variables, the differences due to treatments and seasons are easily shown, and because the marketing perspective is also taken into account. In addition, CIvol can be related to opportunity for growth; that is, the space available for meat growth.

The fact that correlations between CIvol and CIshell are tenuous is of concern. Comparative work is limited until researchers use the same, or both indices. It must also be acknowledged that the culture conditions, and the different sites used, will also limit comparative work. Whilst the issue must be resolved, it will take more studies, such as the comprehensive study by Brown and Hartwick (1988a, b), to enable researchers to encompass the many factors involved.

Appendix B

Normality of initial and final data in Experiments 1 and 2.

One of the assumptions of ANOVA is that the data are normally distributed. The Shapiro-Wilk W test (Tietjen, 1986) was used to test the normality of data for variables (whole weight, shell height, dry shell weight, dry meat weight, CIvol, CIshell, roundness index, cup index, and glycogen content) measured in Pacific oysters (*C. gigas*) on the initial (day 0) and final (days 81 and 124) sample dates in Experiments 1 and 2 (Table B). It is recognised that there were too few replicates to allow for a powerful assessment of normality in the glycogen data sets.

In most cases the Null Hypothesis of normality was retained (NS, $P > 0.05$). Of concern, however, were the highly significant ($P < 0.001$) results shown for dry meat weight ($P < 0.001$) and CIshell ($P < 0.01$) in both the M and C groups, on day 0 of Experiment 2 (Table B). In each group there were some oysters larger than the rest (Figs. B-i, -iv). Due to the high correlation found between whole weight and dry meat weight (c.c. = 0.89, $P < 0.001$; Appendix B), these larger oysters may have caused (Appendix B) a skew in the data, in the upper range, for the dry meat weight (Figs. B-ii, -v). Brown and Hartwick (1988b) showed that CIshell and whole weight are independent ($P > 0.05$). For this reason, it is unlikely that the whole weight affected the CIshell values (Figs. B-iii, -vi).

Further tests on data in Experiments 1 and 2, on other sample dates were found, in most cases, to be normally distributed. In general, there were no consistently non-normal patterns shown for particular variables. For these reasons, parametric techniques were adopted throughout.

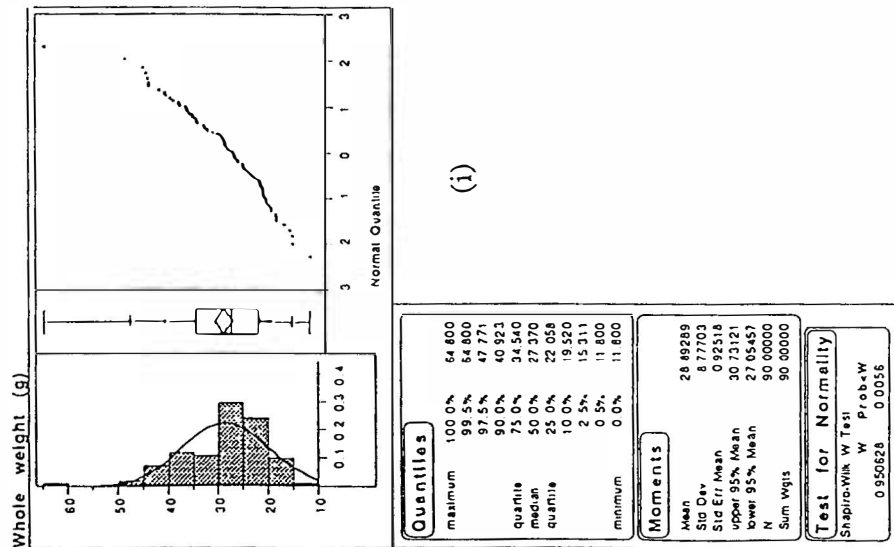
Underwood (1981) argued that dependent variables based on ratios tend not to be normally distributed. Table B shows that the data for four ratios (CIvol, CIshell, roundness index and cup index) were in most cases normally distributed.

TABLE B

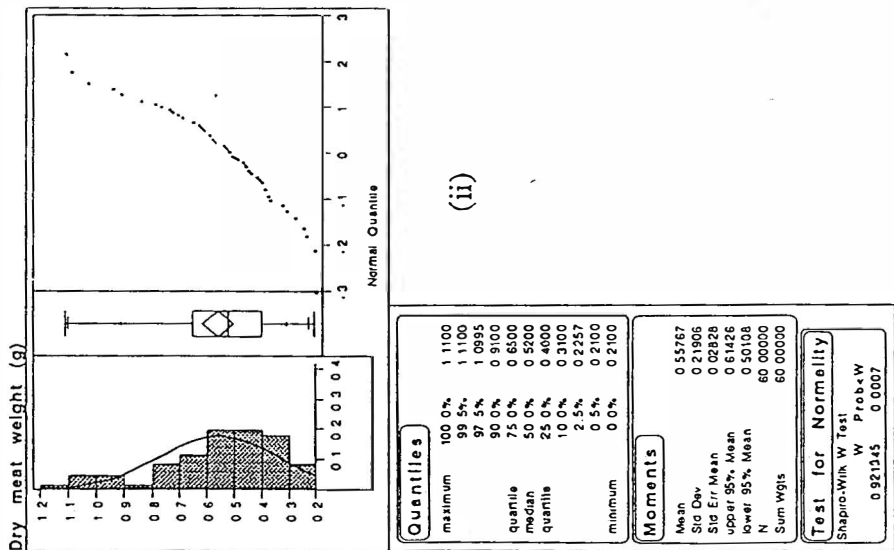
Results of the Shapiro-Wilk W test for normality of initial (day 0) and final (days 81, 124) data for whole weight, shell height, shell height, dry shell weight, dry meat weight, Clvol, Clshell, roundness index, cup index and glycogen content of Pacific oysters (*C. gigas*) measured in Experiments 1 and 2. In most cases, the Null Hypothesis of normality was retained (NS).

	Treatment group	Whole weight (g)	Shell height (mm)	Dry shell weight (g)	Dry meat weight (g)	Clvol	Clshell	Roundness index	Cup index	Glycogen content (g/100 g dry matter basis)
Experiment 1										
Day 0	MM	NS	NS	NS	NS	NS	NS	NS	NS	NS
	M	*	*	NS	NS	NS	NS	NS	NS	NS
	C	NS	NS	NS	NS	*	NS	NS	NS	NS
	n	90	90	30	30	30	30	60	60	6
Day 81	MMH	NS	NS	NS	NS	NS	NS	NS	NS	NS
	MML	NS	NS	NS	NS	NS	NS	***	NS	NS
	MH	NS	NS	NS	NS	NS	NS	NS	***	NS
	ML	NS	NS	NS	NS	NS	NS	NS	NS	*
	CH	NS	NS	NS	NS	NS	NS	NS	NS	NS
	CL	**	NS	NS	NS	NS	NS	NS	NS	NS
	n	90	90	60	60	60	60	60	60	3
Experiment 2										
Day 0	M	**	NS	NS	***	*	**	NS	NS	NS
	C	NS	NS	NS	***	NS	**	*	NS	NS
	n	90	90	60	60	60	60	90	90	12
Day 124	MBH	NS	NS	*	NS	NS	NS	NS	NS	NS
	MBL	*	NS	NS	NS	NS	NS	*	*	NS
	MH	**	NS	*	NS	NS	NS	NS	NS	NS
	ML	NS	NS	NS	NS	NS	NS	NS	NS	NS
	CH	**	*	NS	*	NS	NS	NS	NS	NS
	CL	NS	NS	NS	NS	**	*	**	NS	NS
	n	60	60	30	30	30	30	60	60	6

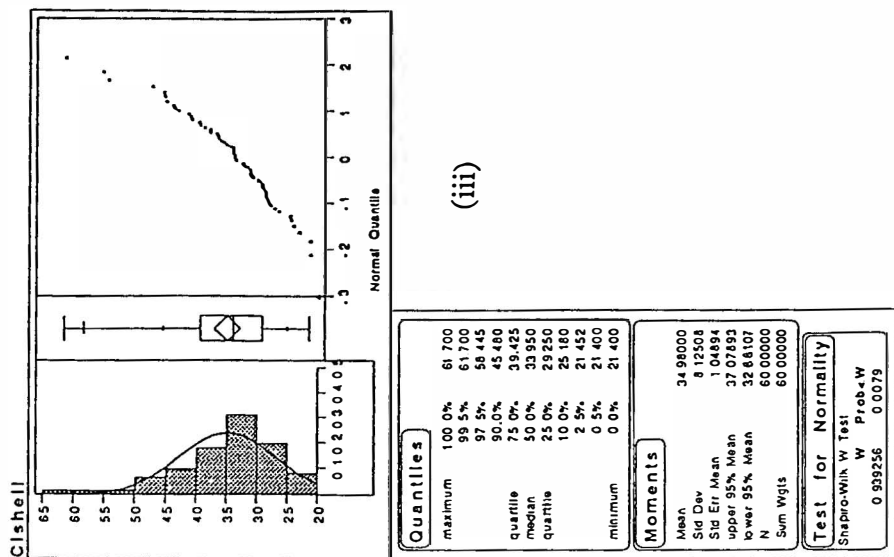
NS, not significant (P>0.05); * = P<0.05; ** = ; P<0.01; *** = P<0.001



(i)

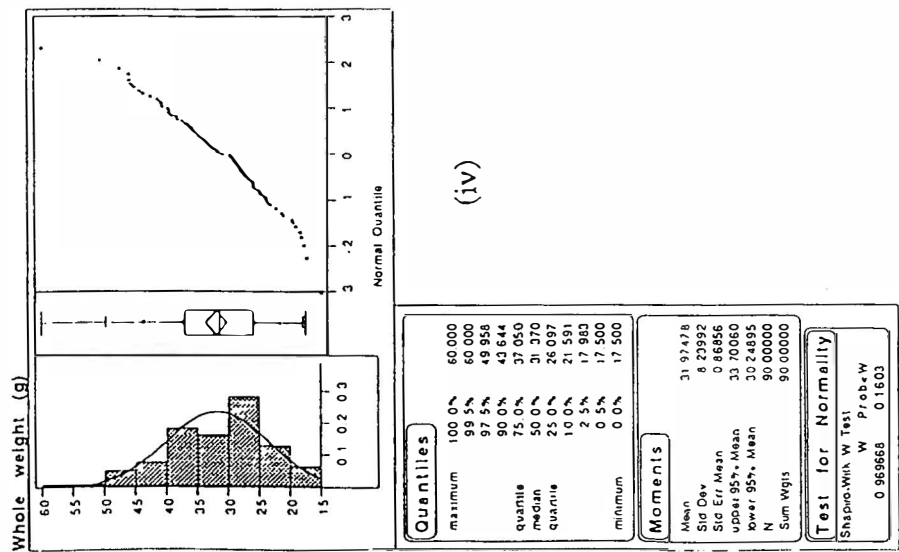


(ii)

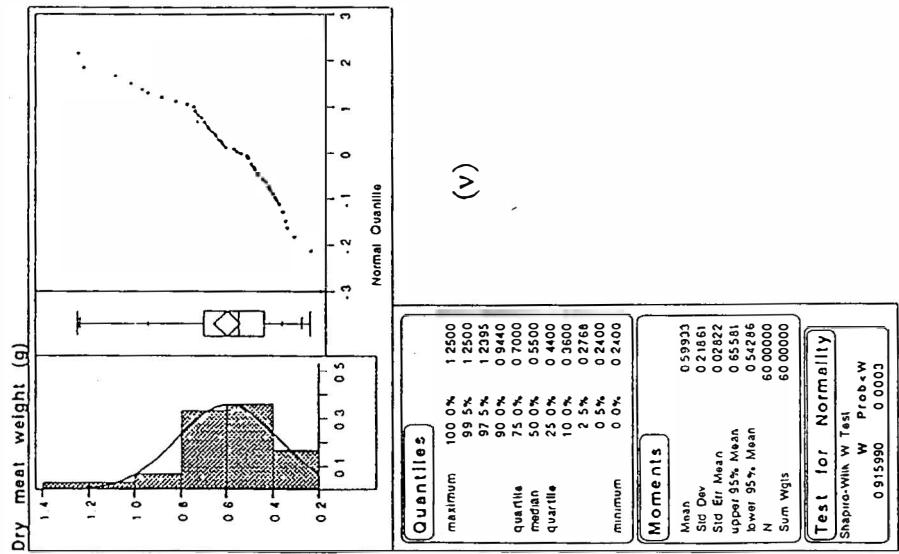


(iii)

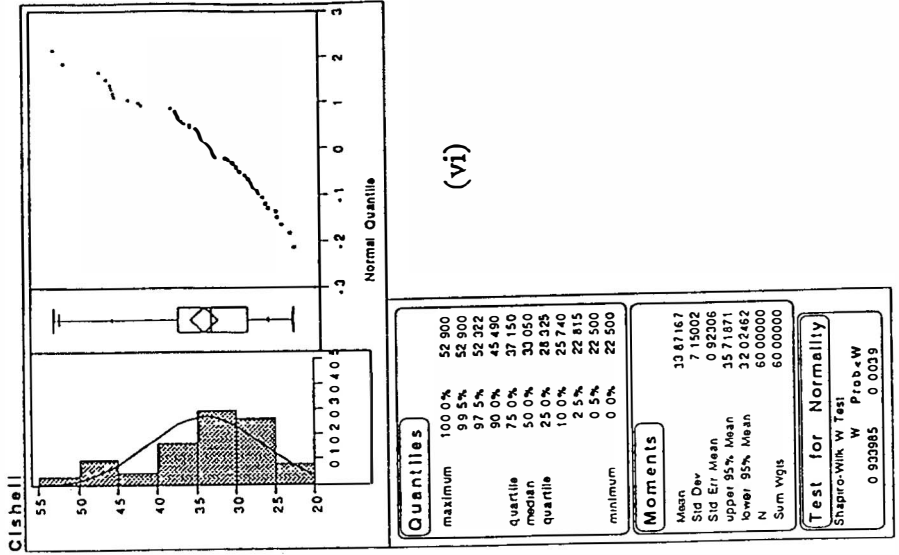
Figs. B-i, -ii, -iii. Frequency distributions, quantiles and Shapiro-Wilk W test for normality of whole weight, dry meat weight and Cisshell data of M group Pacific oysters (*C. gigas*) on day 0 of Experiment 1.



(iv)



(v)



(vi)

Figs. B-iv, -v, -vi. Frequency distributions, quantiles and Shapiro-Wilk W test for normality of whole weight, dry meat weight and Cishell data of C group Pacific oysters (*C. gigas*) on day 0 of Experiment 1.

Appendix C

Correlation analyses of ten performance indices measured in Pacific oysters.

Pacific oysters used for the correlations (Table C) were chosen on the basis that a large sample size be used to improve the power of the analyses. The MML, ML and CL groups measured on the final sample (day 81) in Experiment 1 were combined, because except for a small difference in the dry meat weight (Fig. 9b), shell abrasion (MM, M, C) did not significantly affect the other nine indices (whole weight, dry shell weight, CIvol, CIshell, shell height, shell length, shell depth, roundness index, cup index) measured. Therefore, the Pacific oysters [whole weight 20.5-76.9, shell height 47.9-100.9 (n=270)] used for the correlation analyses represented groups which had been cultured subtidally (0% exposure d⁻¹) on the Little Swanport lease.

Because the numerous correlation analyses ($10 \times 9/2 = 45$) increases P (Type 1 error), an alpha value of 0.01 rather than 0.05 was adopted (Miller, 1966). Clearly, this entails a loss of power.

The correlation coefficient (c.c.) was high for whole weight and dry shell weight (c.c. = 0.98, $P < 0.001$). This is to be expected because the shell represents 60-70% of the whole weight (Walne and Mann, 1975).

Dry meat weight and whole weight were highly correlated (c.c. = 0.89, $P < 0.001$), as were dry meat and shell weight (c.c. = 0.86, $P < 0.001$). It is known that meat and shell growth can be independent (Maguire et al., 1994b). For this reason the correlations may not have been as high, if for example, the sample had included recently spawned oysters whose dry meat weight is considerably reduced during this part of the reproductive cycle (Mann, 1978).

While oyster dimensions (shell height, length and depth) were all significantly correlated with whole weight, dry shell weight and dry meat weight ($P < 0.001$ for each), the correlation coefficients were much lower than for the above relationships (Table C). This indicates the variability of oyster shape. Walne and Spencer (1971) recommended that due to the oyster's highly variable shape that comparative work be based on whole weight, rather than on shell height.

In this study, the CIvol and CIshell were found to be independent of whole oyster weight and dry shell weight ($P>0.01$). Brown and Hartwick (1988b) found via regression analysis that CIvol, but not CIshell, of Pacific oysters ($n=111$) cultured in British Columbia, Canada, was related to their whole weight ("partial correlation coefficient" = 0.502). Maguire et al. (1994b) found that CIvol increased as oysters grew up until spawning or resorption. However, this probably reflects seasonal effects rather than a fundamental relationship between oyster size and CIvol once they are large enough to mature.

As expected, dry meat weight was correlated with CIvol (c.c. = 0.43, $P<0.001$), and CIshell (c.c. = 0.58, $P<0.001$). However, the CIvol and CIshell were not as closely related as might be anticipated (c.c. = 0.63, $P<0.001$). This is discussed below in relation to the oyster's shape.

There was a trend towards larger oysters being less round although the relationships between roundness index and whole weight (c.c. = -0.17) or dry shell weight (c.c. = -0.18) were not significant ($P>0.01$). In Experiment 1 the faster growing L group was more rounded than the H group (Figs. 7c, 8c, 9c, 13c), while the faster growing groups in Experiment 2 (M and C) were more rounded than the MB group in Experiment 2 (Figs. 18c, 19c, 20c, 24c). Clearly, factors other than oyster size were influential in these comparisons.

The cup index was independent ($P>0.01$) of oyster size, based upon weight measurements (whole weight, dry shell weight). This in contrast to Galtsoff (1964), who stated that the shell valves of young oysters are flatter than in larger, older oysters. For this reason, the size range investigated may influence the outcome of such comparisons. Treatment effects on growth also had a strong influence on cup index (for example, the L group versus H group in Experiment 1), again indicating that factors other than oyster size were important.

Shell height and shell length (c.c. = 0.25, $P<0.001$), shell height and depth ($P>0.01$), and shell length and depth (c.c. = 0.21, $P<0.01$) were not closely correlated. This suggests that the shape of Pacific oysters is highly variable. Treatment effects on roundness or cup index also indicate that oyster shape is malleable over lengthy periods.

While the roundness index and shell height were negatively correlated (c.c. = -0.64, $P < 0.001$), there was a positive relationship between roundness and shell length (c.c. = 0.57, $P < 0.001$). This should be the case, since the roundness index ratio equals shell length over depth. Similarly, cup index and shell depth (c.c. = 0.79, $P < 0.001$) were highly correlated, while cup index and shell height (c.c. = -0.49, $P < 0.001$) and cup index and shell length (c.c. = -0.28, $P < 0.001$) were negatively correlated.

For roundness and cup indices there was a trend towards a positive relationship although the correlation coefficient was not high (c.c. = 0.16, $P > 0.01$). Where treatments in this study had an effect on shape, they showed that the roundest oysters tended to have the poorest cup index (see Figs. 13c, 14c, 24b, 25b).

The roundness index and CIvol, or CIshell, were not related ($P > 0.01$). Cup index and CIvol (c.c. = 0.24, $P < 0.01$), and cup index and CIshell (c.c. = 0.20, $P < 0.01$) were related; the deeper the cup, the better the index.

The CIvol and CIshell were not closely related (c.c. = 0.63, $P < 0.001$). The former reflects both shell size and shape while the latter reflects shell size. Clearly the shape of oysters is highly variable and the very low correlation coefficient for dry shell weight and cup index (c.c. = 0.03, $P > 0.05$) indicates that size does not dictate shape.

TABLE C

Summary of correlation analyses of the whole weight, dry shell weight, dry meat weight, Clvol, Clshell, shell height, shell length, shell depth, roundness index and cup index of subtidally cultured Pacific oysters (*C. gigas*). The oysters (L group; n=270; whole weight 20.5-76.9 g; shell height = 47.9-100.9 mm) were measured on the final sample (day 81) in Experiment 1. Each correlation coefficient and significance level are shown. An alpha value of 0.01 was adopted to reduce P (Type 1 error) because of the large number of comparisons.

Variable	Whole wt. (g)	Dry shell wt. (g)	Dry meat wt. (g)	Clvol	Clshell	Shell height (mm)	Shell length (mm)	Shell depth (mm)	Roundness index	Cup index
Whole wt. (g)	1									
Dry shell wt. (g)	0.98**	1								
Dry meat wt. (g)	0.89**	0.86**	1							
Clvol	0.07NS	0.16NS	0.43**	1						
Clshell	0.19NS	0.11NS	0.58**	0.63**	1					
Shell height (mm)	0.64**	0.62**	0.50**	-0.12NS	0.01NS	1				
Shell length (mm)	0.48**	0.44**	0.39**	-0.11NS	0.06NS	0.25**	1			
Shell depth (mm)	0.53**	0.52**	0.58**	0.19NS	0.28**	-0.00NS	0.21*	1		
Roundness index	-0.17NS	-0.18NS	-0.13NS	0.00NS	0.00NS	-0.64**	0.57**	0.14NS	1	
Cup index	0.02NS	0.03NS	0.14NS	0.24*	0.20*	-0.49**	-0.28**	0.79**	0.16NS	1

NS, not significant (P>0.01); * = P<0.01; ** = P<0.001

Appendix D

Growth in shell length and shell depth of Pacific oysters in Experiments 1 and 2.

Shell length and depth dimensions of Pacific oysters in Experiments 1 and 2 were also measured.

Materials and Methods

The same methods as outlined in Section 2.5.2 were used. Shape indices were calculated as in Section 2.2.5.

Results

The shell length and depth of Experiment 1 oysters increased from a mean of 32.6 ± 0.2 mm ($n=180$) and 21.5 ± 0.2 mm ($n=180$) to 40.1 ± 0.3 mm ($n=360$) and 23.8 ± 0.2 mm ($n=360$), respectively (Figs. D-i, -iv). The effect of shell abrasion was usually not significant ($P>0.05$) (Figs. D-ii, -v). Aerial exposure was highly significant; after day 21, the L group grew much faster in shell length than the H group ($P<0.05$, days 42, 64, 81) (Fig. D-iii), and generally, the L group had a greater mean shell depth than the H group ($P<0.05$, days 42, 81) (Fig. D-vi).

In Experiment 2, the mean shell length increased from a mean of 39.1 ± 0.5 mm ($n=120$) to 44.5 ± 0.4 mm ($n=360$) (Fig. D-vii), but only the shell length of four out of the six groups (MH, ML, CH, CL) increased over time. The shell depth increased from a mean of 22.8 ± 0.3 mm ($n=120$) to 25.0 ± 0.2 mm ($n=360$) (Fig. D-x). Shell abrasion was highly significant ($P<0.05$) for shell length after day 38 such that, the MB and C groups had higher shell lengths than the MB group (Fig. D-viii). Shell abrasion did not cause changes in shell depth, except by the final sample, when $C>MB$, M ($P<0.05$) (Fig. D-xi). Aerial exposure had little impact on shell length (Fig. D-ix), or shell depth (Fig. D-xii), although the L group usually had a higher mean shell length ($P<0.05$, day 96), but a smaller mean shell depth ($P<0.05$, day 96), than the H group.

Discussion

The shell length growth patterns were very similar to that of shell height in Experiments 1 (Figs. 8b, c, D-ii, -iii) and 2 (Figs. 19b, c, D-viii, -ix). This shows that the effects shown for shell abrasion and aerial exposure were similar for each variable.

Shell abrasion did not cause changes in shell depth (Figs. D-v, -xi). This is supported by the results shown in Appendices E (Fig. E-iii) and F (Fig. F-iv). Robert et al. (1993) also reported that Pacific oysters cultured in rotational cylinders and in stationary mesh bags had similar shell depths ("width" in his study), despite their dissimilar mean whole weights (32 g compared to 40 g; read from Fig. 4a) by the final sample (read from Fig. 3c). Similar results were obtained by Smith (1994), who found no difference ($P>0.05$) in the shell depth of Pacific oysters cultured in rotational or fixed cylinders (read from Fig. 5.6a).

Aerial exposure caused changes in shell depth. In Experiment 1, the shell depth of the L group was usually larger ($P<0.05$, days 42, 81) than that of the H group (Fig. D-vi). The likely cause of this, apart from faster shell growth, was that the L group had grown larger shell 'flutes' (shell extensions) on their left valve (see Section 2.1), than the H group; this would make the apparent shell depth of the L group larger.

Measurement of shell flutes was not carried out, but examination of their shells, later, showed that the L group had larger flutes than did the H group. This shows that Pacific oysters cultured subtidally (0% exposure d^{-1}) will have increased shell height, length and depth dimensions, compared to those cultured in the intertidal zone (26% exposure d^{-1}). However, the greater increases in shell height and length, compared to shell depth, lead to a poorer cup index ratio in subtidal oysters; this in turn may lead to poorer condition indices (CIvol, CIshell) (Section 4.5; Appendix C).

An opposite result occurred in Experiment 2, because for three out of the last four samples, the H group had a modestly larger shell depth, than the L group ($P<0.05$, day (D-xii). However, since the range of exposures tested in Experiment 2 (0-7% exposure d^{-1}) were smaller than in Experiment 1 (0-26% exposure d^{-1}), and the differences only modest, less confidence can be placed in this result. Why the H group grew more in the shell depth dimension, is not readily explained.

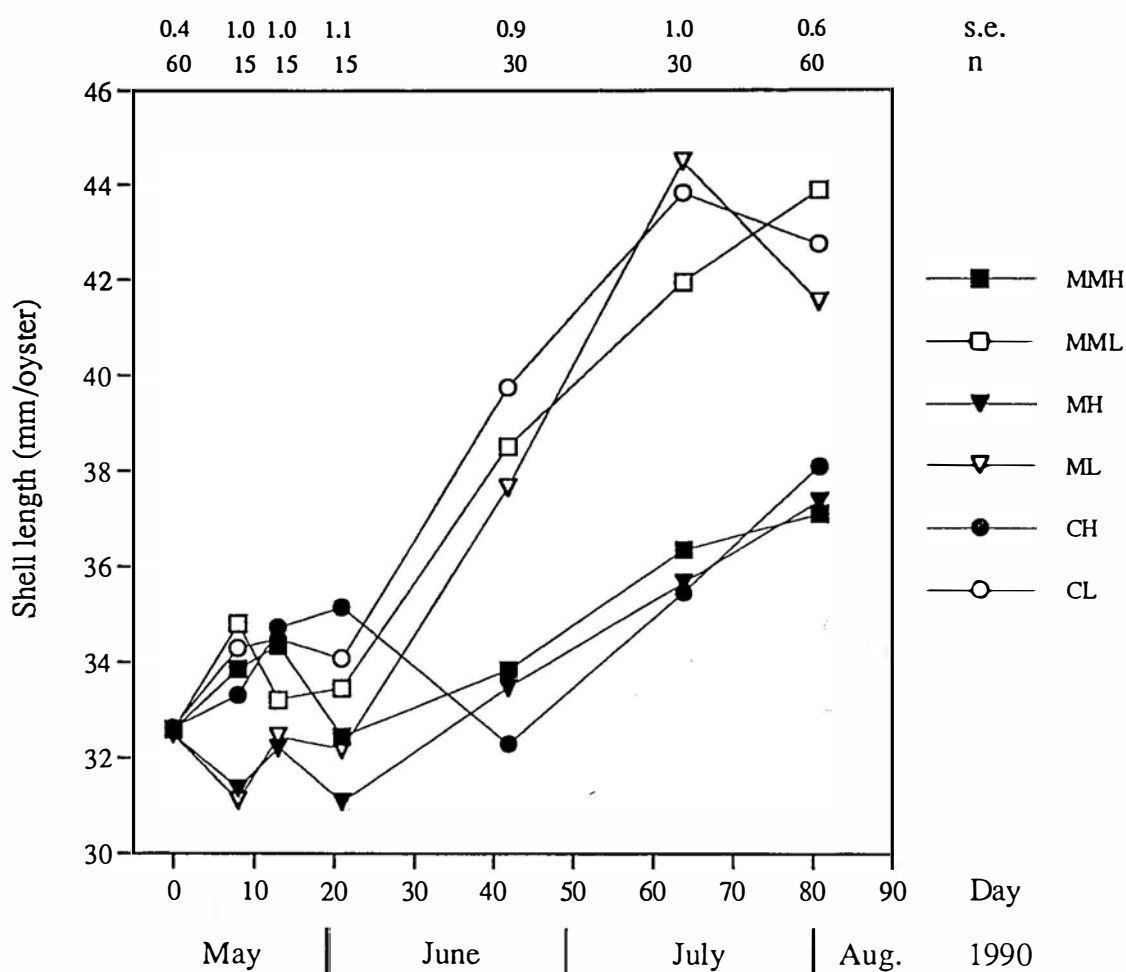
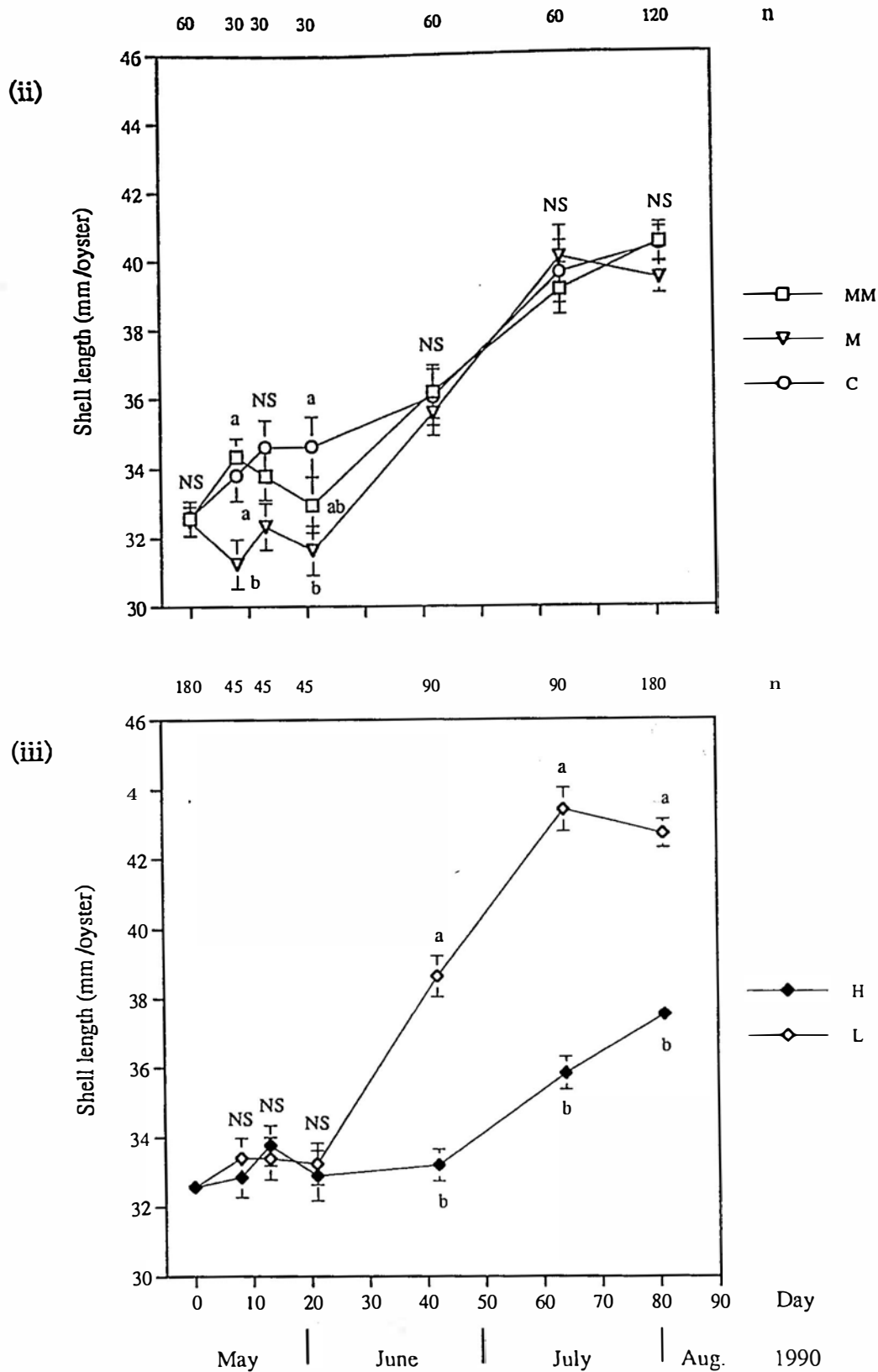


Fig. D-i. Effects of shell abrasion and aerial exposure on the mean shell length of Pacific oysters (*C. gigas*) in Experiment 1. MM, machine-graded twice; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; s.e., pooled standard error; n, sample number.



Figs. D-ii, -iii. Effects of shell abrasion (ii) and aerial exposure (iii) on the mean shell length of Pacific oysters (*C. gigas*) in Experiment 1 (means \pm s.e.). NS, for the same sample date, means do not differ significantly ($P>0.05$); the letters a, b indicate that means differ significantly ($P<0.05$). MM, machine-graded twice; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number.

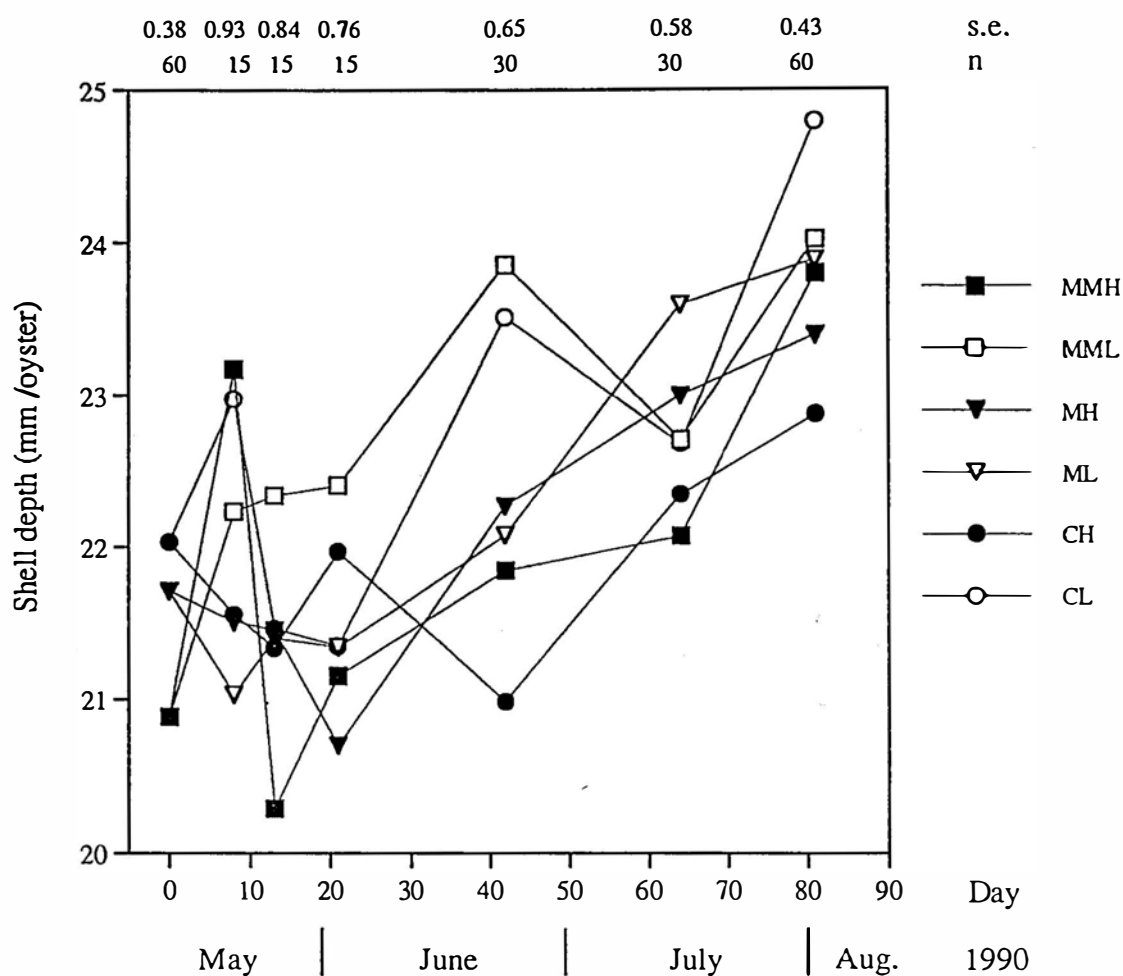
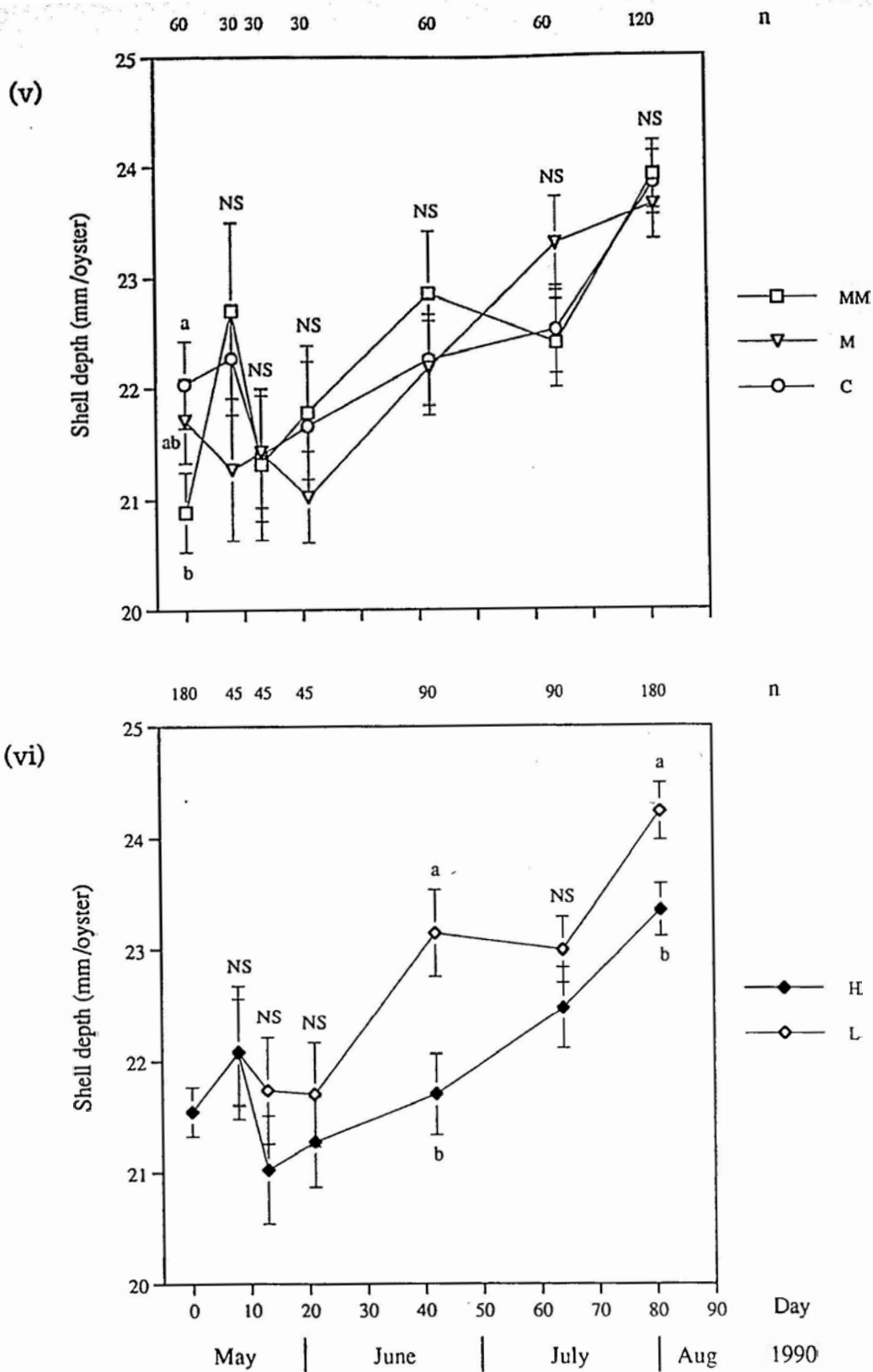


Fig. D-iv. Effects of shell abrasion and aerial exposure on the mean shell depth of Pacific oysters (*C. gigas*) in Experiment 1. MM, machine-graded twice; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; s.e., pooled standard error; n, sample number.



Figs. D-v, -vi. Effects of shell abrasion (v) and aerial exposure (vi) on the mean shell depth of Pacific oysters (*C. gigas*) in Experiment 1 (means \pm s.e.). NS, for the same sample date, means do not differ significantly ($P>0.05$); the letters a, b indicate that means differ significantly ($P<0.05$). MM, machine-graded twice; M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number.

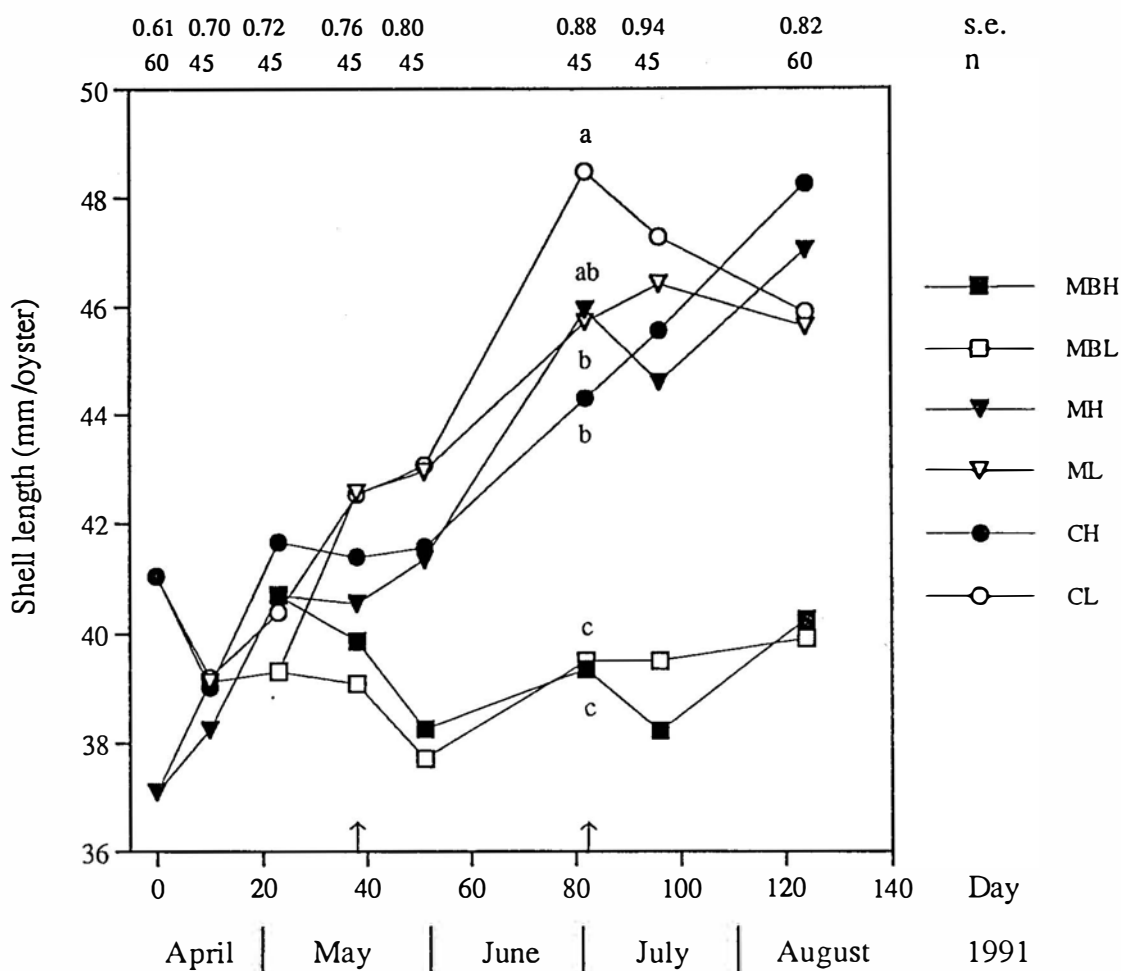
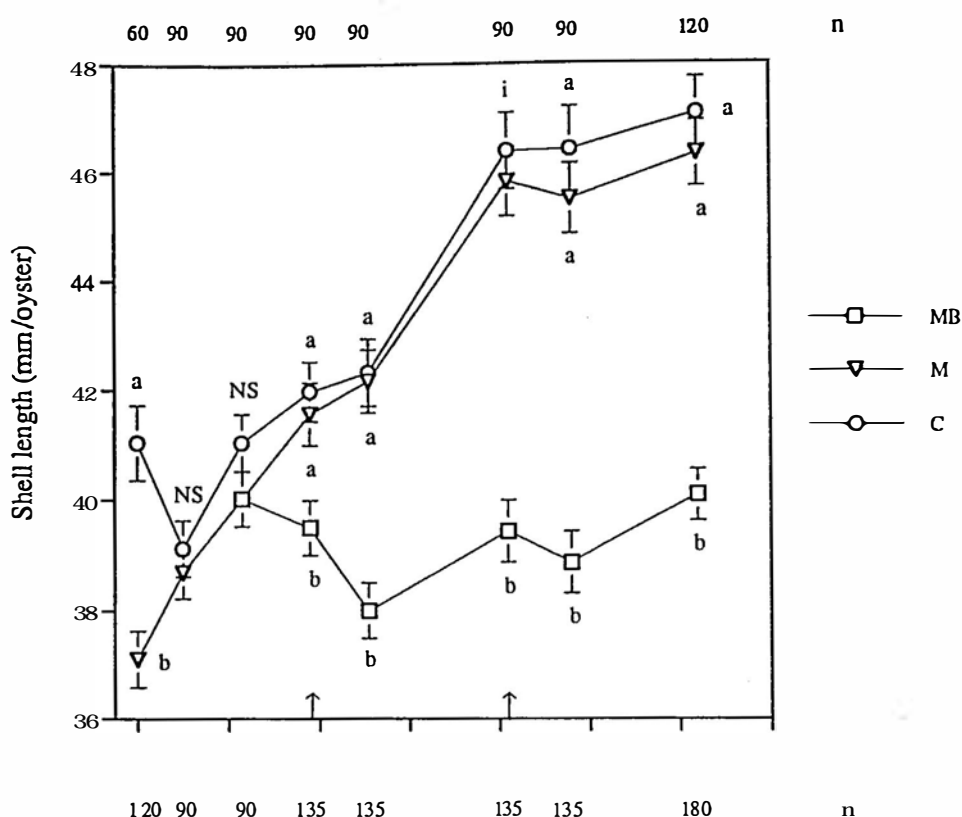
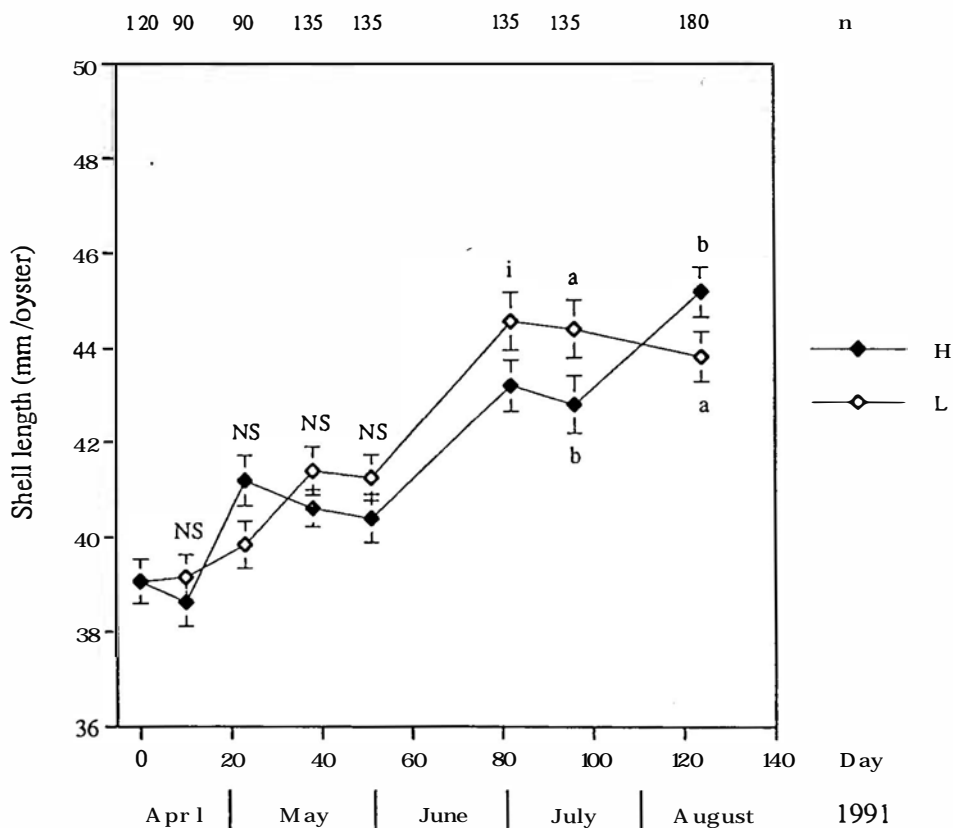


Fig. D-vii. Effects of shell abrasion and aerial exposure on the mean shell length of Pacific oysters (*C. gigas*) in Experiment 2. There was a significant interaction ($P < 0.05$) on day 82, and pairwise comparisons (Fisher's LSD) are shown [means which share common letters do not differ significantly ($P > 0.05$)]. MB, machine-graded once and baskets were shaken on days 38 and 82 (shown by arrows); M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; s.e., pooled standard error; n, sample number.

(viii)



(ix)



Figs. D-viii, D-ix. Effects of shell abrasion (viii) and aerial exposure (ix) on the mean shell length of Pacific oysters (*C. gigas*) in Experiment 2 (means \pm s.e.). NS, for the same sample date, means do not differ significantly ($P>0.05$); the letters a, b indicate that means differ significantly ($P<0.05$); i, for this sample date a significant interaction (Fig. D-vii) prevented statistical comparisons of means based on pooling. MB, machine-graded once and baskets shaken on days 38 and 82 (shown by arrows); M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number.

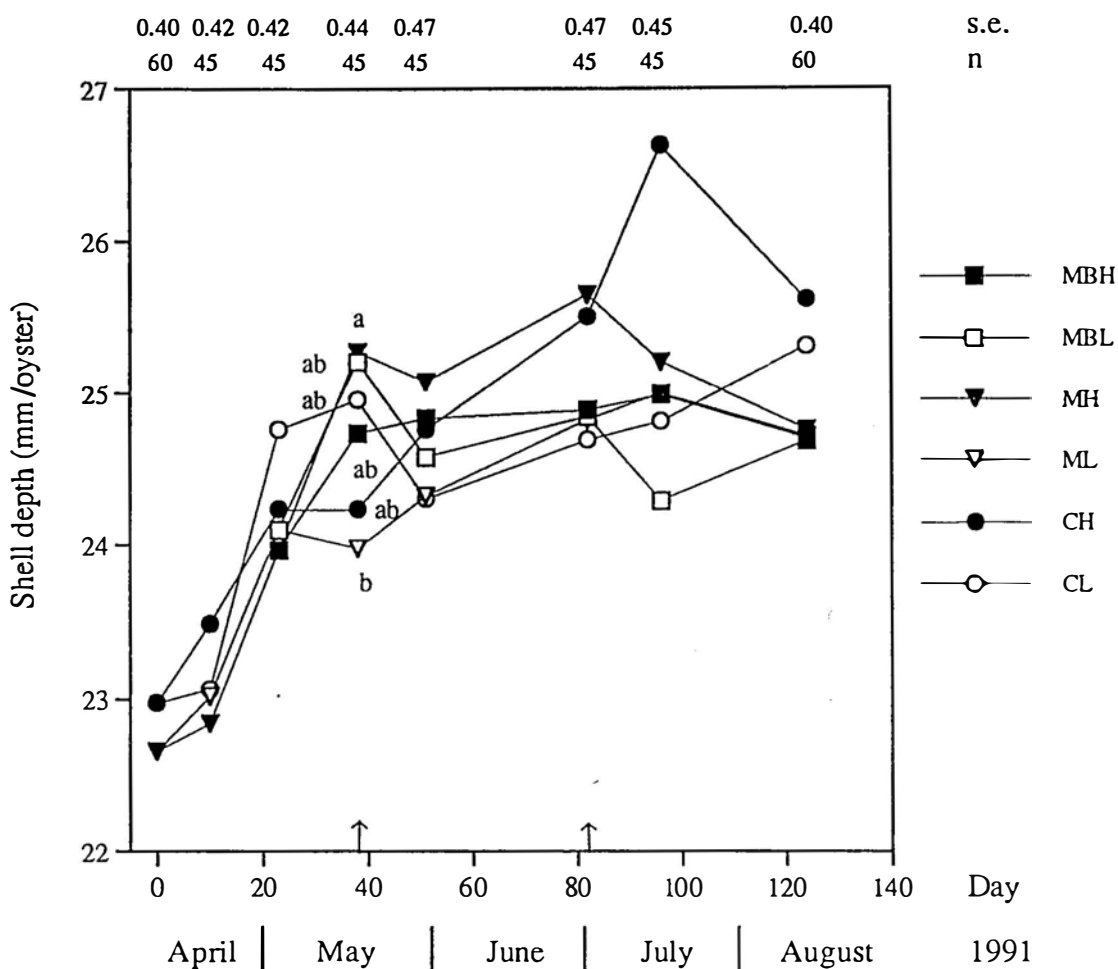
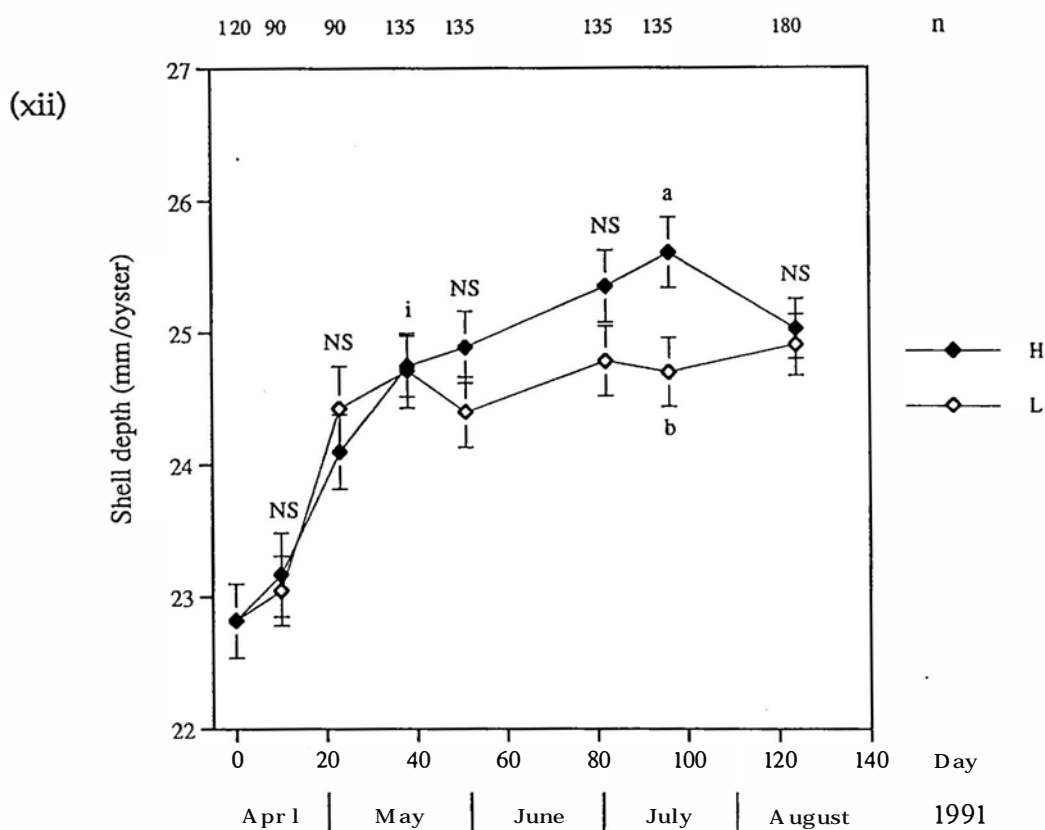
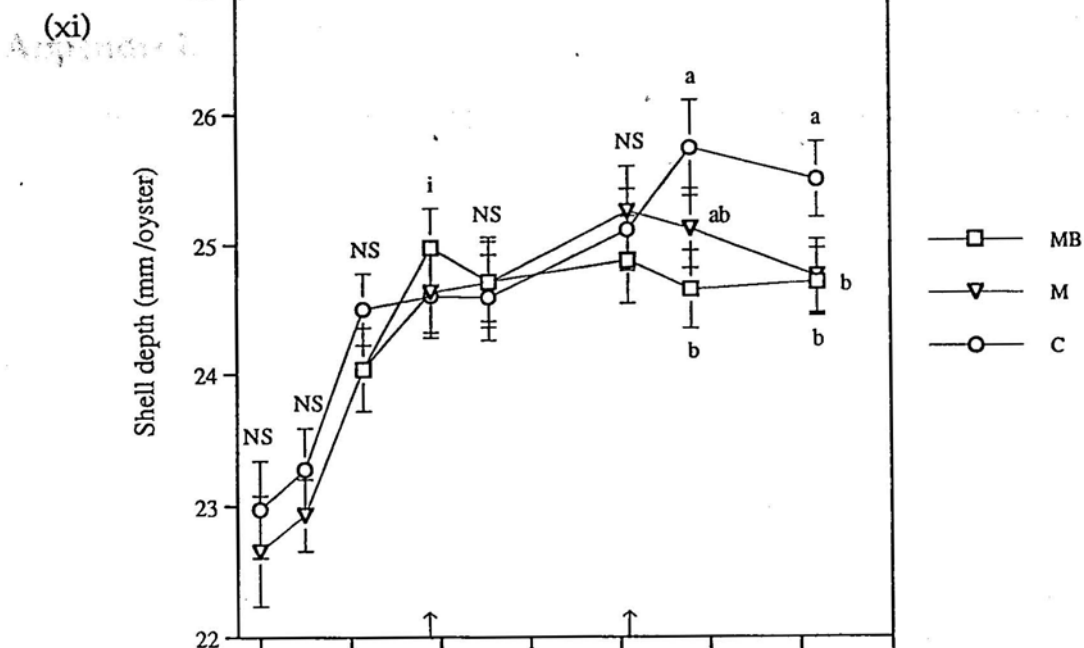


Fig. D-x. Effects of shell abrasion and aerial exposure on the mean shell depth of Pacific oysters (*C. gigas*) in Experiment 2. There was a significant interaction ($P < 0.05$) on day 38, and pairwise comparisons (Fisher's LSD) are shown [means which share common letters do not differ significantly ($P > 0.05$)]. MB, machine-graded once and baskets were shaken on days 38 and 82 (shown by arrows); M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; s.e., pooled standard error; n, sample number.



Figs. D-xi, -xii. Effects of shell abrasion (xi) and aerial exposure (xii) on the mean shell depth of Pacific oysters (*C. gigas*) in Experiment 2 (means \pm s.e.). NS, for the same sample date, means do not differ significantly ($P>0.05$); the letters a, b indicate that means differ significantly ($P<0.05$); i, for this sample date a significant interaction (Fig. D-x) prevented statistical comparisons of means based on pooling. MB, machine-graded once and baskets shaken on days 38 and 82 (shown by arrows); M, machine-graded once; C, control; H, high aerial exposure; L, low aerial exposure; n, sample number.

Appendix E

Additional results showing the shell dimensions and shape indices of Experiment 2 oysters subjected to shell abrasion treatments.

To determine actual shell frill losses (Fig. 3), a sub-sample of Pacific oysters in Experiment 2 were measured at the Pipeclay Lagoon lease, before and after shell abrasion treatments were applied.

Materials and Methods

On day 0 of Experiment 2, 20 Pacific oysters (mean shell height = 76.7 ± 2.0 mm) were randomly sampled from the C group. These were labelled (water-proof texta), and then their shell height and length were measured prior to placing them, along with other oysters, onto a machine grader. Of these, 13 were recovered, and their shell height and shell length were measured to determine shell frill losses. On day 38, half of the M group baskets were shaken for 0.5 min in air; these became the MB group, which were shaken again on day 82. The shell height, length and depth of 30 oysters were recorded before and after treatment, and on both days, 29 oysters were recovered. The roundness and cup indices (Section 2.5.5) were calculated from these data.

The data were analysed using one-factor ANOVA. Homogeneity of variance was assessed using Cochran's test (Sokal and Rohlf, 1981).

Results

Reductions in shell length (Fig. E-ii) were slightly larger ($P < 0.05$, day 38) than reductions in shell height ($P > 0.05$, days 0, 38, 82) (Fig. E-i), while changes in shell depth were negligible (Fig. E-iii). Machine-grading the oysters on day 0 caused a non-significant decline in the roundness index ($P > 0.05$), but subsequent basket shaking had less impact ($P > 0.05$, days 38, 82) (Fig. E-iv). Shaking baskets on day 38 did not improve ($P > 0.05$) the cup index, but on day 82, the cup index was improved ($P < 0.05$) (Fig. E-v).

Actual shell height, shell length and shell depth losses, and the percentage changes are shown in Table E.

TABLE E

Actual losses and percentage decline in the shell height, shell length and shell depth dimensions of Pacific oysters (*C. gigas*), after shell abrasion treatments were applied in Experiment 2.

Shell abrasion treatment	Day	n	Shell height (mm oyster ⁻¹)		Shell length (mm oyster ⁻¹)		Shell depth (mm oyster ⁻¹)	
			mm loss	Decline	mm loss	Decline	mm loss	Decline
			oyster ⁻¹	(%)	oyster ⁻¹	(%)	oyster ⁻¹	(%)
Machine-grading ¹	0	13	3.3 ± 0.4	4.3	5.9 ± 1.0	12.8	-	-
Basket shaking ²	38	29	3.4 ± 0.5	4.6	2.5 ± 0.4	6.2	0.4	1.7
Basket shaking ³	82	29	4.5 ± 0.6	5.8	2.9 ± 0.7	6.9	+0.2	+0.8

¹ M group, machine-graded once.

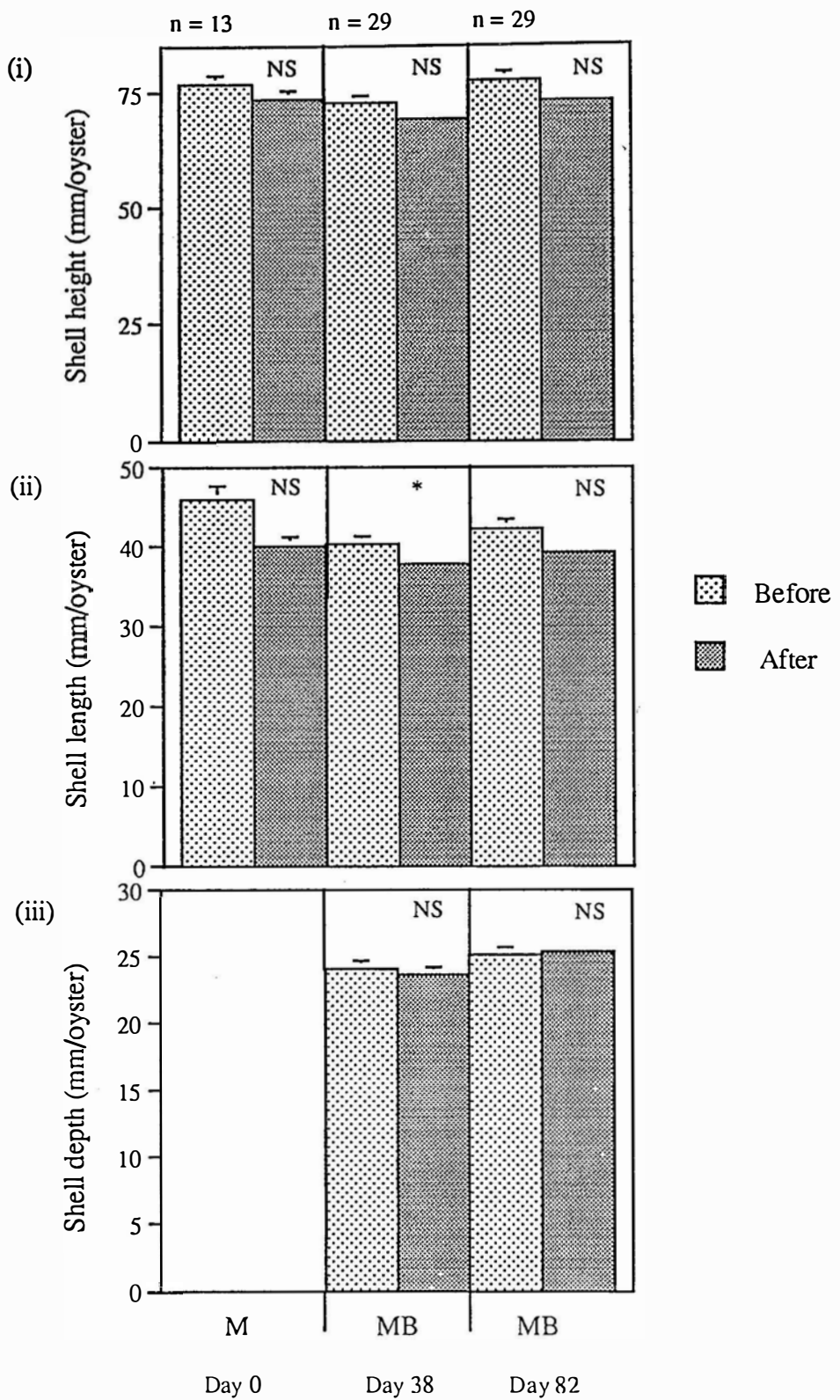
² Half of the M group baskets were shaken, creating the MB group.

³ MB group, machine-graded once and baskets were shaken on days 38 and 82.

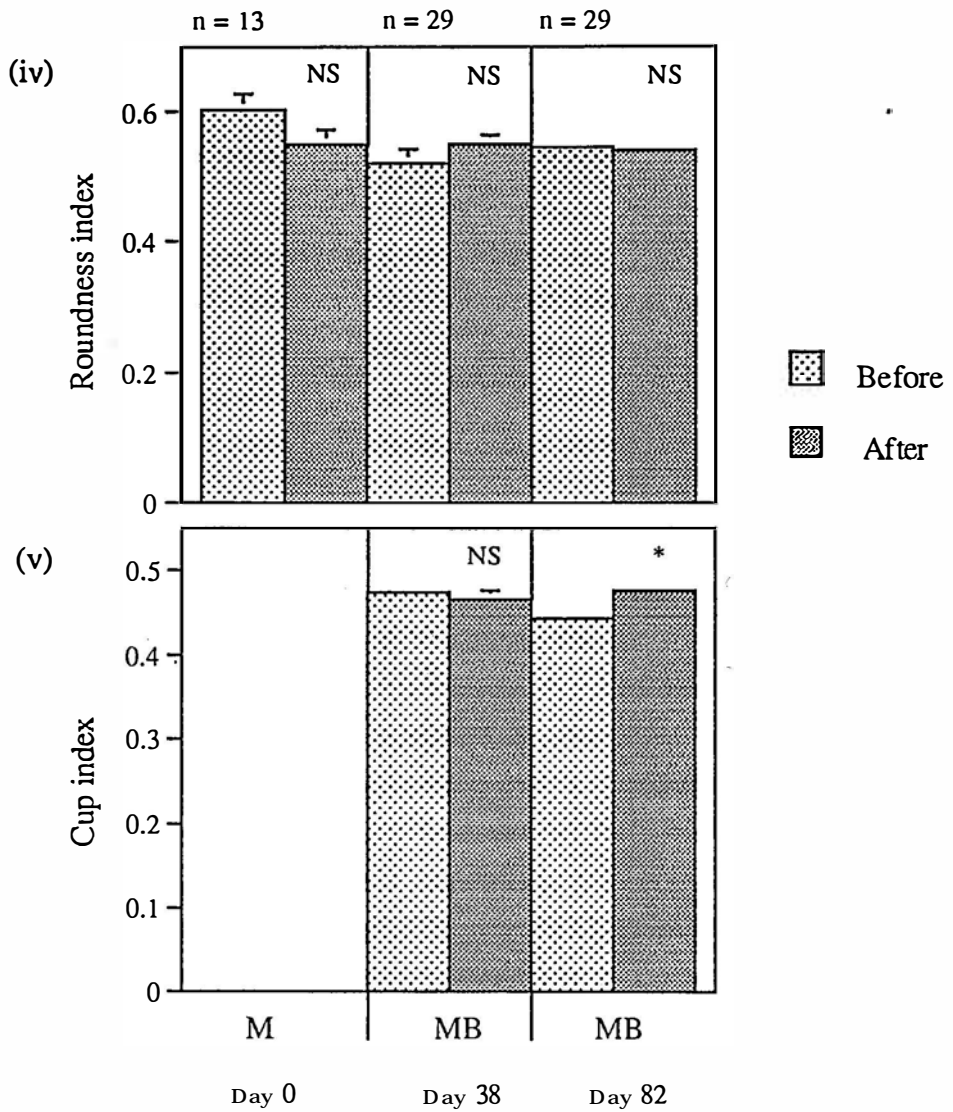
Discussion

The Pacific oysters, prior to the initial machine grading, had large shell frill extensions (see Section 3.4.2.1). The machine-grading did not cause large reductions in shell height (4.3%), but shell length changes were large (12.8%) (Table E). Shell frill growth along the length axis occurs in two directions, but can only occur in one for the height axis (Galtsoff, 1964). Therefore, more shell was removed along the length axis.

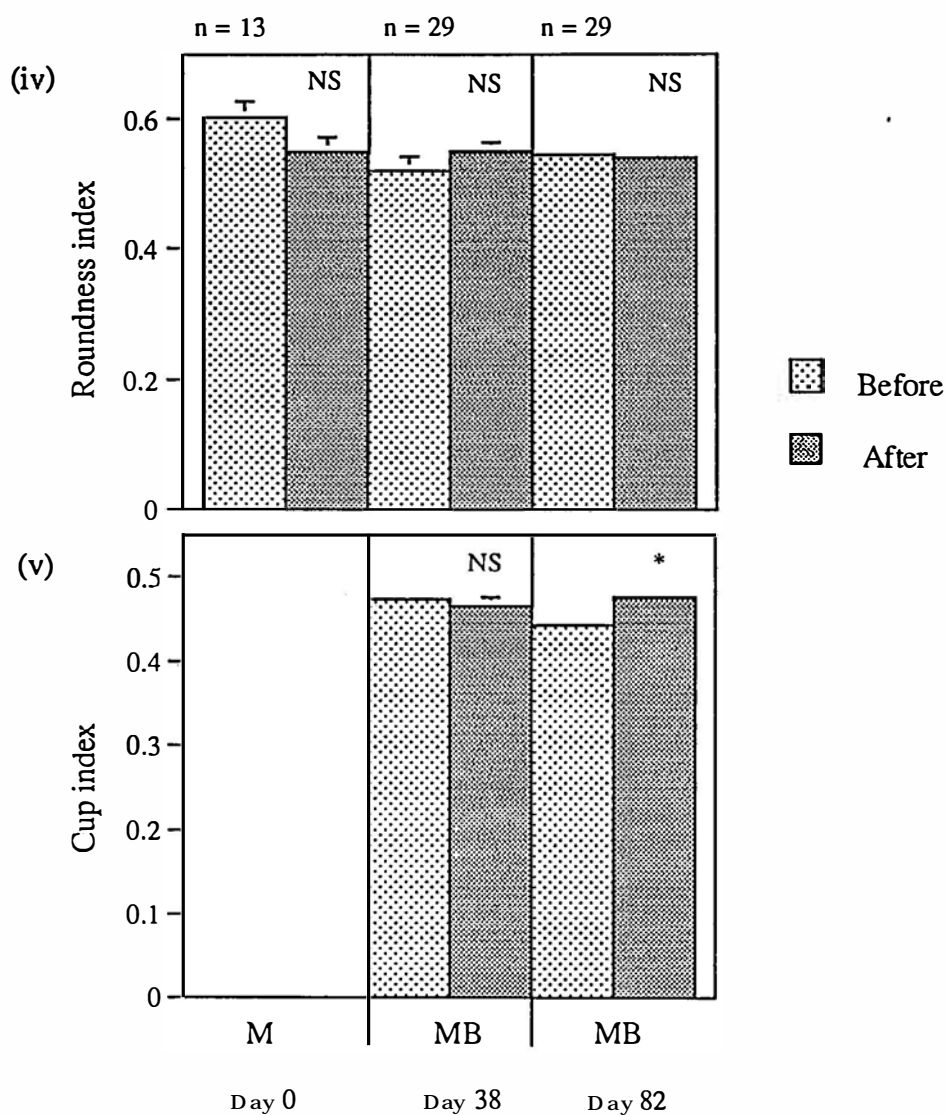
Subsequent basket shaking treatments caused moderate losses (6-7%) in shell length, but these were still greater, however, compared to the shell height losses (5-6%) (Table E). A positive change (+0.2 mm) in shell depth (Table E), indicates that there is some difficulty in measuring this dimension accurately. The accuracy should be improved when larger numbers are measured, but in any case, shell abrasion caused negligible changes in shell depth. Robert et al. (1993), who cultured Pacific oysters in rotational cylinders and compared their growth with bag cultured oysters found, after 14 months, that the shell depth ("width" in their study) of each group was similar ($P > 0.05$) (read from Fig. 3c). Smith (1994) had similar results (read from Fig. 5.6a) when Pacific oysters cultured in rotational cylinders, and therefore subjected to regular abrasion, had a similar mean shell depth, compared to those in fixed cylinders.



Figs. E-i, -ii, -iii. Effects of shell abrasion on the mean shell height (i), shell length (ii) and shell depth (iii) of a sample of Pacific oysters (*C. gigas*) from Experiment 2, before and after shell abrasion treatments were applied. Means \pm SE; NS, means, for the same sample date, do not differ significantly ($P > 0.05$); *, means differ significantly ($P < 0.05$). Data for two aerial exposure treatments were pooled. M, machine-graded once; MB, machine-graded once and baskets were shaken on days 38 and 82; n, sample number.



Figs. E-iv, -v. Effects of shell abrasion on the mean roundness index (iv) and cup index (v) of a sample of Pacific oysters (*C. gigas*) from Experiment 2, before and after shell abrasion treatments were applied. Means \pm SE; NS, means, for the same sample date, do not differ significantly ($P>0.05$); *, means differ significantly ($P<0.05$). Data for two aerial exposure treatments were pooled. M, machine-graded once; MB, machine-graded once and baskets were shaken on days 38 and 82; n, sample number.



Figs. E-iv, -v. Effects of shell abrasion on the mean roundness index (iv) and cup index (v) of a sample of Pacific oysters (*C. gigas*) from Experiment 2, before and after shell abrasion treatments were applied. Means \pm SE; NS, means, for the same sample date, do not differ significantly ($P>0.05$); *, means differ significantly ($P<0.05$). Data for two aerial exposure treatments were pooled. M, machine-graded once; MB, machine-graded once and baskets were shaken on days 38 and 82; n, sample number.

Appendix F

The effect of shaking baskets of Pacific oysters on their whole weight, shell dimensions and shape indices.

This additional experiment was carried out to determine the actual weight loss associated with shell removal. In addition, shell dimensions were measured, and shape indices were calculated.

Materials and Methods

Pacific oysters [mean whole weight = 76.5 ± 1.1 g, mean shell height = 93.2 ± 0.9 mm (n=120)] with large shell frill extensions were selected from a commercial lease, located in Pipeclay Lagoon, Tasmania. These were held in a recirculating system for one day, prior to the experiment.

The oysters were scrubbed, superficially dried with paper towelling, and then labelled (water-proof texta). Each oyster was then weighed and measured. The oysters, in groups of 40, were then shaken in air, in one side of a 12-mm mesh basket unit for 1 min. The shell frill (Fig. 3) removed from each group (n=3) was collected and allowed to air-dry for two days before weighing. The oysters were then re-weighed and measured, however, while doing this, it was noticed that many had lost their shell cavity fluids. For this reason the oysters were resuspended in seawater for a further day, before they were again superficially dried and measured. Roundness and cup indices were determined using the shell height, length and depth dimensions (Section 2.5.5).

Homogeneity of variance was assessed using Cochran's test (Sokal and Rohlf, 1981). The data were then analysed using one-factor ANOVA.

Results

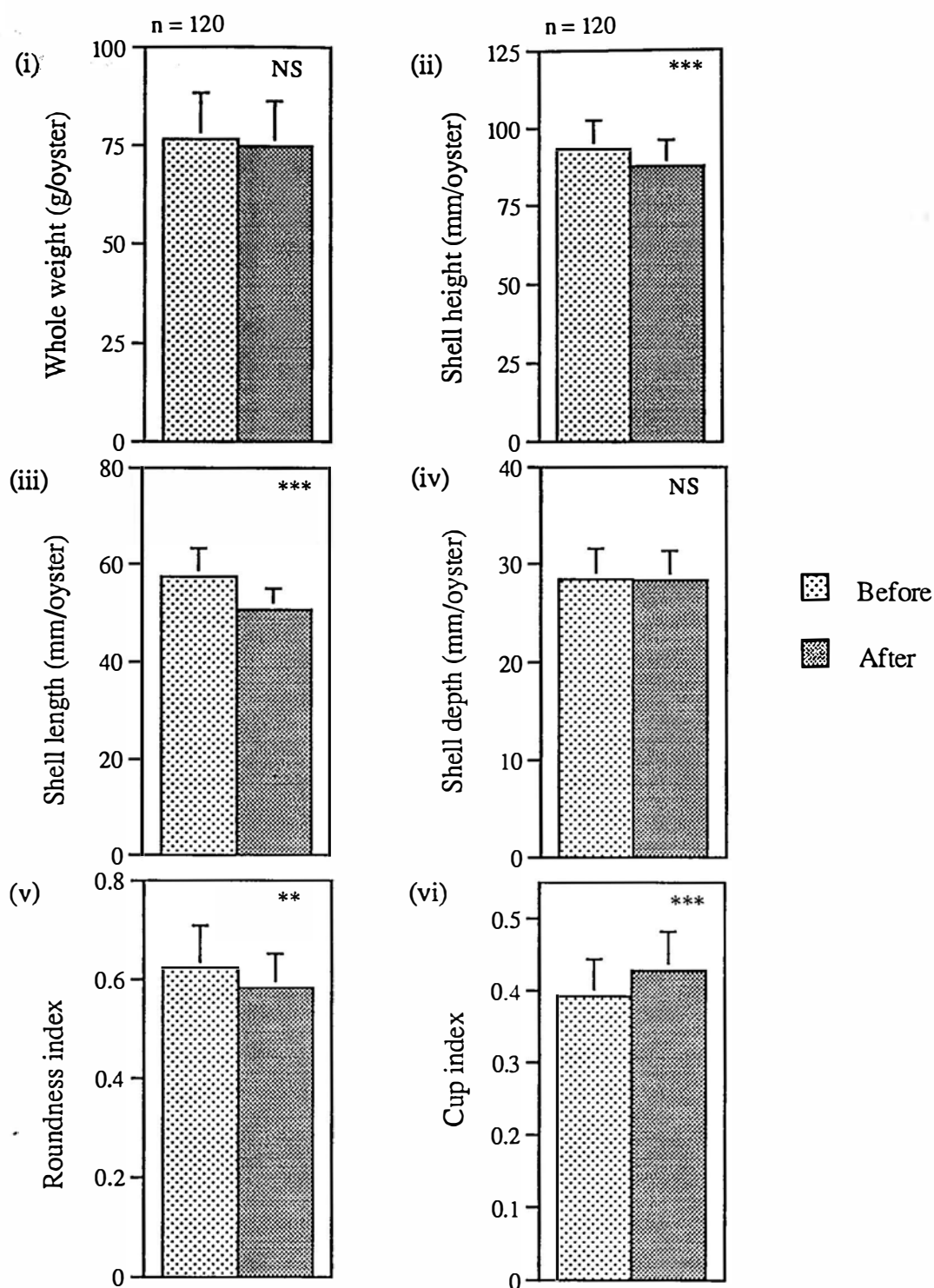
The shell frill retrieved represented 1.9% of their initial whole weight (1.48 g shell frill removed oyster⁻¹). Whole weight did not change significantly ($P > 0.05$) (Fig. F-i). The reduction in whole weight was 2.6% (whole weight loss = 2.00 g oyster⁻¹). Basket shaking did cause significant losses ($P < 0.001$) in shell height (loss of 5.5 mm oyster⁻¹; 5.9% reduction) and shell length (loss of 6.7 mm oyster⁻¹; 7.2% reduction) (Figs. F-ii, -iii). Shell depth did not change significantly ($P > 0.05$) (loss of 0.12 mm oyster⁻¹; 0.4% reduction) (Fig. F-iv). Finally, the oysters became less round ($P < 0.01$) (Fig. F-v), but more cupped in shape ($P < 0.001$) (Fig. F-vi).

Discussion

Losses in whole weight were small (2.6%). Spencer et al., (1992) reported that most of the rough-handling treatments used in their study, caused minimal losses in whole weight (1-2%), of small Pacific oysters (4-8 g mean whole weight). The agitation in air treatments, for 1 or 2 min, however, caused losses of 5 and 7% (mean values), respectively, for small oysters, and 10 and 14%, respectively, for larger oysters (19-24 g), although these probably included fluid loss (Spencer et al., 1992).

As for Experiment 2 oysters (Appendix E), the shell depth did not change ($P>0.05$). Shell height and shell length losses in oysters in this experiment, were 5.9 and 7.2% ($n=120$), respectively, and are similar to the shell height and length losses of Experiment 2 oysters, which were between 4-6% and 6-13% ($n=13-29$), respectively (Appendix E). In this experiment the losses incurred were significant ($P<0.001$) for both shell height and shell length (Figs. F-ii, -iii), but were only significant for shell length ($P<0.05$) on one sample in Experiment 2 (Appendix E). This emphasises the importance of using large sample numbers.

In this experiment, the roundness index decreased ($P<0.01$) (Fig. F-v), but the cupped shape of the oysters improved ($P<0.001$) (Fig. F-vi). In comparison, the roundness of Experiment 2 oysters measured at the lease site, was not improved ($P>0.05$) by shell abrasion (Fig. E-iv). The cup index, however, was improved ($P<0.05$) on day 82 (Fig. E-v). For the majority of oysters, retarding the shell growth of the H group in Experiment 1, and the MB group in Experiment 2, produced oysters which were less round, but which had a better cup shape after 81-124 days of culture (Figs. 13b, 14b, 24b, 25b).



Figs. F-i: -vi. Effects of shell abrasion on the mean whole weight (i), shell height (ii), shell length (iii), shell depth (iv), roundness index (v) and cup index (vi) of a sample of Pacific oysters (*C. gigas*) obtained from a commercial lease in Pipeclay Lagoon, before and after a shell abrasion treatment was applied¹. Means \pm SE; NS, means, for the same sample date, do not differ significantly ($P > 0.05$); ** = $P < 0.01$; *** = $P < 0.001$; n, sample number.

¹ 12 mm mesh baskets were shaken in air for 1 min.

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