OXYGEN CONSUMPTION AND GROWTH OF *MYTILUS EDULIS* ON THE ATLANTIC COAST OF NORTH AMERICA, SOUTH OF NEWFOUNDLAND

Jennifer R. Hum

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Marine Sciences Centre
McGill University
Montreal, Canada

February, 1976

ABSTRACT

In seven natural populations of *Mytilus edulis*, between Newfoundland and Virginia, oxygen consumption and shell growth were measured over a period of 15 months. Seasonal variation in oxygen consumption followed the seasonal variation in temperature at each station (maximum in summer, minimum in winter), except at above optimum (20°C) temperatures. Latitudinal differences in oxygen consumption rates were also temperature-related, with the warmest stations (southern) producing the highest rates throughout the year. Average shell growth followed a similar pattern to that of oxygen consumption, but with complications possibly caused by food availability, especially at midlatitude stations. Growth history and life table characteristics varied over the latitudinal range. No seasonal or latitudinal acclimation (Precht Type II) of oxygen consumption or growth was demonstrated.

SOMMAIRE

La consommation d'oxygène et la croissance de la coquille ont été mesurées sur sept populations naturelles de Mytilus edulis vivant entre Terre-Neuve et la Virginie au cours d'une période de quinze mois. A chaque station, la variation saisonnière dans la consommation d'oxygène suit la variation thermique (maximum en été, minimum en hiver), sauf au dessus d'une température optimale de 20°C. Les différences entre latitudes dans la consummation d'oxygène sont elles aussi liées à la température, les taux les plus élevés s'observant aux stations les plus chaudes (stations au sud). En moyenne la croissance de la coquille suit la même courbe que la consommation d'oxygène, mais avec des irrégularités qui s'expliquent peut-être par la disponibilité en nourriture, particuliérement pour les stations situées aux latitudes moyennes. Le déroulement de la croissance et les caractéristiques vitales varient dans l'intervalle de latitude. Aucune acclimation saisonnière ou latitudinale (type II de Precht) de la consommation d'oxygène ou de la croissance n'a été démontrée.

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NOTE ON THE INTRODUCTION.

The introductory chapters are to provide a context for, and explain some of the problems encountered during, the experiments which are described in the later sections. The study evolved from some research which was done on Mytilus edulis and other mussels in Australia and New Zealand (Hum, 1969, 1971). The present study is concerned with North American M. edulis, and a broad summary of pertinent world research is made in "Introduction (1) Background Literature." This is not intended to be a review of Mytilus edulis literature as a whole, nor as a review of metabolism and growth literature. These two vast subjects are, or will be, well accounted for elsewhere (see Bayne, in prep.), but some detail has been entered into on what might seem peripheral subjects. This detail is to provide a well-referenced basis for the context of this study. The bulk of the introduction is inessential for any reader who is familiar with the metabolism of Mytilus edulis, as it is derived almost entirely from the literature. It simply provides a ready reference to my bias of this subject.

The section on geographic distribution is mainly to point out the wide distribution of the species, its apparent success over a range of habitats, and its suitability to latitudinal studies - both in the problems it creates as a variable species over this range, and the similarities by which widely ranging populations may be regarded as a unit.

Because of this wide distribution, variability, and the number of interested researchers, a discussion on the status of the species is included. The taxonomic status of the M. edulis species complex remains open to controversy and this theme is developed, mainly with respect to form, in the section "Variability within the species."

Research in the taxonomic arena is beginning to relate environmental and physiological factors to the systematic problem: factors affecting metabolic rate and growth of the mussel are expressed visibly as form, abundance and distribution. The present study is mainly concerned with the latitudinal differences in growth and metabolic rate of the mussel in

Atlantic North America, and seems to fit into the context of other mussel research via this interaction of environment and physiology to give a mussel characteristic of its habitat, geographic location and genetic background. This is discussed in "Introduction (2) Latitudinal Aspects of Metabolic Rate Functions," which also includes a brief treatment of metabolic rate functions in poikilotherms other than Mytilus edulis.

INTRODUCTION (1) BACKGROUND LITERATURE.

I. GEOGRAPHIC DISTRIBUTION

Mytilus edulis has a wide distribution in both hemispheres but is not cosmopolitan. It occurs from the subarctic and subantarctic to the warm temperate areas.

In the subantarctic it has been recorded from South America, Kerguelen Island, Auckland Islands and Campbell Island, but from no other subantarctic islands. Southern Hemisphere transitional warm temperate distribution extends into North Island New Zealand, South Australia, Victoria, Tasmania and South America. Mytilus edulis reaches into the warm temperate waters of southern New South Wales, Western Australia and South America. It does not occur in South Africa.

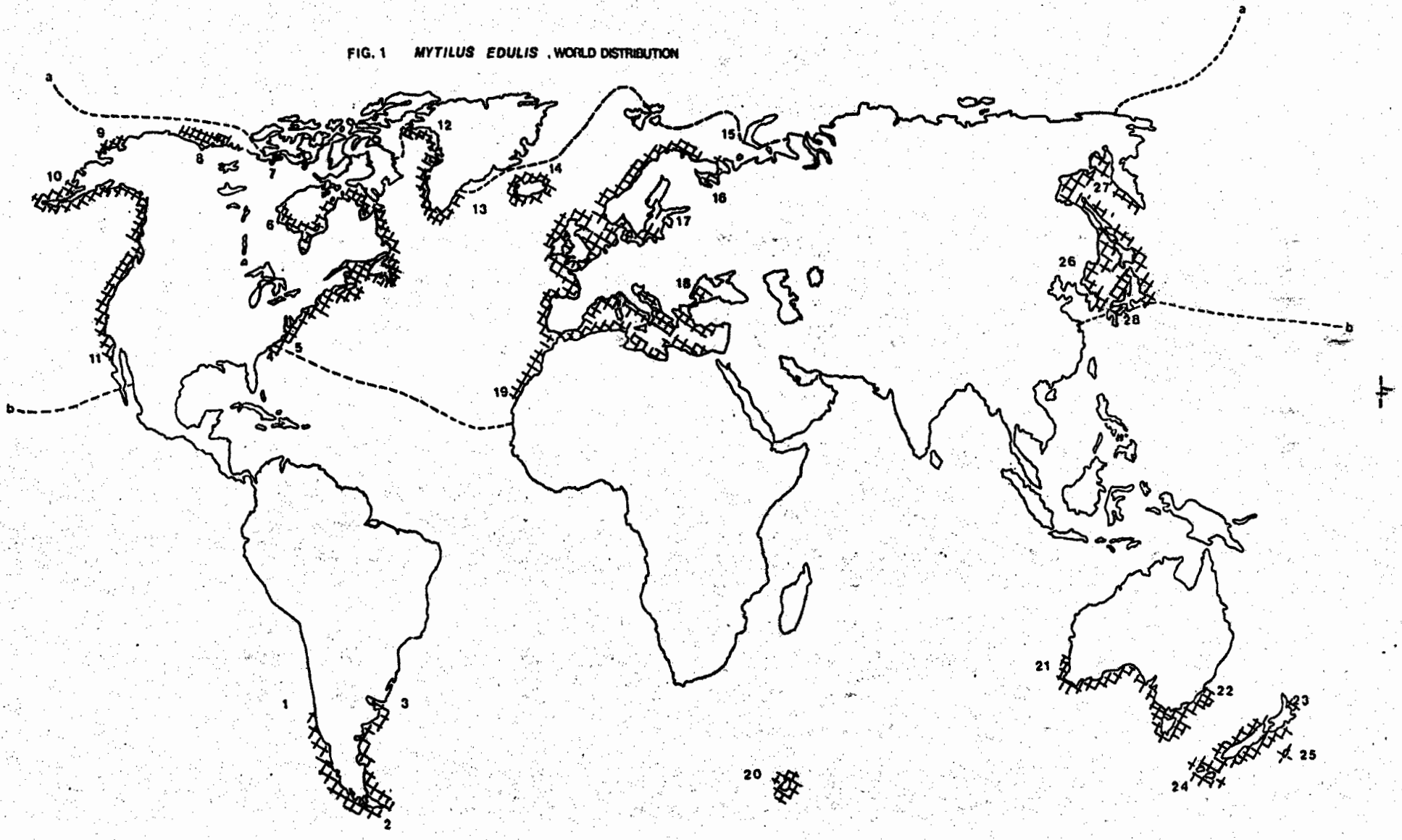
North American distribution ranges from the islands of the Canadian North West Territories to Baja California on the west coast, and the Carolinas on the east coast. Mytilus edulis also occurs in Greenland and Iceland. In Europe it ranges from the White Sea to the Mediterranean, with records as far south as Spanish Sahara in Western Africa, and as far east as Alexandria and the Black Sea (see section on taxonomy). Asian occurrences are recorded from Kamchatka to Korea and the Inland Sea of Japan.

The pattern of distribution, with sources, is shown in Figure 1.

Analysis of distribution is given by Hutchins (1947), Wells and Gray (1960), on southern limits of the North American distribution; Lubinsky (1958), on the Canadian Eastern Arctic; Theisen (1973) & Petersen (1974) on North West Greenland; Knox (1960), summarizing Southern Hemisphere distribution in less detail; and Hum (1969, 1971), on Eastern Australian and New Zealand distribution.

Hutchins (1947) relates North American southern limits to the thermal tolerance of the mussel, concluding that the southernmost occurrence at

FIG. 1 *MYTILUS EDULIS* . WORLD DISTRIBUTION



Beaufort, North Carolina is at the maximum temperature level which the species can tolerate (according to Hutchins at 28°C). Comparing this southern limit with the (less reliable) limits stated for Africa, Asia and Pacific North America, Hutchins found good evidence for the hypothesis of an equatorward distribution limited at the 27°C summer maximum monthly mean isotherm. Wells and Gray (1960) have studied the southern limit of Atlantic North American distribution in more detail. Permanent occurrences, with mussels reaching a large size, were observed to exist from Cape Hatteras northward. Transient occurrences with mussels growing only to about 33mm. during the spring and disappearing in late July exist up to 300 miles further south at Charleston, South Carolina. The pattern is explained in terms of temperature tolerance: Mytilus edulis can survive in the south (Northern Hemisphere) only until the sea temperature reaches the mussel's thermal limit. Thus the southern populations exist only by stocking from the more northern populations.

Lubinsky (1958, 1967, 1971) invokes factors other than temperature as limiting the northern distribution of Mytilus edulis in the Canadian Eastern Arctic. The penetration of Atlantic and Pacific waters into these northern regions seems to be responsible for the gross distribution of the mussel, the northern limit of which follows that of the subarctic zone as delimited by Dunbar (1947). Several occurrences exist beyond what is thought to be the subarctic limit and probably represent incursions of Atlantic water into these regions. Much of the Mytilus distribution in the Eastern Arctic may be due to localized conditions. Low salinities in many areas may be responsible for lack of occurrence, as suggested by severely stunted forms occurring at salinities below 23‰ in the south of Hudson Bay, despite relatively high temperatures.

Low salinity is also an important factor in limiting the distribution of M. edulis in Greenland (Thorson, 1933), but probably of more general importance in the northernmost limitation of the mussel is the sea ice (Petersen, 1974). This has its effect in two ways: (a) The mechanical effects of the sea ice foot on the macrofauna have been noted by Bertelsen (1937), Madsen (1936, 1940) and Just (1967, 1970). Denudation of the macrofauna by this ice foot is still somewhat local however: Theisen(1973)

and Petersen (1974) report survival of Mytilus edulis populations for many years in the tidal zone of Northwest Greenland, subjected to ice foot and shore ice every winter. (b) Petersen (1974) develops a theory that

> "the most important biological effect of the ice-foot is that it foreshortens the biological season. In spring the effect is that the organisms that are frozen solid in the ice cannot start their growth and life-cycles until they have been thawed free. In the autumn the season ends with cold, darkness and being frozen into the ice; but apart from that, it would seem that the animals with pelagic larvae cannot reach the settling stage before the rocks are covered with shore-ice."

Mytilus edulis in the Thule district must originate from larvae carried north by the West Greenland Current. Theisen (1973) suggests that small changes in the hydrography of the West Greenland region will have a large effect on the success of spatfalls near the northern limit of M. edulis distribution. This is attested to by the patchy year classes present in the northern mussel populations. Another influence on the slow development rate may be the short season of primary production in these waters (Madsen, 1936, 1940). The theory of Petersen seems to fit well with the remainder of the mussel's distribution in the Northern Hemisphere (see Figure 1).

Some analysis of Southern Hemisphere distribution has been made in conjunction with wider studies on faunal provinces (Bennett and Pope,1953; Knox, 1960). In a detailed analysis of distribution in eastern Australia and New Zealand, Hum (1971) invoked temperature as the determinant of the equatorward distribution of the mussel: the thermal tolerance coinciding with conditions in the field where mortality occurred, or where growth and development were severely inhibited (see below). Allen (1955) showed that the temperature range for successful larval settlement is 12.5°C to 19°C, with insignificant settlement above 22°C. Local distribution may further be influenced by directions of ocean currents and the availability of suitable substrates (Hum, 1971). In eastern Australia and especially in North Island New Zealand, the prevailing ocean currents tend to retard northerly flux of spat from the regions of maximal development of populations to those fringe areas that would provide suitable conditions. Dispersal is inhibited along the coast by lack of suitable substrate and by intense competition from the subtropical and warm temperate faunas that

inhabit these areas. But development of populations is now being assisted by human activity in the large inlets at the equatorward edge of the mussel's range. Man-made structures are offering both suitable substrate and freedom from competition for at least enough time to allow reproduction to occur. This results in extension of the large populations of the mussel equatorward. (The Chesapeake Bay Bridge-Tunnel in Virginia, U.S.A. may also be providing a staging site that could result in an increase of Mytilus edulis populations southward.)

The phenomenon of bipolarity may be explained by climatic change. Past distribution of Mytilus edulis is more widespread than at present. Fossils occur at Spitsbergen, which is at present north of the mussel's range (Appellöf, 1912), and in Texas which is at present too warm for Mytilus edulis (Ladd et al., 1957). The recent distribution of M. edulis corresponds to that of Aulacomya and Chloromytilus suggesting that they have the same history (Soot-Ryen, 1955; Knox, 1963).

II. VARIATION WITHIN THE SPECIES

The existence of varieties in shell shape, thickness of valves and colour of Mytilus throughout the world has led to some confusion as to the taxonomic status of the group. A brief treatment of this taxonomic problem is relevant to the environmental physiology of Mytilus edulis; in fact the growth and metabolism of the mussel have direct bearing on these taxonomic problems.

The zoological history of Mytilus can be taken as starting in the seventeenth century with the anatomical description by de Heide (White, 1937). Taxonomically the genus was the first described by Linnaeus (1758): "Animal Tethys. Testa bivalvis, rudis, saepius affixa Bysso. Cardo edentulus, distinctus, linea subulata, excavata, longitudinali." This description covers several shells, some of which are now referred to families other than the Mytilidae.

Linnaeus refers to the species Mytilus edulis in "Vermes Testacea" as "M. testa laevuiscula violacea, valvulis obliquis postice acuminatis."

Mytilus edulis was designated type species of the genus Mytilus by Gray in 1847 (Soot-Ryen, 1955).

The present status of Mytilus edulis is taken from Soot-Ryen (1955): those species of the Family Mytilidae with terminal or almost terminal umbones (mytiliform species) are placed in the genus Mytilus. These include M.edulis Linnaeus 1788, M. californianus Conrad 1837, M.crassitesta Lischke 1868, M. giganteus Nordmann 1862. But Soot-Ryen states that the large differences in internal anatomy between these species do not warrant their inclusion in the same genus.

Mytilus edulis as type species has the following characteristics:

> "..anterior position of the umbones, the dysodont teeth on the short anterior margin formed by the radial ridges of the lunule, a small anterior adductor, elongate scars of the anterior retractor well behind the umbones, continuous scars of the posterior adductor and retractors, and the distinctly pitted resilial ridge which fastens the ligament to the nymphae. The posterior part of the mantle margins with tentacules or papillae." (Soot-Ryen, 1955)

A variety of Mytilids had been placed, previous to Soot-Ryen (1955), either in separate species or in some combination with one or more of the other varieties in a separate species. Soot-Ryen advocated the placing of many of the forms into one species: Mytilus edulis, and describing the varieties by means of trinomial nomenclature. An incomplete list of synonyms of Mytilus edulis Linnaeus according to this proposal is given by Soot-Ryen (1955).

The early splitting of this widely distributed species was primarily based on differences in shell morphology. Populations of Mytilus edulis from different places throughout the world, exhibiting a preponderance of some shell shape or other were designated as comprising separate species. However mussels up to 1 cm. in length are remarkably constant in shape and it is now held that the environment during the growth period is largely responsible for modification of the shell form within the one species (Lo Bianco, 1909; Jeffreys, 1863; Forbes and Hanley, 1849; Lubinsky, 1958, 1967; Seed, 1967, 1968).

Extreme conditions, such as those existing at the limits of the distribution of Mytilus edulis, produce mussels of abnormal shape. This is largely due to the erratic periods of growth such as when the mussels are exposed to air for long periods - giving thick, round shells (Williamson, 1907; Coulthard, 1929; Warren, 1936), or to short growing seasons - causing deeply indented shells (Lubinsky, 1958), or to heavy wave action or abrasion (Williamson, 1907; Seed, 1968, 1973).

Shell proportions change with age (Field, 1922; Coe, 1945; Seed, 1968, 1973), and Seed (1968) suggests that the different forms characteristic of different habitats may partly be the product of the age structure of the populations.

Overcrowding causes modification of shape (White, 1937; Savilov, 1957; Savage, 1956; Coe, 1945; Seed, 1968). Density of mussel populations often depends on habitat, and interaction of the density and habitat factors, especially those related to rate of growth, produces mussels of various shapes (Seed, 1968, 1973).

Segerstråle (1957) describes mussels of small size, small width and large height occurring in low salinity (4-5‰) water in the Gulf of

Bothnia. Similar mussels occur in dilute environments in New South Wales and Tasmania (Hum, 1969, 1971).

Medcof and Kerswill (1965) observed that shading decreased the thickness to length ratio in the shells of Mytilus edulis from Bras d'Or Lake, Nova Scotia.

The controversy regarding the taxonomic status of Mytilus edulis and Mytilus galloprovincialis has most recently been summarized by Lubet (1973) and Seed (1971). According to the Soot-Ryen proposal (above) the often separated species M. edulis Linnaeus and M. galloprovincialis Lamarck from boreal Europe and the Mediterranean respectively would be designated varieties of the one species Mytilus edulis, namely M. edulis edulis and M. edulis galloprovincialis. These subspecies, which occur sympatrically in southern England and western France, have led to considerable taxonomic confusion (Lewis and Powell, 1961; Lewis and Seed, 1969; Seed, 1969b,1969c, 1971; and see Lubet, 1973,for history of the controversy.)

A wide variation in shell shape of Mytilus in southwest England was found to be the result of three main factors: crowding, growth rate and age, and these worked synergistically through density dependence (Seed, 1968). Mytilus galloprovincialis is also capable of wide variations in shell characters (Seed, 1969b; Le Gall, 1969). As a result, gross shell morphology is an unsuitable criterion for the separation of the two forms, and Seed (1971) advocates the use of physiological and biochemical approaches.

In southwest England the reproductive cycles of coexisting populations of M. edulis Linnaeus and M. galloprovincialis Lamarck were observed to be out of phase by eight weeks and less distinct in M.galloprovincialis than in M. edulis. Cross fertilization has been successfully induced in the laboratory by Lubet (1959) and Seed (1971), but may not occur in the field in view of the out-of-phase breeding cycles. Growth rates of the two types was different under one set of laboratory conditions. Oxygen consumption rates in the two forms reach their maxima at different temperatures: 20°C for M. edulis in Britain (Read, 1962) and 25°C for M. galloprovincialis in France (Lubet and Lunetta, 1964; Lubet and Chappuis, 1967) but whether this reflects environmental or genetic differences is

unknown. Infestation with Pinnotheres pisum was observed to be different in the two forms (Seed, 1971). No biochemical differences in the pigments has been found (Seed, 1971). Lubet (1959) reports that the number of chromosomes in the two forms is the same.

Mussels resembling these subspecies in gross morphology also occur in the Southern Hemisphere. In eastern Australia 'galloprovincialis' type mussels occur in the north (equatorward) end of the Mytilus distribution range and 'edulis' type mussels occur in the south of the range, i.e., with a similar relation to latitude or temperature as the European counterparts (Hum, 1969). In Australia there is not the burden of the dual taxonomic history of the two forms and currently the Australian mussel is designated Mytilus edulis planulatus Lamarck (Fleming, 1959). Similarly Soot-Ryen (1955) considered certain forms of M. edulis diegensis Coe to have a strong affinity with M. edulis galloprovincialis. This problem has not occurred on the Atlantic seabord of North America - and the Mytilus within the region of the present study belong to the form Mytilus edulis edulis.

III. GROWTH

The versatility of Mytilus edulis in manifesting environmentally determined growth rates can be seen right from the larval stage, where metamorphosis can occur over a size range of 250μ - 400μ (Thorson,1946; Bayne, 1965). After metamorphosis growth may take place for some time in midwater (Nelson, 1928).

Adult growth rate has been examined in the light of many factors: abundance of food, exposure to air, temperature, salinity, water velocity, crowding, solar radiation, age, seasons, wave impact, factors controlling density, etcetera.

Food. Correlation of growth rate in the field with abundance of food has been made by Richards (1946), Coe (1945), Boje (1965), and Le Gall (1969). Coe showed that growth rate in young Mytilus edulis diegensis in California more nearly fitted dinoflagellate abundance than water temperature or solar radiation levels. Richards, in Massachusetts, found that the level of solar radiation was positively correlated with growth rate, probably due to its influence on phytoplankton abundance. Boje found the growth rates under otherwise nearly identical conditions in Kieler Fjord and the Nord-Ostee Canal varied with the amount of food present. Mytilus galloprovincialis also grows fastest during the periods of "vives eaux" in spring (Le Gall, 1969). Larval growth is dependent on food to a certain extent. Field (1922) could not raise larvae beyond a size of 110μ in the laboratory if food was scarce. Bayne (1965) observed increasing growth rate of larvae as cell concentrations of Isochrysis galbana and Monochrysis lutheris were increased. Seed (1969a) states that literature concerning the nutritional aspects of molluscan growth is particularly sparse and needs more research.

Intertidal Exposure. Growth is retarded by exposure to air (Field, 1922; Mossop, 1922; Havinga, 1929; Savage, 1956, Baird and Drinnan, 1957; Baird, 1966; Seed, 1968; Harger, 1970b). It is well known that relaying of mussels from the littoral to sublittoral areas increases growth and

improves condition (Baird, 1966). Coulthard (1929) found that littoral mussels grew at a rate 16 times slower than continuously submerged mussels, with 50% exposure almost inhibiting growth completely. Baird (1966) observed rates of 7.9 and 12 times greater for submerged mussels. Curtailment of growth is caused by deprivation of food and oxygen, possibly combined with a rise in temperature under exposed conditions (Coulthard, 1929). Baird and Drinnan (1957) and Baird (1966) postulated a compensation point where anabolism equals catabolism at 56% exposure in the Conwy Estuary, North Wales. This work is supported by the findings of Coleman and Trueman (1971). Modification of the level of this compensation point by varying exposure to solar radiation (temperature at low tide exposure) was observed by Hum (1971) in Middle Harbour, New South Wales - further suggesting a threshold in the anabolism/katabolism balance.

Rao (1953b) and Rao and Goldberg (1954) postulate differential effects on growth of soft parts and of shell under conditions of exposure and immersion. Calcium for shell growth, coming largely from true solution in seawater is independent of food supply (Rao, 1953b), resulting in heavier shells relative to weight of soft parts in subtidal than in intertidal mussels. The generality of this phenomenon is not supported by the observations of Williamson (1907), Coulthard (1929), Warren (1936), Baird and Drinnan (1957), Seed (1968, 1973) and Hum (1969), that intertidal mussels had thicker and heavier shells relative to meat than did subtidal mussels.

Temperature. Boëtius (1962), Theisen (1968) and Davies (1969) have found the growth rate of Mytilus edulis to be proportional to temperature. The biological zero for growth of the mussel is close to $0^{o}C$ (Boëtius, 1962; Theisen, 1973). Theisen (1968) found that mussels from the Danish Wadden Sea needed approximately 6000 day-degrees to reach a size of about 50mm, whereas Savage (1956) reported that some mussels in the Conwy Estuary needed approximately 15,000 day-degrees to reach this length (the discrepency is due to severe crowding of the Conwy mussels). Davies (1969) grew mussels in cages near the surface of Menai Straits and

these took 4000 to 7000 day-degrees to reach 50mm (average 5000 day-degrees). M. edulis in Disko Fjord took 9000 day-degrees to reach 50 mm (Theisen,1973), over a period of about 10 years at 900 day-degrees per year. Other sub-arctic M. edulis from Godhavn harbour needed 6300 day-degrees (seven years) to reach 50mm. This latter is similar to the Danish Wadden Sea rate, and Theisen has noted that conditions in the two regions are similar - sandy bottom, below low water level, sheltered with tidal currents. Boëtius (1962) reports a similar rate for Copenhagen mussels - at 6000 day-degrees to reach 40mm. Andreu (1957) describes a faster rate per day-degrees for Spanish raft culture mussels (see Theisen, 1973).

Temperature optimum for growth of British M. edulis is between 10°C and 20°C (Bruce, 1926). Coe (1948) estimates it at 17°C - 20°C for Californian M. edulis diegensis, feeding and growth both being slower at 14°C. Laboratory values above 20°C are difficult to obtain because of interference of fouling at high temperatures. Coe has observed feeding up to 26°C. Dodgson (1928) found it maximal at this temperature. But metabolism is also high (Bruce, 1926; Read, 1962; MacIntyre, 1959, 1963, 1967) and may influence growth through the anabolism/katabolism balance (as per von Bertalanffy, 1938; Bělehrádek, 1930, 1935; Baird and Drinnan, 1957).

Temperature optimum for growth can vary between populations however. Bayne (1965), investigating the effect of temperature on growth rates of larvae of M. edulis, found the relative growth rate/temperature curves of larvae from Wales and from Denmark were similar between 11°C and 17°C, but at higher temperatures the growth rates of Welsh mussels remained constant, while those of the Danish mussels declined. This difference reflects the respective ambient temperature regimes of the natural environments.

With reference to low temperature - feeding has been observed down to 0°C and mussels can remain open down to -1.5°C (Loosanoff, 1942). Slow growth at low temperatures results in well defined growth rings (Mossop, 1922; Mateeva, 1948; Seed, 1968). Growth rates vary with season, being generally faster in summer than in winter (Baird, 1966; Coe, 1948; Richards, 1946; Brienne, 1956; Boëtius, 1962). For example Seed (1968) found that 90% of the year's shell growth in English Mytilus edulis occurred from April to September. Maximum increase in tissue weight occurred in the

fall. Seed (1969a) suggests that an interaction of food availability with the seasonal gametogenic cycle may determine the different processes, with temperature in itself playing only an indirect role. M. edulis in Wales follow a different pattern. The largest gains in flesh weight here occur from April to September (Dare and Edwards, 1975) and this is also the season of maximal shell growth (Davies, 1969). The complexity of factors determining the various growth processes is further discussed in the section on nutrition and the gametogenic cycle. Integration of these factors is only in the early stages of investigation, and this only in cool temperate latitudes.

Summer retardation of shell growth in M. edulis planulatus in Lake Macquarie, New South Wales was observed by Hum (1971). This retardation was unlikely to be the result of insufficient food per se, as another species of mussel, Trichomya hirsuta, exhibited maximum shell growth in the same experimental cages at this time. Lake Macquarie is close to the equatorward limit of the distribution of M. edulis, and summer temperatures are above optimum for several metabolic functions of the species. On the other hand, Trichomya hirsuta has a more tropical distribution than M. edulis, and Lake Macquarie lies close to the poleward limit of the distribution of this mussel. The same summer retardation of growth was observed in M. galloprovincialis in Lac de Bizerte, Tunisia, by Le Gall (1969).

Latitude. The degree of temperature-determined limitation on growth processes in Mytilus edulis is reflected in the growth histories of the mussels throughout the geographic range. Mytilus edulis from Greenland (Theisen, 1973), White Sea (Savilov, 1957) and the Canadian eastern Arctic (Lubinsky, 1958) have sigmoid growth curves: growth (development) is slow to start, accelerates after about three years, and continues to be positive until death - which is generally due to external causes like ice denudation (Savilov, 1957) or winter mortality (Blegvad, 1929; Petersen, 1974). Subarctic growth rates may average 4mm per year (Lubinsky, 1958). Ultimate size of northern mussels can be much greater than that in the south or equatorward end of the distribution (e.g. in

Mytilus californianus - Coe and Fox, 1942; Richards, 1928). In more temperate latitudes the growth curve becomes more parabolic than sigmoid, the slow initial phases of growth being accomplished in the larval stage, before settlement (Seed, 1968; Davies, 1969; Hum, 1969, 1971), burying the inflection point in the seasonal variations of growth in the first year. But slow growing mussels in special environments in temperate regions may still show a sigmoid growth curve (Seed, 1968). Growth in most temperate latitude populations approaches a definite limit, implying again the anabolism/katabolism balance and, by comparison with the relatively unlimited growth of the subarctic mussels, a dependence of this balance on temperature. Growth in cool temperate latitudes can average about 50mm per year (Britain: Baird, 1966), or 50mm per two to four years (New England: Field, 1922; Maritimes: Mossop, 1922). In warm latitudes the growth curve is also parabolic - there is rapid early growth followed by early termination of growth to a definite L_∞ (Hum, 1971). Thus after about one year, energy input is entirely consumed in maintenance and possibly also reproductive processes, with none left over for shell growth and the accompanying soft tissue growth. Spanish culture mussels exhibit this type of growth and may grow at a maximum rate of 100mm per year (Wisely, 1967).

Salinity. Salinity affects the ability of the mussel to feed. Valves are closed at about 14‰ (Dodgson, 1928) unless low salinity acclimation has been accomplished (Schlieper, 1955). Mussels may close for a few days during low salinity (Baird, 1966; Hum, 1969; Gilles, 1972). Those which are constantly subjected to low salinities grow slowly and to only a small size (Brandt, 1898, quoted White, 1937; Segerstråle, 1944, 1957; Lubinsky, 1958). Baird (1966) observed differing growth rates over the length of an estuary, depending on season. Winter growth rates were slowest upstream where long periods of low salinity occurred after heavy rain. Bøhle (1972) reports that shell growth of M. edulis from 100% sea water in Norway is highest in 100% sea water, slight in 75% and insignificant in 50% sea water. This corresponds to a reduced filtration activity during the salinity adaptation process. Mussels placed in 75% sea water required four weeks to obtain maximum activity level, but those in 50% sea

water had not acclimated by the seventh week. This implies that when mussels require a long time for adaptation to reduced salinity, the filtration rate and shell growth may be strongly reduced, i.e., varying salinity such as in tidal zone estuaries has a negative effect on growth rate.

Light. Huntsman (1921) observed inhibition of feeding in bright light. Coulthard (1929) found maximum growth in 50% sunlight. Medcof and Kerswill (1965) found that shading increased linear growth, but that thickness was not increased proportionately. This reaction is exploited in mussel culture in Europe where up to a 69% increase in weight is achieved by shade culture (Anonymous, 1968). Seed (1969a) found that mussels growing in the dark had a faster growth rate than those in the light under laboratory conditions. Shell deposition in the dark was yellow-brown, thin and brittle, whereas that deposited in light was thicker and blacker. This was also borne out by field observations - mussels growing on the bottoms of ships and in dense clumps were similar to the laboratory mussels grown in the dark. Seed postulated that light rays may injure the tissues responsible for shell secretion, and deposition of pigment may have a protective value.

Wave Action. In areas exposed to heavy wave action mussel growth is slow (Seed,1968, 1969b). Ultimate size is small (Hum, 1971; Harger, 1970a) and there is considerable modification in shell shape (Seed, 1968). Harger (1970a) reports M. edulis diegensis in California on the open coast growing one-third as much as those in sheltered waters. Maximum size was inversely related to amount of wave impact, as was body weight. The force required to remove mussels from the rocks varied with size, increasing with size for mussels up to 5 cm length and being constant from 5 cm to 10 cm. Harger thus held wave impact to be responsible for the removal of mussels from the substrate in exposed conditions, the apparently smaller L_∞ being the product of population structure and not necessarily of growth curve characteristics. Seasonal growth rate here reflected the effect of wave impact, the slowest growth rates in exposed

situations being in winter during the periods of heavy seas, whereas sheltered mussels exhibited no seasonal variation in growth rate (Harger, 1970b).

Currents. Water movement, in its effects on the availability of food and the removal of harmful wastes, is important for growth. Havinga (1956) reports maximal condition in mussels growing near channels. Feeding behaviour varies with current intensity (Dodgson, 1928; Walne, 1972): mussels often close in stagnant water, and opening is stimulated by currents. Valve opening is widest at current velocities of about 5 m.p.h., but valves almost close at 10 m.p.h. In half-closed mussels filtration is at one-fifth full efficiency (Jørgensen, 1960). Walne (1972) found that filtration rate was positively correlated with water flow rate, and that growth rate was greater for mussels in high flow water than in low flow. Theisen (1973) notes slow growth in sublittoral mussels in Godhavn harbour, probably due to inadequate renewal of water - as indicated by the presence of H_2S stinking mud. Nixon et al. (1971) describe the multiple beneficiary effects of currents in maximizing growth in dense mussel communities.

Competition. Competition with other mussels cuts down food supply and causes physical pressure (Seed, 1968, 1969a; Harger, 1970b), both restricting growth. Growth rates of mussels in places of high population density are slower than in those where predators have reduced the numbers (Havinga, 1956; Savage, 1956; Seed, 1968). Physical and biological factors can act both directly and indirectly on growth rate through effects on population density (Seed, 1968).

Age. As described above in relation to temperature, adult growth in Mytilus edulis from favorable environments in temperate areas generally follows a hyperbolic curve with time, being maximal in the first year and tapering off at a size determined by the environment (Coe, 1945; Seed, 1968, 1969a; Hum, 1969, 1971). For any increase in the length of mussels there exists a corresponding greater increase in mass, and a reduced

feeding efficiency (Fox et al., 1937; Jørgensen, 1949). Energy available for growth and reproduction decreases with increasing size due to limitation in the pumping mechanism proportional to the gill size and respiration rates (Vahl, 1973). Jørgensen (1952b) estimates 84% growth efficiency of Mytilus edulis from 30 mm to 60 mm length and 11% efficiency at 90mm, on the basis of oxygen consumption figures. Age reduction in growth rate may also be attributed to lower metabolic activity in older mussels, as recorded by Zeuthen (1947). However senility is not the primary cause of reduced growth since transplantation can result in renewed growth (Seed, 1969b).

Environmental limits may be imposed by many of the above factors. This can be most easily demonstrated by the relaying of old mussels, which have ceased to grow, to new environments - resulting in renewed growth (Havinga, 1956; Baird, 1966; Seed, 1968). Fast growing mussels often outgrow their environmental limits early and hence are susceptible to mortality during small changes in conditions. This is seen in the relative longevities of low and high latitude mussels. Wisely (1964) reports mussels at the equatorward limit of the distribution living about two years. Theisen (1973) estimates some Northwest Greenland M. edulis to be 24 years old. Savilov (1957) states that high latitude mussels seldom reach the size of environmental limitation as they generally meet with 'accidental' death before this.

Size-dependent mortality in natural populations may obscure evidence of metabolic mortality. Theisen (1968) observed a decrease in mortality rate with increasing size for M. edulis in the Danish Wadden Sea. Seed (1969a) reports that fast growing mussels of the sublittoral in Britain do not get a chance to reach the environmental limit due to predation, whereas slow growing littoral mussels may eventually reach senility.

Limits to growth may be altered by transplantation (see above). Field (1922) showed that old M. edulis which had not grown in length for years could be induced to grow when placed in favourable conditions. Relaying of culture mussels to obtain maximum production is commonly practised. Seed (1968) further demonstrated the effect of the environmental limits to growth by transplants of slow-growing mussels to more favourable

environments - producing as much as 50% increase in growth, and reverse transplants of large fast-growing mussels to unfavourable environments - resulting in high mortality, presumably due to insufficient food to meet the metabolic requirements.

Other factors. Initial size may have an influence on growth rate. For example conditions just after settlement of young mussels may determine the pattern of growth thereafter. Seed (1969a) examined the laboratory growth rates of mussels from the same spatfall but of different initial sizes. Under the same experimental conditions mussels of large initial size had a slower growth rate than initially small mussels. However there was also a large variation in growth rate per group.

Bruce (1926) reported that reproductive activity of Mytilus edulis affected shell growth. Under laboratory conditions approximating those of the natural mussel population, growth was at a standstill throughout, and for some time after, the actual spawning period. None of the more recent studies on M. edulis growth mention this phenomenon. In fact, all indications are to the contrary, with maximum growth periods coinciding with spawning and with high food concentrations in the water (see above). The mechanism of shell deposition is still a highly controversial subject (Digby, 1968) and the possible relation of this mechanism to nutrition and the gametogenic cycle remains obscure.

Genetic differences in growth rates have been recorded for clams (Chanley, 1955) and oysters (Walne, 1958). It is likely that M. edulis and M. galloprovincialis are distinct genetic types (see above). Seed (1971) found marked differences in growth of edulis and galloprovincialis types when kept under identical laboratory conditions. This would indicate physiological differences between the two types, but whether the growth differences would be maintained under natural conditions is unknown. In this case M. edulis had a growth rate of over three times that of M. galloprovincialis throughout the year. There appear to be some inherent differences in temperature relations for Alaskan and Californian M. edulis (Pickens, 1965), for functions other than growth. These may reflect genetic differences as may other dissimilar reactions throughout the wide

geographic range of the mussel.

Parasites have been shown to affect the growth of some bivalves. The copepod Mytilicola intestinalis commonly occurs in Mytilus and appears to be responsible for poor condition in some cases (Williams, 1969). Seed (1969c) reports gill damage and relatively low tissue weight and high shell weight in mussels infected with the pea crab Pinnotheres pisum.

Mussels kept under almost identical conditions may show widely differing growth rates (Coulthard, 1929; Bayne, 1965; Hum, 1969). The effect of position in the clump of mussels has been demonstrated by Harger (1970b): disturbance of the clumps produced higher average growth, probably due to the amelioration of competition within the clump.

Due to the large number of factors which can affect growth rate in Mytilus edulis, comparison of growth rates from several different geographic regions can be misleading. European data are often taken from exploited mussel beds where conditions are optimal for that latitude (e.g. string cultures: Andreu, 1957; Davies, 1969; Mason, 1969; Bøhle, 1968, 1970). Growth data for those mussels beyond the latitudes of possible cultivation are often taken in relatively unfavourable environments (e.g. Theisen, 1973; Lubinsky, 1958; Savilov, 1957). The papers of Seed (1968, 1969a, 1973) and Theisen (1973) demonstrate a variety of growth rates for mussels from different habitats within the one geographic area.

IV. FACTORS AFFECTING METABOLIC RATE

Metabolic rate may be summarized as the rate of the basic respiratory exchange with the environment. The rate of this process is reversibly affected by the rates of the higher processes, and, under suitable circumstances, these can serve as a measure of metabolic rate. In this context they are known as "metabolic rate functions". Frequently studied metabolic rate functions in Mytilus edulis include the rates of enzymatic reactions, heart rate, filtration rate, rate of beating of gill cilia, feeding rate, water pumping rate, excretion rate, rate of growth of shell, reproductive products or other soft tissue, and rate of completion of life cycle or part thereof. The relationship of these functions to the fundamental metabolic rate will be determined by the energy pathways within the whole organism (Vahl, 1973). Relatively little work has been done on the integration of the different rate functions at the level of the whole organism, recent exceptions being the work of Bayne and Thompson (1970), Widdows and Bayne (1971), Gabbot and Bayne (1973) and Bayne (1973) combining data on oxygen consumption, filtration rate and food assimilation efficiency under various conditions.

Functions like the rate of acclimation to environmental variables such as temperature, salinity or oxygen tension are the results of a shift in metabolism rather than a change in rate in the context of metabolic rate function, although these changes may involve a change in rate of the process.

Metabolic rate functions in Mytilus edulis have been studied in the light of a number of factors: notably temperature, but also salinity, oxygen tension, amount of suspended material in the water, current speed, exposure to air, reproductive state, amount of food available, nutritive state, stress, acclimation to various factors, tidal, lunar and inherent rhythms, age, size and latitude. Most of the work on the physiological rate functions has been done in the laboratory. The present study is mainly concerned with the effect of temperature (latitude) on metabolic rate, but as it has been carried out in the environment of the mussels,

rather than in the laboratory, a number of factors other than temperature will be likely to affect the metabolic rate. The remainder of this section will be organized in terms of the factors affecting these metabolic rate functions, especially where they are applicable to the whole organism.

Temperature

Mytilus edulis functions over a wide range of temperature. Several early attempts to establish the upper thermal tolerance were made by Bruce (1926), Ritchie (1927), Henderson (1929), Hutchins (1947) and Reshöft (1961). Ritchie observed that British M. edulis were killed by 14 hour exposure to 28.9°C. The most accurate description of upper thermal tolerance is that by Read and Cumming (1967) who put the limit for Massachusetts mussels at close to 27°C. Australian M. edulis planulatus from Lake Macquarie, N.S.W., reaches its thermal tolerance at just over 28°C, and New Zealand M. edulis aoteanus from Wellington reaches its thermal limit at just over 26°C. (Hum, 1971).

The small differences in tolerance may be due to genotypic differences in the populations from different geographic regions, as observed by Pickens (1965) for Alaskan and Californian M. edulis; or due to resistance acclimation: the mussel has been shown to be capable of shifting its tolerance to high temperatures, as suggested by Henderson (1929) and Schlieper and Kowalski (1956). Pearce (1969) demonstrated higher thermal tolerance in M. edulis from Sandy Hook, New Jersey compared with mussels from Cape Cod, Massachusetts. Also, within the one region (Sandy Hook) intertidal M. edulis had greater tolerance than benthic.

Freidrich (1967) reports that cellular heat resistance of M. edulis from the North Sea and Baltic fluctuates seasonally, dependent on the state of maturity of the gonads and variation in environmental temperature. Over short term increases in temperature the cold resistance is decreased, long term temperature changes equalize the thermal resistance. At "natural" temperatures, between 10°C and 25°C, a slow increase in heat resistance is evident even after seven days readaptation to constant (10°C) conditions.

Heat and cold shocks cause unspecific changes. Increased heat resistance in isolated gill tissue, caused by temperature shock, is associated with a decrease in oxygen consumption. Heat resistance of the enzyme aldolase is increased by heat adaptation of the whole mussel.

It is well known that M. edulis can undergo freezing (Dodgson,1928), with up to 60% of its body fluids frozen. Kanwisher (1955) has observed beds of Mytilus edulis surviving six to eight months frozen solid in ground ice at temperatures of $-20^{o}C$ and below. Mussels at $-15^{o}C$ had 62% of the body water frozen. Petersen (1974) reports Mytilus living in Northwest Greenland which experience temperatures of $-20^{o}C$ or $-30^{o}C$ when exposed to air in winter. In the same day these mussels may be warmed to $1^{o}C$ on the next high tide, or further warmed to $5^{o}C$ by the sun or the foehn (catabatic wind). However Blegvad (1929) has recorded 100% mortality in populations which were frozen for two months. Williams (1970) examined freezing tolerance in Mytilus edulis at $-10^{o}C$. The tissues were injured when 64% of the cellular water was frozen. Adapting the mussel to 150% sea water increased the freezing tolerance to $-15^{o}C$. Adaptation to varying salinity and freezing appear to be independently evolved however.

For short term temperature fluctuations within the mussel's viable range, the rate-temperature (R - T) curve is typified by that of Read (1962) for oxygen consumption. Detectable feeding activity commences at $-1.5^{o}C$ (Loosanoff, 1942). As temperature increases metabolic rate function increases to an optimum, generally at about $20^{o}C$, but this is variable - depending on the temperature history of the mussel (see for example Newell, 1969; Newell and Pye, 1970b). Above $20^{o}C$ the metabolic rate decreases until the lethal point. This type of R - T curve has been demonstrated in part or whole for oxygen consumption (Gray, 1923; Bruce, 1926; Read, 1962; Widdows and Bayne, 1971; Schlieper, Kowalski and Erman, 1958), ciliary activity (Gray, 1923; Schlieper, 1958), pumping or feeding rate (Dodgson, 1928; Coe, 1945; Widdows and Bayne, 1971), and growth in the laboratory (Bruce, 1926; Coe, 1945). Reference to the effect of temperature on growth of the mussel in the field has been made in the section on growth: the same type of R - T curve can be demonstrated for growth rate over a range of latitude (Hum, 1971).

Independence from this simple R - T curve has been demonstrated for a number of functions over short term (non-acclimated) experimental periods. Newell (1967) gives evidence of a temperature independent metabolism in the oxidative activity of M. edulis mitochondria. The rate of succinate and pyruvate oxidation is shown to be relatively unaffected by temperature over a range which is similar to that encountered by mussels on the shore, in this case up to 20°C. Using the data of Glaister and Kerly (1936), Percy and Aldrich (1971) describe a temperature independent region in the R - T curve of Mytilus edulis foot retractor muscle between about 14°C and 25°C. However gill and mantle tissues did not show similar temperature independence - the difference in tissue reaction possibly being related to the relatively low metabolic rate of muscle tissue compared with gills and mantle.

Several laboratory studies reveal the ability of Mytilus edulis to acclimate its metabolic rate functions to changes in temperature. Cell-free homogenate of M. edulis accomplishes thermal acclimation quite rapidly for temperature fluctuations over short periods at temperatures below natural (acclimation) temperature (Newell and Pye, 1970b). Acclimation to higher temperatures is slower. Widdows and Bayne (1971) have shown that acclimation of oxygen consumption and filtration rates in whole mussels is complete within 14 days of a change in ambient temperature. During cold acclimation the energy budget remains in equilibrium, but acclimation to warm temperatures exerts a stress on the mussel, causing mobilization of energy reserves.

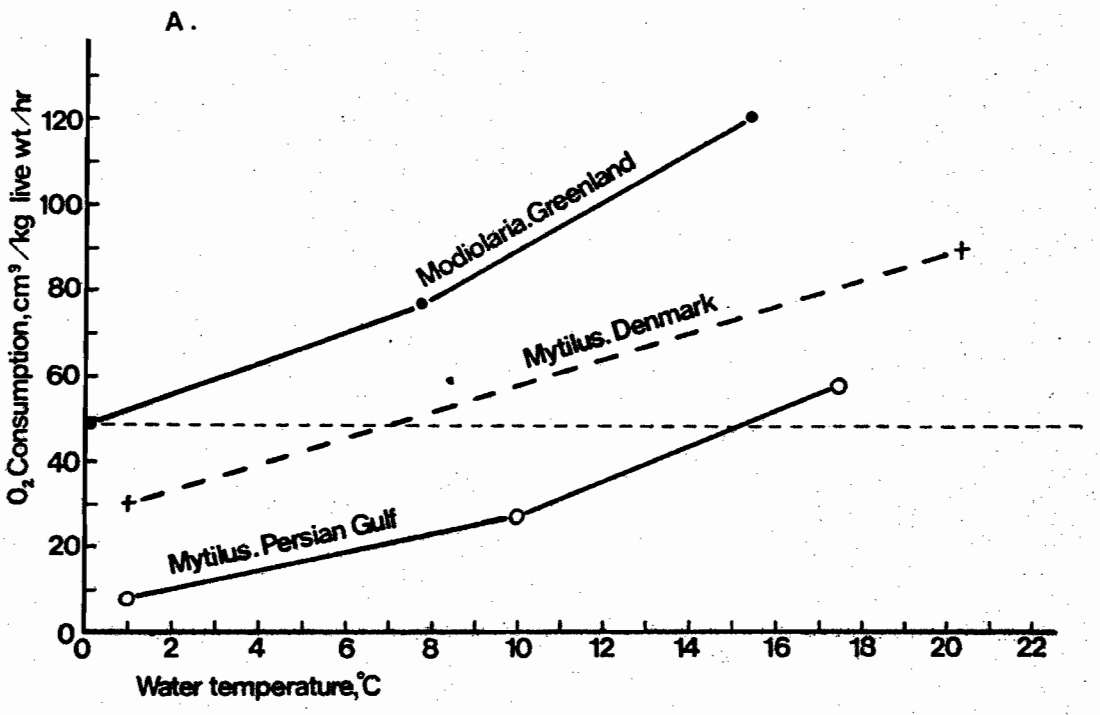
This ability of M. edulis to acclimate its metabolic rate functions to slow temperature changes, suggests that there would be good seasonal acclimation in field populations. The behaviour of M. edulis under natural conditions, however, remains obscure. Bayne and Thompson (1970), Widdows and Bayne (1971), and Gabbot and Bayne (1973) report what they call "seasonal acclimation" of oxygen consumption rate in British M. edulis. This, they say, agrees with the findings of Bruce (1926), Schlieper (1957) and Krüger (1960). In all of these investigations (except below), the seasonal acclimation observed was the result of subjecting mussels to highly artificial temperatures and bears no relation

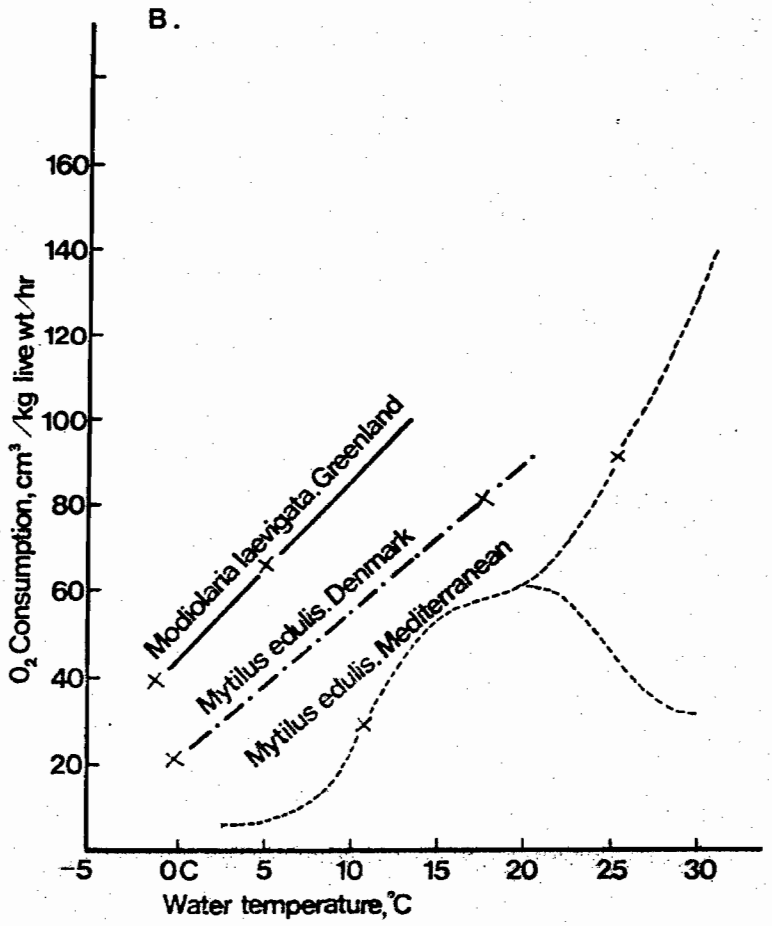
to field conditions. On the other hand, in the study of Bruce (1926: Figure 2, page 839), where oxygen consumption was measured at field temperatures, the mussels did not show seasonal acclimation of oxygen consumption rate. Precisely the opposite finding is reported by Bayne and Thompson (1970: Figure 12, page 543), but the exact method of investigation here is not described.

The work of Pickens (1965) on heart rate of the mussels M. edulis and M. californianus as a function of latitude, intertidal height and acclimation temperature, gives some indication that mussels from colder localities, during some months of the year at least, are as active as those from warmer habitats. Isolated hearts of M. edulis showed ability to acclimate and exhibited a wider range of activity (3°C to 30°C) than in situ - suggesting that in situ control is nervous and not dependent on the heart's ability to respond. Rates of Alaskan M. edulis at their natural habitat temperatures functioned at 68% the rate of Californian M. edulis at their habitat temperatures in summer. But if the Californian mussels were transplanted to Alaskan temperatures (12°C) their heart rate dropped by 40% of the rate at 22°C. This may represent some compensation for temperature between the latitudinally separated populations. However this compensation for temperature was not always clearly exhibited, and complications with other variables, especially vertical distribution, but also food, led Pickens to conclude that on the whole mussel heart rate is not completely regulated to permit the animal to remain relatively independent of environmental temperature.

The classic latitudinal studies on Mytilus metabolic rate are those of Thorson (1936, 1952) and Spärck (1936). Mytilus from the Persian Gulf and from Denmark were compared with Modiolaria from Greenland, in the study of Thorson; while Mytilus edulis from the Mediterranean and from Denmark were compared with Modiolaria laevigata in the study by Spärck. The mussel populations from the different latitudes were found to have comparable oxygen consumption rates at their natural environmental temperatures, despite the differences in these temperatures (see Figure 2). Spärck concluded that the M. edulis from Denmark and the Mediterranean must belong to different physiological races. These populations are

FIG. 2 OXYGEN CONSUMPTION OF MYTILIDS FROM DIFFERENT LATITUDES.
A. FROM THORSON 1952.
B. FROM SPÄRCK 1936.





presently considered as different species by Seed (1971, etc.) and Lubet (1973, etc.), or at least as different subspecies (Soot-Ryen, 1955). Hence neither of the studies is pertinent to the ability of individual mussels to acclimate over a latitudinal range in the manner discussed by Rao (1953a), the time periods involved being more relevant to evolutionary adaptation than acclimation or acclimatization. This may also be true of other latitudinal studies such as those of Pickens (1965) and the present study, where different genotypic populations of the same species may be involved. But as far as this species may be regarded as a unit, these latter studies reveal the metabolic flexibility within this unit.

Oxygen Tension

Mytilus edulis may be exposed to varying oxygen tensions in its natural environment. Short term reductions in available oxygen may occur for intertidal mussels at low tide (Trueman, 1967; Helm and Trueman, 1967), for mussels subjected to anoxic water at low tide - the "oxygen pulse" (Muus, 1967)-and for mussels which are forced to close their valves by low salinity at low tide (Gilles, 1972). Long term oxygen reductions may result from a combination of factors, including valve closure during periods of low salinity after floods (Hum, 1969) and ambient oxygen depletion due to stratification of the water column after floods (MacIntyre,1959,1967).

Tolerance to low oxygen levels has been described by Dodgson(1928), MacIntyre (1959, 1967), Read (1964) and Reish and Ayers (1968). Dodgson noted that survival up to 41 days may occur in deoxygenated conditions at low temperatures. Read found that 50% mortality occurred in sealed seawater jars after 3.1 days at 25°C. MacIntyre found that tolerance depended on temperature, Mytilus surviving anoxia up to 21 days at 15°C, 9 days at 20°C, and 5 days at 25°C. Reish and Ayers report almost 100% survival for 14 days at 0.2 ppm O_2 and 15°C — 16°C. Comparison with some other mussels reveals that Mytilus edulis is relatively poorly adapted to conditions of low ambient oxygen (MacIntyre, 1959, 1967; Read, 1962, 1964; Lent, 1968).

For short term (unacclimated) changes in oxygen tension, the oxygen consumption of Mytilus edulis is governed directly by the oxygen tension

up to a critical level, beyond which it is independent of oxygen pressure. Bruce (1926) describes the insensitivity of Mytilus edulis to low oxygen pressures, the respiratory rate being undiminished until a level of 30% normal pO_2 is reached. Rotthauwe (1958) found oxygen uptake independent of oxygen tension above a critical level of 60% saturation at 19°C. Bayne (1971a) indicates independence of oxygen consumption from pO_2 down to a critical level of 50mm - 70mm Hg., and derives an "oxygen dependence index": $pO_2/Q\ O_2$ against QO_2 which gives a linear relationship below the critical level. However higher metabolic functions are affected by the changes in pO_2 and these react to give regulation of oxygen consumption (see below). The response of Mytilus edulis to reduced oxygen tension is dependent on a number of factors including size (Zeuthen, 1953; Rotthauwe, 1958; Kruger, 1960; Read, 1962; Bayne, 1971a), activity (Bayne, 1971a, 1971b), nutritive stress (Bayne, 1971a), salinity (Bayne, 1971b) and acclimation (Bayne, 1971a, 1971b).

Bayne (1971b) describes the mechanisms for maintaining independence of oxygen consumption from ambient pO_2. During the decline in oxygen tension ventilation rate and frequency and amplitude of the heart beat increased. But at low tensions the ventilation rate and heart frequency declined, while amplitude of heart beat increased. The effects of these reactions on maintaining oxygen consumption are seen by comparison with stressed mussels which are not able to regulate under the same conditions. Other researchers report changes in metabolic rate functions with reduction of ambient pO_2. Schlieper (1955) observed depression of heart rate in oxygen-free water, stagnant water or water rich in CO_2. Similar observations were made by Pickens (1965). Theede et al. (1969) reported that oxygen tension in the water had a direct effect on the activity of the gill cilia and on ventilation rate. Changes during exposure to air (see below), such as depression of heart beat (Trueman, 1967; Helm and Trueman, 1967) may also be explained in terms of inavailability of oxygen.

The percentage extraction of oxygen (or extraction efficiency) from water passing through the mantle cavity varies with pO_2. In fully saturated water the extraction efficiency is low (10% - 15%). But at the lower tensions, at which animals regulate their own oxygen uptake, the extraction

efficiency was higher, reaching a maximum of 30% - 40% at less than 30mm Hg. pO_2. Mussels under nutritive stress could not alter their extraction efficiency under declining oxygen tensions. However on returning to higher oxygen tensions after hypoxia both conformers (stressed) and regulators showed increased extraction efficiency (Bayne, 1971b). Extraction efficiency is also dependent on temperature: Widdows (1973b) has shown that the water convection required to maintain oxygen extraction is inversely proportional to the temperature.

Intertidal Exposure

The behaviour of M. edulis under different conditions of exposure reveals the nature of its metabolic demand in a limiting environment.

Mytilus edulis occurs from the midlittoral to a depth of at least 80 fathoms (Hum, 1969). As described in the above sections on growth and the influence of pO_2 on metabolic rate, the upper vertical limit is generally determined by the metabolic requirements of the mussel (Baird and Drinnan, 1967). The M. edulis populations that are most commonly studied (especially in Europe and North America) are usually described as having their lower limit just below low water mark, although many deeper occurrences have been recorded, for example where there exist fast water currents (Kitching et al., 1959; Hum, 1969, 1971). Larval settlement is usually maximal in shallow water (Engle and Loosanoff, 1944; Chipperfield, 1953; Nair, 1962; Hum, 1969) - due to a number of factors including phototropism (Thorson, 1950; Verwey, 1952), response to hydrostatic pressure (Bayne, 1963) and settlement preferences for certain substrate types which occur only in the littoral (Hum, 1969). Post-settlement and adult distribution in the sublittoral is commonly terminated abruptly by predation (Warren, 1936; Dexter, 1947; Kitching et al.,1959;etc.) or competition with other attached benthos (Lewis, 1953; Hum, 1969, 1971), of physical factors such as deoxygenation (MacIntyre, 1959) and siltation (Hum, 1969).

The mussel thrives best when constantly submerged (Warren, 1939;etc.),

undoubtedly due to the katabolic effects of intertidal exposure to air (Baird and Drinnan, 1957). Helm and Trueman (1967) describe the behaviour of M. edulis under conditions of immersion and exposure as follows:

> "In laboratory conditions of continuous immersion in well-aerated water while siphoning actively, the heart rate of Mytilus remained relatively constant, generally 24/min - 26/min, and showed little change in rate during pedal activity or rapid opening and closing of the valves. Exposure to air led to the progressive, although generally incomplete, closure of the valves and reduction of the heart within 6 minutes of exposure. During exposure the mussels were in general inactive and after about 3 hours the heart rate gradually dropped to below 10/min. Reimmersion . . . led to a brief period of valve closure followed by maximal opening. At the same time there is immediate increase in heart rate and amplitude. . . . The latter is probably indicative of increased ventricular output. . . . Reimmersion after 3 hours of exposure gave rise to a heart rate in excess of that observed during continual immersion which persisted for approximately 10 minutes. Similar results were observed in the field. . ."

The physiology of Mytilus edulis during exposure has been described in terms of anoxia. M. edulis has adapted to littoral existence by being able to reduce its metabolism during periods of aerial exposure, to maintain valve closure so preventing undue water loss, and to repay an oxygen debt effectively (Coleman and Trueman, 1971): the bradycardia during exposure results in reduced metabolism (Schlieper, 1957; Coleman and Trueman, 1971). Valve gape is directly related to heart rate, a reduction in the former leading to a decrease in the latter (Coleman and Trueman, 1971). However an oxygen debt is built up (Schlieper, 1955, 1957; Coleman and Trueman, 1971) and this is repaid when the tide returns, as seen by an overshoot in heart rate and oxygen consumption rate (Helm and Trueman, 1967; Coleman and Trueman, 1971). Only some oxygen may be obtained during exposure by partial opening of the valves (Helm and Trueman, 1967), and this is insufficient to meet the mussel's metabolic needs even at the reduced metabolic level (Coleman and Trueman, 1971). This is in keeping with the conclusions of Baird and Drinnan (1957) that the mussel's intertidal exposure is limited by its metabolic needs. Coleman and Trueman (1971) note that exposure has less noticeable effects on heart rate at low temperatures ($0^{o}C$ - $5^{0}C$) when metabolism is greatly reduced.

The response to aerial exposure is variable and reflects an ability

of the mussel to acclimate its metabolism or learn behaviour patterns appropriate to its environment. Schlieper (1957) compared the responses of M. edulis from the littoral and sublittoral under conditions of aerial exposure. The mussels adapted to intertidal exposure exhibited rapid valve closure, bradycardia and recovery, whereas the sublittoral mussels were much slower to respond. However once the sublittoral mussels had acclimated to the littoral situation their response was no different to that of the littoral mussels. The response of the unacclimated sublittoral M. edulis in this case is similar to that of Moliolus modiolus, a mussel which is seldom uncovered by the tide. Coleman and Trueman (1971) report very slow responses of shell valves and little heart rate suppression in this mussel when it is exposed to air. On the other hand Modiolus demissus, a mussel which occurs higher in the littoral than M. edulis, employs valve gaping during aerial exposure to accomplish evaporative cooling and aerial respiration (Kuenzler, 1961; Lent, 1968).

Tidal rhythmicity in the rate of water transport by Mytilus edulis has been reported by Rao (1954). The rate is maximal at high tide, dependent on the amplitude of the tide in the mussel's environment, and it persists for some time when the mussel is transferred to stable laboratory conditions. However when the mussels are transferred to an environment with a different tidal rhythm there is a prompt shift to the new tidal cycle. Studies by Jørgensen (1960) do not demonstrate this tidal rhythmicity: large variations in water transport rate were observed to be the result of various stimuli, and Jørgensen attributes Rao's results to an artificially low sensitivity of the experimental mussels. Theede (1963) found that North Sea and Baltic Sea mussels which regularly fall dry at low tide did not show a rhythm in the rate of filtration under constant laboratory conditions. Pickens (1965) also found no tidal rhythmicity in the heart rate of M. californianus. Differences in the rates of water transport in M. edulis from different tidal levels have been suggested in analogy with Mytilus californianus by Rao (1953a), Segal et al. (1953) and for heart rate by Pickens (1965). Jørgensen (1960) reported that there were no differences in the rates of water transport of high and low M. edulis in Europe.

Salinity

Mytilus edulis commonly occurs in bays and estuaries where the salinity falls below that of seawater. In the extreme it can occur where the salinity is regularly 4 °/oo - 5 °/oo, in the Gulf of Bothnia and the Gulf of Finland (Segerstråle, 1957) and at 5.5 °/oo near Stockholm (Conklin and Krogh, 1938). Ambient salinities of about 150 °/o seawater may be tolerated by those mussels which withstand freezing of the surrounding seawater and tissue fluids (Williams, 1970).

Behaviour and metabolic activity of the mussel under different conditions of salinity depend on the amplitude and frequency of the salinity variations. The low salinity mussels referred to above only tolerate these conditions as a result of slow acclimation, and high salinity mussels subjected to more rapid changes in salinity to these low levels are not able to withstand the change for long (Dodgson, 1928; Hum, 1969).

Rapid decreases in salinity to low levels, e.g. from seawater to less than 14 °/oo causes closure of the shell valves and cessation of activity including oxygen consumption (Dodgson, 1928; Lubet and Chappuis, 1964, 1966; Gilles, 1972; Bayne, 1973). Closure of the valves isolates the tissues from ambient conditions: salinity inside the mantle cavity can be 24°/oo when outside is 7 °/oo (Milne, 1940). The perivisceral fluid may remain hyperosmotic to the environment for at least 96 hours (Gilles, 1972). Potts (1954) observed that mussels become isosmotic with 50% seawater in about four days if the valves are closed. If the valves are propped open the change is rapid, taking place in about four hours.

Less extreme decreases in salinity cause modification in behaviour and physiology. Valve closure may only be partial or persist for only a short time (van Winkle, 1972; Bayne, 1973), causing flooding of the mantle cavity with low salinity water. At this stage the mussel exhibits poikilosmotic behaviour, the osmolarity of the blood passively flows down the salinity gradient to the lowest level compatible with life (Conklin and Krogh, 1938; Remane and Schlieper, 1958). There is an increase in weight due to osmotic uptake (Maloeuf, 1937), in fact this lack of volume regulation in Mytilus edulis may cause death (Prosser and Brown, 1961).

Gilles (1972) reports that M. edulis has practically no anisosmotic regulatory power: during acclimation to a dilute medium it is the cells which must cope. The mussel can tolerate changes in the osmolarity of seawater of at least 900 mOsM (Lange, 1968b). Total intracellular concentration of ions may be one-half that of seawater (Potts, 1958; Lange and Mostad, 1967) making the corresponding change in the cellular fluid of the mussels about 450 mOsM. Ionic regulation does occur in M. edulis. Under normal circumstances blood K^+ is 30% to 40% higher than that of seawater (Robertson, 1953). Blood chlorides rise and fall proportionately with changes in the external medium (Krogh, 1938, 1939). Foot tissue chlorides are less than one-half those of the blood in seawater and in brackish water (Krogh, 1938). When ambient salinity is reduced intracellular changes allow a large degree of salinity acclimation to occur (as exemplified by acclimation of metabolic rate functions, see below. The volume of gill tissue in osmotically adapted animals is the same at differing salinities (Lange, 1968b). This could be accomplished by secretion of organic solutes: amino acids and taurine (Lange, 1963; Lange and Mostad, 1967) as suggested by the relatively low intracellular chloride concentration in the mussel (Krogh, 1938, 1939; Fox, 1941).

Mussels exhibit optimum activity at their biotope salinity, only changing optima very slowly after alterations in salinity occur. This has been demonstrated for oxygen consumption in whole mussels (Beliaev and Tschugunova, 1952; Schlieper, 1955, 1958; Lagerspitz and Sirrka, 1959) where mussels adapted to either higher or lower salinities than the 'normal' salinity have reduced oxygen uptake compared to the original rate. In vitro gill studies by Lange (1967) agree with whole animal studies: the oxygen consumption of gills from mussels which were adapted to a wide range of salinity exhibited a typical optimum curve when examined at seawater salinity. This is in contrast to earlier studies by Schlieper (1955, 1957), who postulated a relation between hydration of gills and oxygen consumption, on finding that in isolated gills an increased oxygen consumption occurs during decreased ambient salinity. However Lange (1968a) has observed that the volume of gill tissue in osmotically

adapted animals is the same at different salinities. Rate of filtration also exhibits an optimum at the biotope salinity. M. edulis from the Baltic and North Sea have their maximum rates of filtration at their 'normal' salinities (15°/oo and 30°/oo respectively), and even after seven days adaptation to salinity alterations the differences do not disappear (Theede, 1963). Renzoni (1964) found that optima for growth, development and water filtration rates in M. galloprovincialis were at the same salinity as the seawater from which the mussels were obtained. Racial differences may exist between regions with different salinities, but Schlieper (1955) showed that acclimation of oxygen consumption by Baltic Sea mussels (15°/oo) when transferred to the North Sea (30°/oo) was complete. The acclimation of oxygen consumption only took place several weeks after salinity acclimation had been accomplished.

Short term metabolic rate function changes under conditions of altered salinity have been described by van Winkle (1972). Changes in salinity initially inhibit activity of the gill cilia and oxygen consumption of excised gill tissue. If the salinity difference is not too great there is recovery. This was also observed for whole mussels by Bayne (1973). Immediately upon a reduction in salinity the rate of oxygen consumption declined. This was probably due to the inhibition of gill cilia as described by van Winkle. Occasionally the animals closed the shell valves at this time and oxygen consumption ceased. Within six to eight hours of the minimum salinity being reached, recovery of oxygen consumption rate occurred, occasionally resulting in a slight overshoot. Within 24 to 36 hours the rate of oxygen consumption returned to near the previous level.

At low salinities the oxygen consumption may slightly increase or remain constant while ciliary activity decreases (van Winkle, 1972). The decrease in oxygen consumption that would be caused by inhibition of gill cilia here may be masked by the increase in oxygen consumption associated with other activities. Processes of osmotic regulation and excretion require energy (Potts and Parry, 1964). Thus exposure to low salinity has a double effect on the oxygen uptake of the mussel - it both inhibits and activates oxygen consumption (Lange, 1968b). Therefore when considering

oxygen consumption of mussels in environments with changing salinities, a distinction should be made between the demands of mussels in a state of osmotic adaptation and osmotically adapted animals (Bouxin, 1931). This leads to 3 possible levels of oxygen consumption: osmotically adapting, osmotically adapted, and oxygen adapted secondarily to the change in salinity (Lange, 1968b). This is in agreement with the field observations of Schlieper (1955), referred to above.

Bayne (1973) describes metabolic rate functions under the dual stress of decreased salinity and declining oxygen tension. Regulation of oxygen consumption (see section on pO_2) still occurs during acclimation to low salinity, at a slightly reduced rate. This would have ecological significance at low tide where low salinity and low pO_2 may occur simultaneously. The time course for regulation of oxygen consumption under conditions of reduced salinity depends on the magnitude of the salinity change. At lower salinities it takes a greater decline in ambient oxygen to produce an increase in frequency and amplitude of the heart beat.

Nutrition and the gametogenic cycle.

The factors discussed in the previous sections can influence the metabolism of mussels in various combinations, but their effects in combination with nutrition and seasonal changes, notably temperature, are most important in determining the pathways of energy flow within the organism, i.e. which growth processes will occur. Energy is provided by nutrition, procured at various rates and efficiencies - dependent on many factors (Willemsen, 1952; Tammes and Dral, 1955; Jørgensen, 1960, etc.; Theede, 1963; Quraishi, 1964; Davids, 1964; Walne, 1972; Thompson and Bayne, 1972; Tenore and Dunstan, 1973; Foster-Smith, 1975), and directed into different processes according to metabolic demands and level. The integration of these processes is only in the early stages of investigation.

The presence of food itself has an influence on metabolic level. Both chemical and particulate feeding stimuli evoke a feeding response -

stimulating gill cilia to increase pumping and filtration rates (Theede, 1963; Davids, 1964; Thompson and Bayne, 1972). This results in an increase in oxygen consumption rate (Thompson and Bayne, 1972). Removal of chemical feeding stimuli results in a return of activity to the routine level. But removal of particulate (inert or organic) stimuli does not produce a decline in oxygen consumption level, presumably maintained at a high level due to the presence of food in the gut (Thompson and Bayne, 1972).

Three levels of metabolism can be defined for Mytilus edulis on the basis of nutrition: standard, routine and active (Widdows and Bayne, 1971; Thompson and Bayne, 1972; Bayne, 1973). The mussel has a maintenance requirement for food, and animals fed below this level reduce their metabolism accordingly. This reduced rate is known as "standard metabolism". Animals fed above maintenance requirement, but not in the active state of feeding, adjust their oxygen consumption to a "routine" level. Mussels in the feeding state described above exhibit "active metabolism".

Short term temperature changes affect active, routine, and standard oxygen consumption rates differently. For mussels acclimated to 20°C, the effect of short term temperature changes from 10 to 20°C is more pronounced on the active, than on the standard rate (Widdows, 1973). Within these limits is a statistically "routine" oxygen consumption rate (Bayne, Thompson and Widdows, 1973).

Maintenance requirement, standard and routine metabolic rate vary seasonally. The corresponding changes in oxygen consumption may be related in part to the seasonal cycle of gametogenesis, with maximum energy demands occurring during the period of gamete formation (Bayne and Thompson, 1970; Gabbot and Bayne, 1973). For example, at artificially raised temperatures during the period January to April in Britain, M. edulis maintains oxygen consumption above the standard rate even under nutritive stress, due to the increased demand of gametogenic activity (Gabbot and Bayne, 1973). Gabbot and Bayne suggest that there may be a specific mechanism which prevents a reduction in metabolic rate in this period, as long as reserves are available in the body tissues to meet the energy demands of gametogenesis. The body reserves were accumulated in

Table 1. Different spawning periods of M. edulis from different regions.

Locality	Spawning Season	Reference
Scandinavia	Throughout the Year	Jørgensen, 1946 Rees, 1950
Norway, Bergen Harbour	Mar., Apr., May, June Throughout the Year	Rünnstrom, 1927 Nair, 1962
United Kingdom	February to June	Matthews, 1913 Daniel, 1921 Bruce, 1926 White, 1937 Lebour, 1938 Chipperfield, 1953
	(M.ed/M.gall 8 week difference)...	Seed, 1971 Dare and Edwards, 1975
N.W. France	February to March	Berner, 1935 Bouxin, 1955
Spain, Galicia	Spring to Fall, peaks April and September	Bardach, et.al, 1972
Italy	March to April	Lo Bianco, 1899
Near Alexandria	May, June, Jan., Feb.	Fox, 1924
Black Sea	July to September	Borisjak, 1909
Japan	April, Oct. to Nov.	Sugiura, 1959

Table 1 Continued.

Locality	Spawning Season	Reference
Atlantic North America	Autumn (Major)	Stafford, 1912
	Spring (Minor)	Field, 1922
		Battle, 1932
		Engle and Loosanoff, 1944
		Sullivan, 1948
		Wells and Gray, 1960
Pacific North America		
Oakland, California	February to May	Graham and Gay, 1945
Canada	June	Stafford, 1912
New Zealand	Throughout the Year	Ralph and Hurley, 1952
Australia		
Port Philip	Throughout the Year	Allen, 1955
Sydney	June to November	Wisely, 1964
		Allen, 1955
Fremantle	June to November	Wilson and Hodgkin, 1967

the summer and, as the gonad becomes fully ripe and reserves are depleted towards spring, metabolic demand drops and oxygen consumption approaches the standard rate under inactive conditions.

The seasonal biochemical/reproductive cycles are different in M. edulis from the different regions of the world distribution - as seen by the differences in spawning periods (Table 1). The combination of temperature (as per Orton, 1920; Runnström, 1927; and for M. edulis: Allen, 1955) and food availability, determining the storage and utilization of food reserves and resulting in growth and reproductive processes could be expected to vary considerably throughout the world. Analysis of annual cycles of biochemical composition have been made by Daniel (1921), Williams (1969), and Dare and Edwards (1975) in England; by Drzycimski (1961) in the Baltic; by de Zwaan and Zandee (1972) in Holland; and by Fraga (1956) in Spain. In the three northern localities the cycles are similar, with different timing, but the Spanish cycle is more complex - possibly due to the longer spawning period (Dare and Edwards, 1975). Other regions of the global distribution, with different timing of food availability and seasonal temperature changes should produce biochemical and oxygen demand cycles with different characteristics.

Size.

As size increases in M. edulis, from the trochophore stage on, the rate of most metabolic rate functions decreases. This is true of oxygen consumption rate, rate of shell growth, heart rate, and filtration/oxygen consumption ratio. These functions have been shown to be related to size by the equation $Y = a.W^b$, where Y represents the rate of the metabolic function, a is the intercept, W represents the size of the mussel and b is an exponent with values for size-related functions between 0.40 and 1.00 and commonly close to 0.67, i.e. obeying Rubner's surface law. However variations occur, and factors related to size but of secondary importance may here come into play, e.g. growth rate, age, activity, position in life table. Other functions such as Q_{10} or temperature sensitivity also vary with size.

Oxygen consumption provides a measure of total metabolic rate, calorie production or food absorbed. The pattern of oxygen consumption over a range of sizes provides an indication of changes in metabolism over the life span of the mussel. Zeuthen (1947) measured oxygen consumption in M. edulis from the embryo (0.001Y total N content) to bottom stage (to just over 100 mg. total N content). In the embryo stage, oxygen consumption was very low, but once development progressed to the very young trochophore stage oxygen consumption rate rose enormously. Thereafter it dropped quite steeply until the veliger stage. After settlement the rate evened out, but as the mussels reached a size of beyond 1 mg. total N content oxygen consumption rate decreased more and more abruptly. This Zeuthen related to growth rate - which is higher in smaller animals, and a higher ingestion requirement in smaller mussels, as postulated by the finding of Jørgensen (1943) that food filtered off/food combusted is 100 to 200 times higher in larvae than in old Mytilus. Due to a large variation in individual metabolic rates, no equation for oxygen consumption/size was derived by Zeuthen, however it was evident that animals of less than 1 g. (total N content ?) did not obey Rubner's surface law. Further estimates of the dependence of oxygen consumption on size have been made by Rotthauwe (1958) b = 0.676, Krüger (1960) b = 0.70 to 0.93, Read (1962) b = 0.546 to 0.798, and Vahl (1973) who found b equal to approximately 0.75, with variations through the year.

Heart rate has been related to size in M. californianus (and M. edulis?) by Pickens (1965). The slope of the regression lines changed during the year and during long term experiments. Heart rate decreased with size, with b = -0.10 to -0.24.

Studies on filtration and water pumping rates reveal that size is an important factor influencing nutritional input in Mytilus edulis. Jørgensen (1943, 1952a, and 1960) emphasizes the importance of the relation of water transport to oxygen consumption (food required/food available). Young, fast growing lamellibrachs use about twice as much of the absorbed nutrients for growth as for combustion and have correspondingly higher rates of water transport in relation to oxygen consumption than adults. Theede (1963) and Walne (1972) observed decreased weight specific filtration

rates for Mytilus edulis of increasing sizes. According to Walne the relation was variable, depending on outside water flow rate. Vahl (1973) found the exponents (b) for pumping rate (0.60), oxygen uptake (0.75), gill area (0.65), absorption efficiency (-0.02) in the equation $Y = aW^b$, size expressed as dry soft weight. A decrease in energy available for growth and reproduction with increasing size would be caused by the decreased pumping rate in larger mussels, not compensated for by any increase in absorption efficiency. This effect on growth rate is also discussed in the chapter on "Growth" (above).

Size may also affect ability to compensate metabolic rate for changes in temperature and other variables. Rao (1953a), and Rao and Bullock (1954) observed higher Q_{10} in larger Mytilus californianus compared with smaller mussels in several populations. Size dependence varied in populations from different latitudes and habitats, being lower in high latitudes and sublittoral populations. Pickens (1965) also found Q_{10} to be greater in large Mytilus (presumably californianus, as no data was presented for M. edulis). Read (1962) observed differences in Q_{10} for different sizes of M. edulis. However the Q_{10} for each size group also varied with temperature range, and a large overlap of data led Read to doubt the significance of Q_{10} dependence on size.

INTRODUCTION (2) LATITUDINAL ASPECTS OF METABOLIC RATE FUNCTIONS.

From the preceding chapters it can be seen that latitudinal studies on Mytilus edulis would involve a complex combination of factors. The integration of knowledge on the metabolic responses of M. edulis to these factors, notably temperature, and of knowledge of other organisms - especially those taxonomically close to M. edulis, but also those with a similar thermal biotope (eurythermal temperate), in contrast to organisms which would differ widely (e.g. stenothermal tropical, Antarctic, etc.) allows some general predictions to emerge.

I. METABOLIC RATE IN RELATION TO THERMAL BIOTOPE

There is an extensive literature on the differing abilities of poikilotherms to compensate their metabolic rates for latitudinal differences in temperature (see reviews by Rao and Bullock, 1954; Bullock, 1955; Precht, 1955, 1958; Prosser, 1955; Kinne, 1963 a,b, 1970; Dunbar, 1968; Vernberg and Vernberg, 1972; Newell and Bayne, 1973). During the first half of the century the preoccupation in this field was mainly with the absolute level of metabolic rate, i.e. whether or not poikilotherms escape the Arrhenius equation with respect to latitudinal differences in temperature. Relevant papers include those of Mayer (1914), Hörstadius (1925), Runnström (1927, 1930, 1936), Spärck (1936), Thorson (1936, 1946, 1950, 1952), Fox (1936, 1938, 1939), Fox and Wingfield (1937), Wingfield (1939), Moore (1939, 1942 a,b) Scholander et al. (1953).

Since this time the details of capacity to regulate metabolic rate have been investigated in a wide range of aquatic poikilotherms from different thermal biotopes. Examples include the studies of Peiss and Field (1950), Roberts (1952, 1953), Rao (1953a), Marshall and Orr (1955), Conover (1959, 1960, 1962), Demeusy (1957), Wohlschlag (1957 - 1964), McWhinnie (1964), Vernberg and Vernberg (1970), Lasenby and Langford (1972), Holeton (1973, 1974), George (1974) and De Vries (1974). The treatment of growth rates and life cycles in the same context has been reviewed by Dunbar (1968).

This accumulation of data, on different taxonomic groups of poikilotherms from different parts of the world with different thermal regimes, reveals a wide range of metabolic responses to thermal characteristics. It is apparent that these responses are dependent on the thermal regime of the species, the history of the thermal biotope which it inhabits, and the evolutionary history of the species. This is illustrated by examples of acutely-measured R-T curves for fish (De Vries, 1974) and isopods (George, 1974) from antarctic, arctic, temperate and tropical regions. These papers give cases of very good latitudinal adaptation of metabolic rate (i.e. cold and warm water forms have comparable rates of oxygen consumption at their

respective habitat temperatures) and also show R-T curves which characterize the range of temperature of the habitat (i.e. stenothermal versus eurythermal). Antarctic forms, representing a relatively old fauna in a cold, thermally stable habitat, consume oxygen at a respectable rate, but only within the narrow limits of their natural habitat. Beyond these limits (1 or 2°C) metabolic rate is severely depressed, in fact, death occurs. This represents very fine adaptation to a long stable environment, and one exception to this pattern - the zoarcid fish Rhigophila dearborni, is probably a relatively recent immigrant to the region (Wohlschlag, 1964). Shallow water arctic forms, which inhabit a cold but fluctuating thermal environment (both in the long and short term), exhibit R-T curves typical of eurythermal animals. The level of metabolism is high over a wide range of temperatures. Similarly, temperate forms, which undergo large seasonal variations in temperature, have a comparable metabolic rate over a wide but different range of temperature. Tropical forms are again stenothermal, functioning at a slightly higher rate over a narrow range of temperature.

These patterns are all very tidy, but they have come in for recent criticism on the basis of technique. Holeton (1973, 1974), working on arctic fish, has obtained much lower values for metabolic rate than those of previous studies (e.g. Scholander et al., 1953; Wohlschlag, 1957). Holeton attributes this discrepancy to an unnaturally high metabolic rate in the earlier studies caused by the handling of very sensitive cold-water fish. This problem with differences in results has occurred before (e.g. Fox and Wingfield, 1936-9; Berg, 1953 and Thorson, 1952), and suggests that the metabolic type is dependent on more than temperature and temperature-related evolution. For example food levels may be of great importance - it would be maladaptive for a high arctic poikilotherm to require a large energy input for maintenance of a high metabolic rate when food is scarce (Dunbar, 1968; Holeton, 1973). In this case poikilotherms may actually be exploiting a low level of metabolism, determined or not by temperature, so that they can exist in a low energy environment. The ability of poikilotherms to evolve enzyme systems which will function, under conditions of low temperature, at rates comparable to those of the

temperate organisms, has been suitably demonstrated (Hochachka and Somero, 1973; Hazel and Prosser, 1974), but the only way that long-lived poikilotherms may be able to persist in low energy environments may be to deny this strategy.

II. LATITUDINAL STUDIES ON METABOLIC RATE OF OTHER MYTILIDAE.

There is some information on the effect of latitude on the metabolic rate of Mytilidae other than Mytilus edulis. Interspecific studies include those of Thorson (1936, etc.) and Spärck (1936). These have been discussed above under "Factors affecting metabolic rate: Temperature." and are summarized in Figure 2. More analogous to the present study are the investigations on Mytilus californianus by Rao (1953a), Dehnel (1956) and Pickens (1965) in which metabolic rate function is examined over a range of latitude. Pickens' study involves both M. edulis and M. californianus and is discussed with respect to M. edulis elsewhere. The studies of Rao and Dehnel are on M. californianus only. Mytilus californianus has a wide latitudinal distribution, similar to that of Mytilus edulis, on the Pacific coast of North America.

It may be noted at this stage that in many publications concerning the growth and metabolism of Mytilus edulis, reference is made to the mussel "Mytilus" (= M. edulis or M. californianus) as if the properties of these mussels are interchangeable. For my own purposes this has been very misleading. These two mussels may have a great deal in common, but the distinction should be kept when discussing latitudinal differences in metabolic rate functions, for which there is little information on Mytilus edulis. The tendency to lump these two species is particularly prevalent in reviews referring to the papers of Coe and Fox (1942), Fox and Coe (1943), Coe (1945), Rao (1953a) and Dehnel (1956). Similarly it is hard to untangle the information (even though it may be the same) for the two species in the paper by Pickens (1965).

Rao (1953a) has done some experiments on the variation of water propulsion in Mytilus californianus from different latitudes. The major conclusion of this study was that "the absolute rate as well as the weight-specific rate of pumping is greater at any temperature in mussels from higher latitudes than in those of the same weight from lower latitudes".

Rate at minimal habitat temperatures were found to be equal, except in large mussels which have higher water propulsion rates at high latitudes. These conclusions appear to differ with the ideas presented for Mytilus edulis below. But a look at Rao's experimental approach reveals that his results have little bearing on the question of latitudinal adaptation in the context of the present study.

The mussels in Rao's study came from Los Angeles (Lat. 34° 00' N), Fort Ross (Lat. 38° 31' N) and Friday Harbor (Lat. 48° 27' N). They were transported to one laboratory and kept at their respective environmental temperatures of 16, 10 and 6.5°C for some weeks. The mussels were then placed into water of various temperatures and the rate of water propulsion acutely measured for each locality and size. Thus, for each experimental temperature, mussels acclimated to different temperatures were compared under different magnitudes of temperature change. For example, at an experimental temperature of 20°C mussels from Los Angeles, Fort Ross and Friday Harbor experienced temperature increases of 4, 10 and 14°C respectively. Under these circumstances, and if M. californianus responds to high temperature stress in the same way as M. edulis (cf. Widdows and Bayne, 1971), the high water propulsion rate exhibited by the high latitude mussels may have been the result of the magnitude of the temperature change imposed on the mussel during the experiment. This is not a response to the absolute level of the temperature and says nothing of the level of metabolism at which the mussels naturally functioned in their original environments.

The latitudinal interpretation of Rao's studies may be contrasted to the latitudinal comparison of heart rate in M. californianus made by Pickens (1965). Pickens' results appear to differ from those of Rao: little latitudinal compensation in heart rate was exhibited in the later study. But this was probably due to the method of investigation. Pickens' mussels from Alaska, Washington, California and Mexico were kept at habitat temperatures for only a short period before acutely-measured R-T curves were estimated. A variety of results with respect to acclimation over the R-T curves were obtained, but at their habitat temperatures northern mussels (Washington) functioned at about half the rate of southern

mussels (Mexico). The experimental variation in temperature which occurred during estimation of the R-T curve could have had a disturbing effect on the mussels, so that by the time that the habitat temperature was reached, the mussels may have been reacting to a new thermal regime. This approach may be compared with that of the present study in which mussels remained at habitat temperature throughout the experiment and were not led up to it via the R-T curve.

The studies of Rao and Pickens show that M. californianus from different latitudes function at metabolic rates characteristic of their environments, but they do not show that there is latitudinal compensation for temperature.

Dehnel (1956) describes the rate of shell growth in populations of Mytilus californianus from California and Alaska. The rates were measured over short periods at the probable times of maximum growth at each locality. The Californian mussels had a higher growth rate than the Alaskan, but Dehnel concludes that this is due to a number of non-temperature factors, and if correction is made for these, "the actual discrepancy in intrinsic growth rate is small or absent". This means that at 9°C an Alaskan mussel can grow as fast as a Californian mussel at 16°C, i.e. latitudinal adaptation of growth rate may occur. No information on growth rate for other periods of the year is available for latitudinal comparison, but Coe and Fox (1942) indicate that food may be limiting for growth of Californian mussels. There is also no information on latitudinal differences in growth curves or life tables in M. californianus.

III. METABOLIC RATE OF MYTILUS EDULIS AS RELATED TO LATITUDE.

(A summary of the preceding chapters in latitudinal context.)

Mytilus edulis has a wide latitudinal distribution. Over this range it exhibits a variety of metabolic responses to its environment, which alter its morphology to such an extent that there has been, and still remains, controversy as to the taxonomic status of the species. The success of M. edulis as an old species (since Miocene) containing wide variability, is, in my opinion, largely due to its ability to exploit ecotone type environments, including thermal ecotones. These not only necessitate eurythermicity, but in a poikilotherm, demand either excellent thermal acclimation of metabolic rate functions, or a wide tolerance of different metabolic levels. Different metabolic responses have been demonstrated in some of the higher metabolic functions of M. edulis: growth, reproduction, life span, form. The level at which this flexibility comes into play remains undefined. The aim of the present study is to examine the flexibility of metabolic rate at the level of the respiratory exchange with the environment. Measurement of oxygen consumption rate not only indicates the sum of metabolic rates within the organism, but (in its relation to temperature in this case) may indicate the metabolic level at which flexibility is first exhibited.

The distribution of the mussel includes regions where the average annual water temperature is 1°C and others where it is 20°C. Different latitudes also offer different local ranges of temperature, for example the Atlantic North American extreme of 26°C cf. the small annual ranges of only a few degrees in some subarctic waters. Timing of temperature changes also varies with latitude: rate of change of temperature is dependent on the annual range of temperature and on the rate of seasonal shifts, for example the changes induced by turnover of the water column or introduction of new current systems. Thus the metabolic effects of latitudinally-related temperature changes will run from the immediate R-T curve (e.g. Read, 1962), through short term acclimation (e.g. Widdows and Bayne, 1971), to long term acclimation as exemplified by regional

differences (e.g. Pickens, 1965) and genetic differences or evolutionary adaptation (e.g. Thorson, 1936 etc.; Spärck, 1936). These effects have all been discussed in detail above.

For these simple temperature responses a combination of levels of temperature adaptation will be present in any one population at any time. The environment is not static like the laboratory. Temperature changes will occur with every tide, with day and night, dependent on local weather, be constantly changing through the seasons and in the long or short term with fluctuations in local current systems, for example as might be occurring in West Greenland (Theisen, 1973).

The literature on temperature-related metabolic rate functions predicts a high degree of temperature acclimation for Mytilus edulis. But these studies have been done under the relatively static conditions of the laboratory and usually only on one or two populations of M. edulis. It remains to be seen whether M. edulis can acclimate its metabolic rate to temperature changes under field conditions.

Apart from the added complexity of the thermal regime in the field, there are several other factors which may influence the mussel's ability to acclimate to temperature changes under natural conditions. These include other environmental factors such as salinity, oxygen tension, food availability, etc., which may induce stresses on the mussel to the extent that they affect temperature acclimation ability, and which may also cause metabolic rate changes masking temperature-induced metabolic rate changes (see above). Also, the combination of inputs from the local environment, especially those of a seasonal nature, at any one latitude will determine a pattern for the mussel's biochemical or gametogenic cycle, growth rate and life span. A summary of latitudinal differences in growth and metabolism of M. edulis is made in Table 2, from the text in the previous sections. These characteristics of the mussels themselves will in turn modify temperature responses.

Table 2 suggests large differences in metabolic processes over the range of latitude occupied by M. edulis. Life span, growth rate and the shape of the growth curve show not only variation from one geographic region to another, but unidirectional change over most of the latitudinal

TABLE 2. Growth and metabolism of *Mytilus edulis* in relation to latitude, arranging information from preceding chapters into a latitudinal context:

Region	Annual water temperature	Metabolic rate functions
subarctic	-2 to +4°C.	possible freezing mortality activity at -1.5°C sigmoid growth curve slow growth rate all growth in summer no L_∞ long life span*
cool temperate	0 to 13°C.	parabolic growth curve moderate growth rate maximum growth in summer L_∞ approached moderate life span gamete development in warm periods
warm temperate	15 to 23°C.	parabolic growth curve fast growth rate maximum growth in winter, spring or autumn definite L_∞ short life span gamete development in cool periods occupies high food, O_2 habitat
subtropical	to 26°C.	settlement with little growth short life span no gamete development high O_2 requirement for survival
	above 26°C.	mortality.

* "life span" refers to metabolically-determined life span.

range, representing a latitudinal trend. In warmer, as compared with cooler latitudes, growth is initially faster, there is a definite limit to size and the life span of the mussels is shorter. This indicates a generally faster life cycle in lower latitudes, and is possibly suggestive of a higher overall metabolic rate. Soft tissue accumulation in the form of stored glycogen is also high in intermediate latitudes in summer. However the anabolic metabolic rate functions, as exemplified by growth and reproduction, follow a typical R-T curve with latitude (temperature). As the extremes of the equatorward distribution are reached, growth and reproduction are thwarted, in fact, the trend in this direction is evident in summer in some of the milder regions of the distribution. Suppression of these major growth processes at high temperatures suggests the following alternatives:

1. Temperature-induced metabolic rate suppression at above 20°C may decrease the rate of filtration and other energy procuring processes.

2. Metabolic requirements of M. edulis may not be satisfied at the (still) high rate of metabolism predicted by the acutely-measured oxygen consumption R-T curve at these temperatures. Spärck (1936) predicted that high latitude poikilotherms would starve at low latitude temperatures. Katabolism may exceed anabolism, resulting in zero or negative growth. That is the relation $dW/dt = A-K$ (von Bertalanffy, 1949) is controlled by temperature such that different equilibrium levels for size or reproductive development exist at different temperatures. The relation $V = a(T + \alpha)^b$ (Bělehrádek, 1955) may be applied to final size, life span and growth processes.

3. The high temperatures may exert a stress, as described by Widdows and Bayne (1971) for mussels undergoing warm acclimation. Energy required for growth may be demanded by other processes - which is just another way of saying $K > A$.

4. A combination of high katabolic demand and suppression of energy procuring or conversion processes may occur.

The low tolerance of M. edulis to conditions of depleted oxygen at warm temperatures and its apparent preference for high oxygen and food

habitats at low latitudes suggest that total metabolic rate (oxygen consumption) may be higher at low latitudes than in cooler regions. If oxygen demand is in fact higher at low latitudes some of the increase could be attributed to katabolic processes: combustion versus growth processes, and would fit in with the observations on growth and life span of the mussel. Older mussels do use a greater percentage of their food for maintenance processes, and it is not unreasonable to suggest that the balance between these two directions of energy flow is temperature determined, particularly as low latitude mussels get older sooner. The latitudinal trend in this direction is not limited only to the extreme equatorward populations of M. edulis, but is evident throughout the distribution.

On the other hand, the high degree of temperature acclimation exhibited by Mytilus edulis in the laboratory, together with the aura created by the latitudinal studies of Thorson and Spärck, seem to predict that the mussel would acclimate its metabolic rate (oxygen consumption) to the high temperatures of low latitudes. The present study is an attempt to resolve this problem. Using the Thorson and Spärck studies as a basis, a comparison of growth and total metabolic rate, measured as oxygen consumption, is made over a range of latitude: Newfoundland to North Carolina, during all seasons of the year.

STATIONS.

The two major determinants of temperature in the range of Mytilus edulis are latitude and time of year. In Atlantic North America M. edulis is distributed from subarctic waters to approximately Cape Hatteras, North Carolina. The coast from Newfoundland to North Carolina spans 13^{o} of latitude and provides temperature contrasts from stable cold (Newfoundland to Maine), through a boundary region (Cape Cod to Cape Hatteras) to a stable warm region (Cape Hatteras - south) and covers almost the entire thermal spectrum of the M. edulis distribution. The coastal waters are influenced by the climatic extremes of the adjacent continent, which cause the greatest seasonal temperature fluctuations of any ocean waters in the world. This is especially marked in the boundary region, where seasonal fluctuations in coastal water temperature of up to $26^{o}C$ have been recorded (Parr, 1933). In contrast the coastal waters of Maine and of Carolina experience ranges of about $11^{o}C$. Figure 4 shows the approximate temperature variations at the experimental stations throughout the year.

A comparison of latitudinally-separated populations of M. edulis with respect to metabolic and growth rates would only be meaningful on this coast if all periods of the year were taken into consideration. A close schedule of metabolic rate measurement was therefore needed, limiting the study to readily accessible stations on the coast. Populations of M. edulis from Newfoundland to North Carolina are accessible by road: a van was fitted out for living and laboratory.

Eight major stations were established (Figure 3). Conditions in the littoral and shallow sublittoral, where M. edulis occurs, are determined further by local factors. At each experimental station, unique combinations of physiography, tides and weather determined the relative influences of marine, estuarine and terrestrial factors. This was especially evident in the cases of salinity and ambient oxygen concentration (see Figures 5 to 48). Substrate availability was also important in determining the sites of mussel populations within each region that

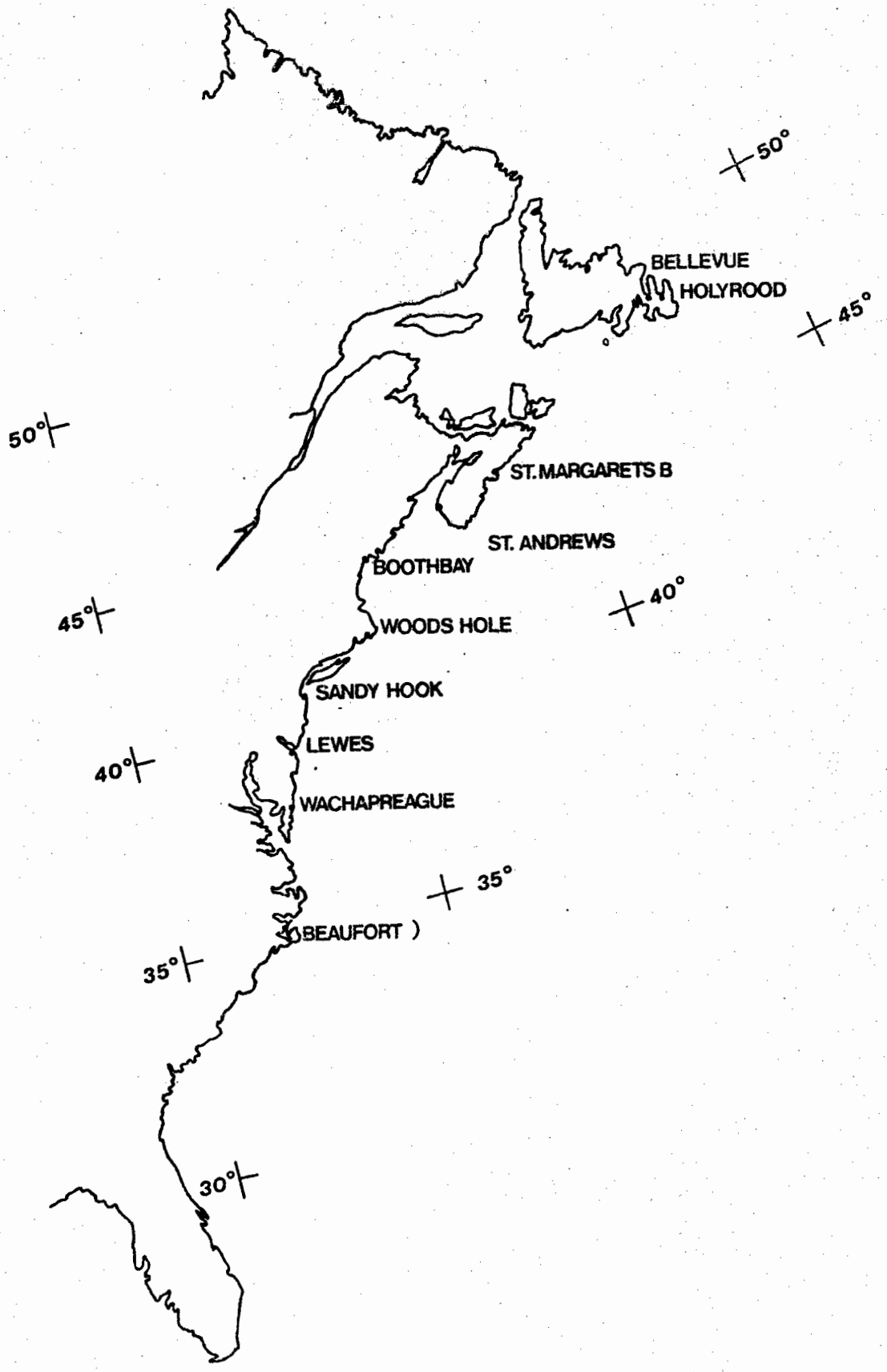


FIG. 3 Location of experimental stations.

was chosen for study. Each experimental station represented a compromise between several factors, with the basic criterion being workability on a healthy mussel population.

Each station was visited every two months: a suitable interval for growth study measurements (Hum, 1969, 1971), also a reasonable period in which to accomplish the logistics involved in the circle between Newfoundland and Carolina and back. The entire study was continued for 15 months: each station being visited 7 times, to give a total year's readings with overlap for the first (trial) run down the coast.

Further description of the study localities is provided by Buchanan (1975), and some is also given in the text following where relevant to the growth and metabolism studies.

OXYGEN CONSUMPTION STUDY.

I. METHODS.

The comparison of oxygen consumption rates in M. edulis populations over the range of latitude required a quick, robust, comparative method, adaptable to a wide range of ambient conditions.

When possible, experiments were carried out right on the sites of the mussel populations: at Holyrood, St. Margaret's Bay, Sandy Hook and Lewes. "In situ" studies were impracticable at St. Andrews and Wachapreague where tidal velocities were too great to keep the experimental equipment stable. At Boothbay Harbor it was more convenient to use the laboratory aquarium system than the harbour floor as the experimental environment. No oxygen consumption studies were done at Woods Hole.

The respirometer was closed: a 500 ml. wide-mouthed bottle with ground glass stopper.

Oxygen concentration was determined by standard Winkler technique (Strickland and Parsons, 1968).

Mussels of length 4.0 to 5.5 cm. were selected from sublittoral populations at each site, scrubbed clean and placed individually in respirometer bottles. The open bottles, in a crate were then lowered to the bay floor - close to the original site of the experimental mussels. Here they remained overnight. By morning the mussels had usually completed byssal thread secretion and appeared to be settled into their new substrate.

Measurement of oxygen consumption commenced 12 hours after collection of the mussels. Two control bottles and from 10 to 24 bottles containing mussels were filled slowly with fresh seawater from the site of the mussel population, sealed under water and returned to the sublittoral situation. Two water samples were taken for determination of the original oxygen concentration. A single experiment usually ran for 2 hours (1 hour for higher temperatures or low original oxygen concentration). At the end of this period the contents of the wide-mouthed

bottles were siphoned carefully into 250 ml. B.O.D. bottles and measured for oxygen concentration. The mussels were returned to the sublittoral site in open bottles for a 1 hour rest period.

During the early part of the study, measurements were generally made every 3 hours for 24 hours: 2 hours sealed, 1 hour open - to establish whether fluctuations in light, tide, temperature, salinity and oxygen concentration, as well as any inherent rhythms of the mussels affected the oxygen consumption during the experiments. Only temperature, salinity and oxygen concentration were found to affect the mussels' activity, and these factors were not necessarily time dependent, allowing a more flexible experimental schedule during the latter part of the study.

On completion of the oxygen consumption measurements the experimental mussels were examined and measured. Oxygen consumption was calculated as ml. O_2 consumed per gram wet (blotted) tissue weight.

II. COMMENTS ON METHOD.

The respirometry used in this study was of necessity a compromise between accuracy, feasibility and reproducibility of the mussel's natural environment. Some comments on the context of the results is therefore in order.

Any method which involves disturbing the mussels must place demands on the metabolism and hence affect the oxygen consumption. Bayne (1971a) reports that a 12-15 hour period for equilibrium in an experimental chamber is sufficient to give linear responses to changes in environmental (pO_2) factors. The settling period allowed in the present study was at least 15 hours. In some cases during the present study, the first experimental run gave a higher value for oxygen consumption than the later runs. This could be attributed to the demand of settling into a new substrate, or to the disturbance caused by the new stimulus of movement of the respirometer and complete water renewal at the commencement of the experiment. One obvious metabolic demand was the secretion of a new byssal thread. Mussels usually secreted these during the overnight settling period. Exceptions existed where the mussels were apparently stressed by high temperatures or low oxygen concentrations at Sandy Hook and Lewes during the summer, and during subzero temperatures and possible nutritive stress at Holyrood in winter. Byssal thread secretion was both rapid and successful under all but these experimental circumstances.

Simulation of the mussel's natural environment in the respirometers was of course only approximate. Temperature was the major factor under consideration, and under the rigorous circumstances of the study the advantages of a closed respirometer outweighed those of an open respirometer. The most obvious disadvantage to the closed respirometer is the decrease in ambient oxygen and increase in carbon dioxide and metabolites in the chamber as the experiment progresses. Some trials were made at Holyrood in September 1971 and a 2 hour experimental period was found to be optimal (at these temperatures and ambient oxygen levels). For periods of less than 1 hour the manipulations of the respirometers

could have interfered with the measured oxygen consumption rate of the mussels. Beyond a period of 4 hours the oxygen consumption was inhibited. At the higher temperatures and lower ambient oxygen levels of the southern stations in summer, an experimental period of 1 hour was optimal. However at Lewes and Sandy Hook initial ambient oxygen levels were occasionally low enough to have an effect on oxygen consumption rate, and the further lowering of oxygen level during the experimental run could not be avoided by the closed respirometry. The following graphs demonstrate a direct relationship between ambient oxygen and oxygen consumption by the mussels, the problem being that some of the low values for oxygen consumption could have been caused by decrease of oxygen level in the experimental chamber:

Figure 29.	Sandy Hook.	1 Sept. 1971
36.	Lewes.	6 Sept. 1971
40.	Lewes.	6 May 1972 (also low salinity)
41.	Lewes.	1 July 1972 (few data)
42.	Lewes.	3 Sept. 1972 (also low salinity)

No measurements of pCO_2 or metabolites were made in this study. Both are known to inhibit oxygen consumption in M. edulis (Jørgensen, 1960). The rate of circulation of water by M. edulis varies over a wide range and is dependent on many factors. A common maximal rate of 30 ml. water pumped/mussel/minute represents a re-circulation of the experimental water 3-6 times every hour. Circulation in such a chamber has been shown to be fairly complete (Jørgensen, 1960), and considerable re-circulation through the mussel could be expected. In this respect the closed system could be expected to produce an under-estimate of the oxygen consumption.

A further inhibition of metabolism may have been incurred by the lack of water circulation in the bottles. Mussels accustomed to a fairly turbulent environment were studied under conditions where the only water circulation was provided by themselves. Currents stimulate filtration (Walne, 1972), and in this regard the closed respirometer would again provide an under-estimate of oxygen consumption. Similarly the amount of dissolved and particulate food in the water affects metabolic rate. At recirculation rates of 3-6 times during the experimental period, and

TABLE 3.

Type of Study	O_2 cons.ml/g.dry/hr.	Region	Author
	0.15 to 1.5	Mass. U.S.A.	Read, 1962
Over Year	0.6 to 1.8	U.K.	Bayne and Thompson, 1970
Standard	0.2		
Routine	0.4	U.K.	Gabbot and Bayne, 1973
Active	0.6		
Starved	0.2		
Fed	0.5	U.K.	Thompson and Bayne, 1972
After Feeding	0.35		
Acclimated (temp)	0.2 to 0.5		
Unacclimated	to 0.8	U.K.	Widdows and Bayne, 1971
At Field Temp.	0.2 to 0.45		
In Declining pO_2	0.4 to 2.4	U.K.	Bayne, 1971b
Var. Salinity & pO_2 (15°C.)	0.0 to 1.7	U.K.	Bayne, 1973
Close Respirom. Mussel of 1g dry wt.	1.4	Denmark	Vahl, 1973
Mussel of 30 mg dry wt. Tissue Prep.	(1.0 to 3.0) by 10^{-2}	U.K.	Newell and Pye, 1970a
Northern Stations	0.00 to 2.00	Holyrood to Boothbay	Present study
Southern Stations	1.00 to 3.50	Sandy Hook to Wachapreague	Present study

under the normal efficiency of particle retention (close to 100%), particulate food could be expected to be removed by the mussel early in the experiment. Active metabolic rate, if present at the commencement of the experiments, would be replaced by routine metabolic rate as food is depleted from the water and particulate food in the gut is metabolized. Under the circumstances of the study it was impossible to control the prior feeding activity of the mussels and hence metabolic rates recorded here can be considered as approximately routine unless the mussels were under nutritive stress, e.g. at the northern stations in winter.

The oxygen consumption values obtained in the present study agree reasonably well with those of other studies. Converting the values of the present study to ml. O_2 consumed/g. dry weight/hour, some comparisons are made in Table 3.

For the present study values obtained at the northern stations are comparable to those of other studies. Oxygen consumption rate at the southern stations, however, was well above any of the records in Table 3. Most of the data in Table 3 come from regions which are thermally equivalent to, or a little warmer than, the northern stations of the present study.

III. RESULTS.

The results of the oxygen consumption study are presented in Appendix Table 1. For ease of interpretation, graphical representation of this table is made in Figures 5 to 48 in the text following. The data are summarized on a per visit basis in text Table 4 which allows a comparison of seasonal variation in oxygen consumption between stations. This is represented graphically, over the year - in Figure 49, and per ambient temperature - in Figure 50. For a less complicated comparison between stations, the regression of temperature on oxygen consumption over the year has been made for each station. The calculations are presented in Appendix Table 2, the results are summarized in text Table 5 and presented graphically in Figure 51.

Graphical Presentation of Oxygen Consumption Study Data.

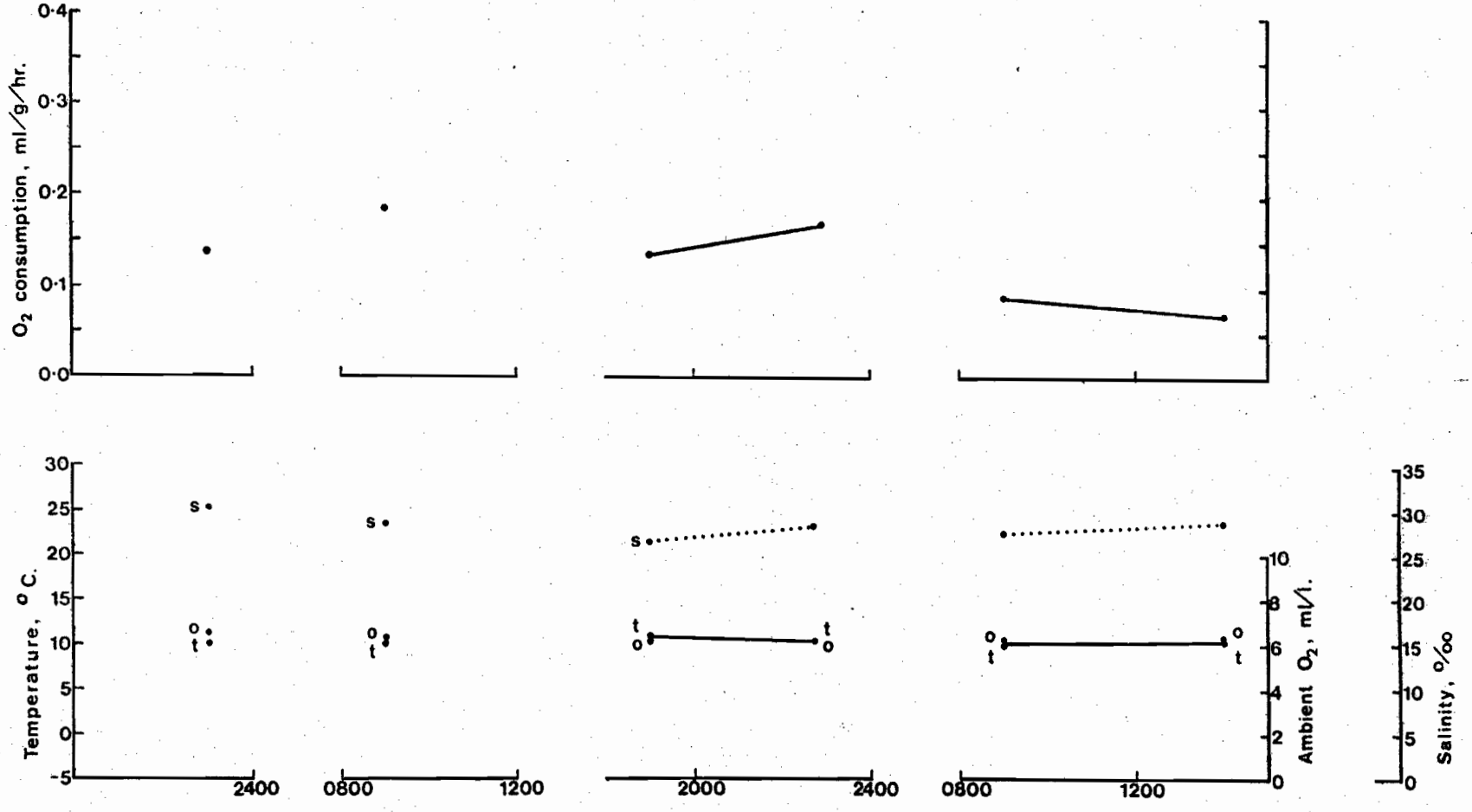
Figures 5 to 48 show mean oxygen consumption rates ($n \doteq 10$), compared with ambient experimental temperature, salinity, and oxygen concentration. These are plotted on a time axis of 1 to 3 days (hours shown along abscissa) for each sampling station.

Bellevue and Holyrood. Figures 5 to 10.

No figure is included for 6 February, 1972. The salinity during this period was too low for the mussels to open, and on two runs taken, oxygen consumption was zero. Observations of mussels in the field were made prior to the experimental runs. Even at salinities greater than 16°/oo the mussels under the ice (temperature -0.2°C) remained closed for long periods. Byssal thread secretion and hence attachment in the experimental bottles was poor: some mussels did not attach over a three day period, those that did only secreted a few fine threads. Oxygen consumption rate was low at Holyrood and at other stations at temperatures similar to those recorded on 6 February, and in view of the lack of activity observed in the field, it is probable that oxygen consumption was near zero for Holyrood on 6 February.

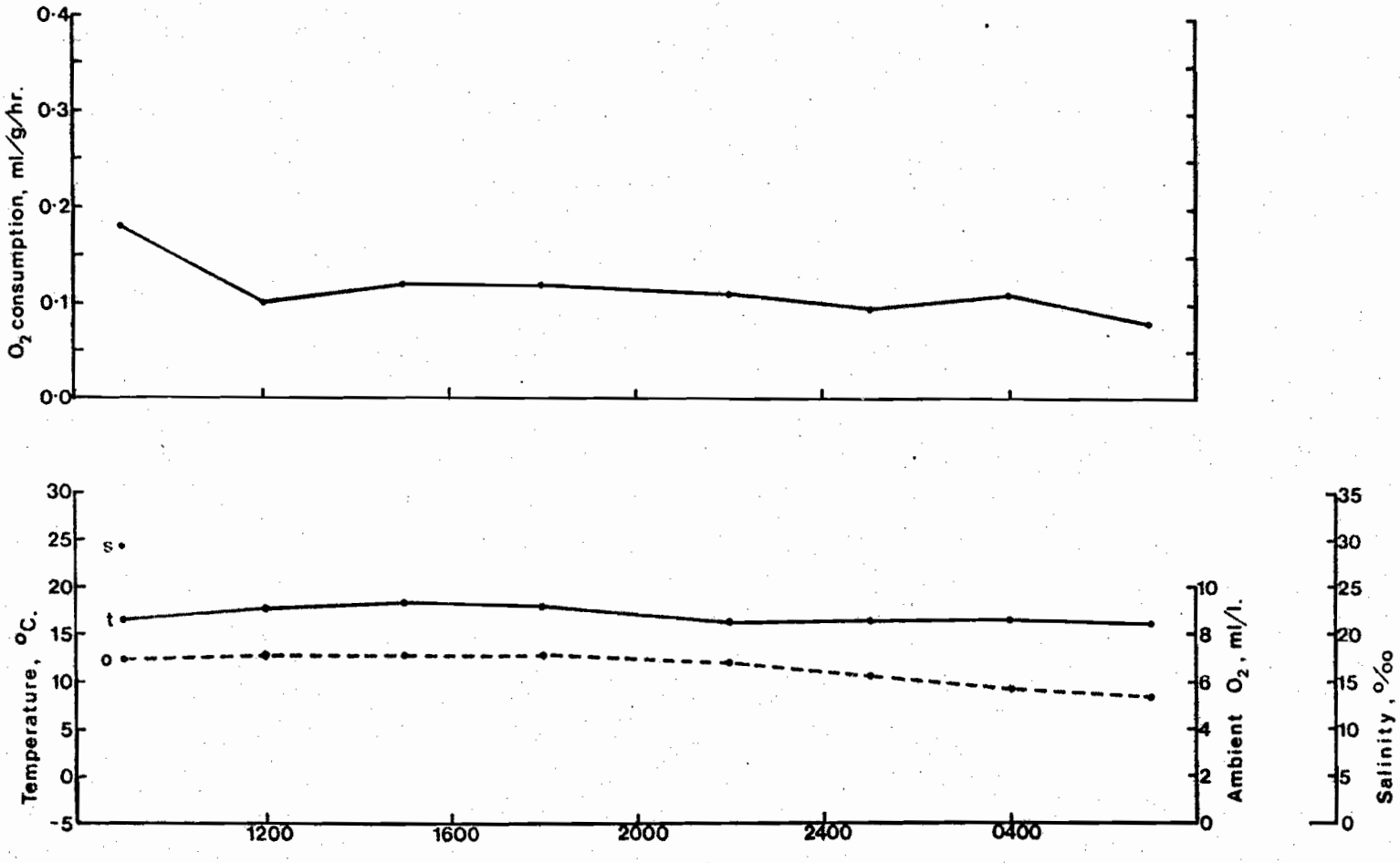
Due to the low air temperatures and near freezing point of the water on 6 December 1972 at Holyrood some difficulty was caused in the measurement of oxygen concentration by icing up of the respirometer bottles. This may account for the high oxygen consumption values obtained for Runs 3 and 4. Salinity in Runs 4 and 5 was below 10°/oo, and Run 5 should be taken as the correct value for oxygen consumption at this salinity.

Salinity again affected oxygen consumption on 8 April 1972 and 7 June 1972. On 8 April oxygen consumption was low but dropped even lower when salinity fell below 15°/oo. On 7 June the mussels closed when salinity dropped to about 15°/oo.



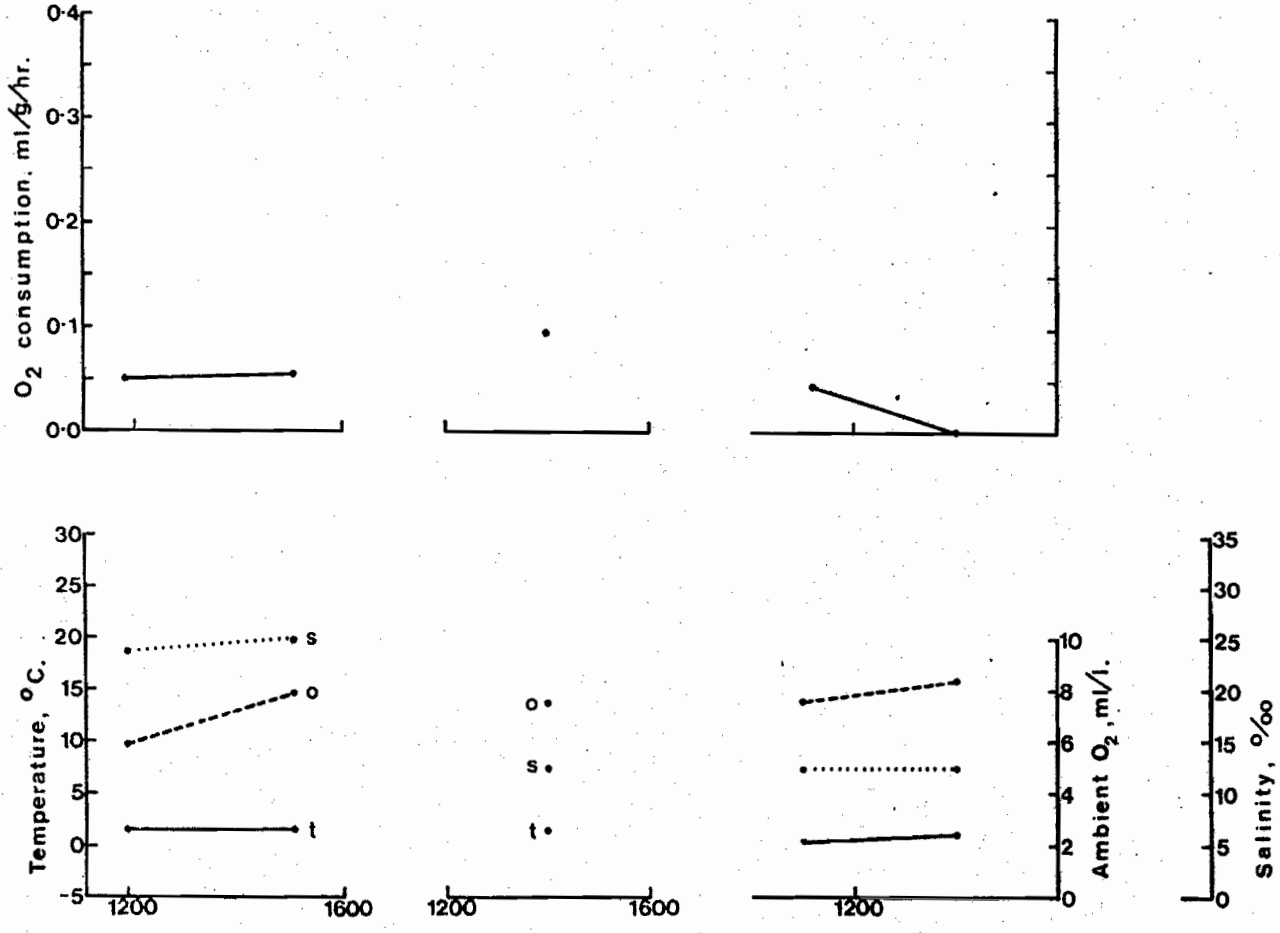
BELLEVUE 6 Oct 71
HOLYROOD

Fig. 6



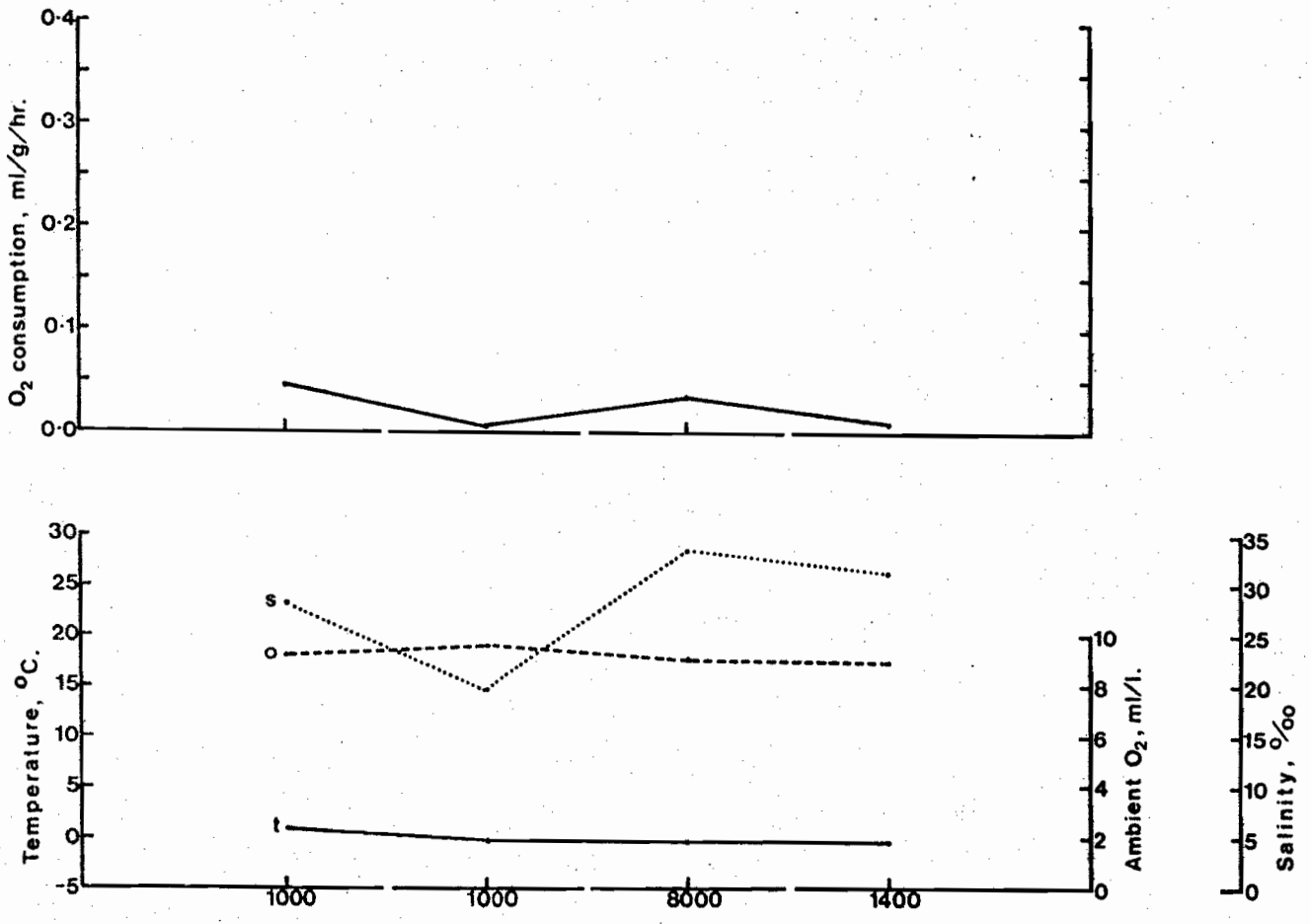
BELLEVUE 1 Aug 71

fig. 5



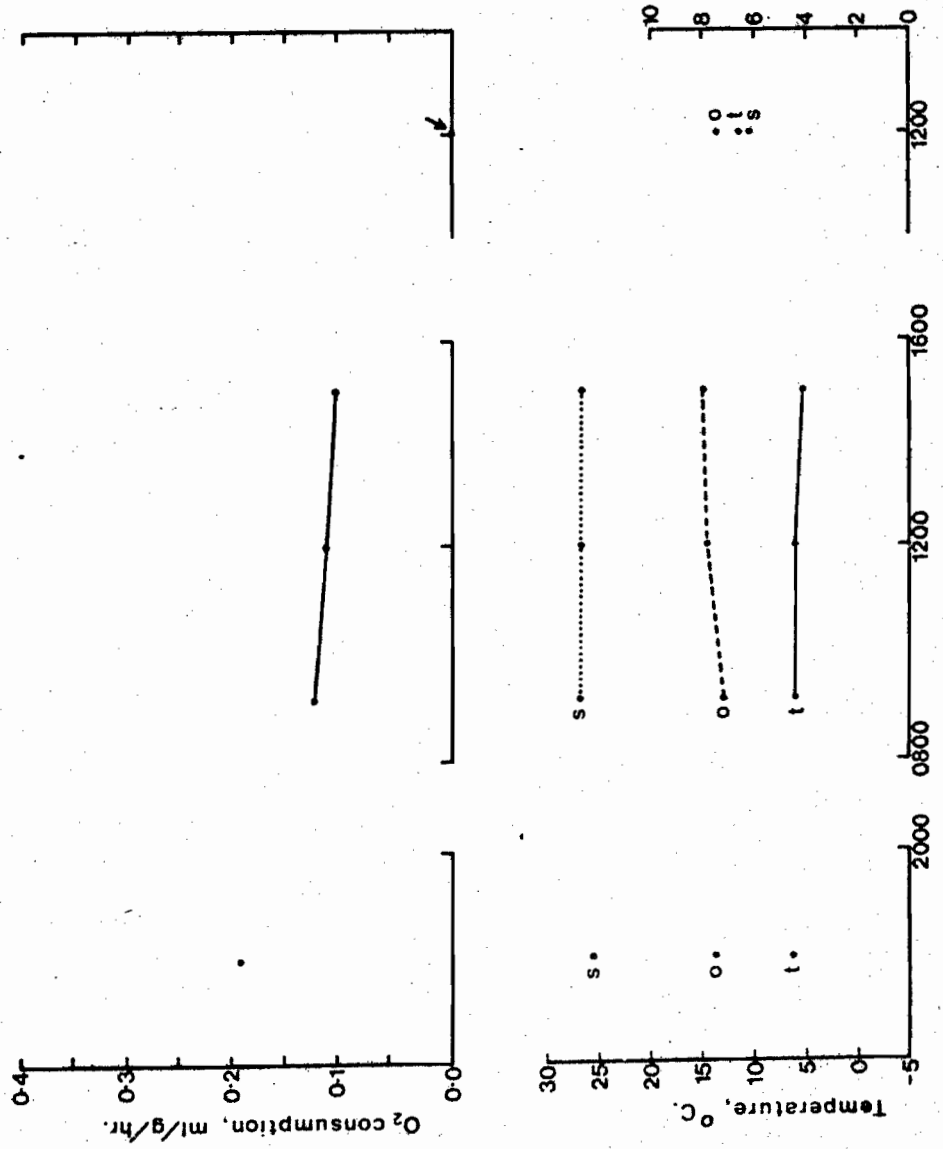
BELLEVUE 6 Dec 71
HOLYROOD

Fig. 7



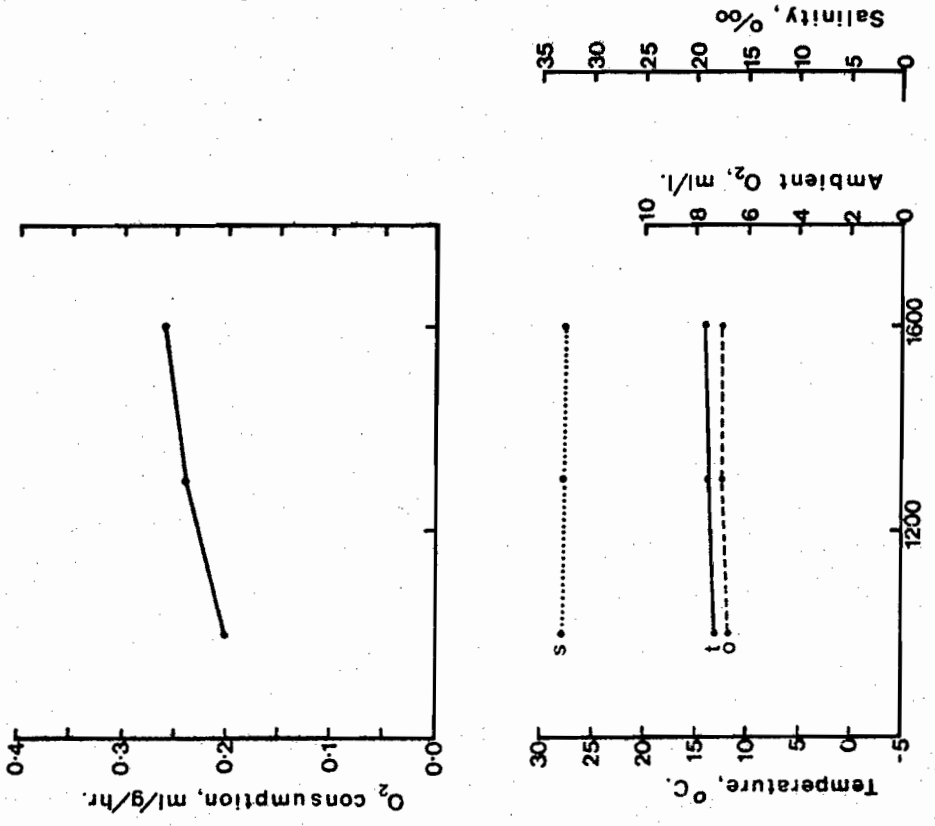
HOLYROOD 8 Apr 72

Fig. 8



HOLYROOD 7 Jun 72

Fig. 9



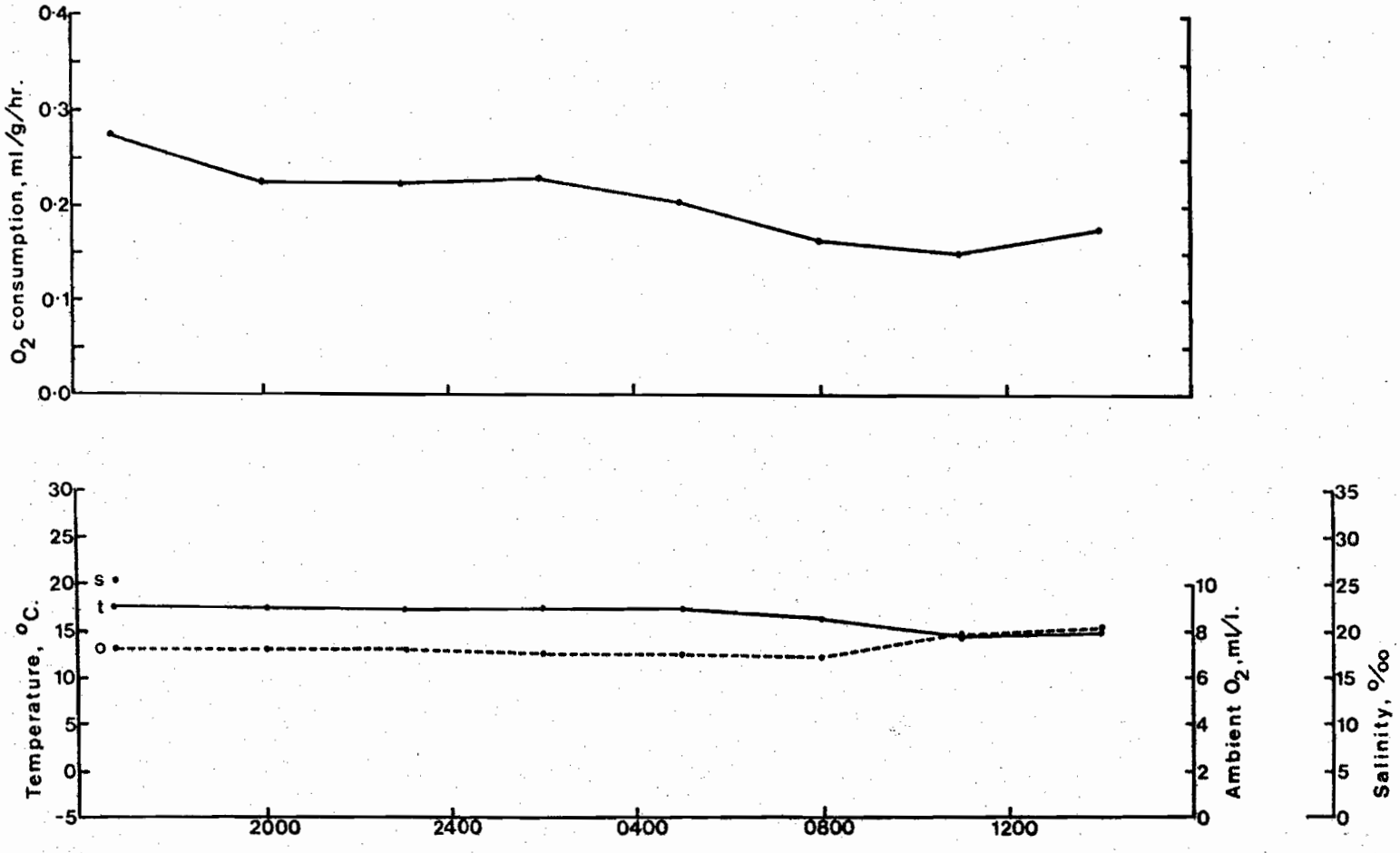
HOLYROOD 2 Aug 72

Fig. 10

St. Margaret's Bay. Figures 11 to 16.

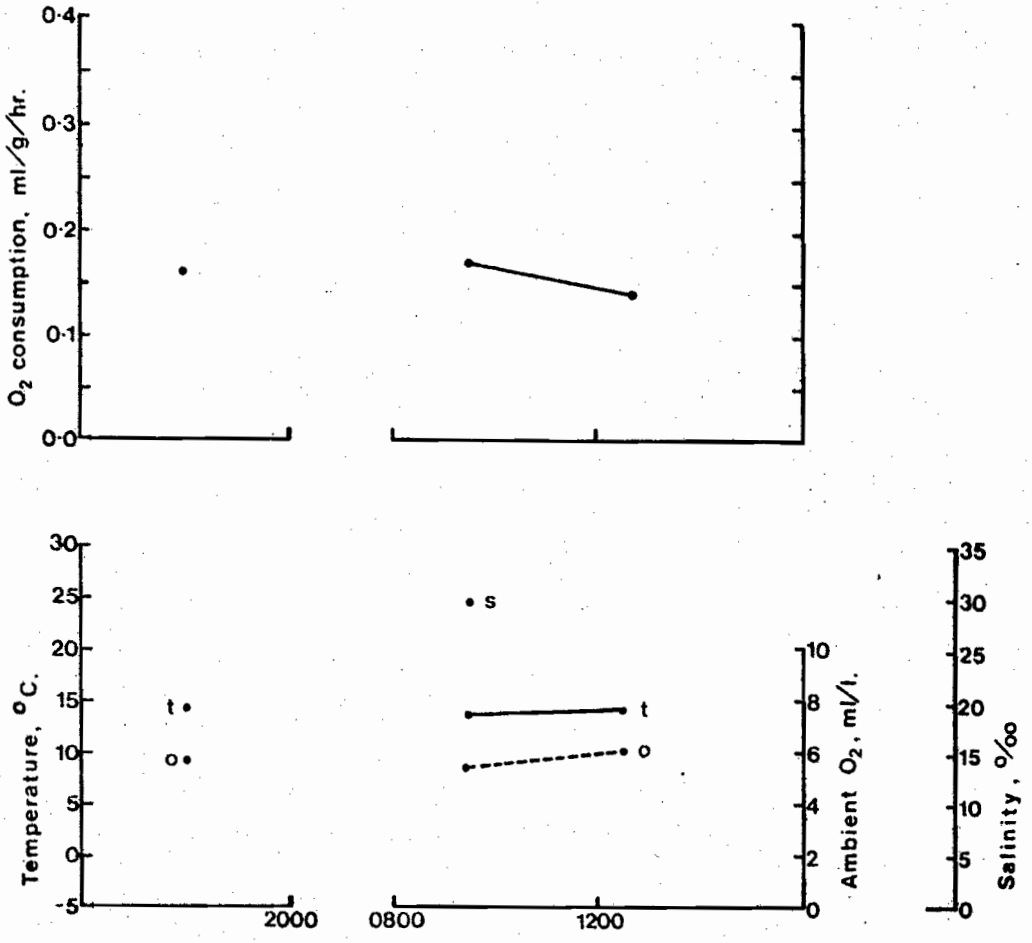
No oxygen consumption data were obtained for early February, 1972. Activity and oxygen consumption were probably very low at this time (see comments for Holyrood, 7 February, 1972).

On 15 April, 1972 low salinity on Run 1 caused a depression in oxygen consumption.



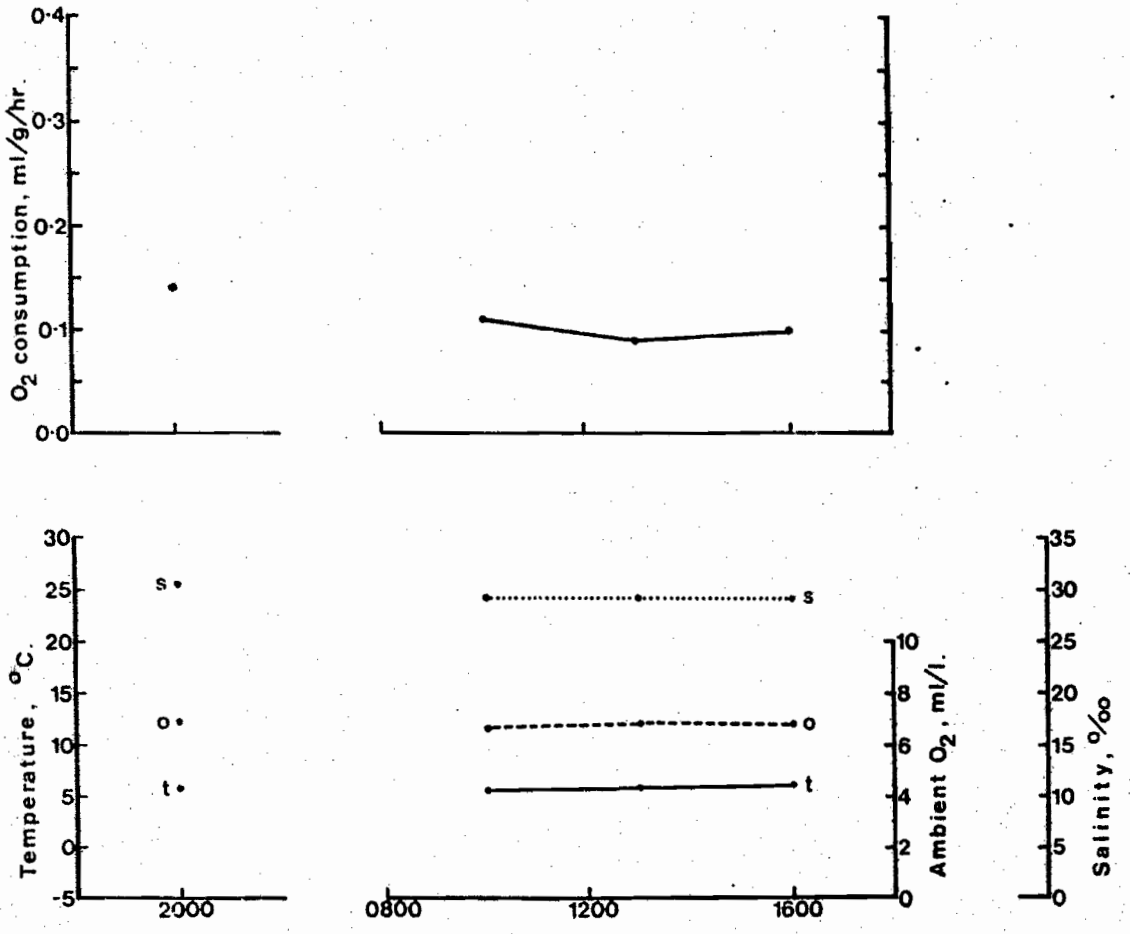
ST. MARGARET'S BAY 7 Aug 71

Fig. 11



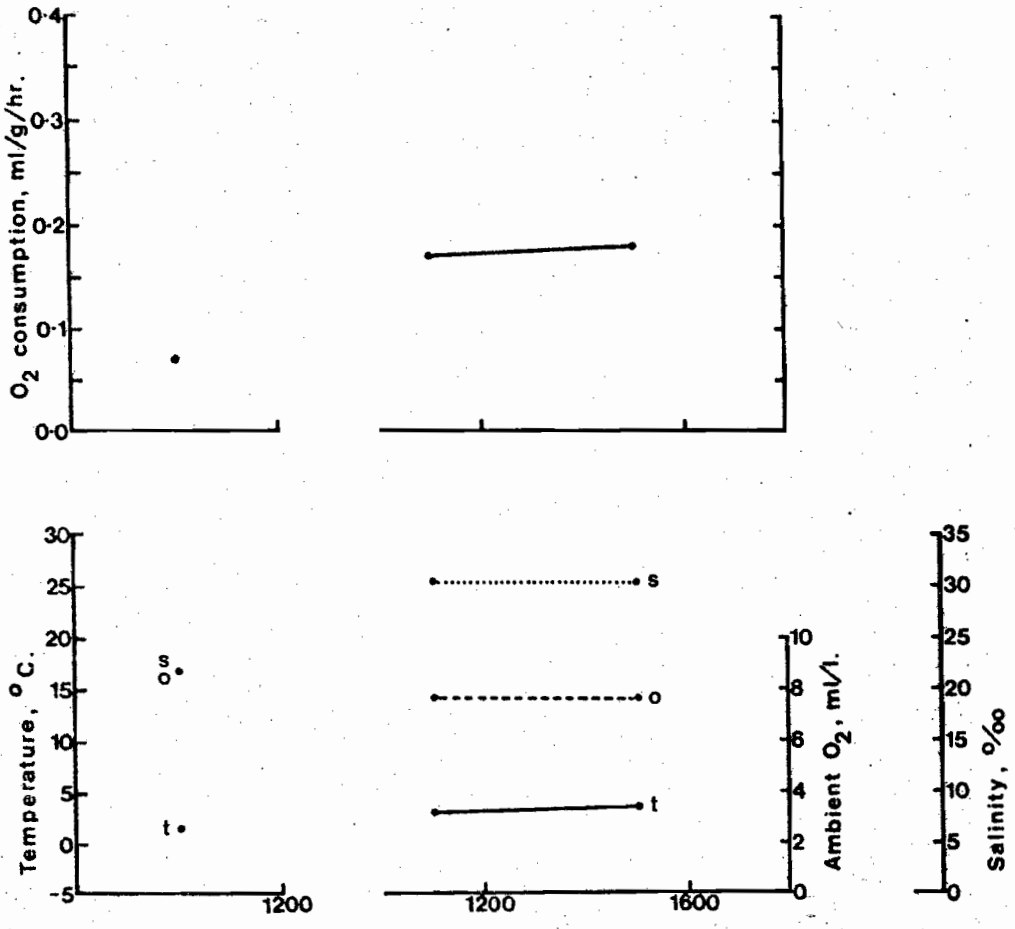
ST. MARGARET'S BAY 14 Oct 71

Fig. 12



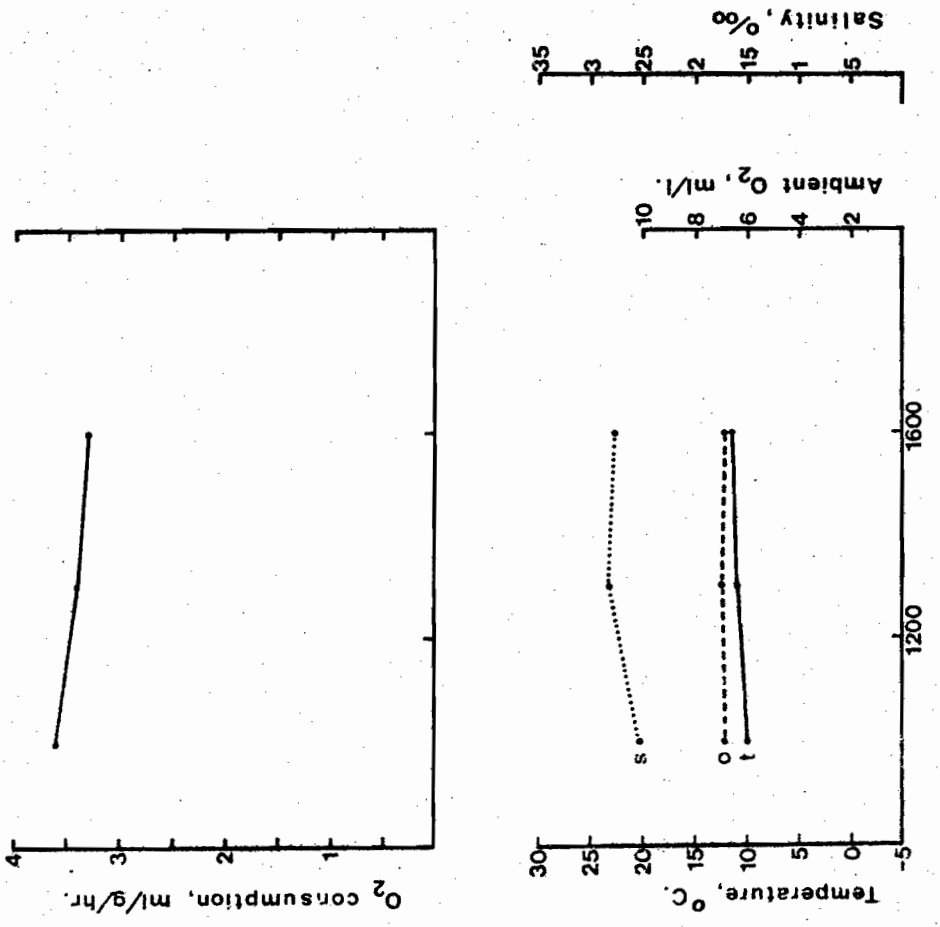
ST. MARGARET'S BAY 12 Dec 71

Fig. 13



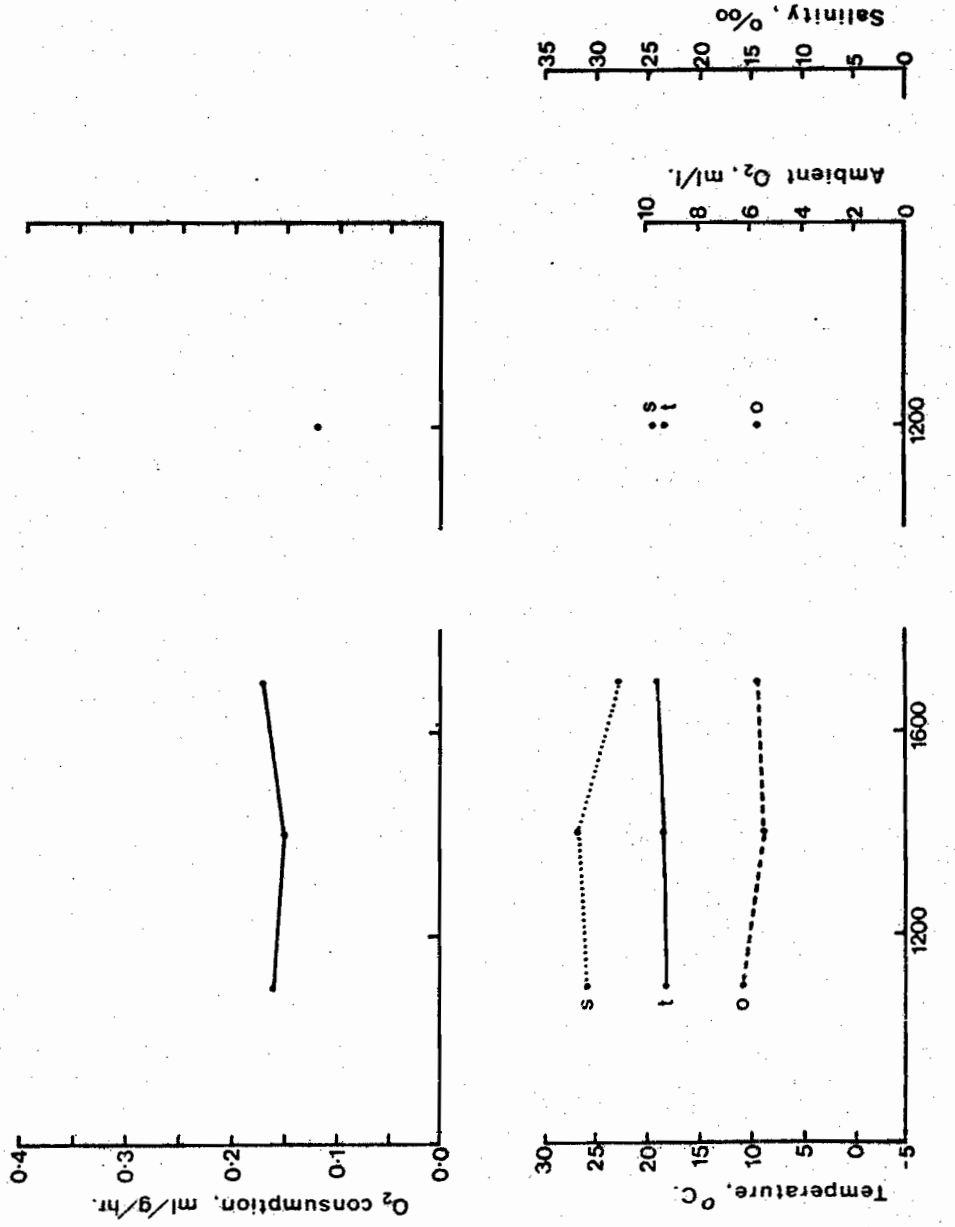
ST. MARGARET'S BAY 15 Apr 72

Fig. 14



ST. MARGARET'S BAY 12 Jun 72

Fig. 15



ST. MARGARET'S BAY 10 Aug 72

Fig. 16

St. Andrews. Figures 17 to 21.

Due to initial difficulties with the tides at St. Andrews, no reliable data were obtained for September to November, 1971. The earliest data for St. Andrews were on 15 December, 1971.

Conditions were effectively uniform throughout each experimental period except on 19 June, 1972 when small changes in salinity may have produced the small changes in oxygen consumption.

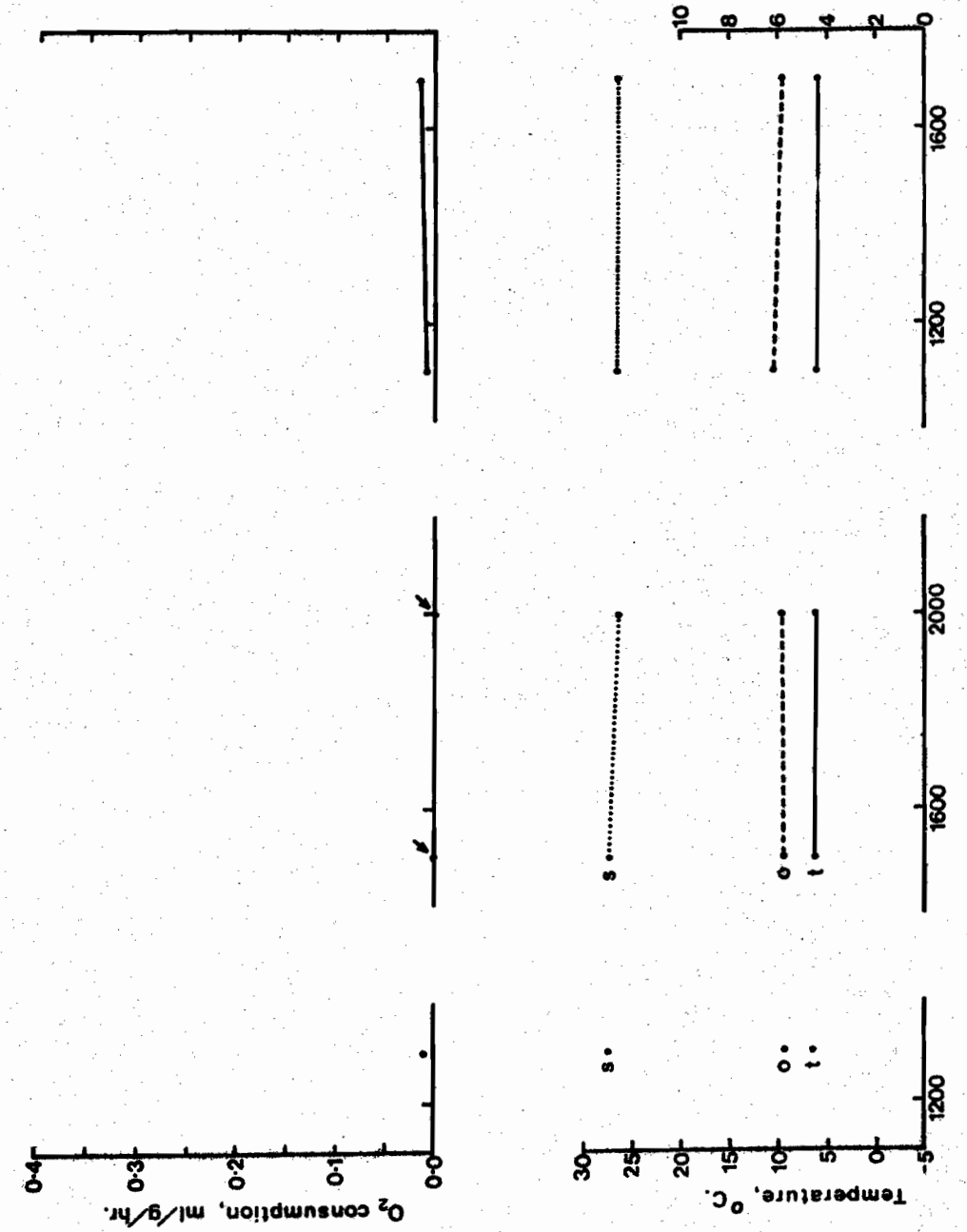
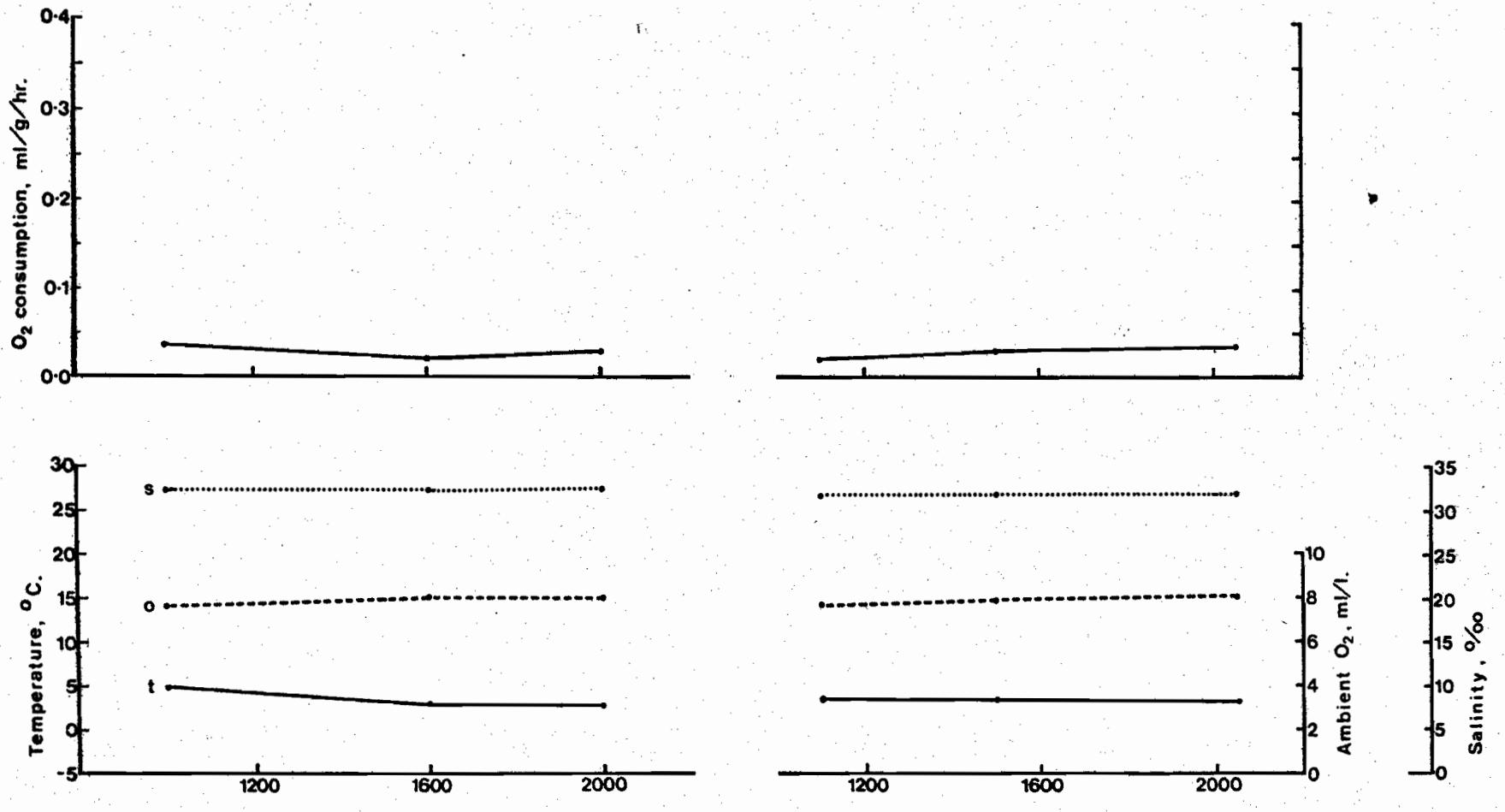
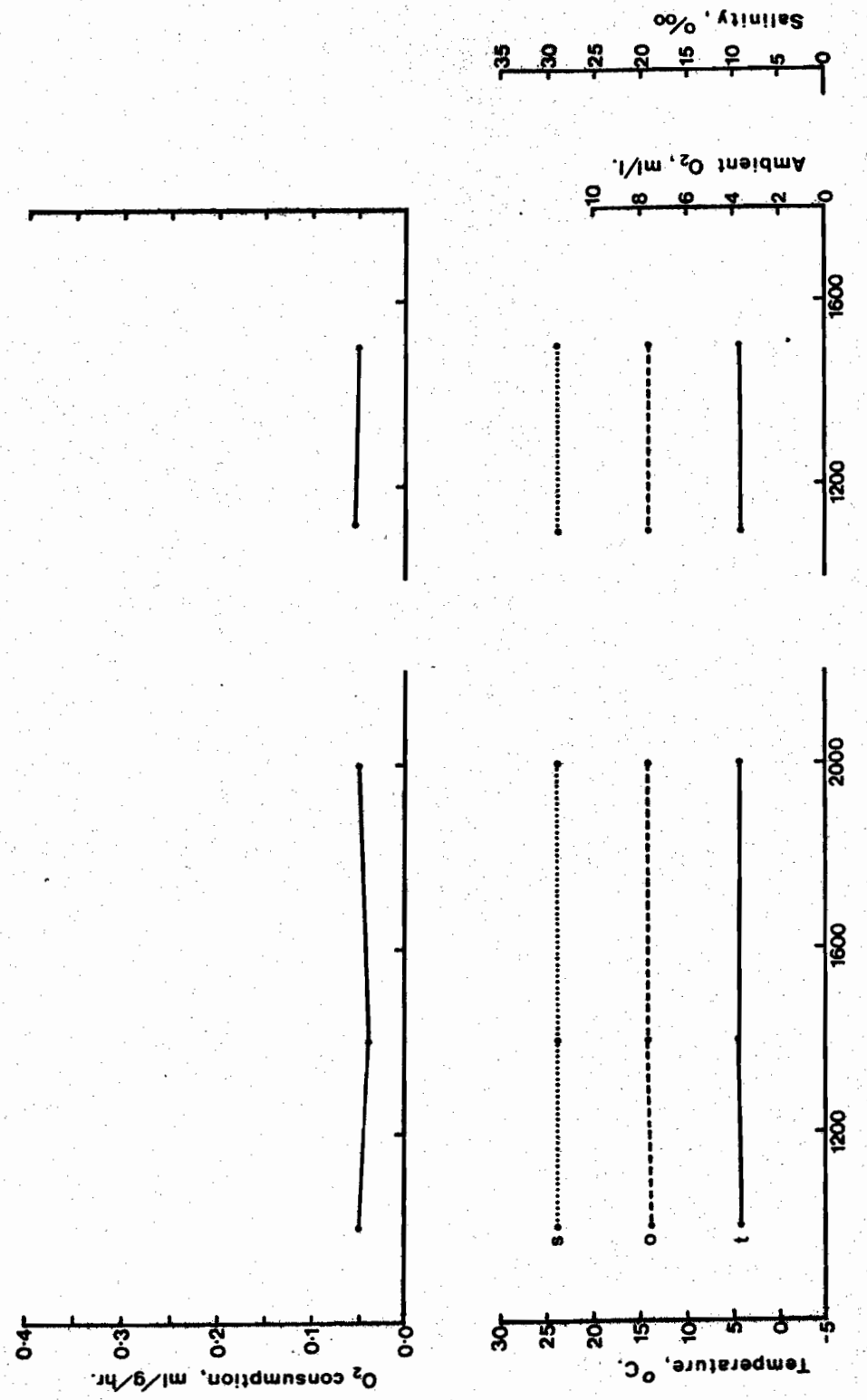

O2 consumption, ml/g/hr.
0·0
0·1
0·2
0·3
0·4
Temperature, °C.
30
25
20
15
10
5
0
-5
s
o
t
1200
1600
2000
Ambient O2, ml/l.
0
2
4
6
8
10
Salinity, °/oo
0
5
10
15
20
25
30
35
ST. ANDREWS
15 Dec 71

Fig. 17



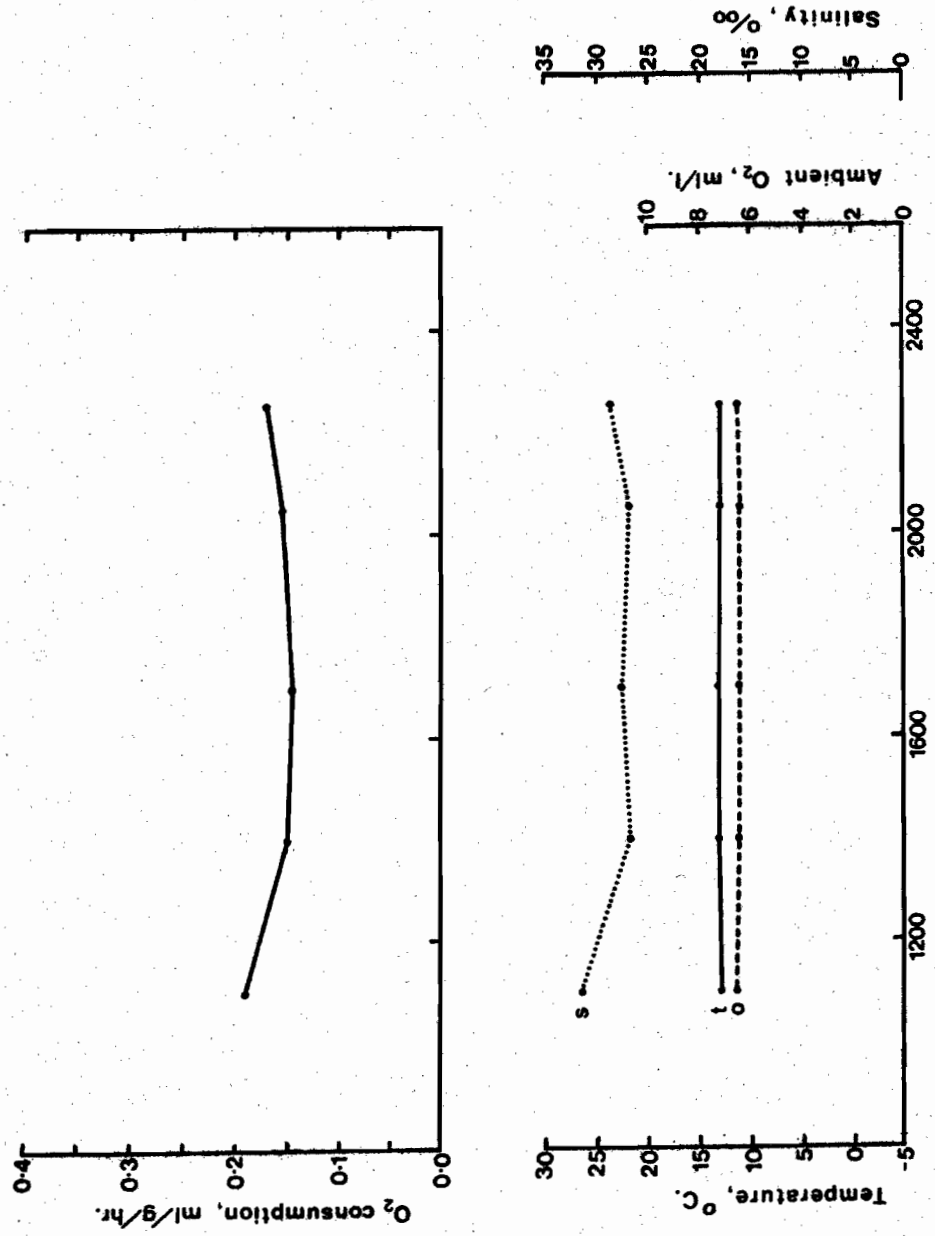
ST. ANDREWS 15 Feb 72

Fig. 18



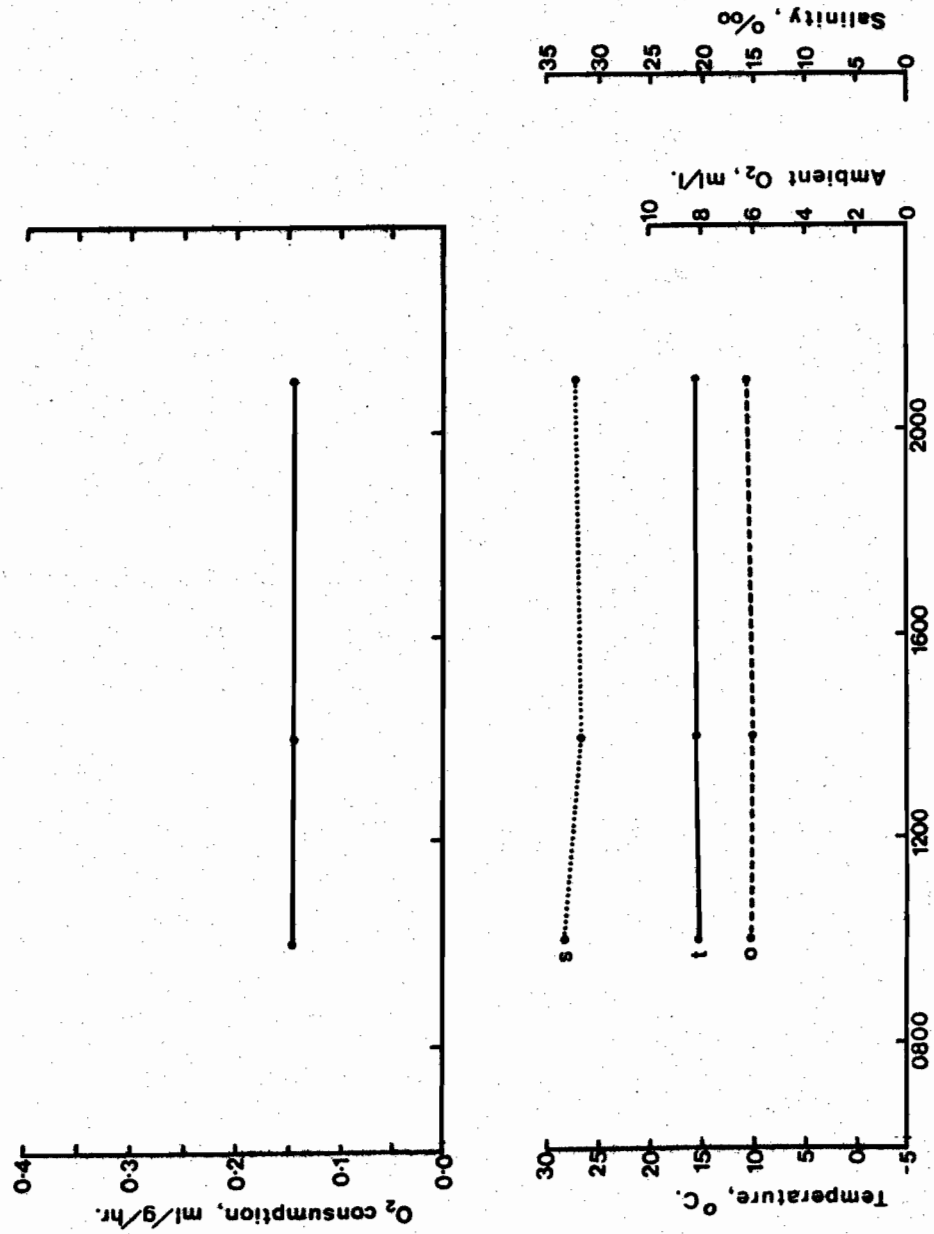
ST. ANDREWS 19 Apr 72

Fig. 19



ST. ANDREWS 19 Jun 72

Fig. 20

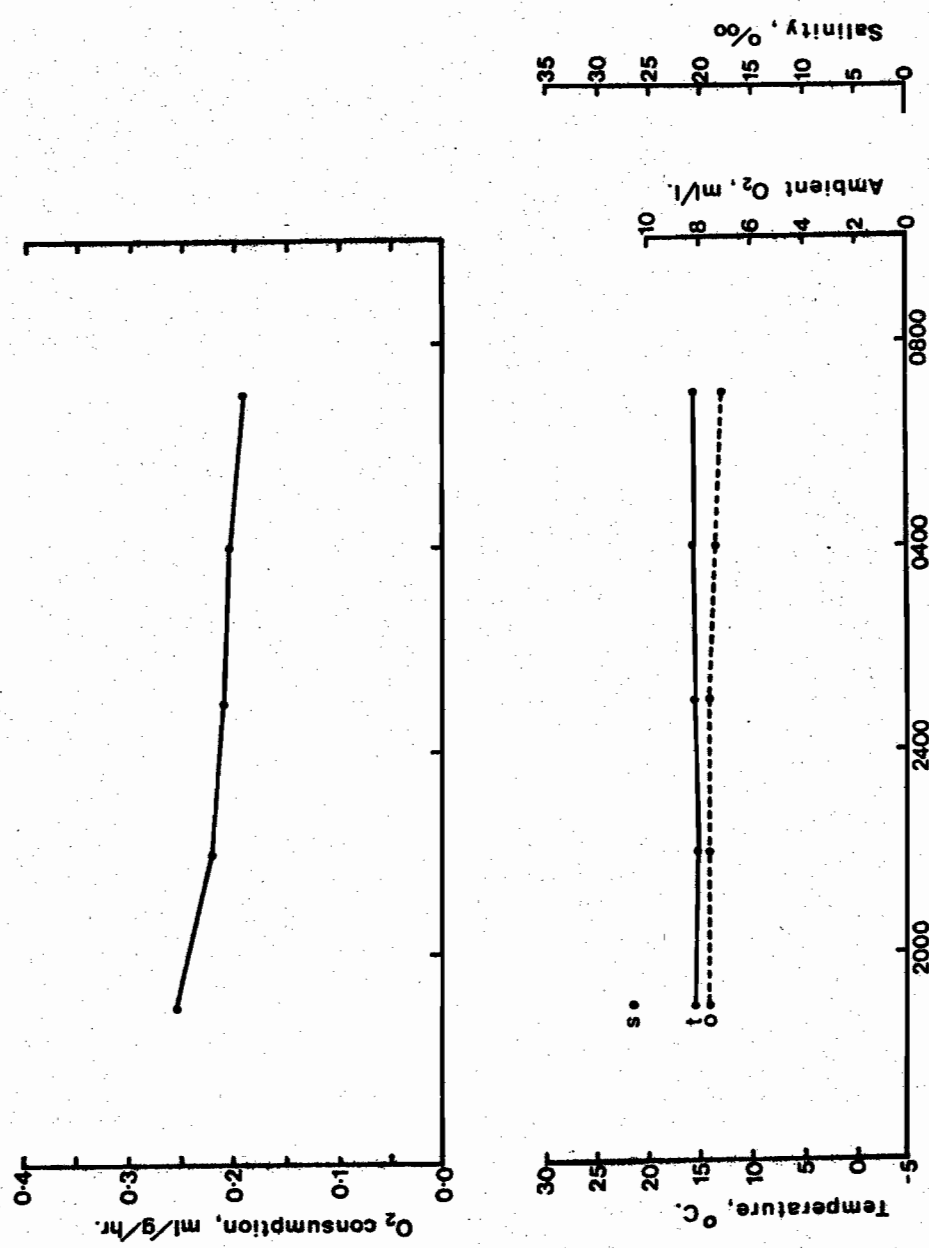


ST. ANDREWS 16 Aug 72

Fig. 21

Boothbay. Figures 22 to 28.

A complete set of data was obtained for Boothbay. Oxygen consumption and measured environmental factors were effectively uniform throughout each experimental period.

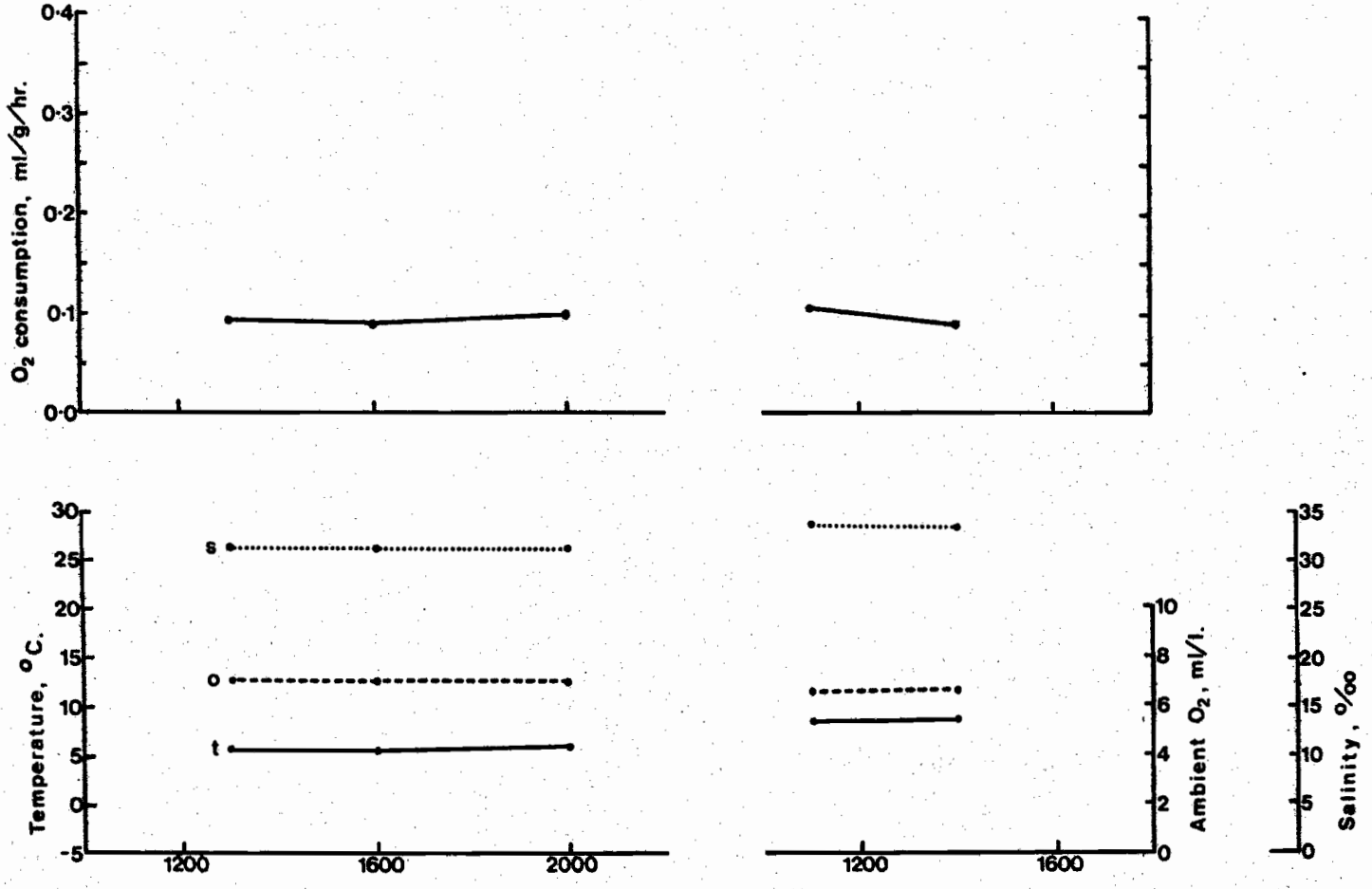


BOOTHBAY 17 Aug 71

Fig. 22

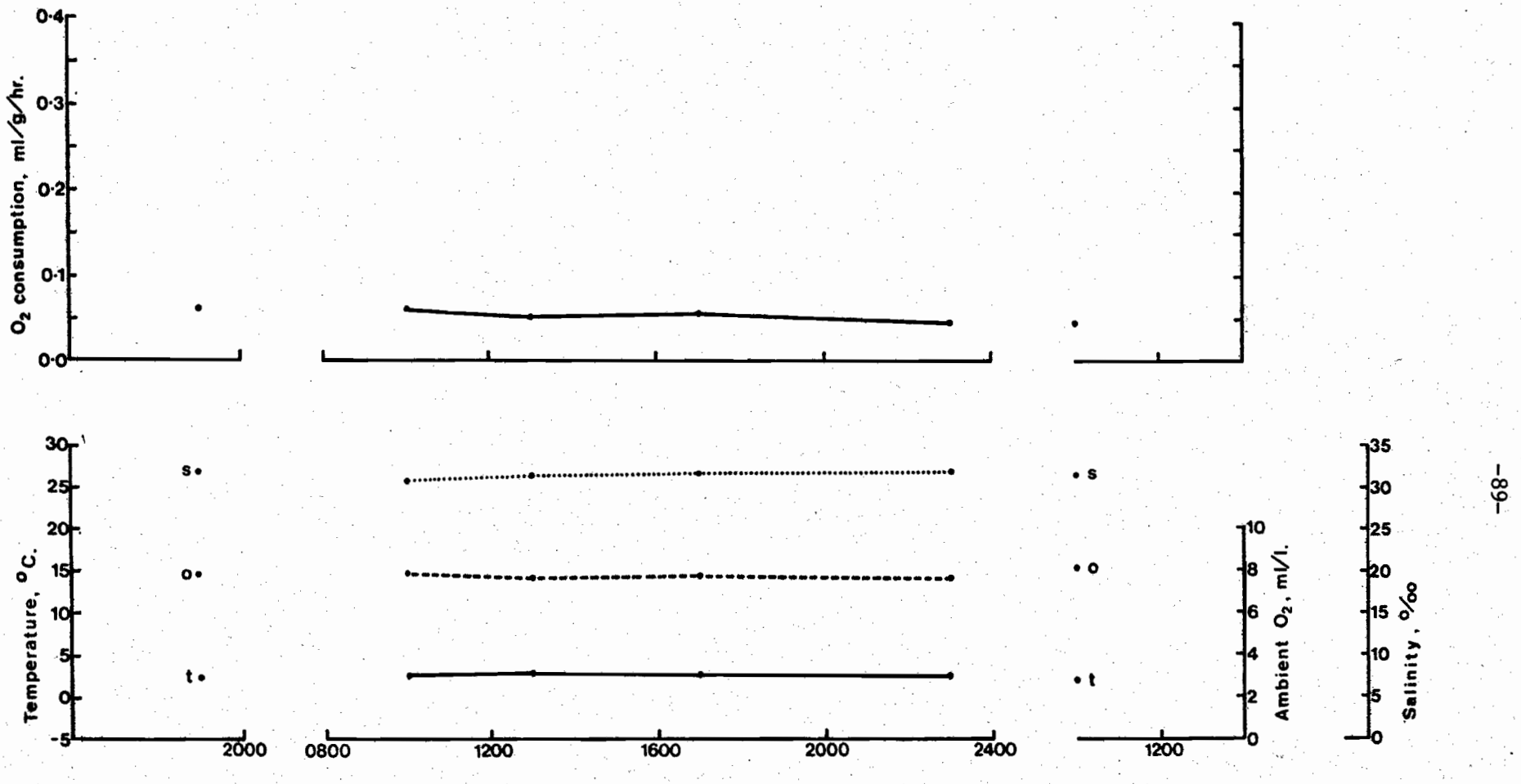
BOOTHBAY 21 Oct 71

Fig. 23



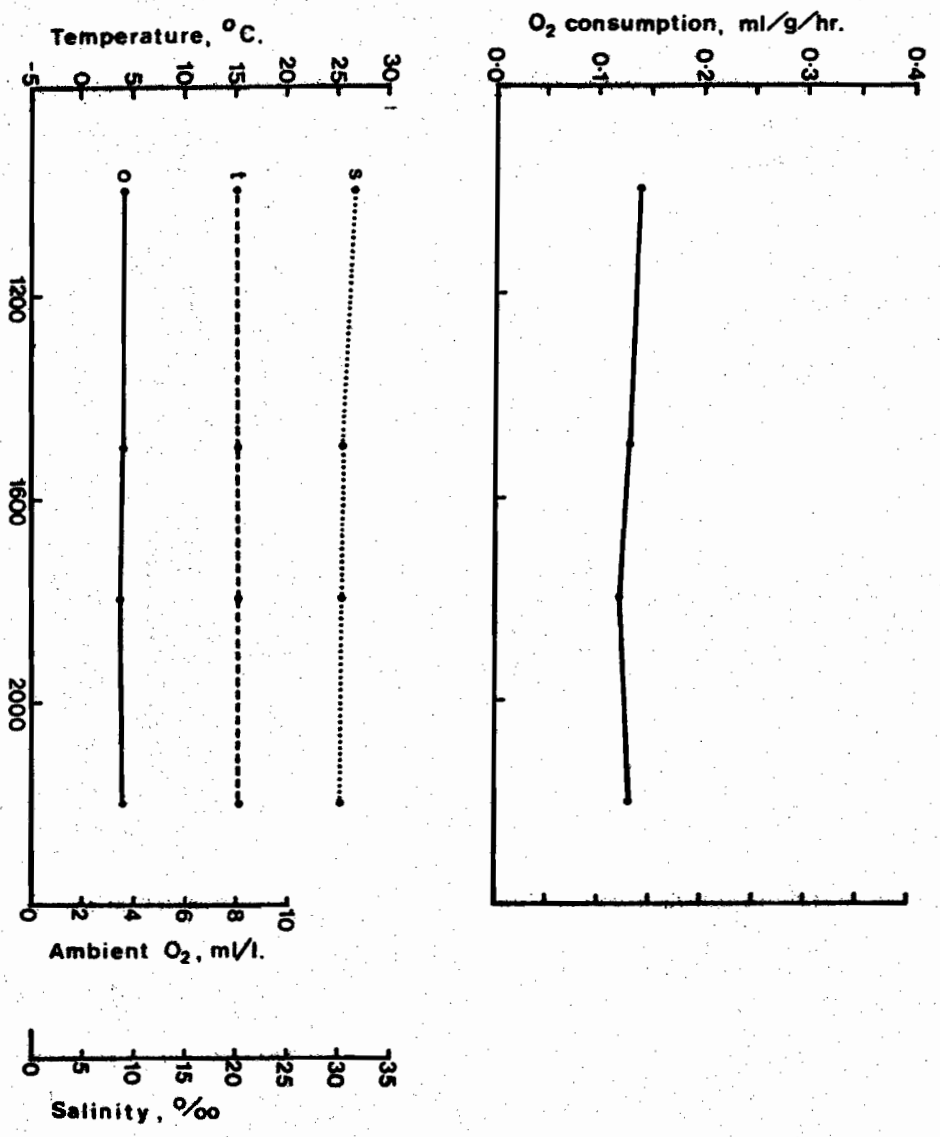
BOOTHBAY 20 Dec 71

Fig. 24



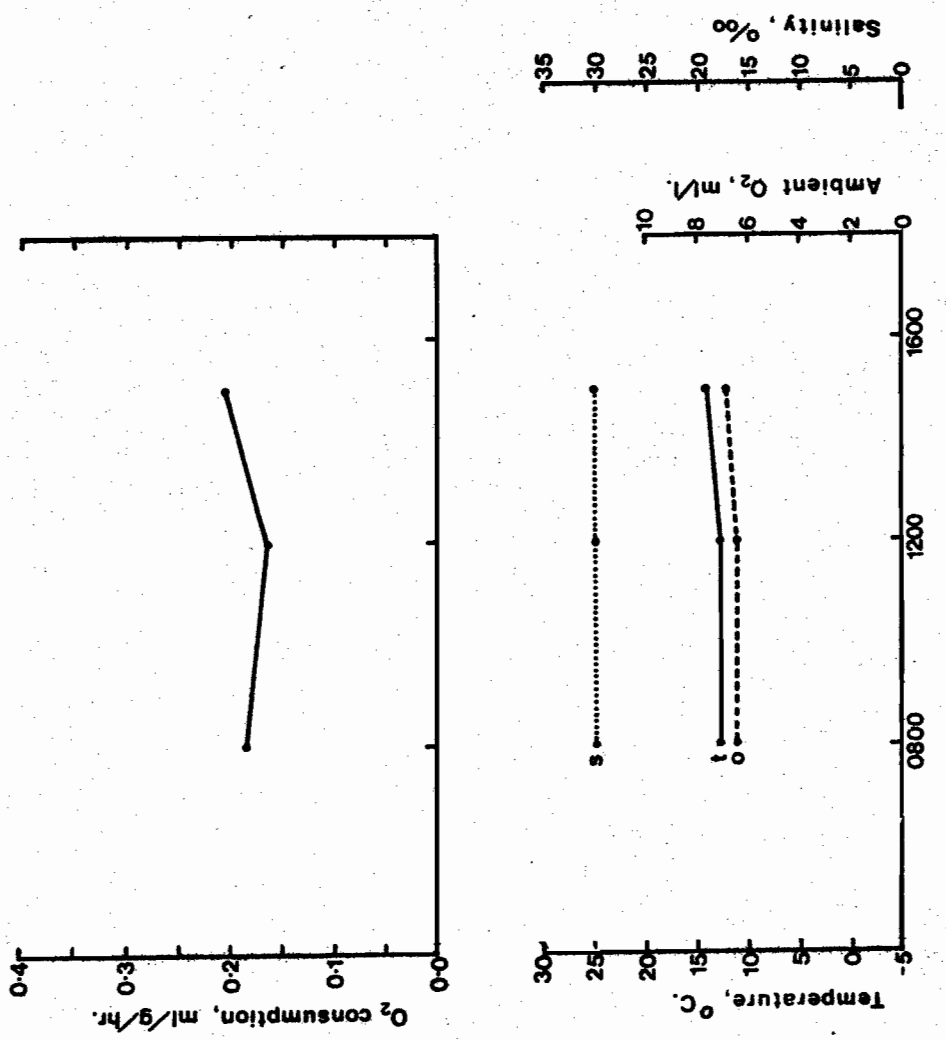
BOOTHBAY 19 Feb 72

Fig. 25



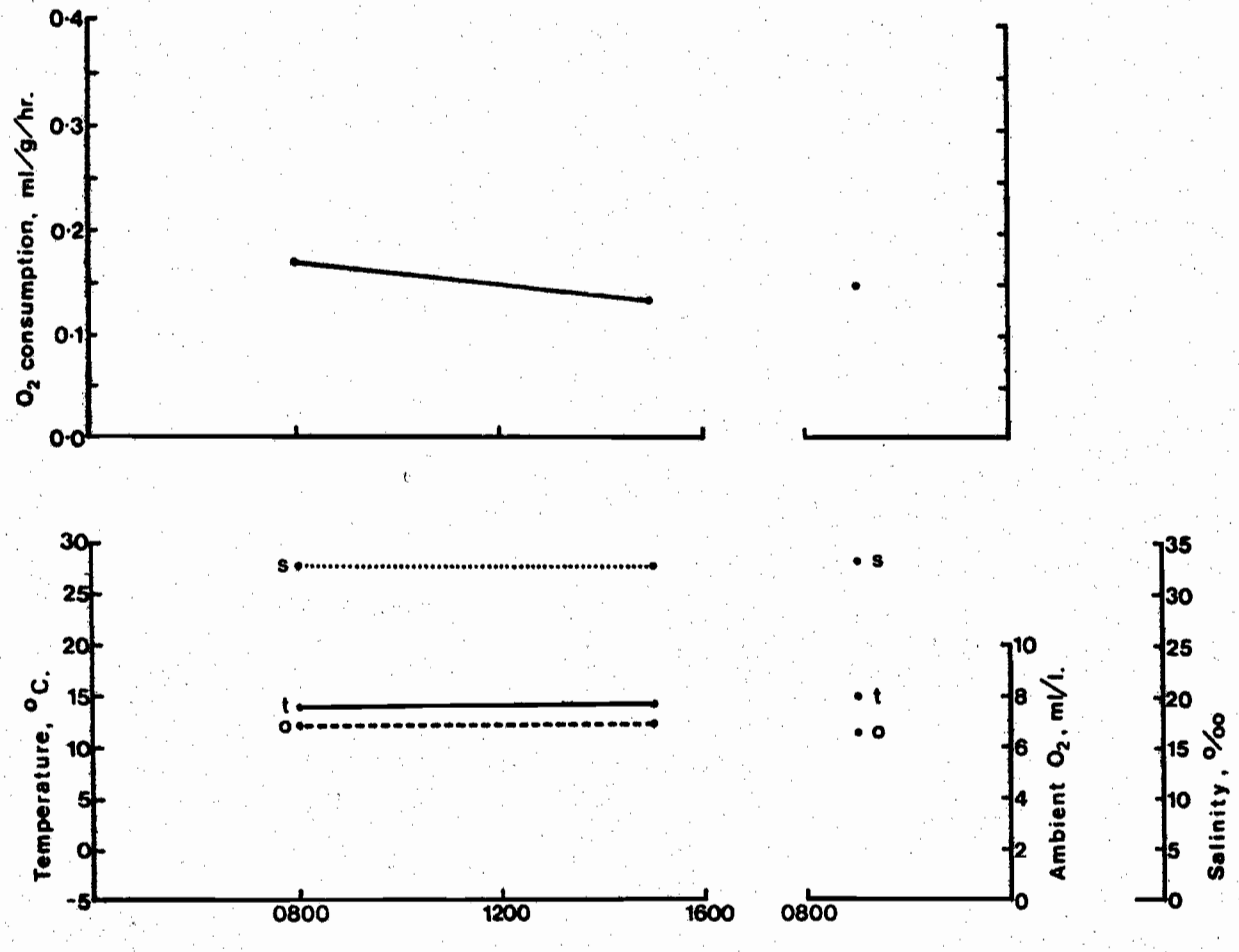
BOOTHBAY 23 Apr 72

Fig. 26



BOOTHBAY 20 Jun 72

Fig. 27



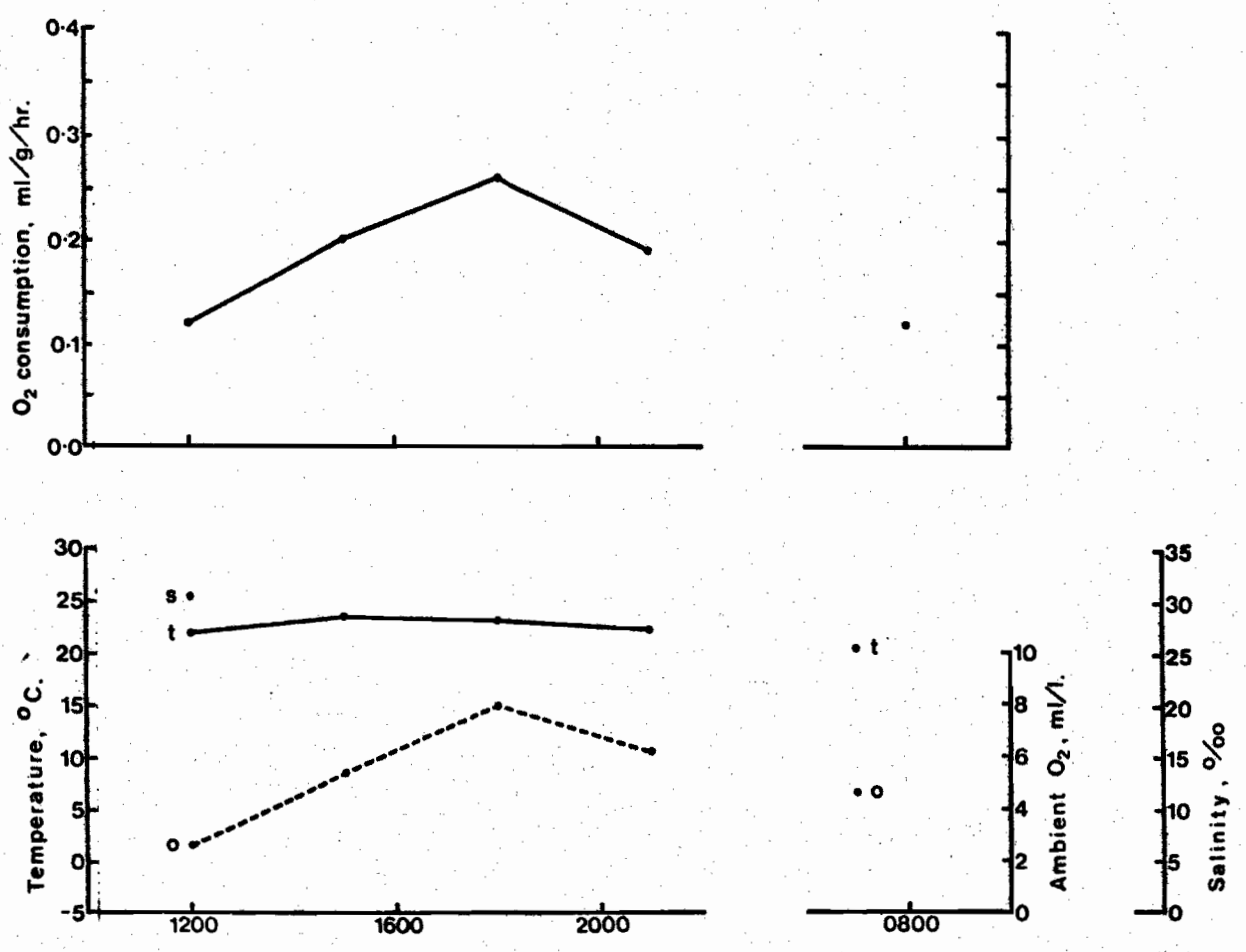
BOOTHBAY 20 Aug 72

Fig. 28

Sandy Hook. Figures 29 to 35.

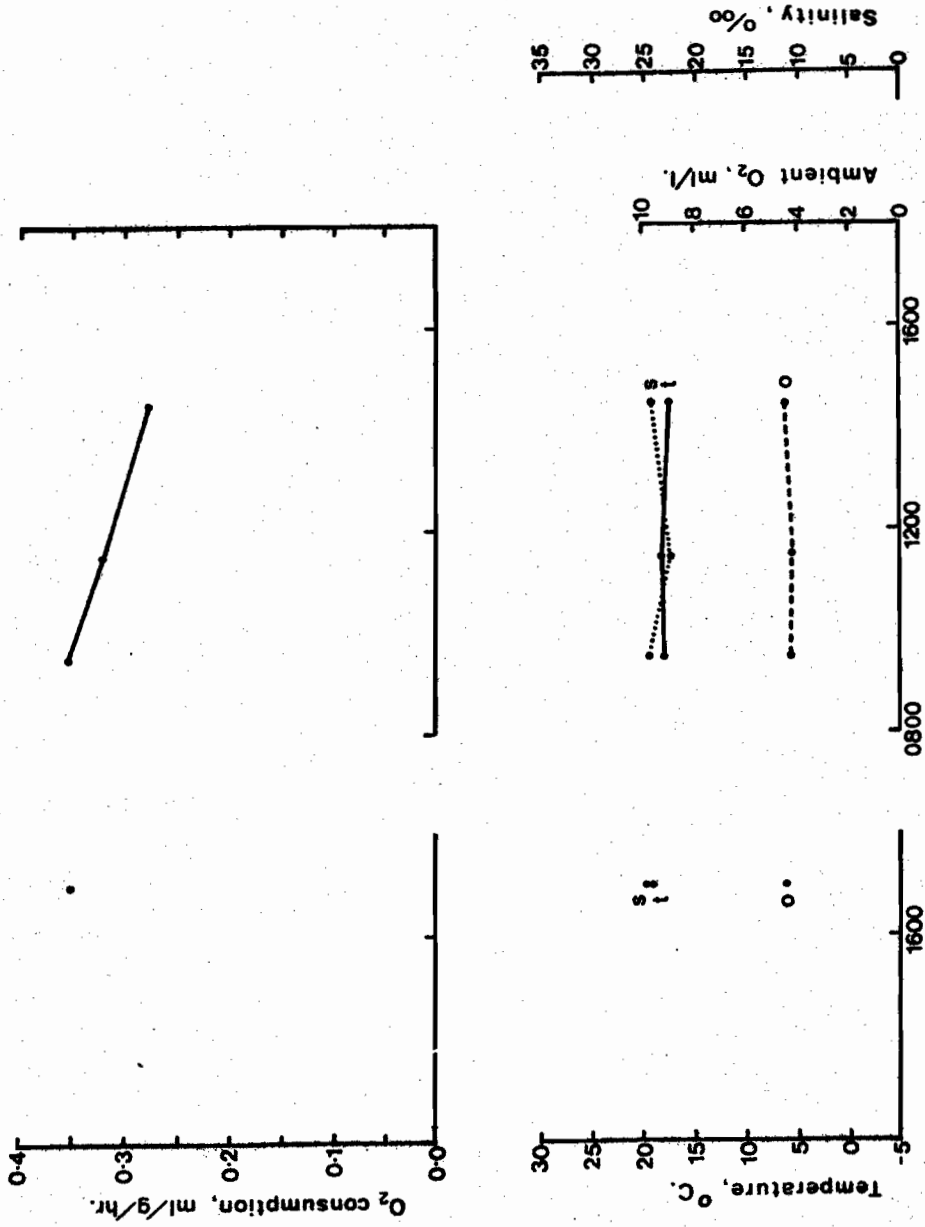
A complete set of data was obtained for Sandy Hook. Most of the results were straightforward, except for 1 September, 1971 where post-flood conditions caused wide variations in ambient oxygen levels. On 2 November, 1971, 29 June and 9 August, 1972 low ambient oxygen was again recorded.

The general level of oxygen consumption values on 1 September was probably depressed below 'normal' values for these temperatures - despite the supersaturation in ambient oxygen recorded in Run 3. Twice during the experimental period, samples of open water from the experimental site contained no measureable oxygen. Local populations of mussels and other organisms were undergoing catastrophic mortality. The mussels that were obtained for the oxygen consumption study, although apparently the most healthy in the area, exhibited poor response to stimuli, secreted no byssal threads and spent much of the time gaping wide. A combination of high temperatures and low ambient oxygen levels - possibly after salinity stress, imposed on initially unhealthy mussels was probably responsible for the mortality of most of the Sandy Hook mussel population at this time.



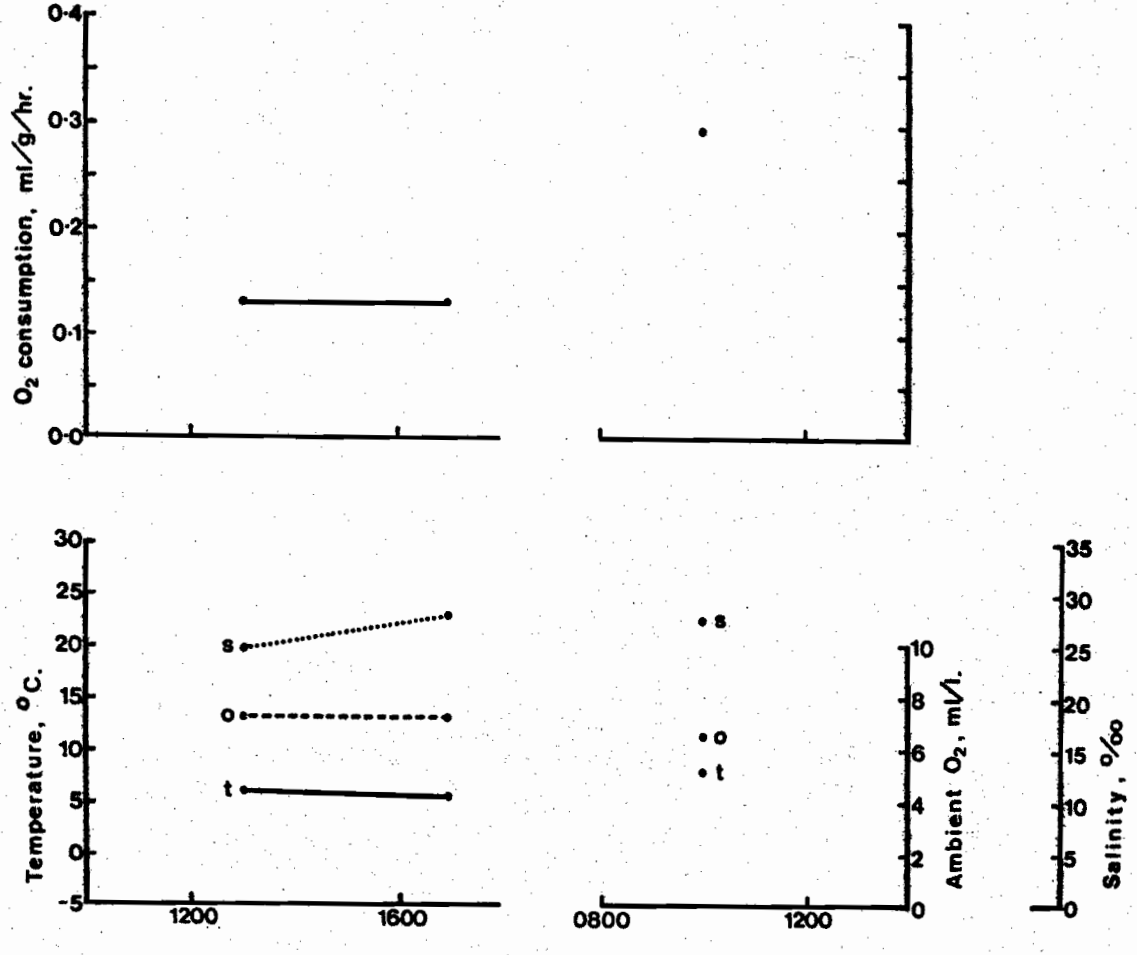
SANDY HOOK 1 Sept 71

Fig. 29



SANDY HOOK 2 Nov 71

Fig. 30



SANDY HOOK 27 Dec 71

Fig. 31

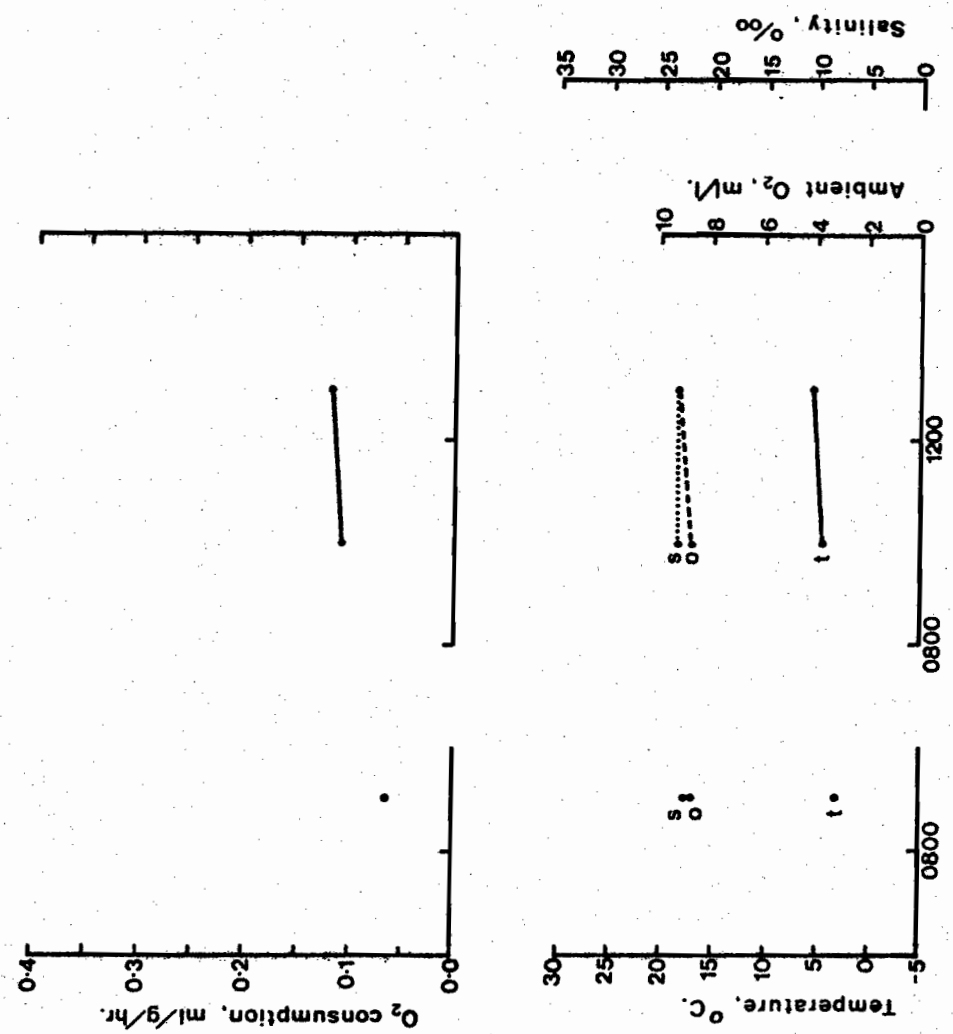
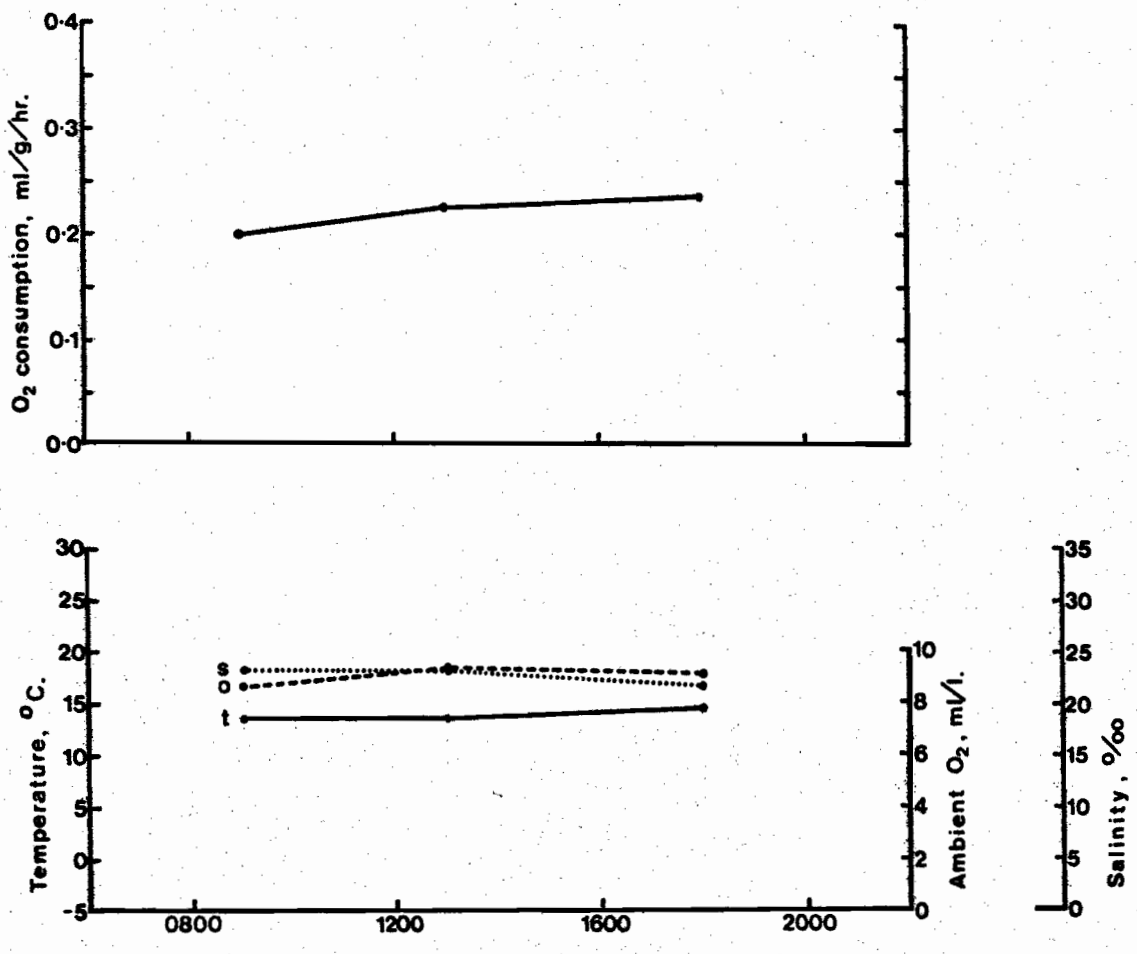
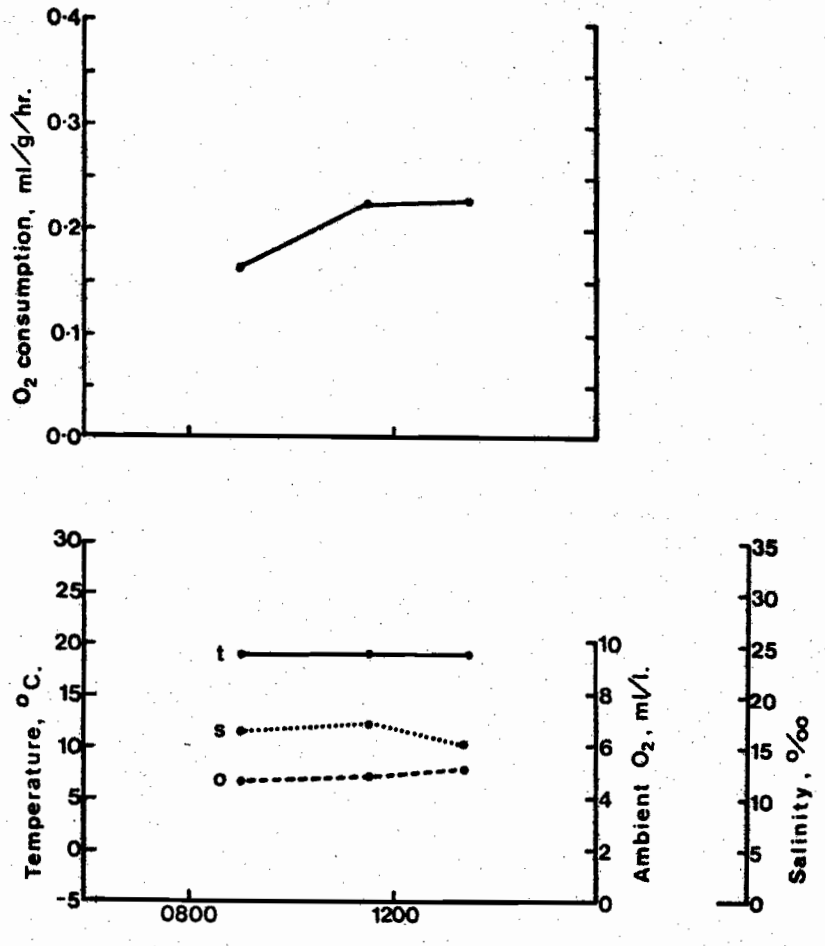

Salinity, ‰
35
30
25
20
15
10
5
0
Ambient O_2, ml/l.
10
8
6
4
2
0
s
t
0800
1200
Temperature, °C.
30
25
20
15
10
5
0
-5
s
t
0800
O_2 consumption, ml/g/hr.
0·4
0·3
0·2
0·1
0·0
SANDY HOOK
1 Mar 72

Fig. 32



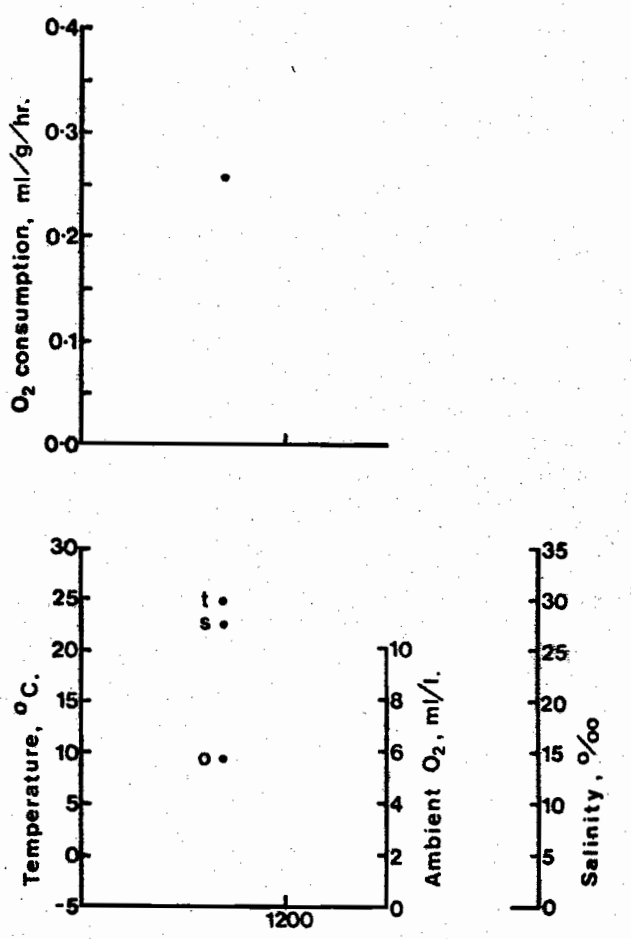
SANDY HOOK 4 May 72

Fig. 33



SANDY HOOK 29 Jun 72

Fig. 34



SANDY HOOK 30 Aug 72

Fig. 35

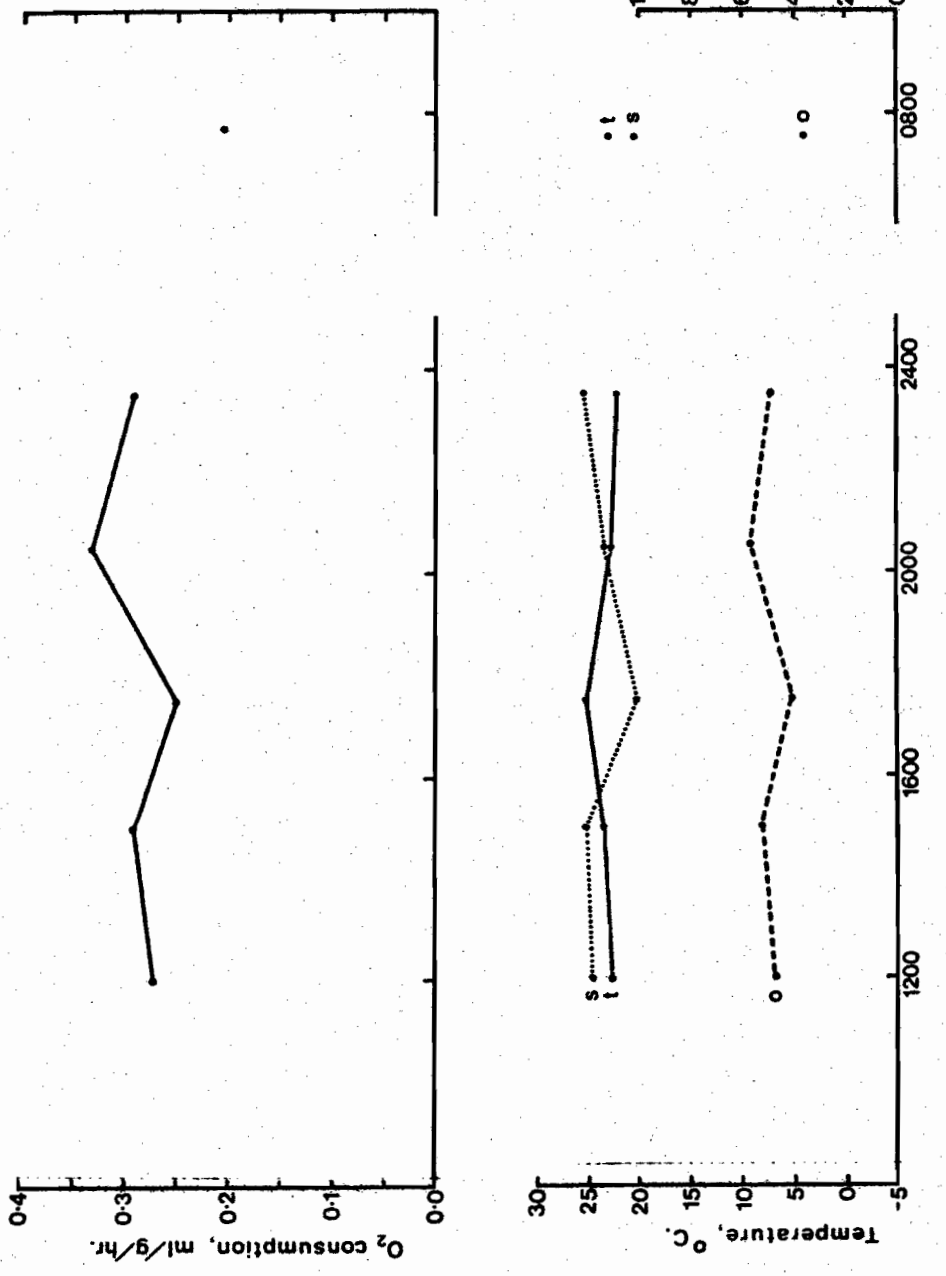
Lewes. Figures 36 to 42.

A complete set of data was obtained for Lewes. Due to fluctuating conditions in the narrow tidal channel where the experiments were carried out, a number of factors had pronounced effects on the oxygen consumption of the mussels.

On 6 September, 1971 the inlet was recovering from the same flood recorded at Sandy Hook on 1 September. Ambient oxygen was low and salinity varied with the tide. Figure 36 shows that oxygen consumption of the mussels was affected by ambient oxygen levels, with a possible secondary influence from salinity. The general level of oxygen consumption was probably depressed below 'normal' for these temperatures.

Four experimental runs were made on 5 November, 1971 (see Appendix Table 1) but only Run 2 is depicted in Figure 37. Heavy siltation in the respirometer bottles prior to the other runs caused closure of the mussels and may have affected oxygen consumption values.

Figure 40 shows correlation of oxygen consumption with both salinity and ambient oxygen concentration on 6 May, 1972. Low salinity (less than $15^{o}/oo$) on the outgoing tide caused the mussels to close, and withdrawal of oxygen from the surrounding water was reduced to zero. This tidal pulse in salinity and oxygen concentration was again recorded on 3 September, 1972, with closure of the mussels and cessation of oxygen consumption at salinities below $12^{o}/oo$. No overshoot in oxygen consumption that might indicate repayment of an oxygen debt was recorded after return of salinity to favourable levels in either case.



LEWES 6 Sept 71

Fig. 36

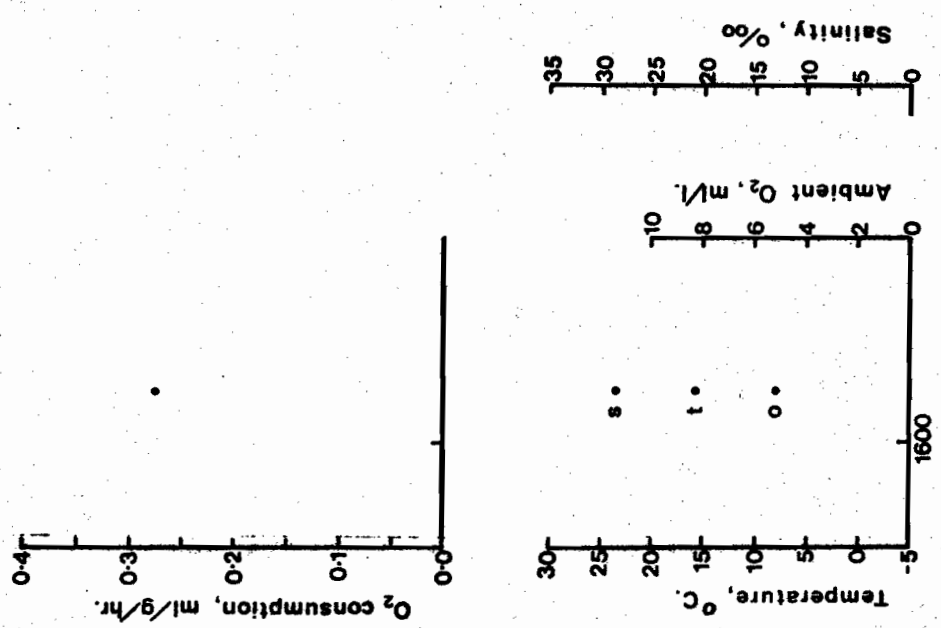
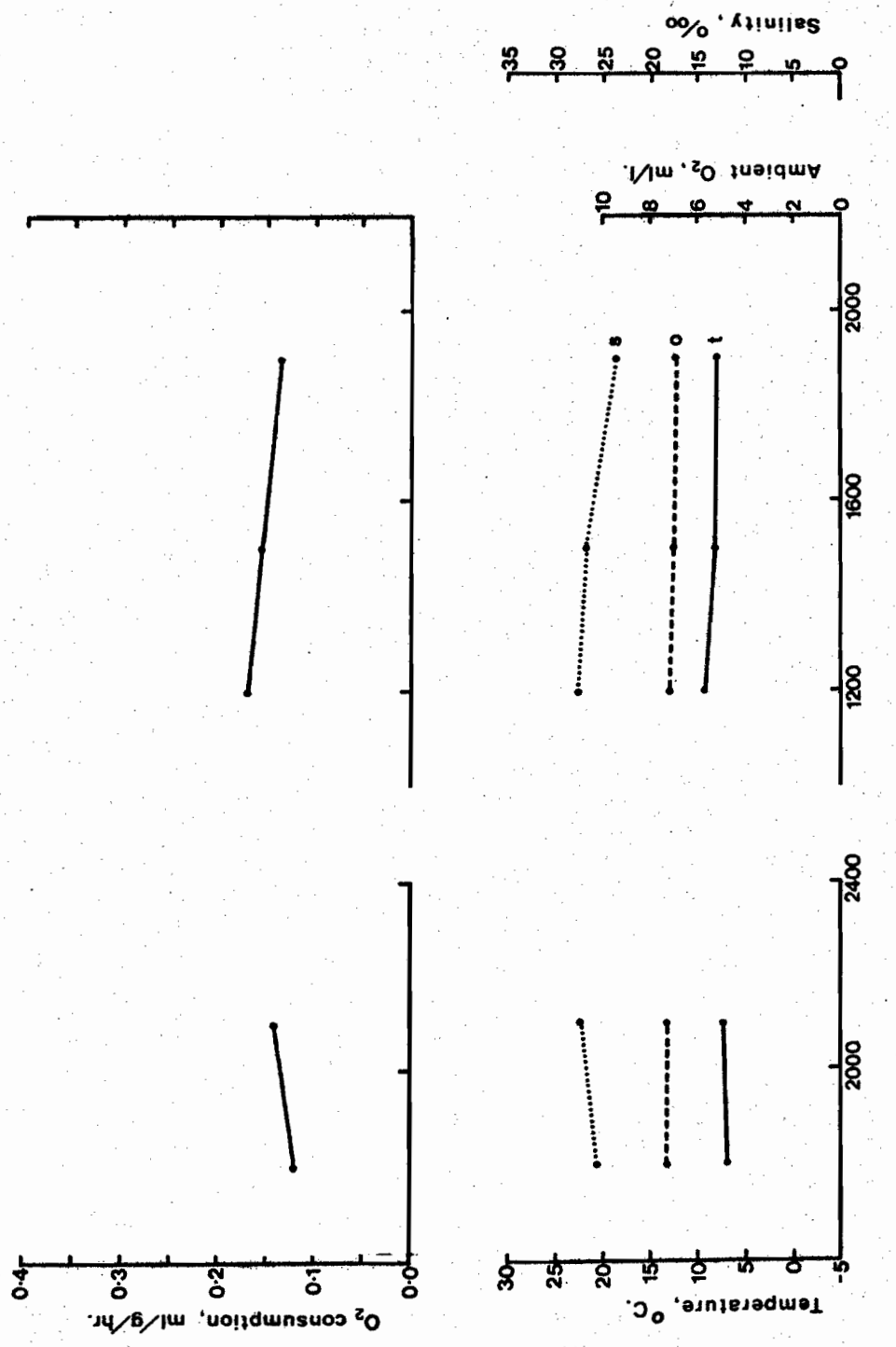

O2 consumption, ml/g/hr.
0·0
0·1
0·2
0·3
0·4
Temperature, °C.
30
25
20
15
10
5
0
-5
s
t
o
1600
Ambient O2, ml/l.
0
2
4
6
8
10
Salinity, °/oo
0
5
10
15
20
25
30
35
LEWES 5 Nov 71

Fig. 37



LEWES 30 Dec 71

Fig. 38

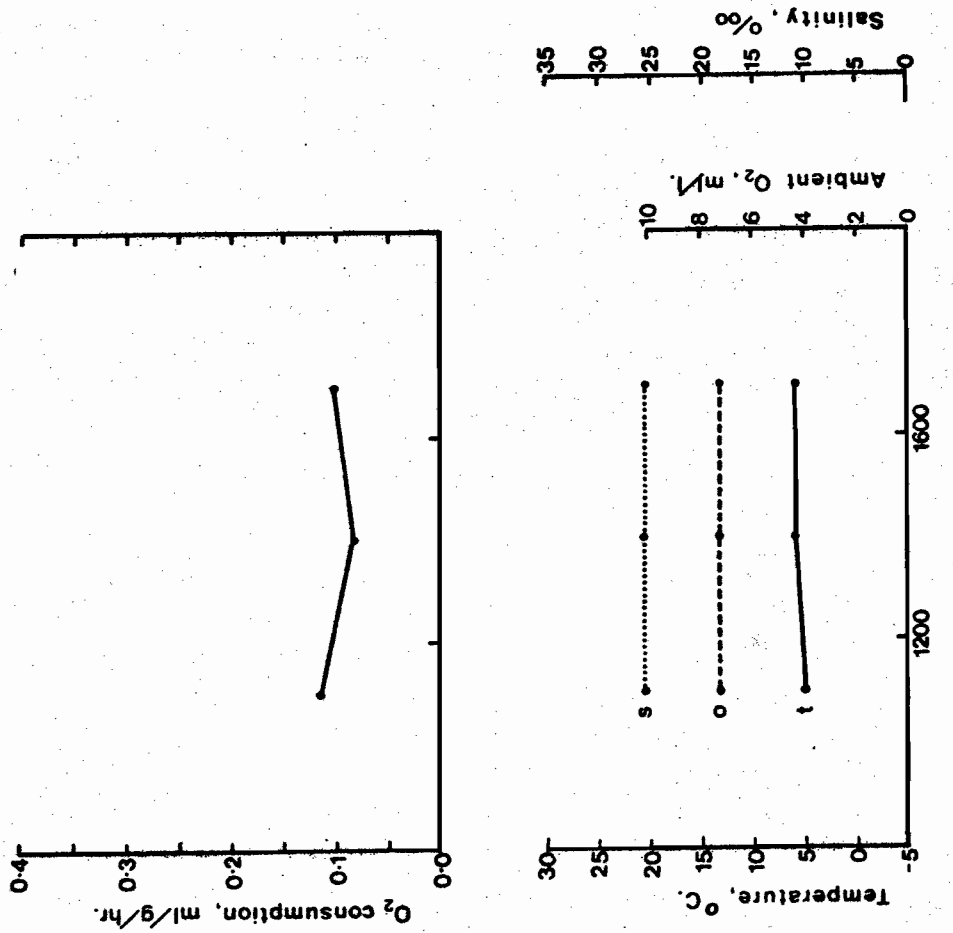
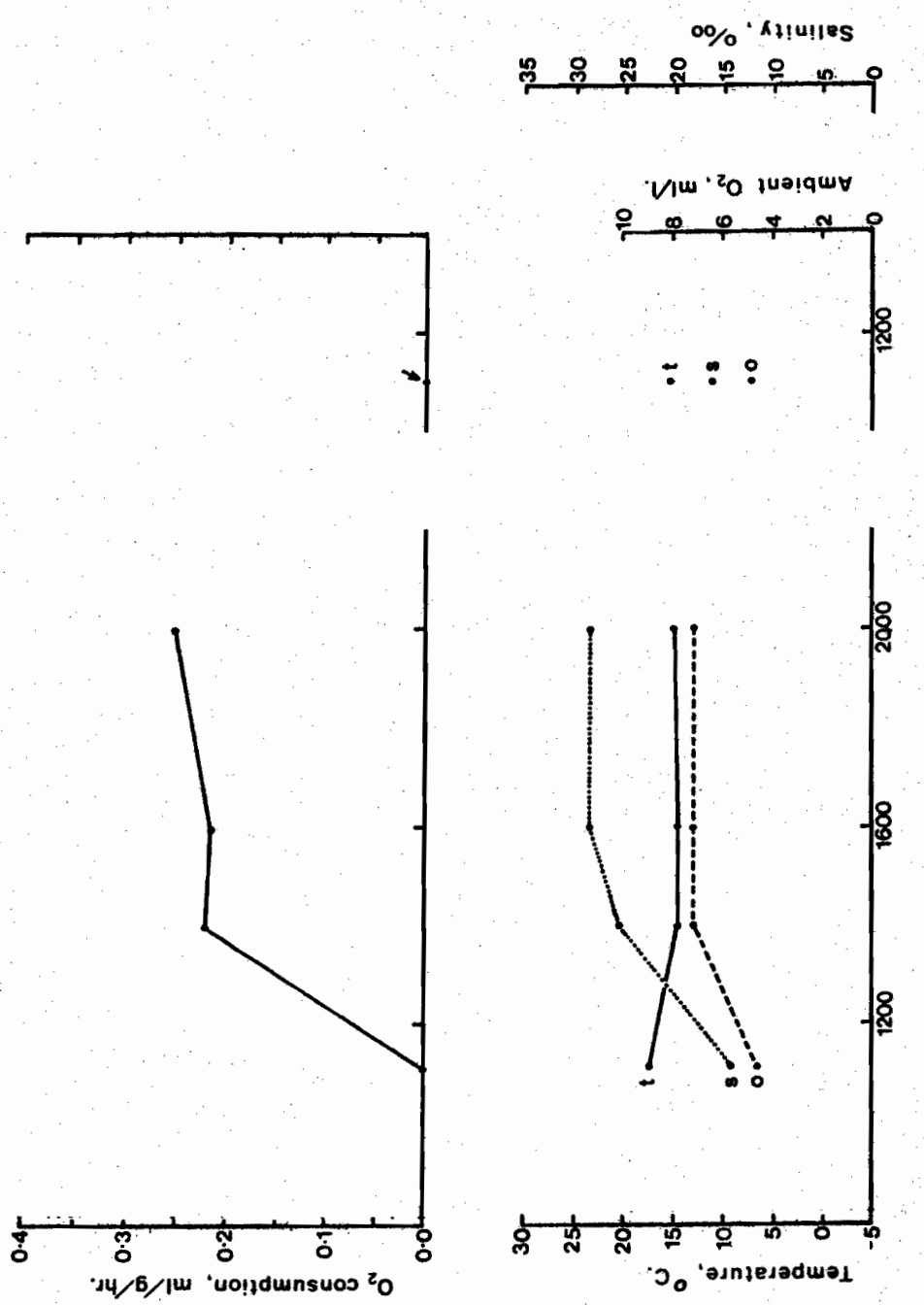

O2 consumption, ml/g/hr.
0·0
0·1
0·2
0·3
0·4
Temperature, °C.
30
25
20
15
10
5
0
-5
s
o
t
1200
1600
Ambient O2, ml/l.
0
2
4
6
8
10
Salinity, °/00
0
5
10
15
20
25
30
35
LEWES 5 Mar 72

Fig. 39



LEWES 6 May 72.

Fig. 40

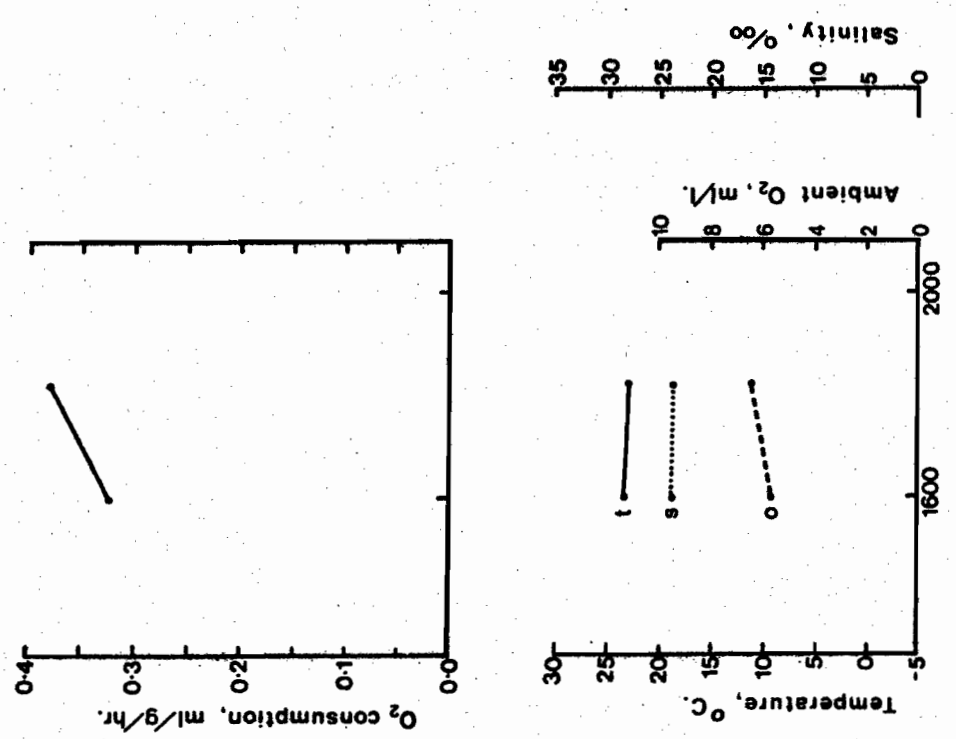

O2 consumption, ml/g/hr.
0·0
0·1
0·2
0·3
0·4
Temperature, °C.
30
25
20
15
10
5
0
-5
t
s
o
1600
2000
Ambient O2, ml/l.
0
2
4
6
8
10
Salinity, °/oo
0
5
10
15
20
25
30
35
LEWES 1 Jul 72

Fig. 41

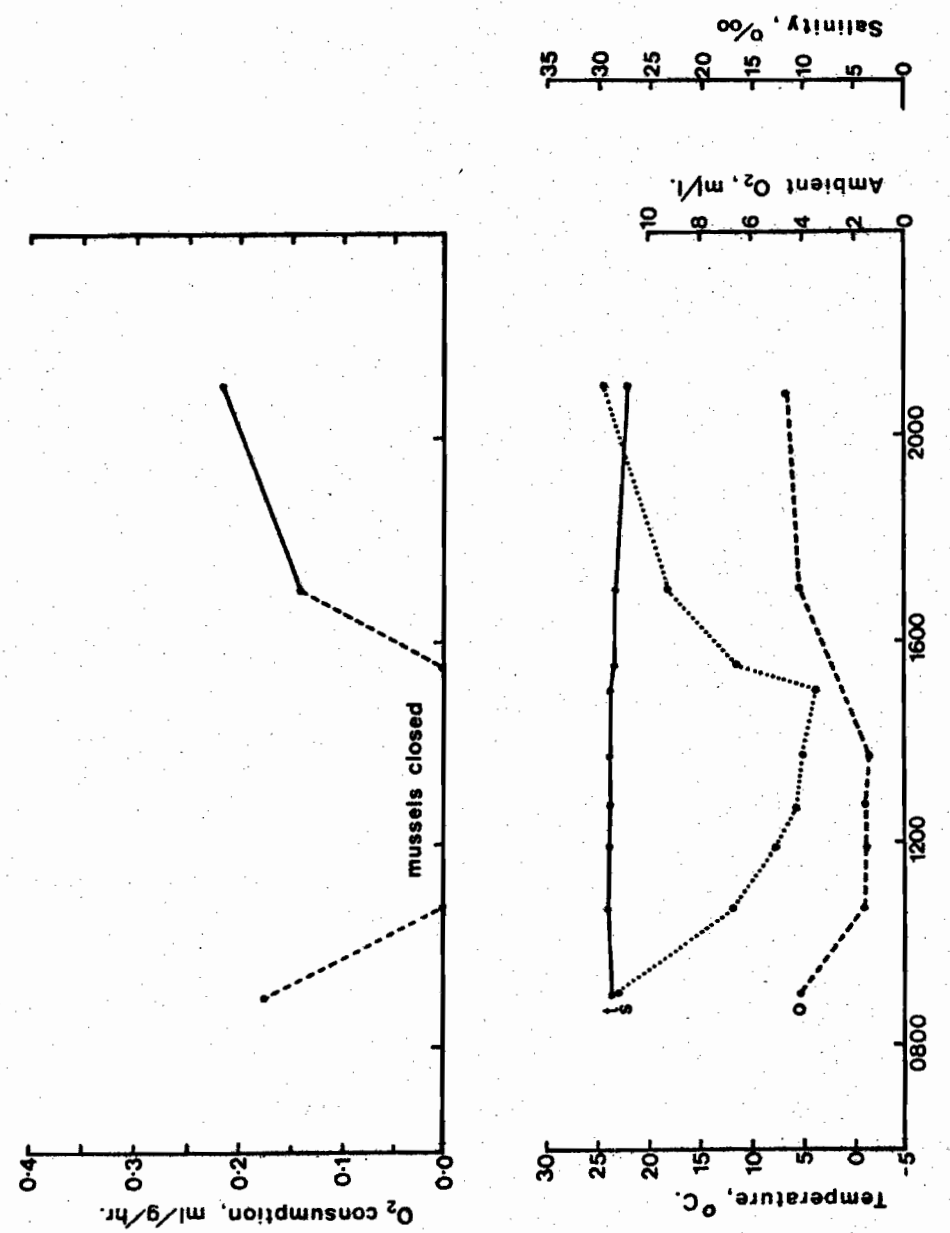

O2 consumption, ml/g/hr.
0·0
0·1
0·2
0·3
0·4
mussels closed
Temperature, °C.
30
25
20
15
10
5
0
-5
0800
1200
1600
2000
Ambient O2, ml/l.
0
2
4
6
8
10
Salinity, °/oo
0
5
10
15
20
25
30
35
LEWES 3 Sept 72

Fig. 42

Wachapreague. Figures 43 to 48.

A complete set of data was obtained for Wachapreague. Low ambient oxygen concentrations on 6 July and 8 September, 1972 may have affected oxygen consumption of the mussels.

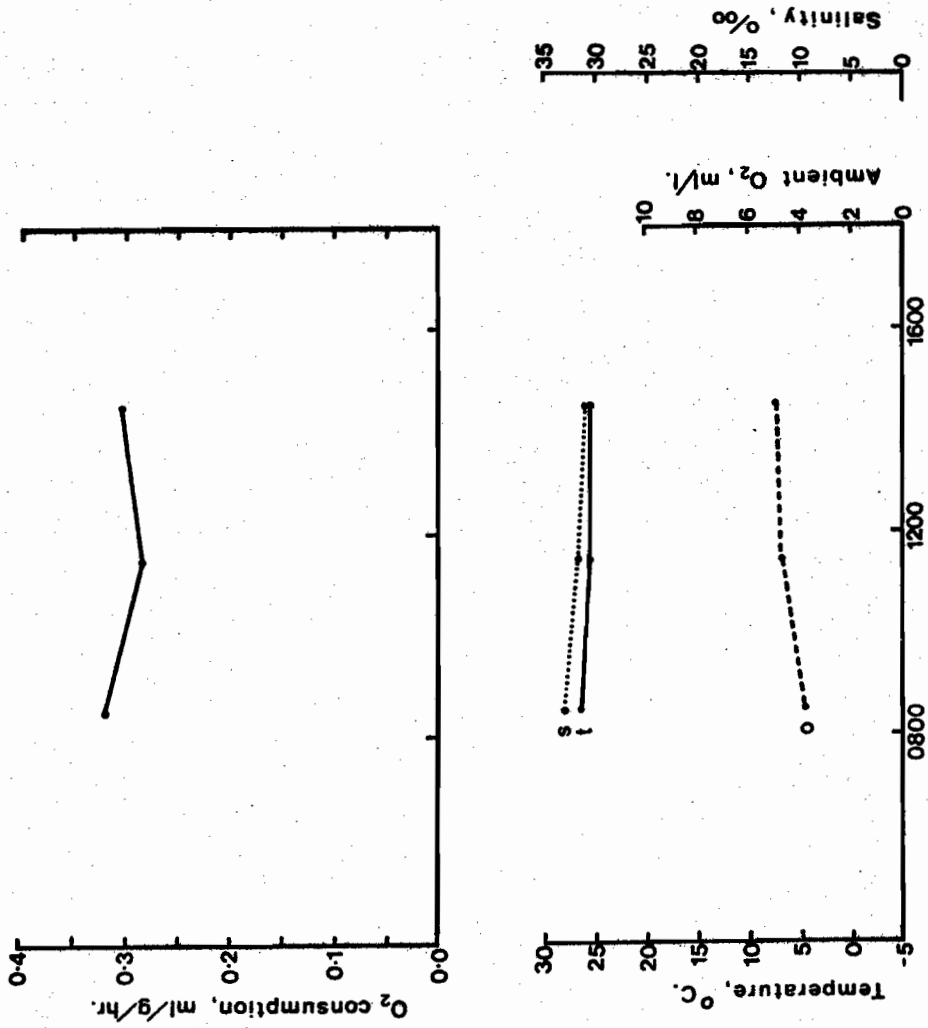
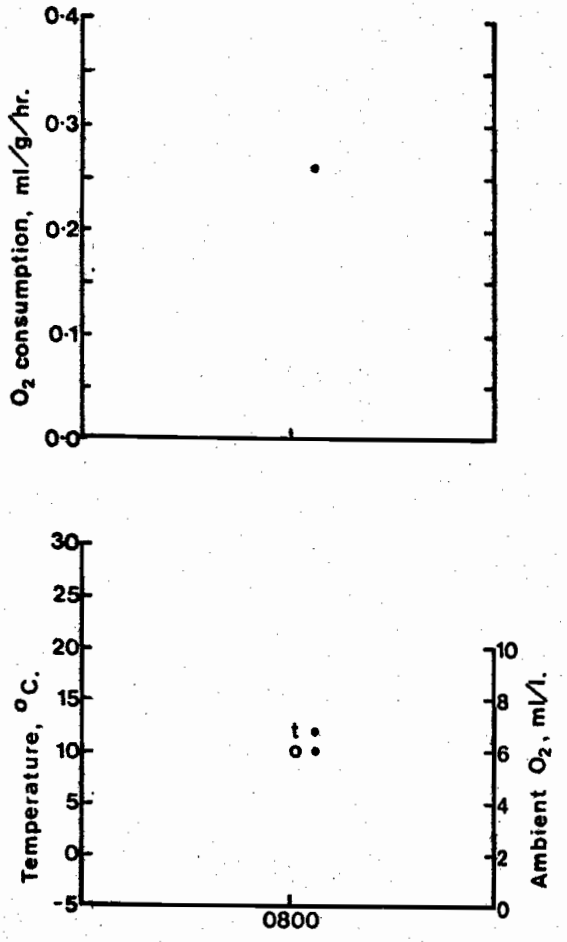
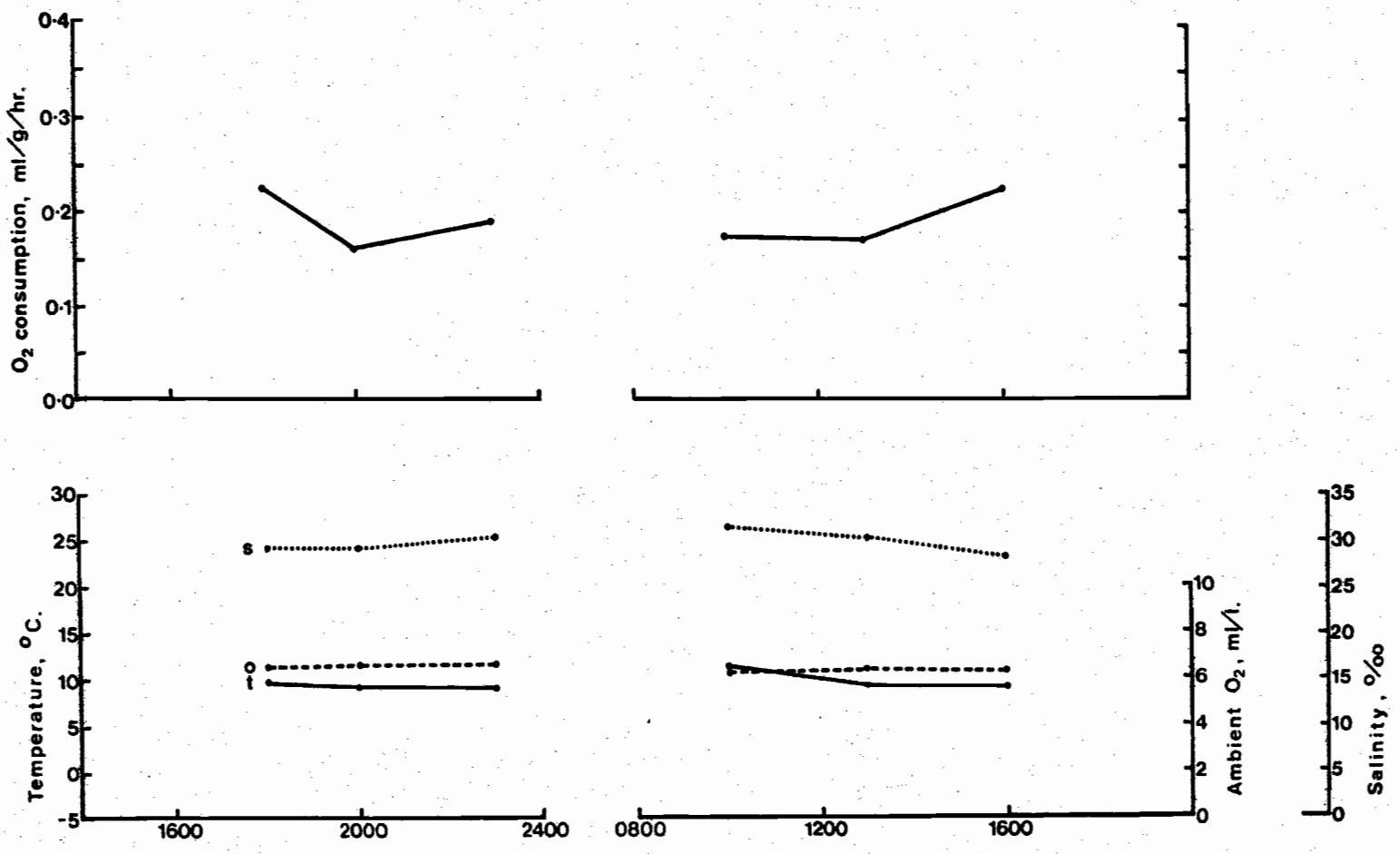

O2 consumption, ml/g/hr.
0·0
0·1
0·2
0·3
0·4
Temperature, °C.
30
25
20
15
10
5
0
-5
Ambient O2, ml/l.
0
2
4
6
8
10
Salinity, °/oo
0
5
10
15
20
25
30
35
0800
1200
1600
S
t
o
WACHAPREAGUE 9 Sept 71

Fig. 43



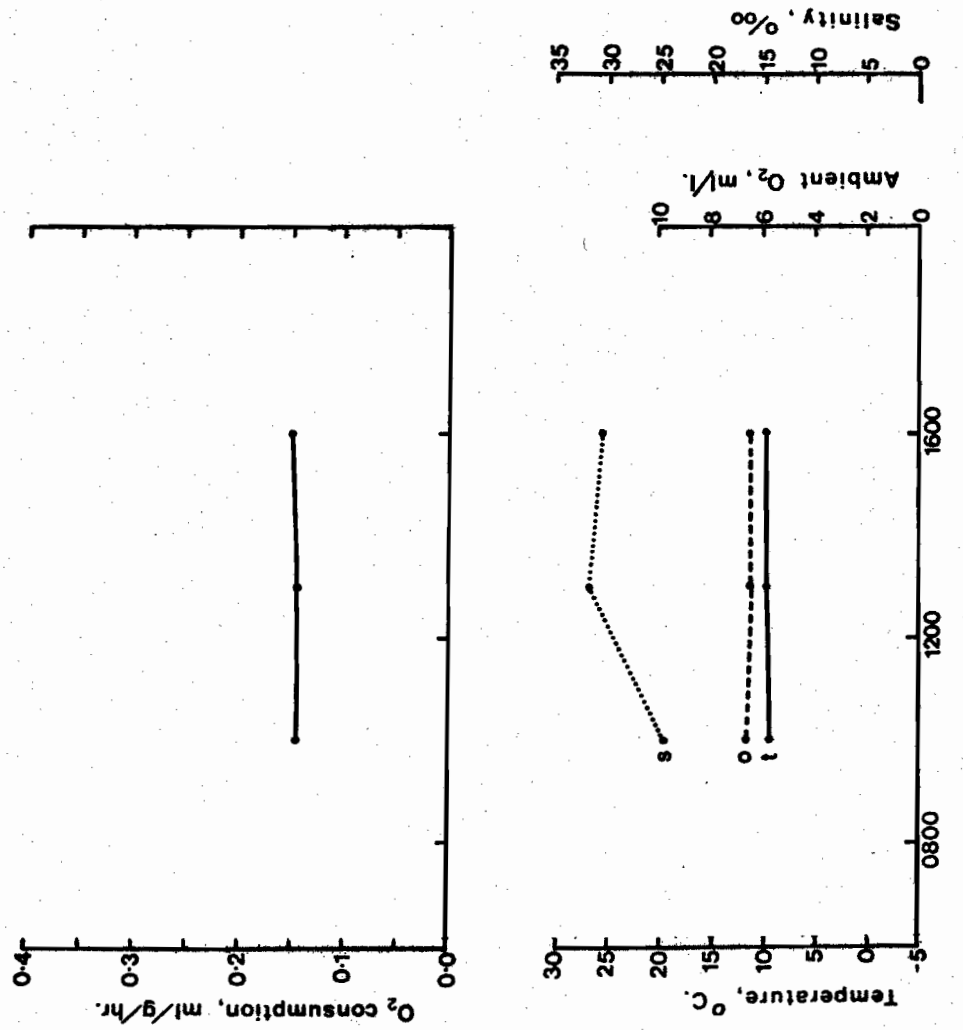
WACHAPREAGUE 9 Nov 71

Fig. 44



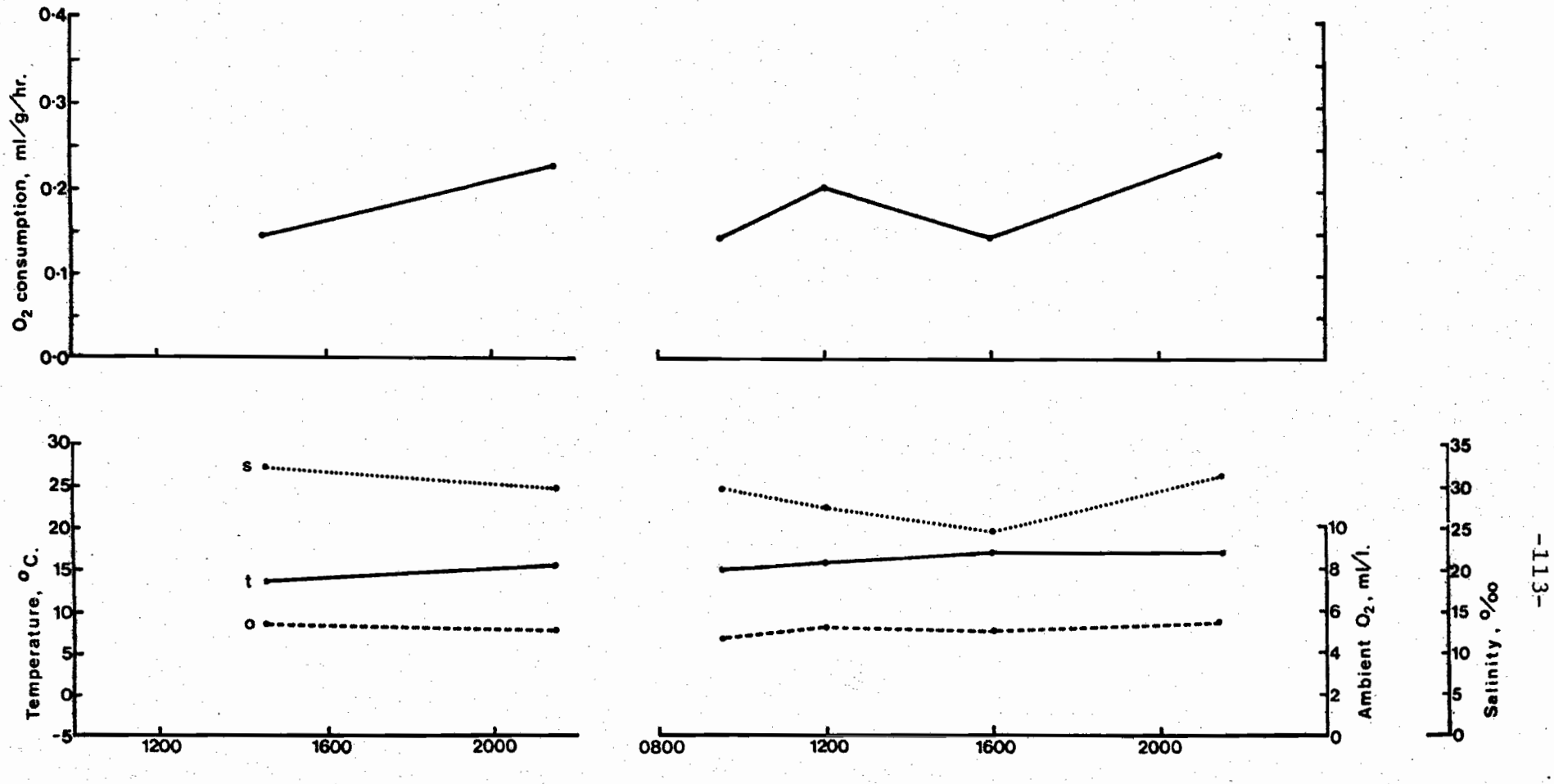
WACHAPREAGUE 4 Jan 72

Fig. 45



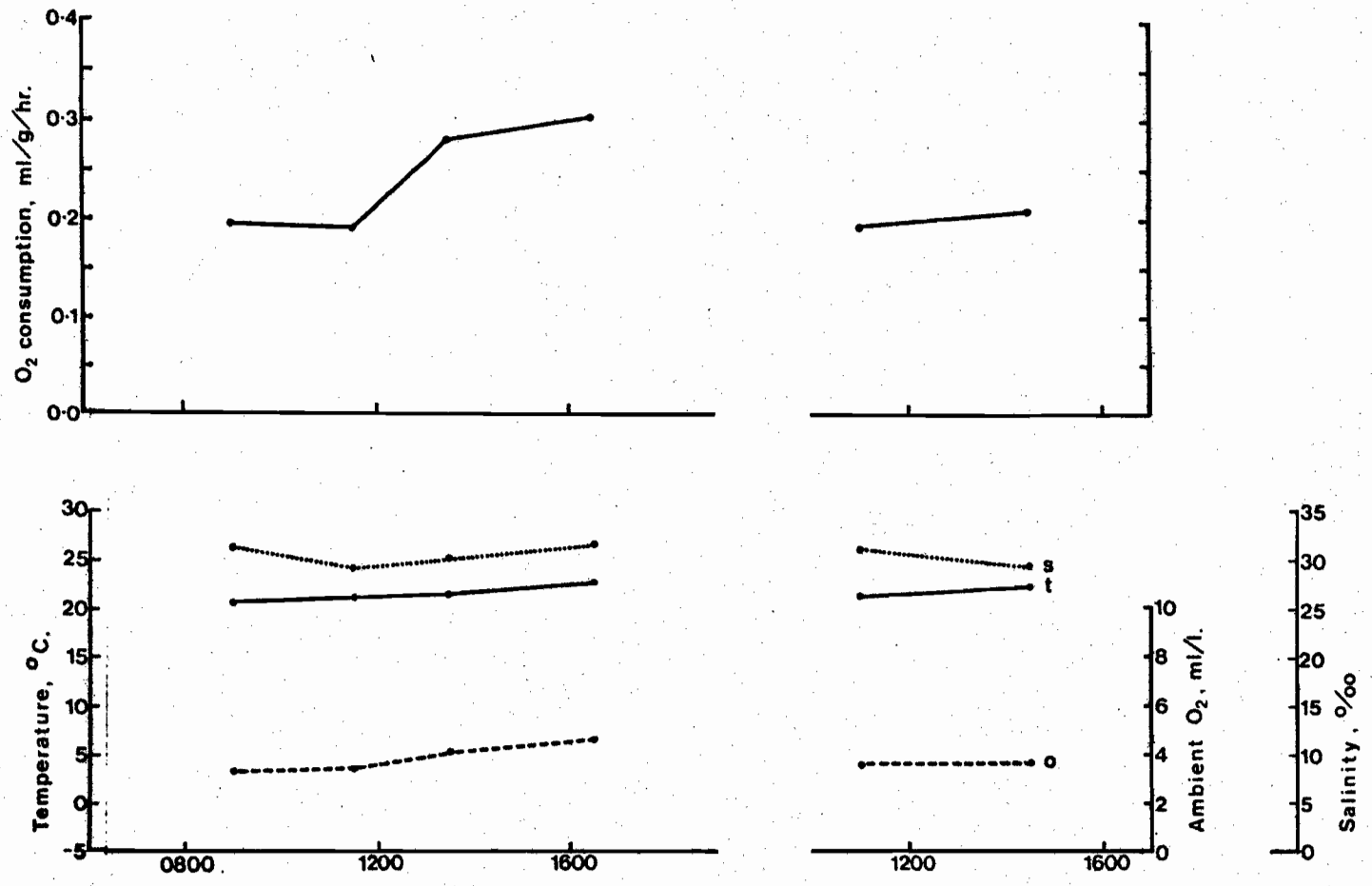
WACHAPREAGUE 7 Mar 72

Fig. 46



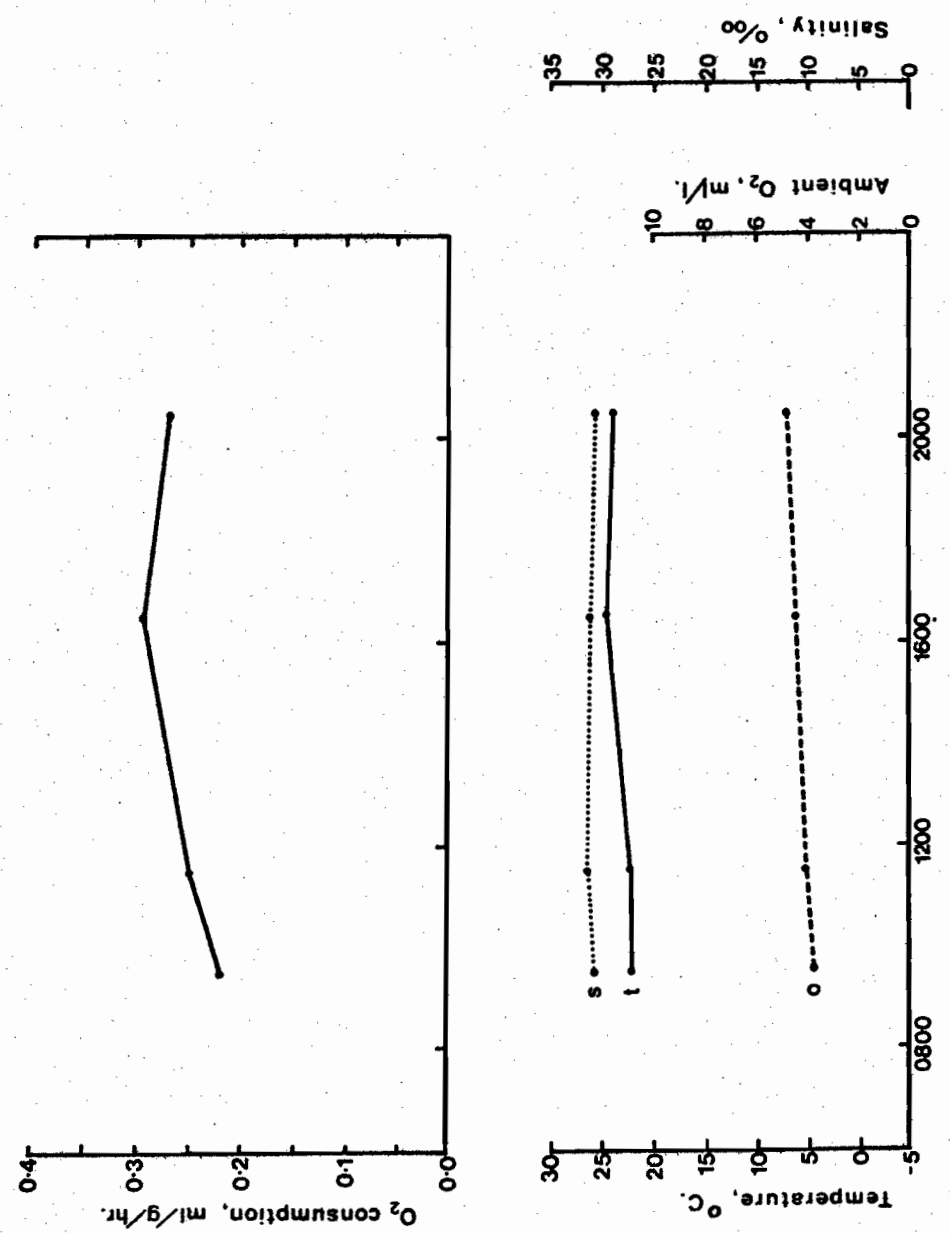
WACHAPREAGUE 10 May 72

Fig. 47



WACHAPREAGUE 6 July 72

Fig. 48



WACHAPREAGUE 8 Sept 72

Fig. 48a

IV. SEASONAL AND LATITUDINAL VARIATION IN OXYGEN CONSUMPTION.

TABLE 4. Seasonal variation in oxygen consumption. Mean oxygen consumption and mean temperature per station per visit. For graphical representation see Figures 49 and 50.

STATION	DATE	t^{o} C.	O_2 ml./g./hr.
Bellevue	1 Aug. 71	17.0	0.12
Holyrood	6 Oct. 71	10.4	0.13
	6 Dec. 71	1.2	0.05
	8 Feb. 72	-0.2	0.00
	8 Apr. 72	-0.1	0.03
	7 Jun. 72	5.8	0.05
	2 Aug. 72	13.6	0.12
St. Margaret's Bay	7 Aug. 71	16.6	0.21
	14 Oct. 71	14.1	0.15
	12 Dec. 71	5.9	0.06
	15 Apr. 72	1.5	0.04
	12 Jun. 72	10.8	0.17
	10 Aug. 72	18.5	0.15
St. Andrews	15 Dec. 71	6.2	0.05
	15 Feb. 72	3.4	0.03
	19 Apr. 72	4.2	0.05
	19 Jun. 72	12.9	0.16
	16 Aug. 72	15.5	0.15

TABLE 4. Continued.

STATION	DATE	t^{o} C.	O_2 ml./g./hr.
Boothbay	17 Aug. 71	15.5	0.22
	21 Oct. 71	12.3	0.21
	20 Dec. 71	6.9	0.10
	19 Feb. 72	2.5	0.06
	23 Apr. 72	4.0	0.13
	20 Jun. 72	13.2	0.19
	20 Aug. 72	14.5	0.15
Sandy Hook	1 Sep. 71	23.2	0.22
	2 Nov. 71	18.1	0.33
	27 Dec. 71	6.5	0.19
	1 Mar. 72	4.3	0.10
	4 May. 72	13.8	0.22
	29 Jun. 72	19.0	0.22
	30 Aug. 72	24.5	0.26
Lewes	6 Sep. 71	23.5	0.27
	5 Nov. 71	16.4	0.31
	30 Dec. 71	7.9	0.15
	5 Mar. 72	5.6	0.11
	6 May 72	14.9	0.23
	1 Jul. 72	23.1	0.36
	3 Sep. 72	22.7	0.20
Wachapreague	9 Sep. 71	25.8	0.31
	9 Nov. 71	12.0	0.26
	4 Jan. 72	9.5	0.19
	7 Mar. 72	9.6	0.15
	10 May 72	15.7	0.21
	6 Jul. 72	21.8	0.23
	8 Sep. 72	23.2	0.26

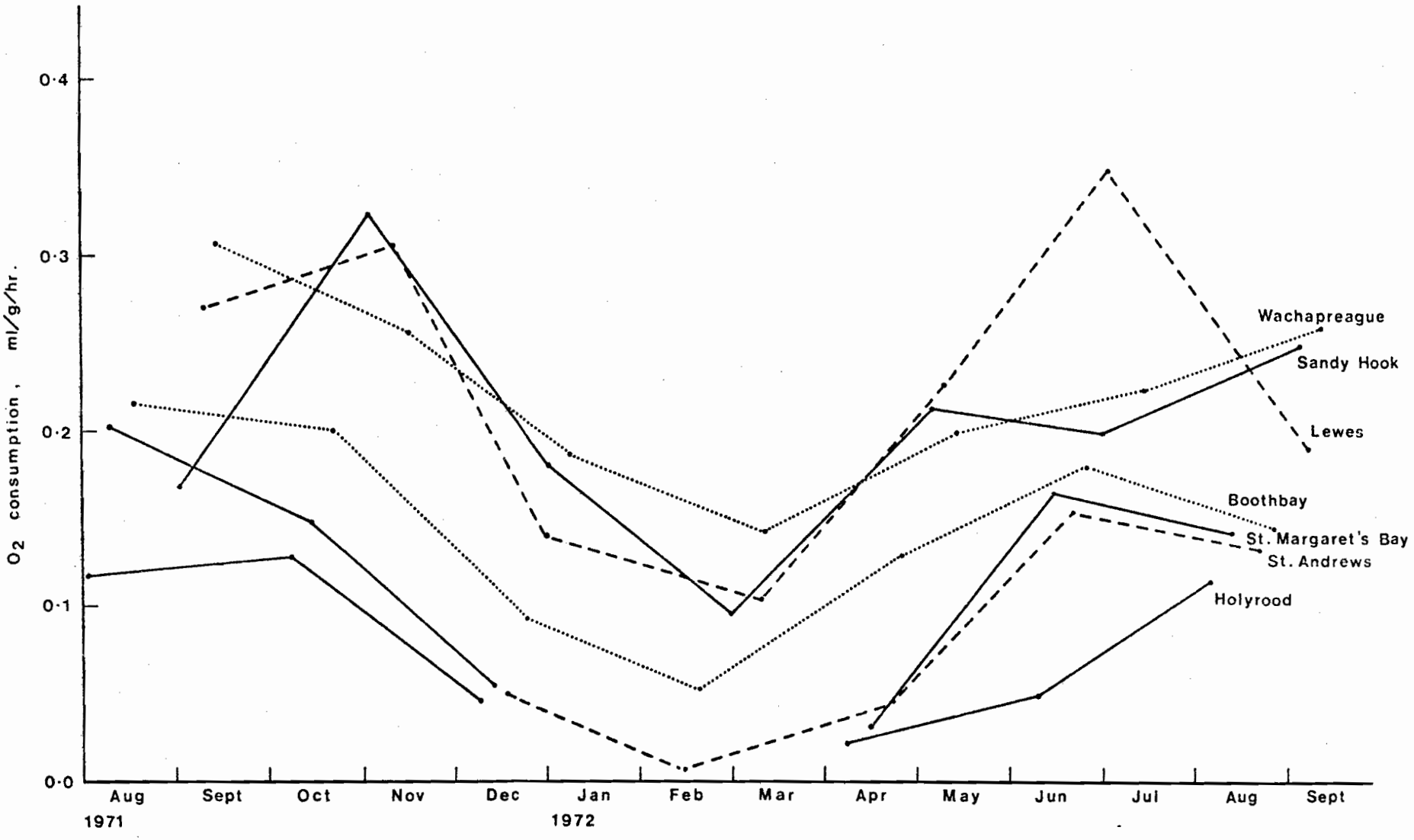


FIG. 49 Oxygen consumption in latitudinally separated *M.edulis* over one year.

Seasonal Variation in Oxygen Consumption. Figure 49.

The seasonal pattern of oxygen consumption follows that of temperature at each station (see Figure 4, which shows the seasonal variation in temperature at the experimental stations). Oxygen consumption rates are maximal in summer and minimal in winter. The marked variation in the rate indicates a lack of compensation for seasonal changes in temperature.

This pattern is similar to that found by Bruce (1926) for the oxygen consumption, measured at field temperatures throughout the year, of Mytilus edulis from the Irish Sea. The "seasonal acclimation" of metabolic rate functions, reported by Newell and Pye (1970a), Bayne and Thompson (1970), and Widdows and Bayne (1971), comes into a different context to the present study and that of Bruce cited above (see Introduction). The results of Widdows and Bayne (1971), for oxygen consumption rates at high temperatures, are in agreement with the present study. At 20°C only partial acclimation (Precht Type III) of oxygen consumption rate was found by Widdows and Bayne, and this is comparable to the situation at the three southern stations of the present study.

The lack of seasonal acclimation, in spite of the experimentally demonstrated ability of the mussel to compensate for short term temperature changes, may be due to a number of factors. On the Atlantic coast of North America, the seasonal temperature variations are large, and may not allow time for complete acclimation to any existing temperature situation. Thermal acclimation may be further affected by energy availability, for example food may be limiting in winter, especially at the northern stations. These possibilities are further discussed below, with reference to other characteristics of the mussels.

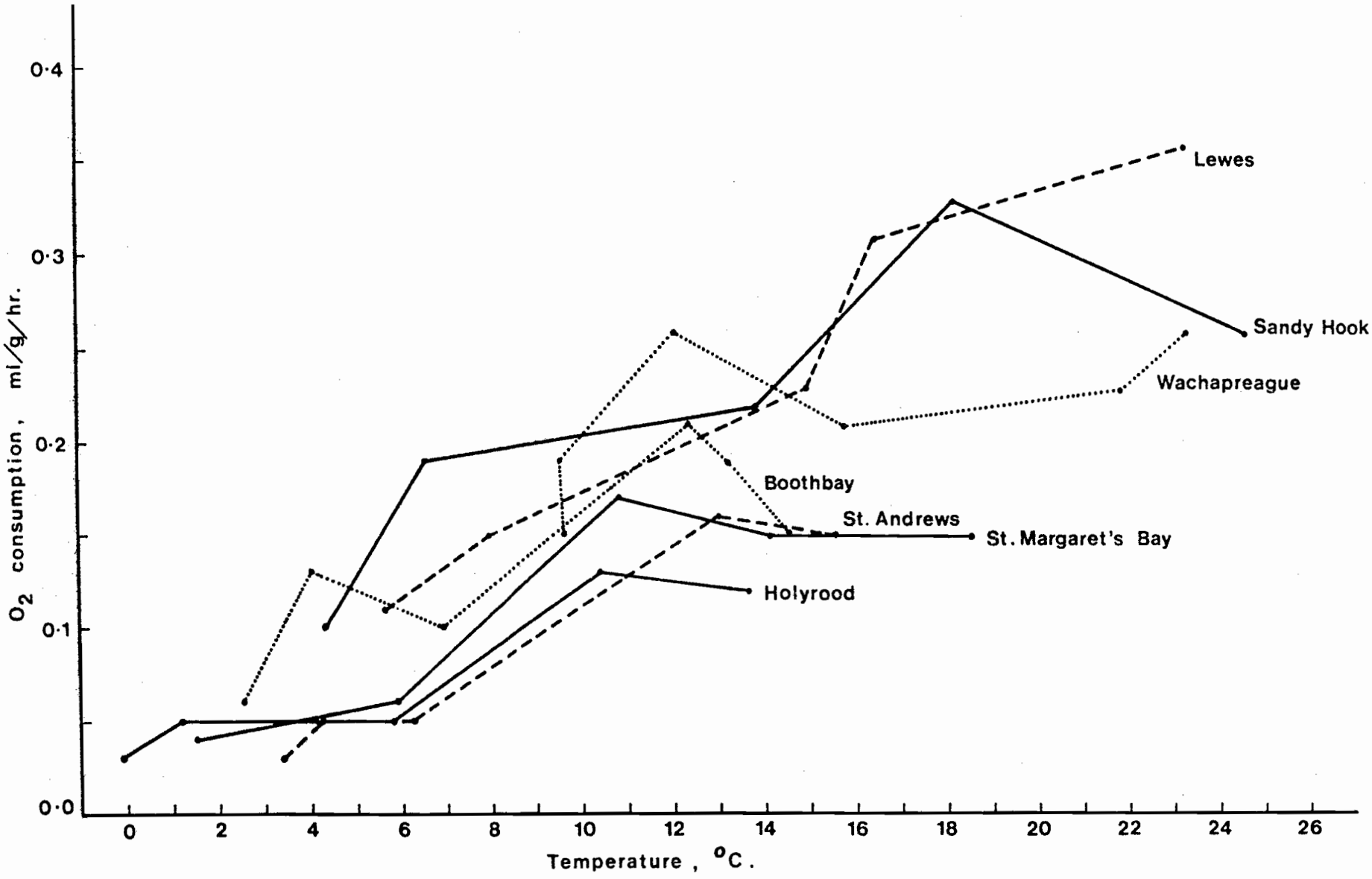


FIG.50 O_2 consumption in latitudinally separated *M. edulis* plotted against mean temperature per visit.

Effect of Temperature on Oxygen Consumption. Figure 50.

In Figure 50 the oxygen consumption data from Table 4 (Figure 49) are replotted against ambient experimental (field) temperature. This shows more clearly than in Figure 49, that temperature is an important seasonal variate related to oxygen consumption rate.

The individual curves in this representation approach the ideal suggested by Bullock (1955: Figure 5 on page 334) in a comparison of "Hypothetical R-T curves showing the relation between the usual, acutely measured, temperature effect on cold-adapted and on warm-adapted individuals and the possibly more natural curve when temperature is changed slowly or time for acclimation is available at every temperature." But any acclimation can still only be considered partial, due to the constant variation in temperature which must exist in the field over the seasons, and to other factors which will affect the mussel's ability to acclimate - e.g. environmentally imposed stresses, biochemical/gametogenic cycle (see Introduction). Other regions of the mussel's distribution, exhibiting a less seasonally variable thermal environment, e.g. Spain, would undoubtedly come closer to approaching the ideal fully acclimated R-T curve, than the curves of the present study.

The shapes of the curves in Figure 50 are irregular. This irregularity is to be expected because of the number of variables present in a long-term field study. Data affected by low ambient salinity and oxygen concentration have been omitted from Figure 50. But there was no way of controlling for pre-experimental factors such as environmental stress or length of (thermal) acclimation time. (The curve for Wachapreague in Figure 50 is highly irregular. Reference to Figure 49 shows that this is due to seasonal influences. The seasonal curve in Figure 49 is regular, and the lack of regularity in Figure 50 is probably lack of acclimation to a changing thermal regime.) If some shape is to be given to the surves, two possible features are:

(a) a similarity to the typical, acutely measured R-T curves: oxygen consumption increases directly with temperature to an optimum, beyond which it levels out or decreases. This feature is noticeable to some extent in all of the curves, and might represent acclimation of each

population to its environmental thermal regime. Summer suppression of metabolism of M. edulis would be expected at the southern stations in view of the near lethal temperatures which exist there.

(b) At the northern stations there appears to be a temperature-insensitive region at the lower end of the local temperature range. If this interpretation is valid, the feature may be relevant to the work of Percy and Aldrich (1971) on M. edulis, Newell and Northcroft (1967), Newell and Pye (1971) on several invertebrates, Halcrow (1963) on copepods, and Halcrow and Boyd (1967) on amphipods. These studies describe what is considered to be temperature-insensitive regions at the lower ends of R-T curves. The number of data points used in these studies are not impressive. The authors do not offer any suggestions of the physiological significance of these temperature-independent regions apart from the usual adaptive value. If such a phenomenon existed it could be helpful to the organism, but the evidence for a temperature-insensitive region here is not overwhelming.

The stations have roughly similar curves over their respective temperature ranges, but these are different temperatures for each station: from -0.2 to +17°C at Holyrood, and from +9.5 to +26°C at Wachapreague. That is, the metabolic activity of each population is adapted to the range of temperatures which normally occurs at the site of the population over the year. (At this point the question of genetic versus phenotypic adaptation is usually brought up.)

For complete adaptation the curves should not be displaced vertically as they are here, with the cold adapted populations exhibiting the lowest metabolic rates and the populations from warm environments exhibiting the highest rates. This represents a lack of adaptation. This feature is further discussed with reference to Table 5 and Figure 51.

Effect of seasonal variation in temperature on oxygen consumption.

The irregularity of the oxygen consumption/temperature curves in Figure 50 and the regularity of the oxygen consumption/season curves in Figure 49 suggest that the oxygen consumption pattern throughout the year may be the product of the combined effect of temperature per se and rate of change of temperature, i.e. some seasonal acclimation may be taking place.

For each station and each visit the rate of change of oxygen consumption was compared with the rate of change of temperature over the two month period between experiments. The correlation of rate of change of temperature/rate of change of oxygen consumption was high ($r = 0.66$ to 0.84) considering the range of factors affecting oxygen consumption and the above optimum temperatures which existed at the southern stations (and these had the lowest r values).

Comparison of individual values of d O cons/d temp suggests only some seasonal acclimation of the oxygen consumption rates. In many cases the temperature would be on the increase and little or no increase in oxygen consumption would occur. This effect occurred mainly at the high temperature end of the R-T curve however, and in view of the non-linearity of laboratory R-T curves, the phenomenon may have represented the reaction to above optimum temperatures for oxygen consumption in mussels adapted to their particular thermal regimes.

TABLE 5. Regression of oxygen consumption (y) on ambient experimental temperature (x) over the year, using means of all readings for the last 6 visits: Oct.-Nov. 1971 to Aug.-Sept. 1972, i.e. omitting Aug.-Sept. 1971. Q_{10} taken for mid 10°C of local temperature range.

Station	Annual mean exp temp °C	Annual temp range °C	Annual mean *Mytilus* O_2 cons ml/g/hr	Regression	Q_{10}
Holyrood*	5.12	max 13.6 min -0.2 ra 13.8	0.06	y = 0.02 + 0.008x	3.66
St. Margaret's Bay*	8.57	max 18.5 min 0.0 ra 18.5	0.10	y = 0.02 + 0.009x	2.80
St. Andrews**	7.03	max 15.5 min 3.4 ra 12.1	0.07	y = 0.00 + 0.011x	3.75
Boothbay	8.90	max 14.5 min 2.5 ra 12.0	0.14	y = 0.06 + 0.009x	2.00
Sandy Hook	14.37	max 24.5 min 4.3 ra 20.2	0.22	y = 0.11 + 0.007x	1.41
Lewes	15.05	max 22.7 min 5.6 ra 17.5	0.23	y = 0.08 + 0.010x	1.58
Wachapreague	15.27	max 23.2 min 9.5 ra 13.7	0.22	y = 0.15 + 0.005x	1.25

*Midwinter readings were not successful at these stations, values of 0.0 are inserted in the regression.
**Only 5 readings were made at St. Andrews: Nov 1971 is missing. This does not fall at the extremes of the thermal range at that station, but results are not strictly comparable with the other stations.

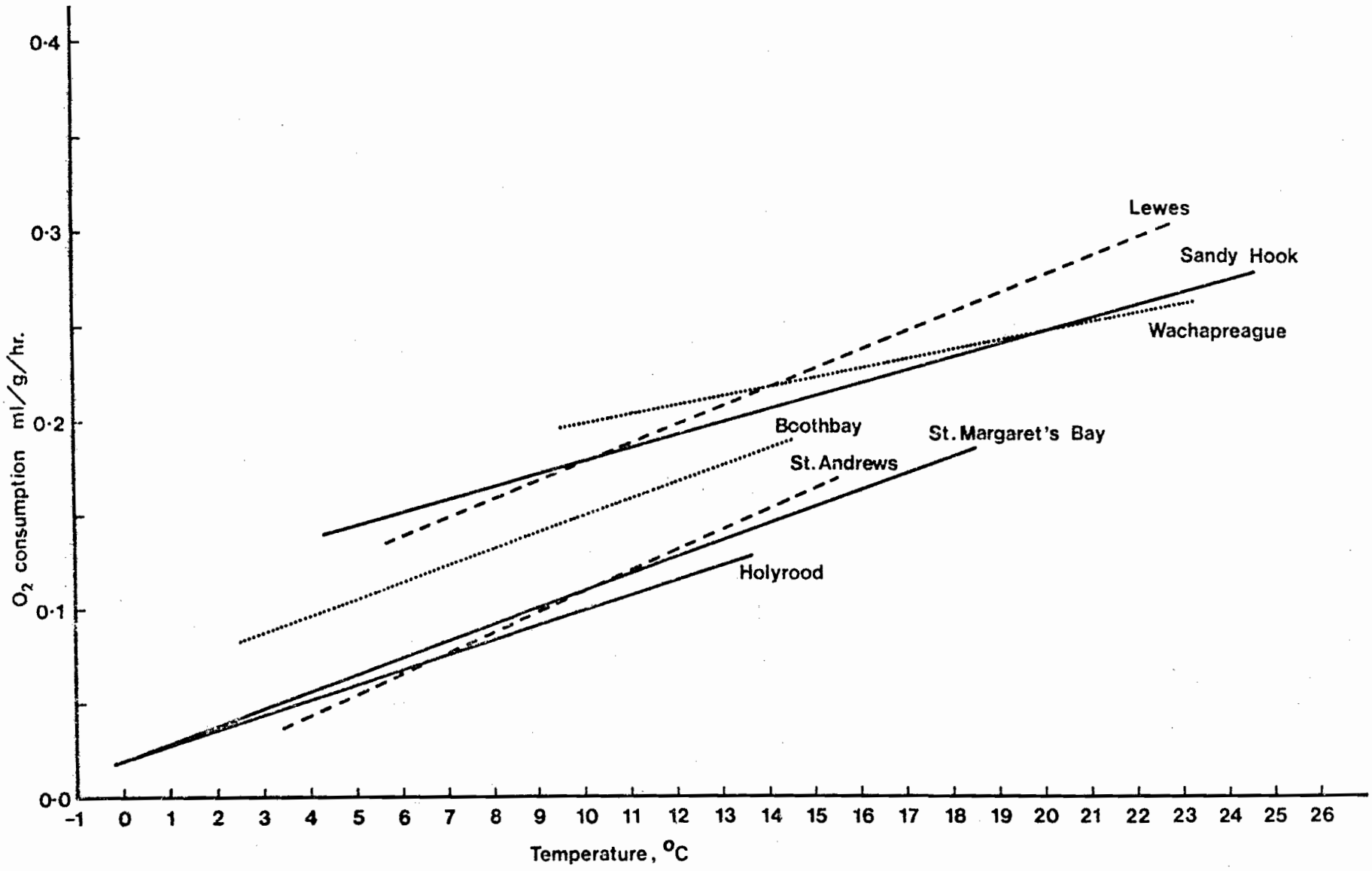


FIG.51 Qo_2 as a function of temperature in latitudinally separated *M.edulis* regression over years readings.

Latitudinal Variation in Oxygen Consumption. Table 5 and Figure 51.

Table 5 and Figure 51 simplify the data of Figure 50 to show the latitudinal differences in oxygen consumption rate. R-T regression lines are displaced vertically such that the northern stations have lower oxygen consumption than the southern stations. This is the characteristic displacement described by Prosser (1958) as Type IIA translation. At the normal environmental temperatures that exist at each station throughout the year, compensation for latitudinal differences in temperature do not exist or are very slight.

Reference to Table 5 shows that the vertical displacement of the R-T regression lines corresponds to the order of annual mean experimental temperature. The correlation of annual mean oxygen consumption to annual mean temperature for all stations over the year, is high ($r = 0.98$). The Q_{10} of this regression ($y = 0.04 + 0.17x$) between 5 and 15°C is 4.4, which despite the objections to use of the Q_{10} values for comparison between each station, (see below), is greater than any Q_{10} for any individual station. This is just another way of saying that each station has an R-T curve typical of its environment, and that little or no latitudinal adaptation exists. This is significant in that these stations, Sandy Hook in particular, probably represent the greatest range of water temperature over the year for any Mytilus edulis in the world, and lack of sufficient time for seasonal acclimation here should render the Q_{10} value for the year at its maximum.

No detailed studies of this sort have been done for Mytilus edulis (see Introduction). The closest would be those of Thorson (1936) and Spärck (1936) which describe a high degree of latitudinal adaptation for different species of Mytilidae.

Analogous intraspecific studies to the present one are those of Rao (1953a) and Pickens (1965) on Mytilus californianus. The present results agree well with those of Pickens, who found that the heart rate of M. californianus at natural environmental temperatures was only partially compensated for temperature over the range of latitude from

Washington to Mexico. The results of Rao on pumping rate are not in accord with those of Pickens or of the present study (see Introduction).

The values of Q_{10} for the mid 10°C of the annual environmental temperature range at each station are listed in Table 5. They indicate the inapplicability of Q_{10} as a measure of metabolic sensitivity to temperature differences in this case. The ratio of Q_{10}/annual mean experimental temperature here is predominantly dependent on the size of the denominator in the Q_{10} $(R_t + 10/R_t)$, in this case, low for the northern stations and high for the southern stations. The Q_{10} values listed in Table 5 are useful only in that they re-emphasize the lack of latitudinal adaptation between the stations.

The slopes of the R-T regressions, listed in Table 5 and shown in Figure 51, provide a clearer assessment of temperature sensitivity than Q_{10} in this study. The differences in slopes may be related to the individual values plotted in Figure 50. The variations in slopes are not the product of a common factor, rather they show the susceptibility of oxygen consumption rate to a number of factors (see below).

GROWTH STUDIES

I. INTRODUCTION.

The growth studies were primarily intended to compare oxygen consumption with the rate of an ongoing metabolic process, i.e. one that could be referred to a known point in any one mussel throughout the study year. Indices such as condition and gametogenic or biochemical states were less suitable than growth for this purpose, due to the short term changes that can occur in these parameters. Shell growth, more obviously than these other processes, leaves evidence of its course over the entire year.

Growth parameters also indicate the metabolic pattern of the mussel, summed over its lifetime. They give an estimate of lifespan, the variations in metabolic rate over this time, and the environmental limitation on metabolic processes for both short terms (seasonal) and long terms (lifespans). Growth studies are also a means of evaluating the comparative suitability of various environments for mussels.

II. FIELD METHODS.

At each station, 100 to 400 mussels of all available sizes were taken from the local population, tagged individually (Howitt Plastics, individually numbered fish tags), measured with vernier calipers to the nearest millimeter for maximum length, height and width (as defined by Seed, 1968), and replaced close to their original position in cages of chicken wire. Further measurements were made every two months for over one year, or as long as the experimental material survived.

Measurement in this way has the effect of disturbing the mussels every 2 months. Adverse effects to growth are minimized by careful handling. This disturbance evens out competition between mussels such that mussels exhibiting maximum or minimum growth rates due to their positions in the clump during one growth period, may have their roles reversed during the next growth period. Harger (1970b) reports that this type of disturbance increases the average growth rate of the clump. Disturbance appears to be atypical of the natural mussel populations observed in this study, but is common enough in dense beds of mussels on soft substrates (see Dodgson, 1928) or in high current situations (Hum 1969, 1971).

This method of growth estimation is relatively time consuming and has a low return compared with the use of modal length frequency distributions in natural populations or the use of counted annual disturbance rings. Size frequency distributions were not used because of the number of factors affecting population structure and because of the unstable nature of mussel populations (Field, 1922; Fischer-Piette, 1935; Coe, 1946, 1956; Havinga, 1956; Pequenant, 1963; Hosomi, 1967, 1968, 1974; Hum, 1969, 1971; etc.). Although annual growth rings have been used to plot growth curves by many researchers (Mossop, 1922; Meteeva, 1948; Weymouth, 1923; Orton, 1926; Seed, 1968; etc.), the wide range of latitude, and multiple factors affecting growth in the present study would render growth rings misleading as a measure of annual growth.

In view of the many factors known to affect growth in Mytilus edulis (see Introduction), care was taken to provide for comparability of growth

study habitats. Mussels for growth studies were taken from the healthiest populations in their area. In these populations growth appeared to be least inhibited by such factors as crowding, abrasion, pollution, etc. All mussels were of sublittoral origin, from 0-6 metres below L.W.M., and from areas with good water circulation.

III. ANALYSIS.

The data procured during the growth studies lent themselves to various types of analyses, depending on factors unique to each station.

Long Term Growth.

When mussels survived beyond the one year experimental period, long term growth rates (several years) were estimated using the Ford-Walford plot (Ford, 1933; Walford, 1946) to give the parameters of the von Bertalanffy growth equation (Beverton and Holt, 1957). In this analysis it was assumed that mussel growth does not vary significantly from year to year, i.e. that 1971-72 was an average year for growth. The lengths of individually marked mussels of all sizes available at time t + 1 (= fall 1972) were plotted against lengths at time t (= fall 1971). From the regression of l_{t+1} on l_t, with a slope of e^{-K}, estimates of L_∞ and K of the von Bertalanffy growth equation were obtained. Such analysis was possible only at Holyrood, St. Margaret's Bay and Woods Hole.

The growth study at Sandy Hook lasted almost a year. A combination of data obtained from the population growing in the proximity of the growth study cage and the ten months of individual growth study data provided an estimate of growth over more than one year for comparison with the three studies above.

Larval settlement could be estimated at Sandy Hook by observation of spat growth in 1971-72. Holyrood and St. Margaret's Bay spatfalls could not be estimated due to the slow growth in the early years at these latitudes. No significant spatfall occurred at the Woods Hole site over the study period.

No estimate of long term growth could be made at St. Andrews due to persistent predation of the growth study mussels. Some data for this locality are provided by Mossop (1922).

The habitats of Mytilus edulis at Lewes and Wachapreague were of an unstable nature. Maintenance of growth studies at these sites proved impossible for any length of time. The data of Buchanan (1975), from test panels at these stations in 1971-72, provides estimates of early growth: settlement to 6 months at Lewes, and settlement to 8 months at Wachapreague.

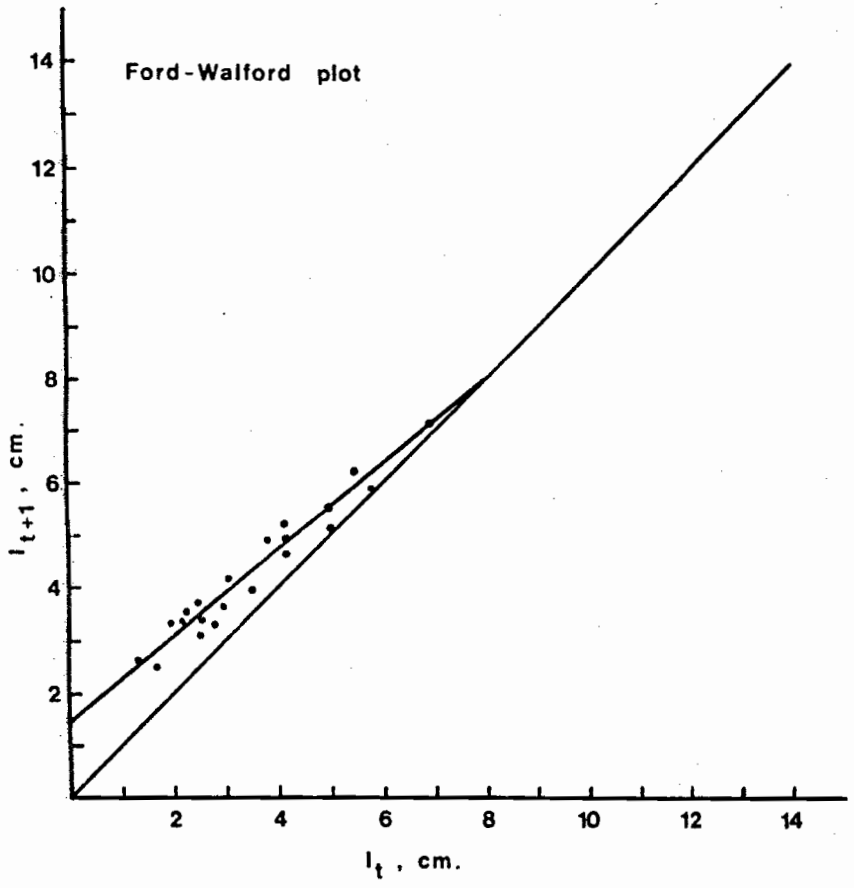
Short term growth.

Estimates of seasonal variation in growth rate were afforded by the 2 monthly measurements at each station. Since a large range of sizes of mussels was used in each experiment, allowance had to be made in the calculations for age- or size-dependent variation in growth rate. This was accomplished by dividing the mussels into approximate age categories estimated from the growth curves (see Appendix).

IV. RESULTS.

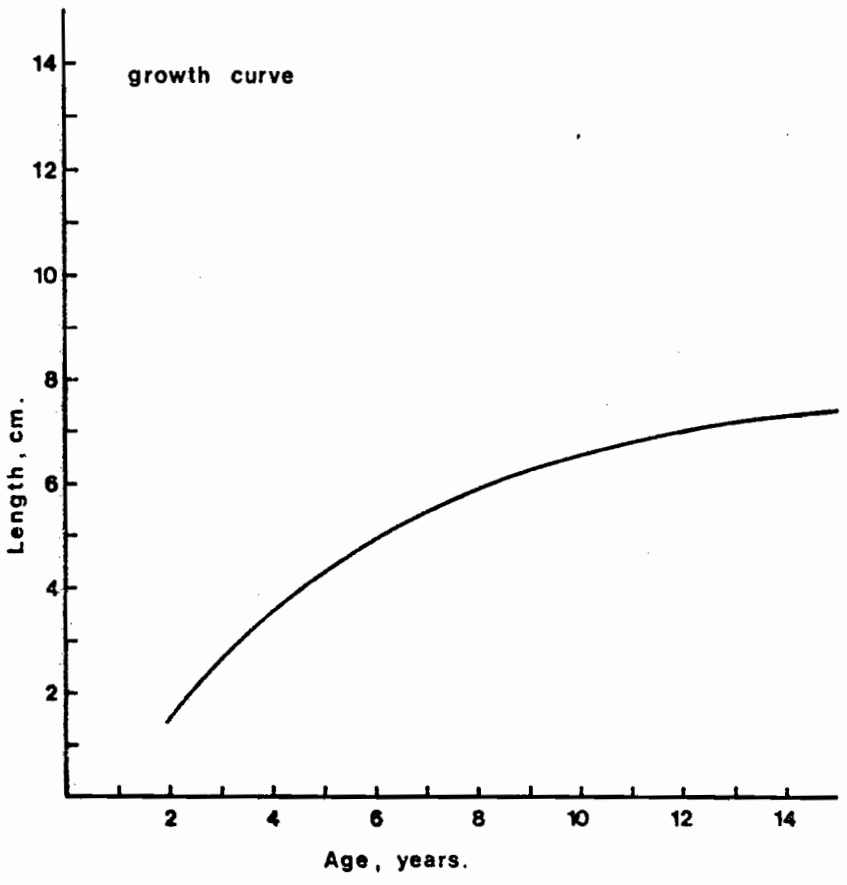
Data from the growth studies are listed in Appendix Tables 2 to 15, together with details of analysis. Parameters estimated for the von Bertalanffy growth equation are given in text Table 6. These and other growth characteristics are presented graphically from Figures 52 to 65 and discussed in the text following.

Fig. 52



HOLYROOD

Fig. 53



Holyrood.

The growth curve for Holyrood M. edulis (Fig. 53), as estimated by the Ford-Walford plot (Fig. 52), is valid between shell lengths of 1.5 to 6.7 cm. The correlation coefficient for the Ford-Walford plot is 0.97 and the linear relation of l_{t+1}/l_t exists at less than the 5% level. No lack of linearity is evident in the Ford-Walford plot at either end of the data presented; and the plot of $(l_{t+1} - l_t)/l_t$ (not shown) indicates a line (von Bertalanffy equation) rather than a curve (Gomperz equation) for mussels of length greater than 1.5 cm (see Thiesen, 1973).

These results indicate that:

i) any point of inflection of the growth curve must lie below a size of 1.5 cm, i.e. growth study mussels are at or beyond the size of maximum growth and here exhibit a von Bertalanffy type growth curve rather than a Gomperz type.

ii) growth approaches a limit (L_∞) at about 8 cm.

Mussels of length less than 0.89 cm could not be labelled for the growth study. Estimates of early growth come from other sources. There are data for first year growth, obtained from rope collectors placed by the present author near the site of the growth study and from ropes placed by R. Miller (FRB, St. Johns) at a nearby wharf. In a previous year, Miller observed 3 spatfalls of M. edulis from June to October. The earliest spatfall grew as much as 1 cm between June and November. The autumn spatfall exhibited negligible growth over winter, reaching a length of only 1 mm by the following spring. This autumn set was overtaken by the set of the following June; i.e., over-wintering at the early post-settlement stage was inhibitory to growth. Data obtained by the present author on a set which occurred between October and November 1971 are similar to those of Miller. These mussels reached a mean size of 1.5 mm by June 1972. Another spatfall occurred between April and June 1972; no growth data were obtained for these mussels beyond June 1972.

A spatfall which occurred between August and October 1971 at Bellevue, Conception Bay, at a shallow sublittoral site comparable to

that at Holyrood, exhibited a growth rate intermediate between that of the early summer and autumn spatfalls at Holyrood. Growth in the 2 month period reached an average of 5 mm shell length.

Thus, in any one population of first year mussels, there may be several (3) cohorts at the end of the first growing season. The position of the first growth check will be different for each spatfall. The ensuing growth will depend on the stage of growth or development when the first winter has its effect. Mussels of the autumn spatfall will soon be overtaken by those of the following summer, but they will exhibit more growth checks. Analysis of second year growth requires a detailed following of the several cohorts in growing populations or employing a large sample size to follow growth checks. These data are not presently available.

Estimation of the age of growth study mussels will be dependent on second year growth, and will be different for the different spatfalls (will the autumn spatfalls ever recover?). Early summer spatfalls have almost reached the size of growth study mussels by the end of the first summer, and for these spatfall could be estimated at about 15 months prior to the commencement of the growth study, although the effect of the first winter is unknown.

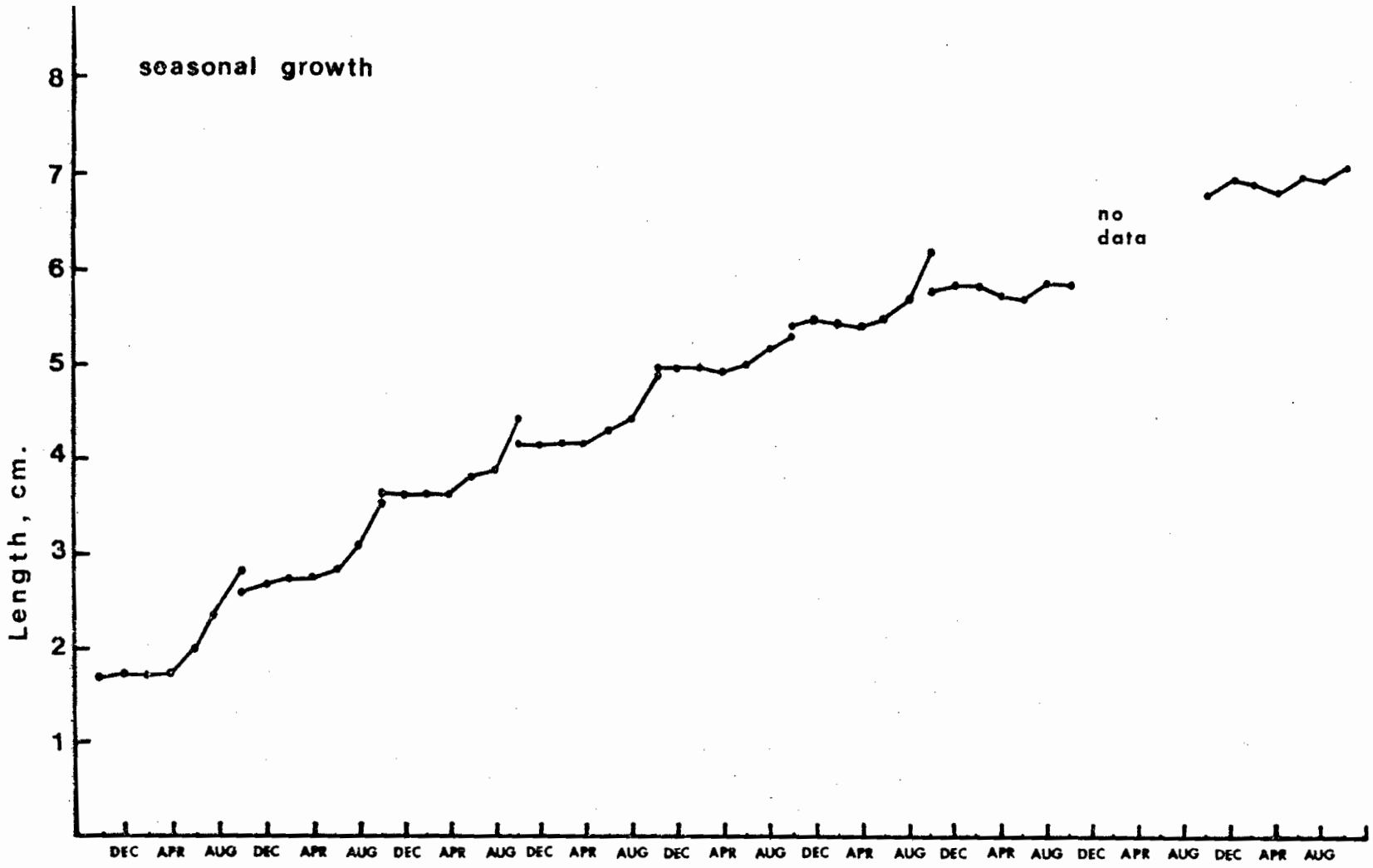
The maximum length (L_∞) of about 8 cm estimated from the growth study data appears to be typical of Mytilus edulis of the shallow sublittoral habitat at Holyrood. Population samples of mussels from sublittoral sites in the vicinity yielded mussels of maximum size between 7.5 and 8.0 cm. Beach drift samples had mussels up to 8.5 cm shell length. These large mussels had close growth checks during the later years, and the shell margin exhibited considerable wear indicating that growth in shell length may have been negative over a period of some years. Apart from the metabolically determine L_∞ in this population, a size dependent mortality was observed to affect population structure: during the winter months more large individuals than small were dragged above the mussel zone by moving ice.

Age at final size can be estimated by two methods for this population of mussels. Both methods are unsatisfactory in such long-lived bivalves. From the Ford-Walford plot and resulting growth equation, age

at L_∞ is estimated to be greater than 15 years. The validity of this value is dependent on the rate of early growth (see above) and on the assumption that growth for 1971-72 was typical of that for other years (see below). The growth curve estimated in this way may be compared with the growth histories of individual mussels as revealed by their growth checks which are quite distinct at this latitude. The oldest mussel found was 8.5 cm in length and had 22 obvious growth checks, but many of the earliest checks were deleted by shell erosion. Growth was erratic over its lifetime: good and bad series of years for shell growth were represented by spaced and close growth checks respectively. Shell erosion deleted parts of several years' growth checks, indicating the range of apparent growth and the range of final lengths which may occur. Few of the larger mussels exhibited in their growth checks the totally regular growth depicted in the von Bertalanffy growth curve. No consistent pattern of growth perturbation could be derived from the population growth check data. Growth irregularities of this sort are not surprising in slow growing shallow sublittoral mussels which have been observed to undergo disturbances by ice and salinity change (see O cons. study), and perhaps gravel and sand erosion, and which almost certainly will be subjected to variations in direct growth factors from year to year.

The growth curve exhibited by the Holyrood growth study mussels is typical of M. edulis from one environment only. (It may be considered representative of the respiration study mussels.) Other populations of M. edulis in northeastern Newfoundland undoubtedly exhibit different growth curves, although these have not been worked out in detail. Brief comparisons with other populations are as follows: Some open coast littoral mussels at Logy Bay do not appear to grow larger than 15 mm, probably due to crowding, exposure to air, wave action and eventual removal of most of the population by ice. In contrast, sublittoral channel mussels at Bellevue, Conception Bay, growing under conditions of strong tidal water flow and possibly warm, food-rich, diluted coastal lagoon water during the growing season, grow larger and faster than the mussels at Holyrood. The possible effect of increased energy input in this

Fig. 54



HOLYROOD

exploitable mussel bed would be interesting to compare with the apparently low energy input of the Holyrood growth study population.

A modified growth curve is presented in Figure 54, showing the effects of season on growth of M. edulis of various sizes. Seasonal changes are most marked in small mussels and barely detectable in those mussels approaching the maximum shell size. Mussels up to a length of 5 cm exhibit a consistent pattern of seasonal growth: growth is minimal or absent from November to April, increases from May to July, and is maximal from August to November. Mussels of shell length greater than 5.5 cm exhibit irregular growth and occasionally negative growth. This can be attributed to the negative balance of the slow growth rate and the natural abrasion of the shell margin during the long season of inactivity. The seasonal pattern of shell growth at Holyrood is discussed further in comparison with other seasonal changes (see Figure 64 below).

Fig. 55

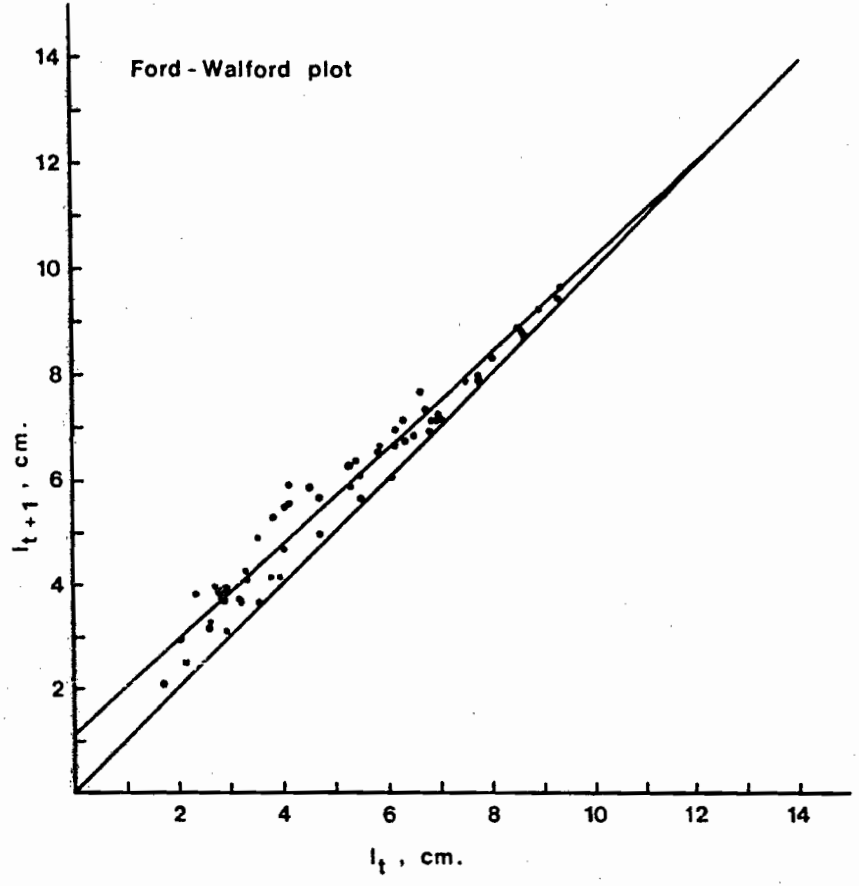
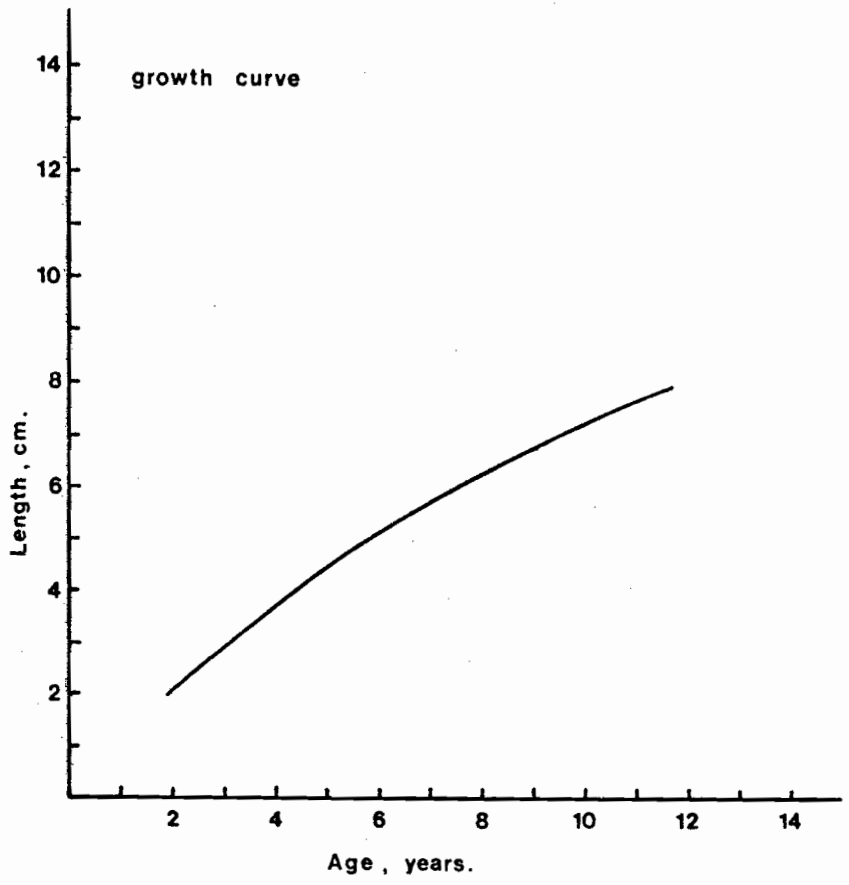


Fig. 56



ST. MARGARET'S BAY

St. Margaret's Bay.

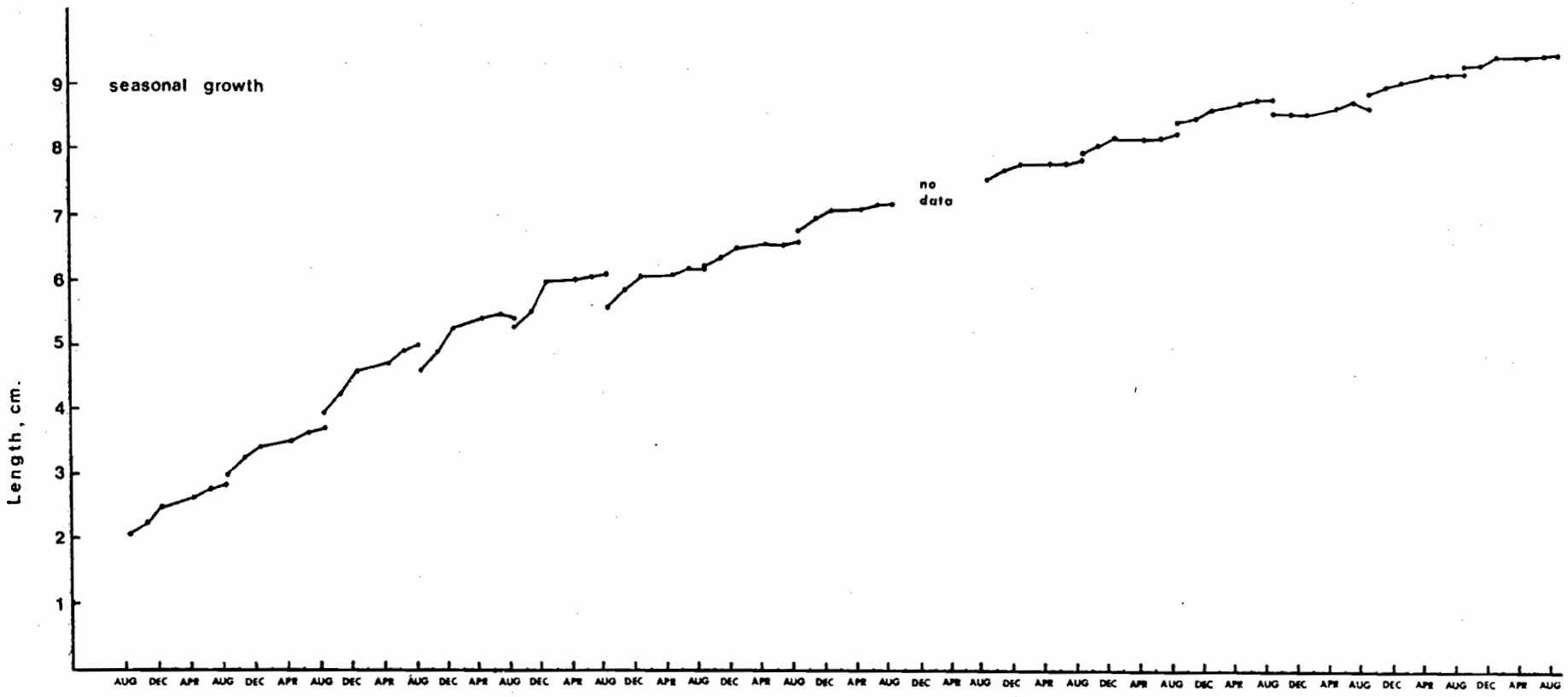
The Ford-Walford plot (Fig. 55) for St. Margaret's Bay M. edulis defines a growth curve between shell lengths of 2.0 and 10.0 cm. The correlation coefficient for the Ford-Walford plot is 9.79 and the linear relation of l_{t+1}/l_t exists at less than the 5% level. A lack of linearity is suggested in the Ford-Walford plot by the spread of data between l_t values of 2.0 and 6.0 cm. This is more clearly exhibited in the plot of $(l_{t+1} - l_t)/l_t$ (not shown), inferring that the Gomperz equation (Gomperz, 1825) may be more applicable to growth of the mussels of this size than the von Bertalanffy equation. The Gomperz curve has an inflection point and, for the present data, the period of maximum growth rate is indicated at a shell length of about 4.0 cm.

In larger mussels, the tendency to approach a final length is not very marked. According to the regression for the Ford-Walford plot, L_∞ is at about 12.00 cm, but this is an extrapolated value. The largest mussels found in the area were between 10.5 and 11.0 cm in length. Data for mussels older than these may or may not reveal an increased divergence of the Ford-Walford plot from the $l_{t+1} = l_t$ line. The possibility of obtaining such data from a natural population is diminished by the great age of large mussels and the abundance of predatory starfish which denude great areas of the mussel populations.

Data by which to refer the growth curve to time of spatfall were unobtainable during the study period. No substantial spatfalls occurred on rope collectors, wooden panels or amongst the mussel population at the experimental site between August 1971 and August 1972, so that first year growth was not observed.

The seasonal pattern of growth for the various sizes of mussels at St. Margaret's Bay is shown in Figure 57. Short term variations in growth rate are more marked in small than in large mussels. For mussels of less than 5 cm length the pattern is similar to that at Holyrood. Growth is most rapid in autumn, very slow during the winter, and increases again in spring and summer. The growth rates during the summer of 1972 were adversely affected by quantities of creosote originating from wharf

Fig. 57

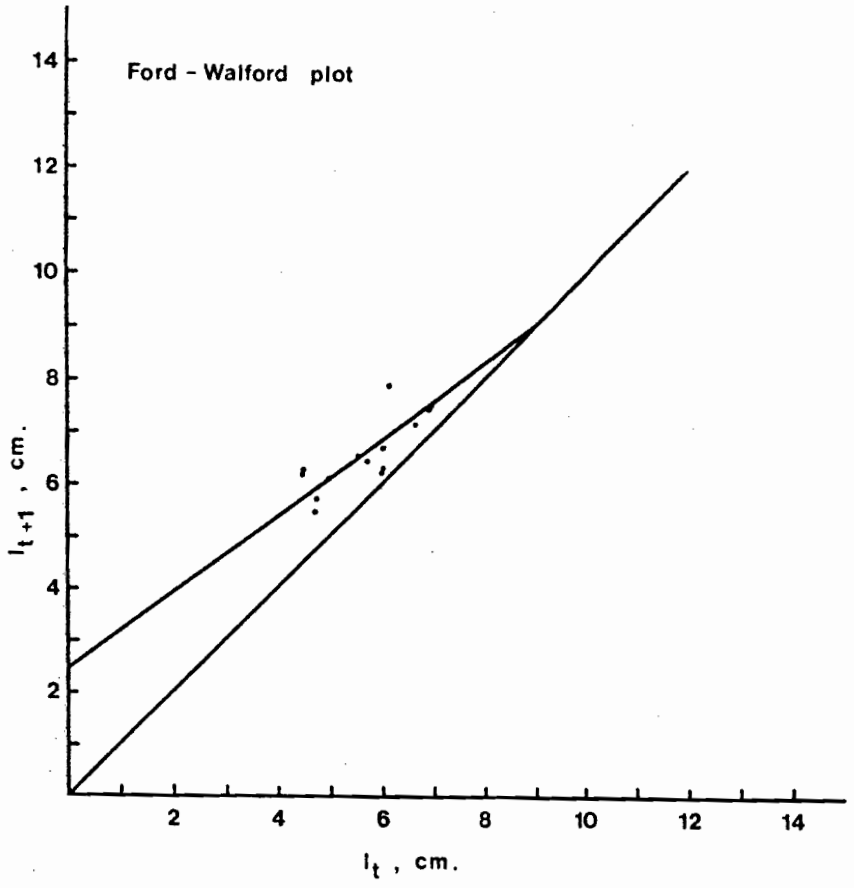


ST. MARGARET'S BAY.

construction in May. Creosote caused softening of the shell margins, but no obvious internal damage occurred to these mussels. Mussels of lengths less than 5 cm would probably have grown at a greater rate during the summer of 1972 if they had not been affected by the creosote. Seasonal variation in growth of large mussels was not marked, and the effect of creosote may have been minor to this age group.

The retardation of growth by creosote in the summer of 1972 renders the 1971-72 growth rates an under-estimate for normal years. However, the shape of the growth curve obtained from the growth study is probably typical, as the dominant growth periods have retained their character. The curve will be damped though by the lack of growth during the second growing season. That this effect is not too important in the growth of the mussel over its life span is demonstrated by comparison with growth check data for the natural mussel population. Mussels of 5 to 6 cm in length had 7 growth checks, as would be predicted by the von Bertalanffy growth curve from the growth study data. Age at maximum length for this pattern of growth would be of the order of 20 years.

The pattern of seasonal growth is further discussed in relation to other characters of the mussels in the next section (see Figure 65).



WOODS HOLE

Fig. 58

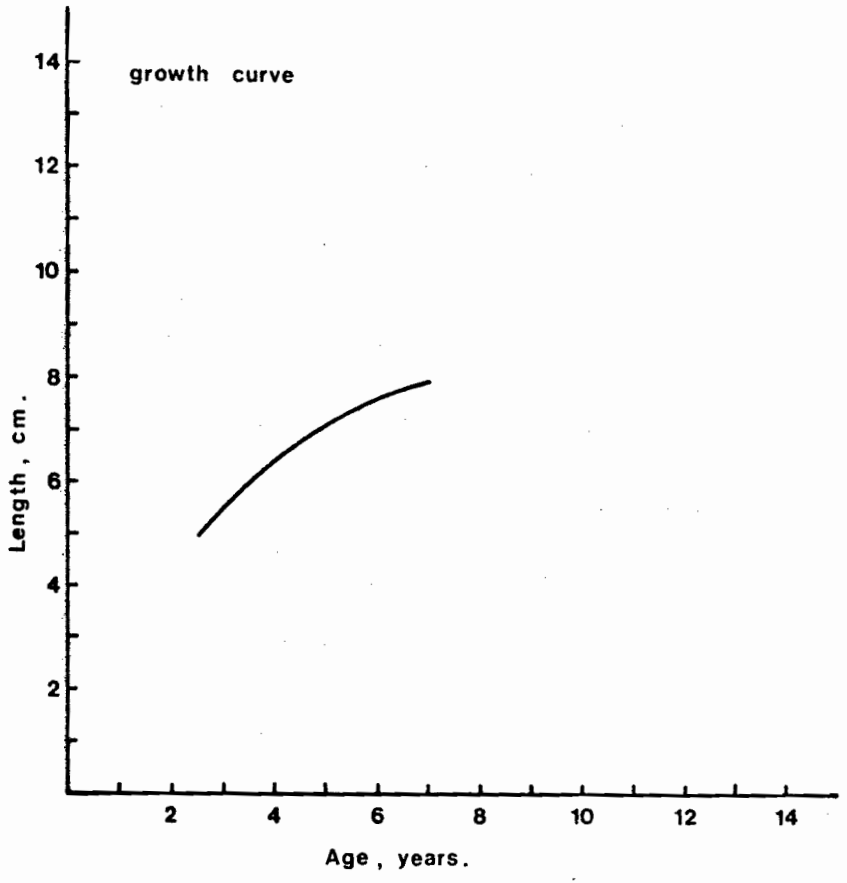
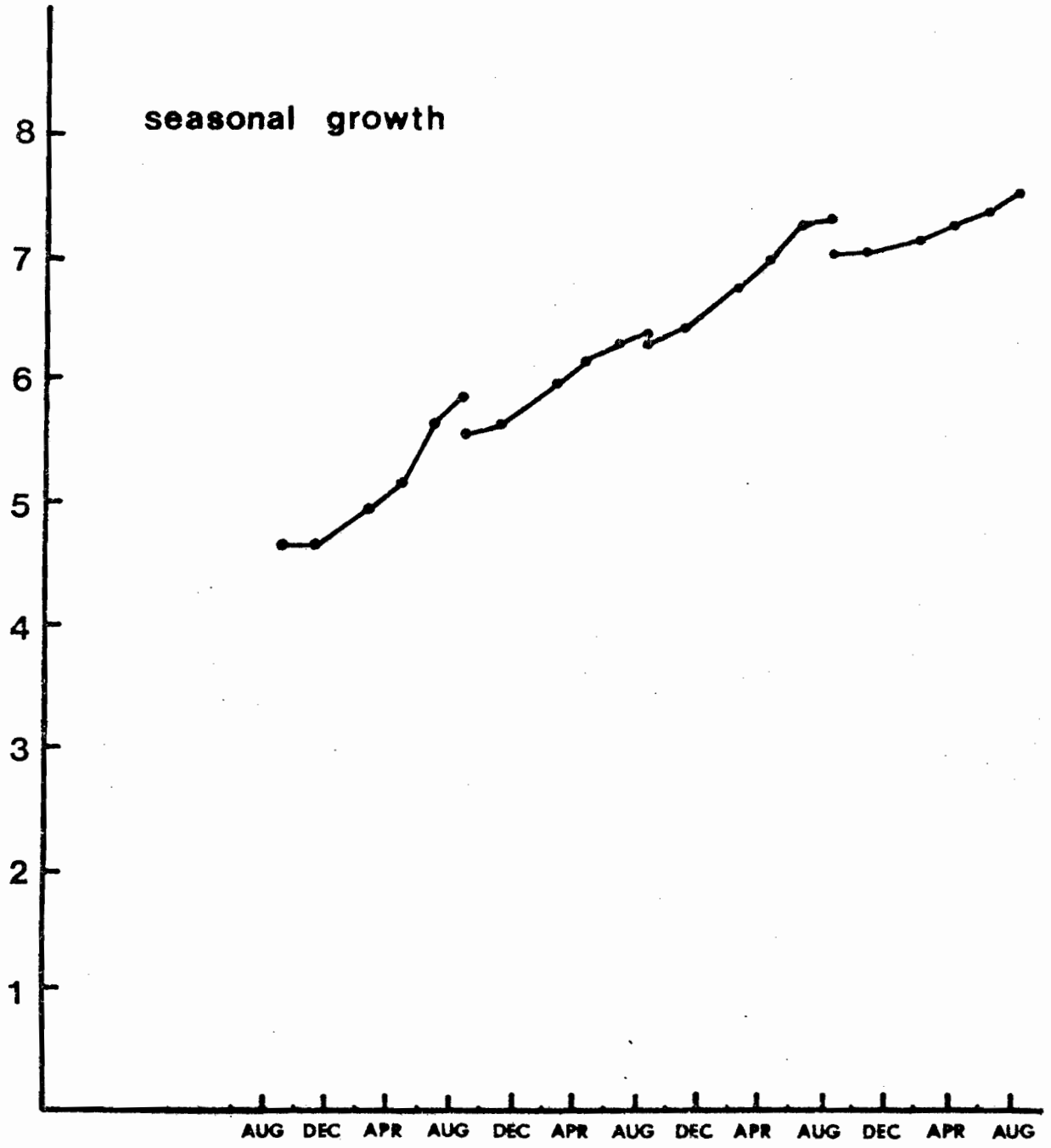


Fig. 59

Fig. 60



WOODS HOLE

Woods Hole.

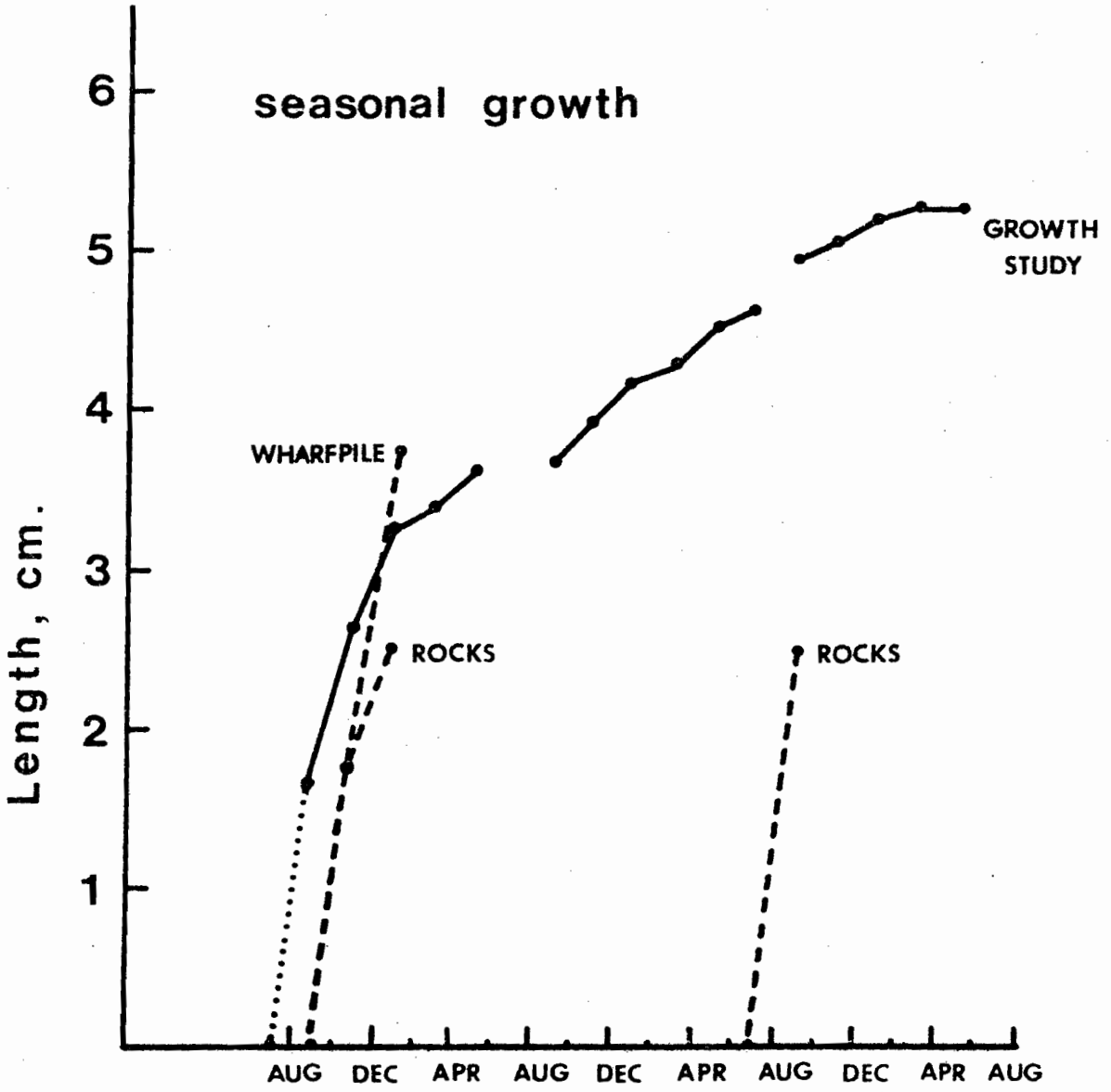
The uniform population of Mytilus edulis on the wharfpiles at Woods Hole provided material for the growth study between shell lengths of 4 - 8 cm. The Ford-Walford plot (Figure 58) and the growth curve (Figure 59) can only be considered valid between these lengths. The rest of the information (below) is extrapolated. No substantial spatfalls occurred on rope collectors, wooden panels or amongst the natural mussel population during the study year, so no estimate of early growth was made.

The Ford-Walford plot has a correlation coefficient of 0.81 with a linear relation of l_{t+1}/l_t existing at less than the 5% level. The spread of data is not sufficient to determine the relative applicability of the von Bertalanffy and Gomperz equations. The high value of K (0.32) for the von Bertalanffy relation suggests that any point of inflection of the growth curve must occur at a relatively early stage (cf. Holyrood and St. Margaret's Bay) and that the von Bertalanffy is the more relevant curve.

The growth study data predict an abrupt levelling of the growth curve at about 8 cm shell length. The maximum length attainable under these conditions is about 9 cm. This is greater than the length of any of the mussels observed in the field (maximum 7.5 - 8.0 cm), due to the age of the mussel population on the recently constructed wharf.

Figure 60 shows the seasonal pattern of growth in a modified growth curve for Woods Hole. Growth does not follow the seasonal pattern of temperature. The short term variations in rate are similar to those observed by Richards (1946). Short term growth is discussed in more detail in the next section (see Figure 70).

Fig. 61



SANDY HOOK

Sandy Hook.

Due to the short life span of Mytilus edulis at Sandy Hook, the growth curve (Figure 61) is complicated by short term factors. The growth pattern and life span are determined by the interaction of the age/growth curve with seasonal growth variations.

Data for early growth come from observations of summer spatfalls on rocks and wharfpiles. These mussels grew at rates of 1.0 to 2.5 cm/month, depending on location and time of spatfall.

The growth study population yielded data for a curve between 1.5 and 5.4 cm shell length. Mussels of 1.5 cm had no growth checks and were probably the result of a spatfall in spring or early summer. Growth of these mussels was rapid over late summer and fall, comparable to that of the recently settled mussels (above). Their rate of growth decreased over winter, probably due to low temperature, and although it increased again with the higher water temperature in spring, the initial rapid growth was never recovered. By the end of the first year the mussels reached a length of 3.5 cm.

In the second year the mussels increased their length by only 1 cm. Growth was most rapid for this age group during summer, it decreased in winter, and increased again in spring. But during the third summer growth decreased. This was probably the result of environmental stresses (above optimum temperature, low ambient oxygen levels) acting on mussels which were already close to their metabolic limit for growth and age in this environment.

The interaction of temperature, L_∞ and metabolic demand was more clearly shown by third year mussels (see also Figure 69). These accomplished a total annual growth of only 0.3 cm. There were two seasonal minima, one in winter and one in summer. The final summer minimum coincided with the L_∞ observed in field populations.

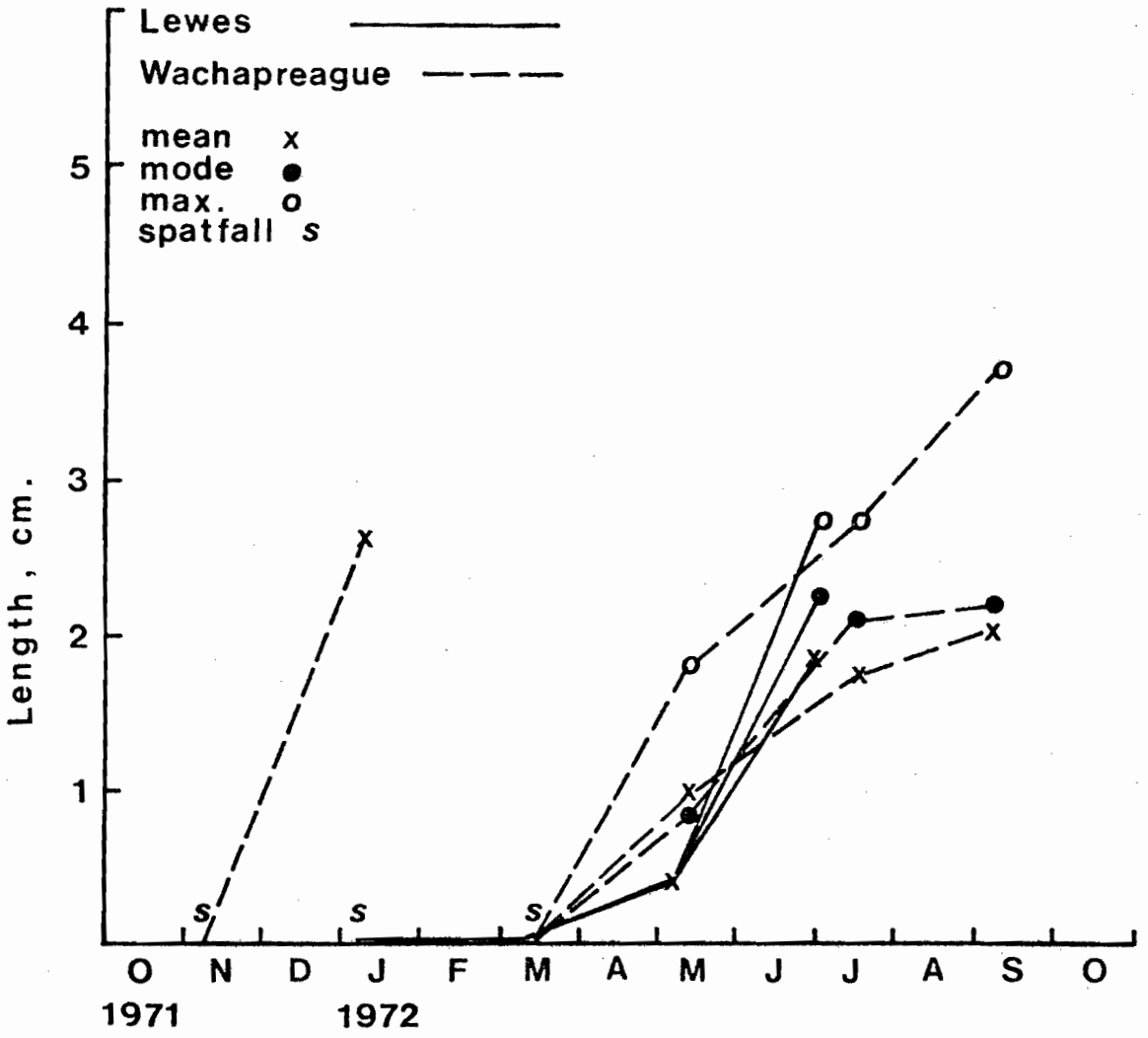


FIG. 62 Growth of test panel *M. edulis* at Lewes and Wachapreague, from the data of Buchanan (1975).

Lewes and Wachapreague.

Figure 62 is the graphical representation of growth data obtained by Buchanan (1975) for mussels which settled on wooden test panels at Lewes and Wachapreague during 1971-72. The data provide a measure of the growth of M. edulis from spatfall to an age of 6 months at Lewes, and to an age of 8 months at Wachapreague.

At Lewes a spatfall occurred in January 1972. The growth of the mussels remained negligible over winter, increased only slightly during spring, and accelerated to a rate of over 1 cm per month in early summer. At this stage the mussels fell prey to their own bulk and no further growth data was obtained. The growth rates observed at Lewes reflect the seasonal variation in temperature. During January and February the temperature remained below 5°C, from March to April below 10°C, in May less than 15°C and in June temperatures ranged from 15-20°C. At no stage for which growth data are available did the temperatures go above optimum (20°C), and the curve depicted in Figure 64 suggests a direct effect of temperature on growth of the mussels.

At Wachapreague there were two spatfalls which provided growth data. The spatfall of November 1971 grew rapidly to reach a mean size of 2.5 cm by January 1972. By March the mussels had fallen off the panel due to their bulk, and no further growth data was obtained. Another spatfall occurred at Wachapreague in March 1972. This also grew rapidly, but not as fast as the November spatfall. For this spatfall there was a marked difference between the rate at which the bulk of the population (mean, mode) grew and the maximum rate of growth of a mussel on the panel. This difference could be attributed to crowding. Thus these data probably do not reveal the metabolically-determined rate of growth of M. edulis at Wachapreague, but a rate imposed by physical compression. The mean and modal rates of growth decreased with time, whereas the maximum rate remained high throughout the 8 month period. These data show that growth can persist at a rate of at least 0.75 cm per month over the first summer of attachment. But no conclusions can be made about the shape of the growth curve or the seasonal variation in growth under these circumstances.

Because of the unstable nature of the mussel populations at Lewes and Wachapreague it is impossible to estimate L_∞ or the ultimate age that mussels at these localities might achieve if left to their own metabolic devices. Mussels at Lewes were adversely affected by a number of factors and exhibited several growth checks in any one year. No large mussels were found, the maximum length was 6.1 cm, but mussels of this size were rare. Most of the population had the appearance of being stunted, and widespread mortality occurred from time to time. The largest mussels of the Wachapreague population were of length less than 6.5 cm and mussels of over 5.5 cm were common. But the prevalence of sand denudation and high currents at this site makes this observation useless as an estimate of metabolic L_∞.

V. LATITUDINAL VARIATION IN GROWTH.

Growth of Mytilus edulis varies between the different stations. Variation exists in several growth parameters and may be attributed to a number of causes, both latitudinal and local in origin. There are many ways of comparing growth at different latitudes (see Introduction), but the most satisfactory for this study is the comparison of the growth curves over the life spans of the mussels.

The growth studies from Holyrood, St. Margaret's Bay, Woods Hole and Sandy Hook provide sufficient data to allow comparison of the growth curves over a good portion of the adult life of the mussels. Figure 63 shows the comparison of growth curves from these stations and Table 6 gives the respective parameters of the von Bertalanffy growth equation. The data on growth of M. edulis at Lewes show seasonal variations in growth so large that they impose their pattern on the growth curve over the short lifespan of the mussels, rendering a von Bertalanffy treatment irrelevant.

But for those stations which do provide von Bertalanffy or Gomperz type growth curves some broad latitudinal comparisons can be made. The stations are discussed in order of latitude, starting with the warmest and southernmost: Sandy Hook.

TABLE 6. Growth parameters estimated from one year's growth study data, see above. L_∞ given in cm.

Station	Ford-Walford plot	Constants for von Bertalanffy equ'n	
		L_∞	K
Sandy Hook	$l_{t+1} = 3.65 + 0.341_t$	5.55	3.53
Woods Hole	$= 2.50 + 0.721_t$	8.92	0.32
St. Margaret's Bay	$= 1.08 + 0.911_t$	12.00	0.09
Holyrood	$= 1.43 + 0.821_t$	8.00	0.19

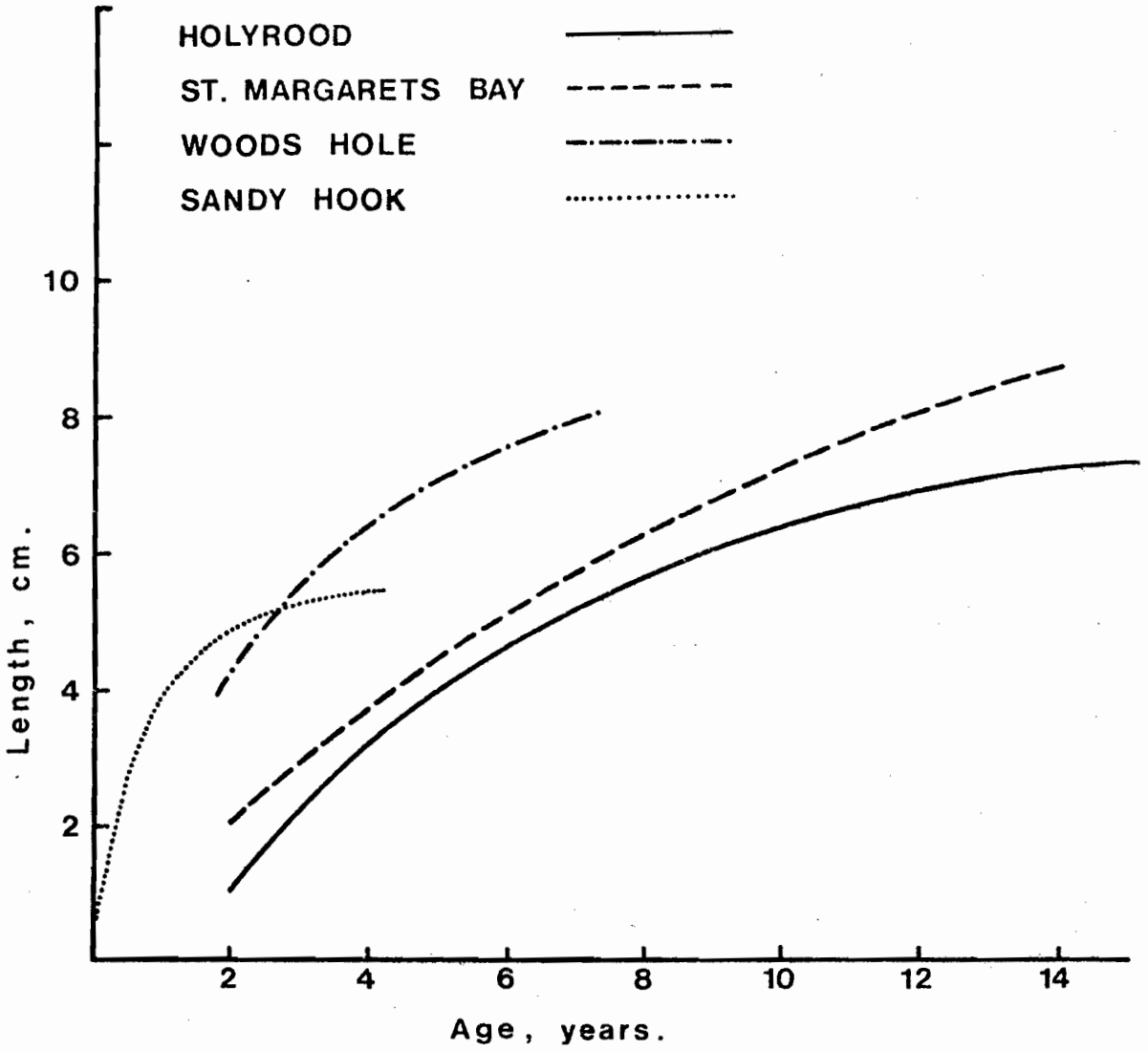


FIG. 63 Latitudinal comparison of growth curves.

Of the four stations in Figure 63, Sandy Hook allows the fastest initial growth, but also has the highest K value and the lowest L_∞ value, i.e. growth reaches a limit at an early stage, at a length of 5.5 cm and an age of 4 years.

Woods Hole mussels exhibit the second fastest initial growth rate, and if the von Bertalanffy equation is extrapolated beyond the range of data, i.e. if growth continues to follow the same pattern in time, a levelling of growth will occur at an age of about 8 years and a length of 8.0 to 9.9 cm.

At St. Margaret's Bay early growth is slower than at either of the above stations, perhaps even slower than suggested by extrapolation of the St. Margaret's Bay growth curves in Figure 63 (settlement time unknown). Beyond a length of 4 cm, growth is still relatively slow compared with the early growth rates of mussels from the southern stations, but it shows little tendency to reach a definite L_∞. The present data show that at a length of 10 cm growth is still positive, and continuation of growth along this pattern would produce an ill-defined L_∞ at about 12.00 cm after more than 20 years. But further divergence from a L_∞ beyond the data presented remains a possibility.

At Holyrood growth is initially slow. There is no suggestion of sigmoidicity in the growth curve. The slope of the von Bertalanffy curve is comparable to that of St. Margaret's Bay in the early stages, but the Holyrood curve has a higher value for K and the growth slows down markedly after about 12 years at a length of 6.5 - 7.0 cm with a predicted and observed L_∞ at 8.0 cm at an age of more than 20 years.

The results of this comparison are largely in keeping with the temperature-metabolic theory of growth determination put forward in the Introduction. High temperature (low latitude) gives rapid growth in the initial stages, but is also correlated with an early levelling of growth rate, a low L_∞ and early mortality (e.g. Sandy Hook). Low temperature gives a sigmoid curve with slow growth throughout the long life span and no definite L_∞ (e.g. St. Margaret's Bay).

The growth curve of Woods Hole mussels is intermediate between that of Sandy Hook and St. Margaret's Bay and as such fits into its latitudinal

context. That of Holyrood Mytilus shows the slow initial growth rate characteristic of high latitude mussels (although no sigmoidicity is evident from the present data), but differs from the ideal latitudinal pattern in possessing a definite L_∞. It is tempting to postualte that low energy input (food, water circulation) is the reason for this discrepancy. High latitude mussels in sub-optimal environments do exhibit high K values in their growth curves and have small maximum size, e.g. the low salinity mussels of Hudsons Bay (Lubinsky, 1958) or the open coast mussels of Newfoundland (see above). There are several factors at Holyrood which may contribute to the determination of L_∞ at 8.00 cm.

Latitudinal variation in growth is often discussed in terms of absolute growth (see Introduction), i.e. growth per year in mussels of unspecified age, or more suitably growth in the first year. Treatment of growth data from the literature in this way is unsatisfactory except to show that a range of growth rates occur, and treatment of the present data in this way shows why.

Growth varies with age, following a sigmoid or hyperbolic function, and reference to Figures 52 to 62 shows that at any station the rates of growth are dependent on the age of the mussel with respect to its life span. Comparison between stations must allow for this difference. There are also marked seasonal shifts and these may affect gross growth characteristics in two ways. At northern stations winter growth is negligible. This appears to have a deleterious effect on first year mussels of the autumn set and such comparisons as 'growth in the first year', 'growth to the first 5 mm' or 'growth per day-degrees' must be qualified as to time of spatfall. At the southern stations where growth is fast and life span short, the seasonal effect is a major characteristic in the growth pattern (e.g. Lewes). Again time of spatfall is important, not in determining only the first 50 mm of growth, but in determining the whole shape of the growth 'curve' (see Figure 64).

In studies that are largely concerned with temperature, growth from different regions is often compared in terms of day degrees to reach a certain state (see Introduction). The applicability of this tool may be evaluated by comparison of some of the stations in the present study (see Table 7).

TABLE 7. Annual mean temperature, length of time and number of day-degrees for M. edulis (from latitudinally-separated populations) to reach 50 mm shell length.

Station	To Reach 50 mm		
	Time	Mean annual temperature	Day-degrees
Holy rood	7 yrs	5.12°C	13000
St. Margaret's Bay	6 yrs (±)	8.46°C	18500
Woods Hole	3 yrs	11.28°C	12500
Sandy Hook	2 yrs	14.37°C	10500
Wachapreague	8 mths (extrap.)	19.82°C	5000

Except for the mussels at Wachapreague, the number of day-degrees taken to reach a length of 50 mm is high compared with those in the literature (see Introduction). The growth site at Wachapreague seems particularly favourable to growth of M. edulis, providing high temperatures throughout the year, as well as abundant food and fast currents giving unlimited oxygen supply. Sandy Hook mussels suffer from several factors which render their growth relatively low per day-degrees. The existence of two growth minima - one in summer and one in winter, slows growth to the extent that a 50 mm mussel is two years old, i.e. experiences 4 growth minima, two of which are related to day-degrees. Adverse factors not related to temperature also exist here. Growth of M. edulis at Woods Hole is already independent of seasonal temperature changes (see Figure 68) and in the long term is independent of day-degrees. St. Margaret's Bay mussels have a slow growth rate per day-degrees. This may be due to the sigmoidicity of the growth curve as well as short term temperature-independence of growth rate caused by creosote poisoning in the early summer of 1971. The low energy environment of Holyrood, postulated above, could be expected to produce a low growth rate per day-degrees.

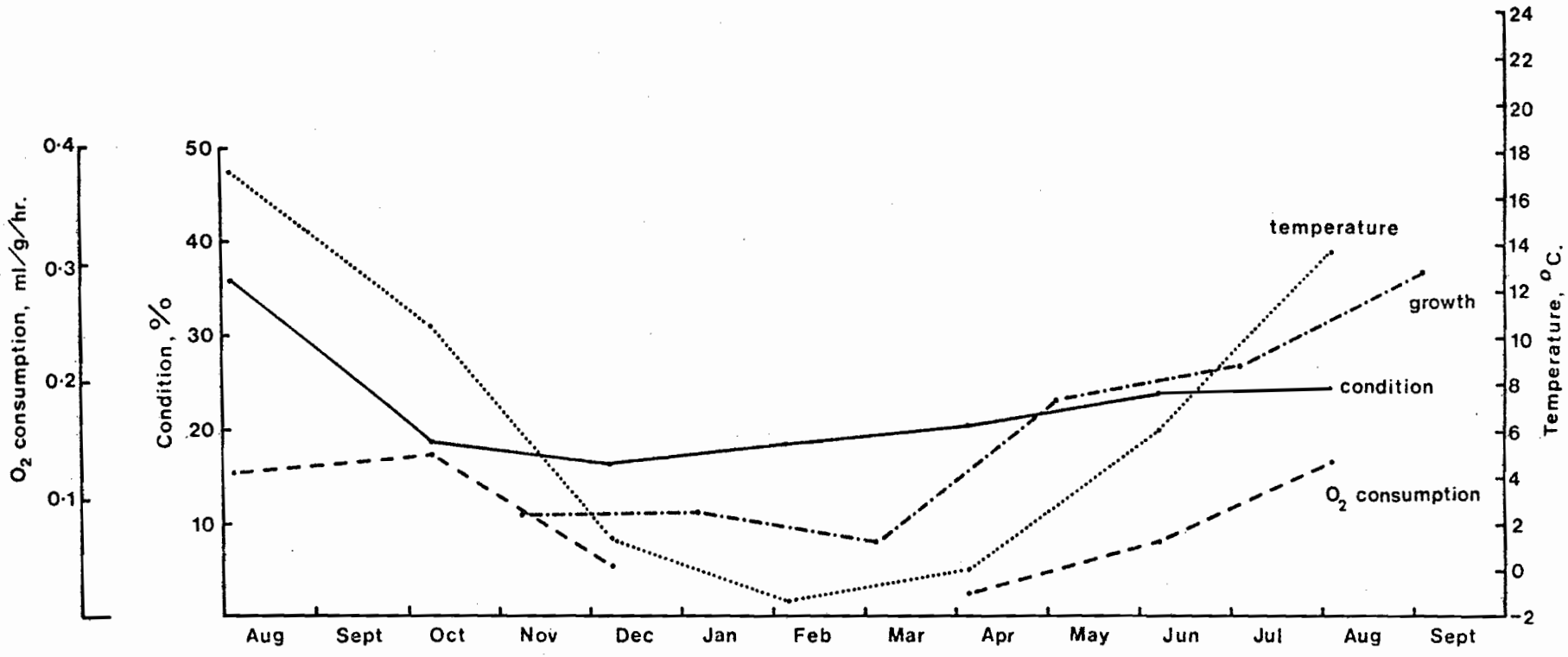
INTEGRATION OF OXYGEN CONSUMPTION, AND GROWTH STUDY RESULTS.

In the introductory chapters (see "Metabolic rate of M. edulis as related to latitude.") the thesis was put forward that the metabolic rate, imposed on M. edulis by the various environments in which it finds habitat, determines the major accumulative growth processes of the mussel. For example, if food and other factors are not limiting, the rate of shell growth, shape of the growth curve, ageing, environmental limitation of (shell) growth and lifespan are determined by a largely temperature-induced metabolic rate. Temperature may also determine the level at which other environmental factors are limiting to metabolic rate and growth processes.

The integration of oxygen consumption, and growth study results, which follows in this chapter, evaluates this hypothesis over different time periods and different latitudes (and environments, where equality inevitably could not be met). Section I, on seasonal comparison of oxygen consumption, and growth studies, considers the immediate relation between temperature, oxygen consumption and growth at each station. Section II is a discussion of the cumulative effect of this interaction, in producing mussels with life table characteristics peculiar to their respective environments and latitudes.

The parameters plotted in Figures 66 to 73 are taken from data in the previous chapters. Temperature is as per Figure 4. Oxygen consumption rates for each station are as per Figure 49. Growth values are taken from growth study data for mussels of the size used in the oxygen consumption studies (4-6 cm) and these have been estimated in Appendix Tables 5, 8, 9, 12 and 15. Condition is taken as the mean of the 10 respiration study mussels for the ratio of meat weight to total weight expressed as a percentage. Some evaluation of gonadal state is made (text), but the gametogenic cycle in M. edulis is generally shorter than the sampling frequency in this study, and details of the reproductive cycle cannot be ascertained with accuracy.

Fig. 64



HOLYROOD

I. SEASONAL COMPARISON OF OXYGEN CONSUMPTION, AND GROWTH STUDY RESULTS.

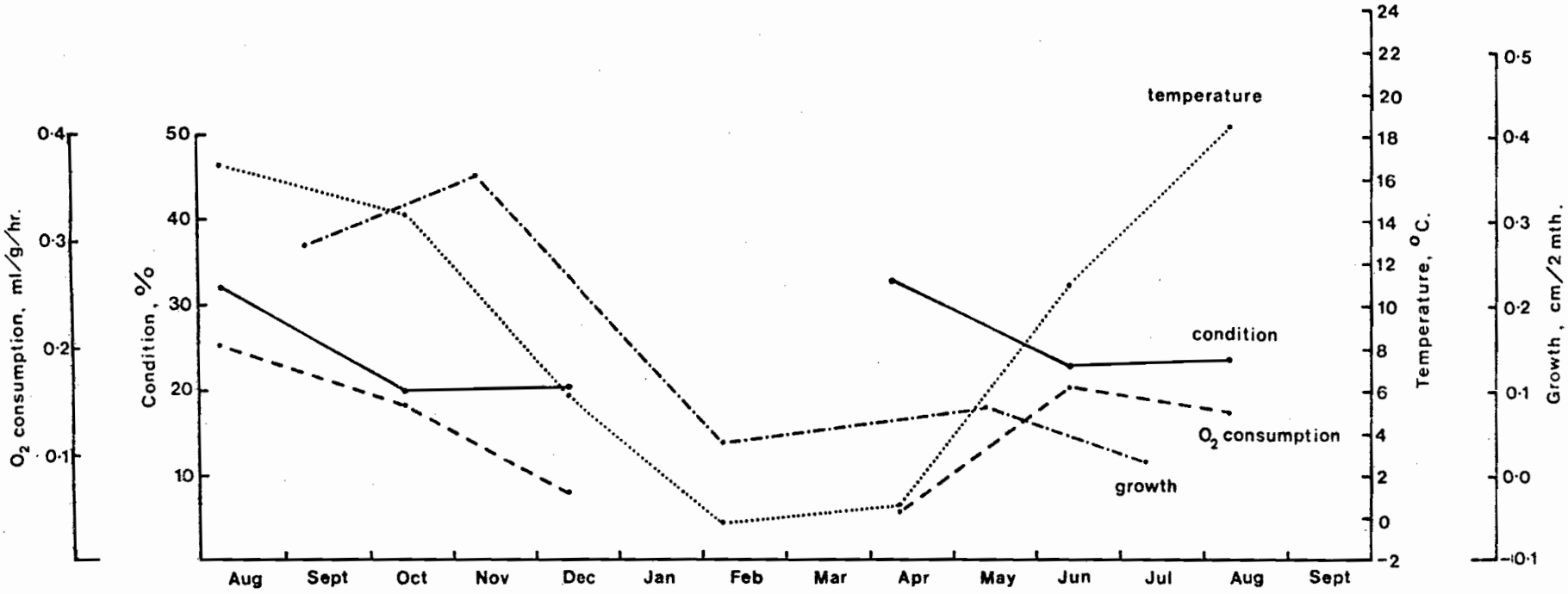
Holyrood. Figure 64.

Oxygen consumption was maximal in summer and minimal in winter. The rate of oxygen consumption did not follow the seasonal temperature changes directly, for during the period of maximum temperatures, in August, oxygen consumption was not as high as would be expected if no thermal acclimation occurred (see also Figure 50).

Shell growth followed the same seasonal trend as oxygen consumption, being greatest in the summer months. No summer levelling of the growth rate, analogous to that of the oxygen consumption rate, was revealed by the growth study data. Low shell growth in winter may be correlated with the low activity rates indicated by the oxygen consumption values at this time, but may also be caught in a viscious circle with low energy resources, due to lack of food from the water, and lack of storage products in the mantle (see below).

The seasonal pattern of condition was related to temperature and the gametogenic cycle. In August condition was high, the mussels had been active over summer, and the gonads were full. Condition dropped abruptly over autumn, due to the loss of gametes at the autumn spawning. Over the winter, condition improved gradually, but the mantle remained transparent from October to at least early February, i.e. remained free of both stored glycogen and gonadal material. Slightly improved condition was recorded over the spring and summer months. This corresponded to a mixture of gonadal states. Regeneration of gametes commenced in February, and spawning occurred some time prior to early April. By June most of the mussels were again full with gametes. In August the gonads were spent and some regeneration of gametes was taking place. It appears that spawning took place several times over the warmer period of the year, and not just in spring and summer.

Fig. 65



ST. MARGARET'S BAY

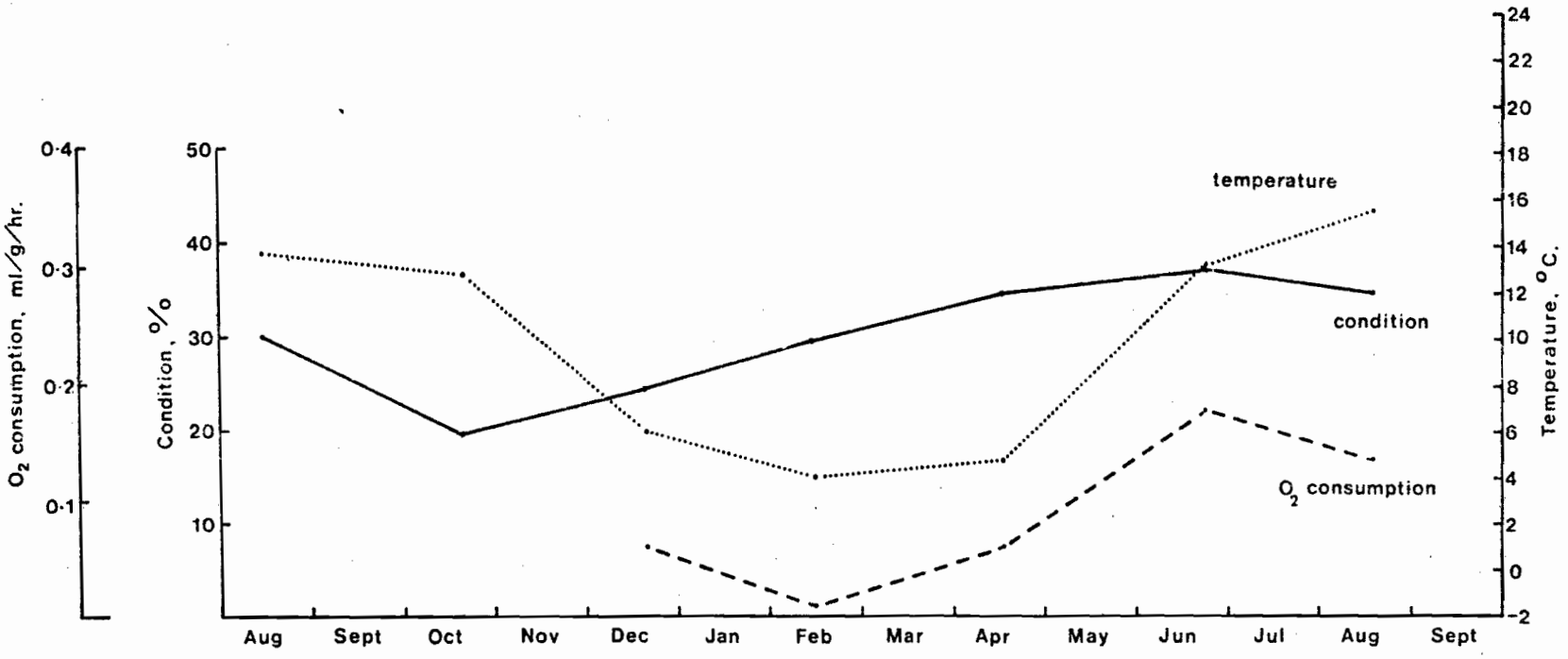
St. Margaret's Bay. Figure 65.

Oxygen consumption was maximal in summer and minimal in winter. During the hottest month (August) of the second year, oxygen consumption, though it remained high, did not follow the increase in temperature.

Shell growth was high during the first summer and increased over fall. This fall increase could have been due to increased food but Platt and Irwin (1968) report a relatively high level of primary production in St. Margaret's Bay throughout summer. Growth dropped sharply over the winter, corresponding to lower temperature and decreased activity, as revealed by the low oxygen consumption rate. Growth increased slightly over spring, but did not regain momentum in the second summer. The summer retardation was due to the introduction of creosote to the waters around the mussel population in May 1972 (see above).

The condition/gametogenic cycle for St. Margaret's Bay was harder to interpret than that of Holyrood. The good condition of summer 1971 reflected mantles full of storage products, most mantles containing 50% glycogen reserve and 50% regenerating gametes. This state probably represented the conversion of glycogen to gametes. Temperatures were also highest at this time. The sum of these two effects was probably reflected in the high oxygen consumption rate at this time. Over autumn the average condition fell, possibly due to spawning but a great range of mantle states was observed at this time. Condition remained low over December, corresponding to little or no reserves in the mantles. During April condition was high, mantles were full, but whether of glycogen or gametes is unknown. This period would correspond to high phytoplankton levels in the bay (Platt and Irwin, 1968; Platt, 1971). It did not coincide with high oxygen consumption levels, or temperatures. Condition again fell over summer. By August many of the mussels had spawned or were spawning. Average condition was fairly low.

Fig. 66



ST. ANDREWS

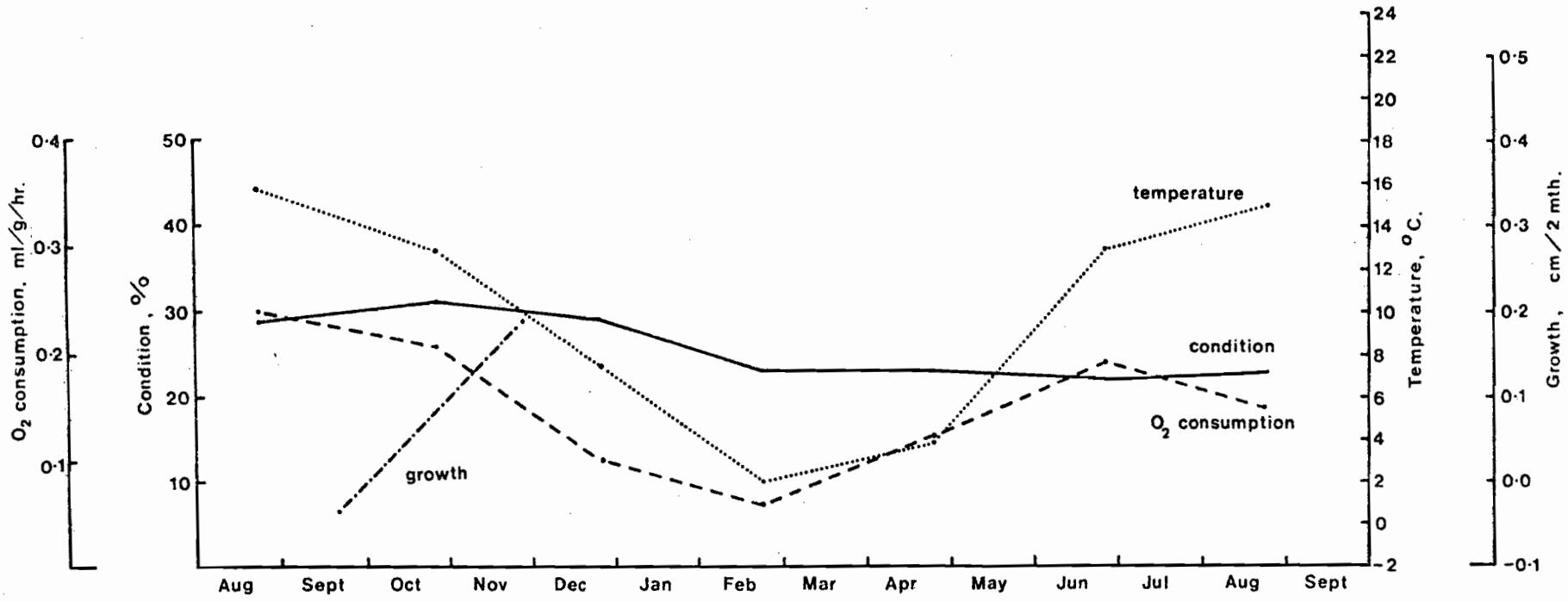
St. Andrews. Figure 66.

Rate of oxygen consumption follows temperature, with the usual exception in the warmest period of the year.

There are no growth data for the study period, but the data of Mossop (1922) indicates that growth is suppressed in winter to the extent that strong growth rings are formed.

Condition followed a similar pattern to that at Holyrood and St. Margaret's Bay. In August condition was high, mantles were full of gametes. Condition decreased abruptly over autumn, corresponding to release of gametes. Over winter there was a steady increase in condition, more marked than that at Holyrood. Mantles remained free of gametes in most of the population until April, when condition was as high as that of the ripe population of August. Condition was high at all sampling times between April and September. According to Battle (1932, 1934), spawning and regeneration of gametes takes place throughout the summer period at approximately monthly frequency. This would not have been picked up by the two-monthly sampling intervals used in the present study.

Fig. 67



BOOTHBAY

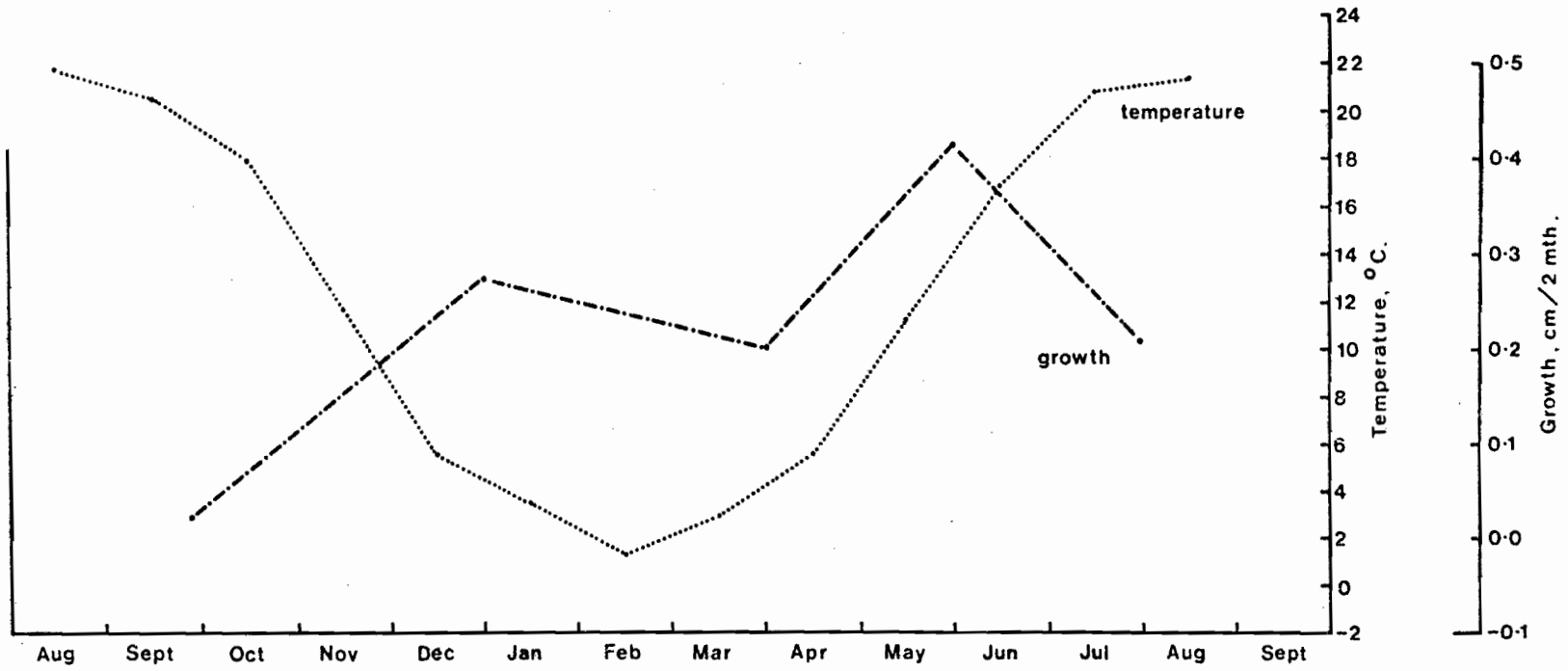
Boothbay. Figure 67.

Oxygen consumption was again highest in summer and lowest in winter, with the exception of August 1972 where oxygen consumption values did not follow the rise in temperature. The high rate of oxygen consumption in spring may be the result of high phytoplankton levels, producing an active metabolic rate.

Shell growth data does not span sufficient time to allow comparison with the other properties of the mussels. Growth was initially slow during late summer and increased markedly over fall. This pattern was similar to that observed at St. Margaret's Bay and Woods Hole. It may have been due to a number of factors including the level of phytoplankton in the water (see Richards, 1946 and Woods Hole, below), and thinning of the originally dense cage population by starfish which settled from the plankton and devoured first the small, and finally the larger mussels in the cage.

The cycle in condition was different to that at the other stations. There was little variation through the year. Condition was highest during the late summer and fall. A slight drop in condition by December corresponded to spent mantles, in only some of the population. This state continued through until April. During summer the mantle contained storage products, either glycogen or gametes, but these did not improve condition noticeably. Spawning apparently occurred just prior to the late August sampling, the mantles were spent and condition was at its lowest. This may account for the low oxygen consumption recorded at this time (cf. other periods where gametogenesis may have been taking place).

Fig. 68

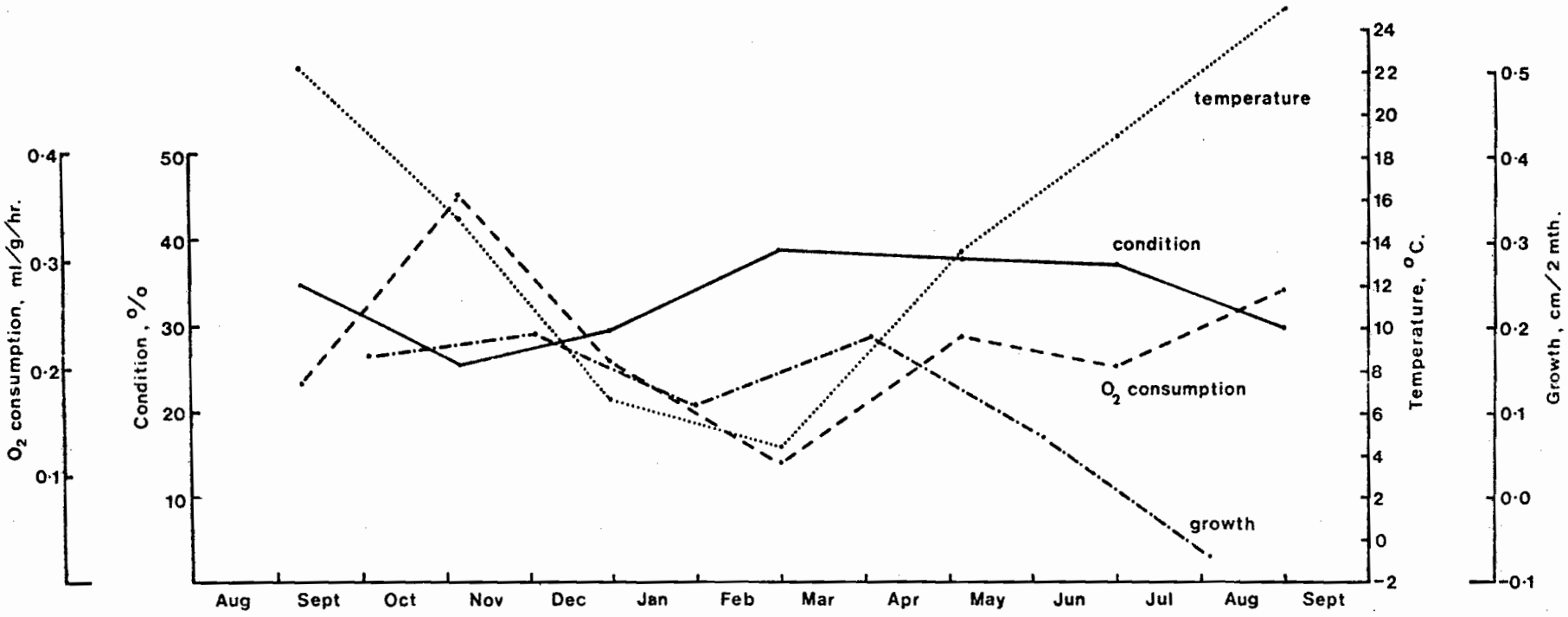


WOODS HOLE

Woods Hole. Figure 68.

Shell growth was the only parameter for which data were obtained for comparison with the seasonal cycle of temperature at Woods Hole. Growth was not correlated to temperature, at least not seasonally. It was lowest during the first late summer period, then increased markedly over fall and early winter in a manner similar to that recorded for St. Margaret's Bay and Boothbay. Late winter growth was slower, but the rate increased again in spring and early summer. By late summer it had fallen again. This pattern is identical to that observed by Richards (1946) who put forward an hypothesis based on available food. Phytoplankton in these waters is maximal in spring and another peak occurs in fall, these periods correspond to those of maximum growth of the mussels. Summer fogs keep illumination down, suppressing phytoplankton growth, and hence probably mussel growth. The relevance of this theory is dependent on the mechanisms of shell growth: whether or not shell growth is dependent on food, feeding rate or tissue growth (see "Introduction: Growth").

Fig. 69



SANDY HOOK

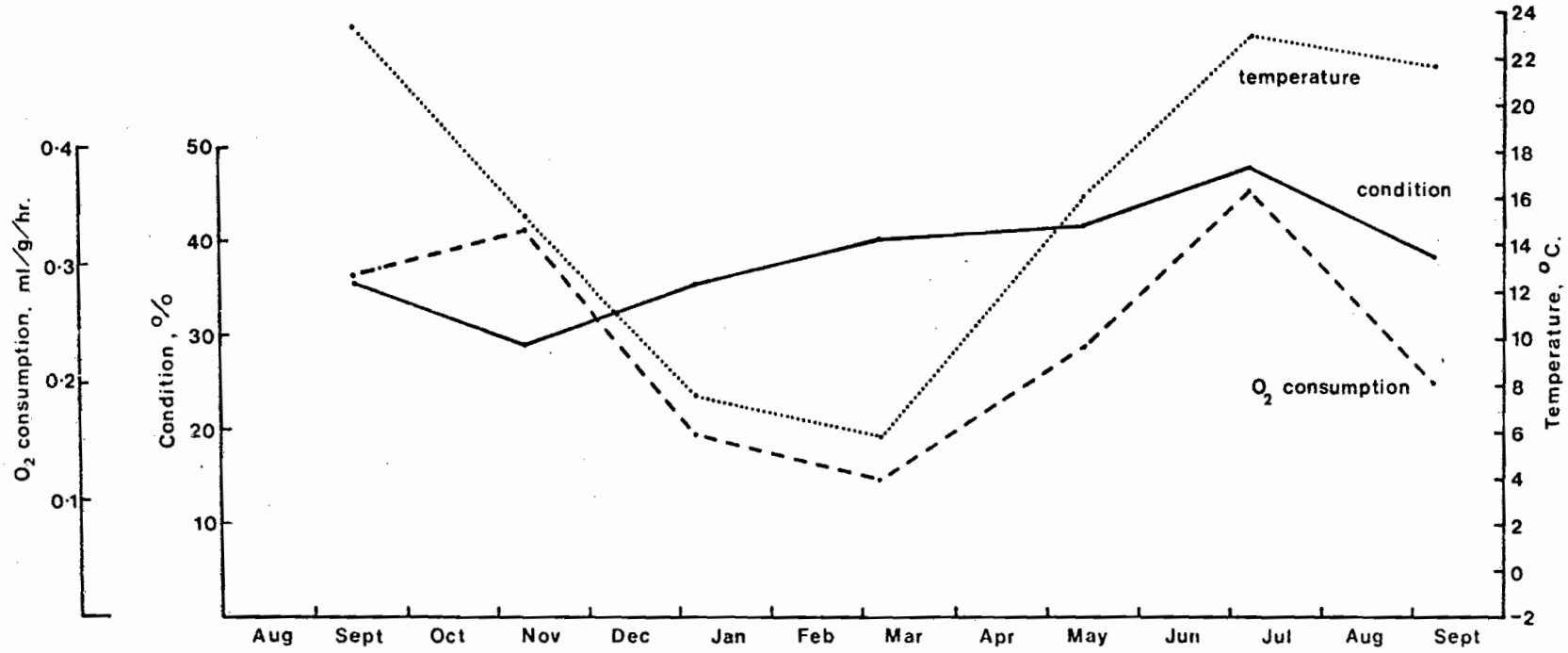
Sandy Hook, Figure 69.

Oxygen consumption followed temperature only during the cooler months of the year. Maximum oxygen consumption was observed in fall, with another peak in spring. Minimum oxygen consumption occurred in winter, but further lows were observed in summer. The low oxygen consumption recorded in summer 1971 was largely due to factors other than the above-optimum temperatures which occurred then. These included post flood stresses, low ambient oxygen and poor health of the mussel population. The general summer suppression in oxygen consumption may be largely attributed to above optimum temperatures.

Similarly shell growth showed two optima, in spring and in fall. There was depression of growth in winter, but the major depression occurred in summer. This latter depression occurred during a time of near lethal temperatures.

The cycle in condition was similar to that of the northern stations, with the exception of Boothbay. Condition was high at the end of summer. Spawning occurred between September and November, and resulted in a decrease in condition. A gradual increase in condition occurred over winter. Analysis of the gametogenic cycle was not complete enough to interpret the changes which occurred in the mussels over spring and summer.

Fig. 70

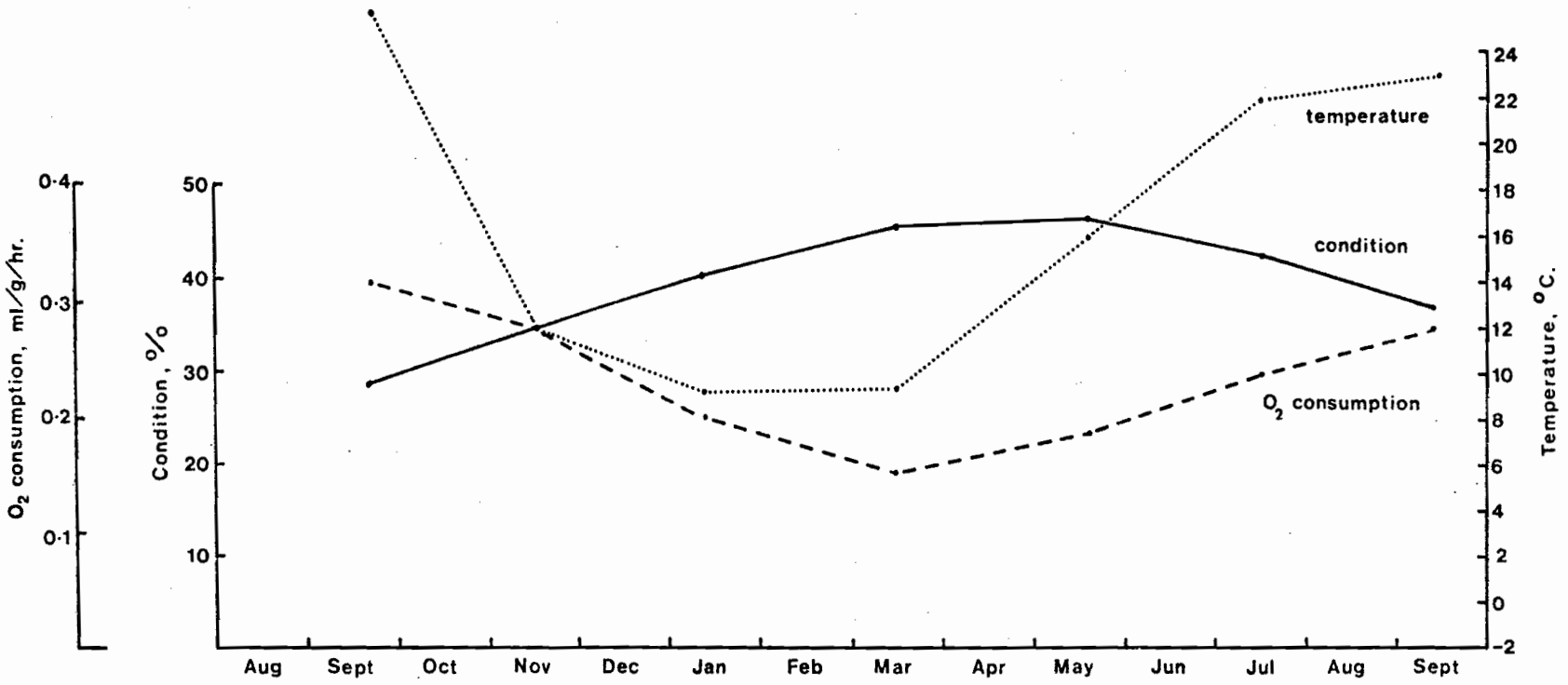

temperature
condition
O_2 consumption
O_2 consumption, ml/g/hr.
Condition, %
Temperature, °C.
0·4
0·3
0·2
0·1
50
40
30
20
10
24
22
20
18
16
14
12
10
8
6
4
2
0
-2
Aug
Sept
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sept

LEWES

Lewes. Figure 70.

Oxygen consumption followed temperature over the cooler parts of the year, but was depressed at the near-lethal temperatures of summer. Growth data are not available for mussels of respiration study size (4-5 cm), but are available for mussels of the first 6 months after spatfall, which occurred in January. The growth of these mussels was related to temperature (see Figure 64) from January to June. No summer growth data were obtained. Condition of the mussels may be related to the gametogenic cycle, the drop in condition from September to November may represent spawning, and the general increase over winter and spring is a consequence of repletion of gametes. The maximum condition recorded, in September 1972, represents the stage of conversion of storage glycogen to gametes.

Fig. 71



WACHAPREAGUE

Wachapreague. Figure 71.

Oxygen consumption rate again followed temperature over the year, with a less marked suppression in summer than at the other southern stations. This relative lack of summer suppression was in part due to the high ambient oxygen levels at Wachapreague (cf. Sandy Hook and Lewes), but may also have been a result of the relatively small annual range of temperature at Wachapreague. No growth data for respiration study sized mussels are available and data for growth of spat mussels over a period of 8 months do not reflect any temperature characteristics. Condition was lowest over summer, increased over autumn and winter and dropped again in summer. Gonads appeared to be regenerating over summer and were full during the cooler months.

Discussion.

From the data in Figures 64 to 71 some general conclusions can be drawn with respect to the interaction of temperature, metabolic rate and growth rate. On the whole, oxygen consumption is positively correlated with growth rate, i.e. when the mussels are active, shell growth is proportional to this activity. Exceptions occur as follows:

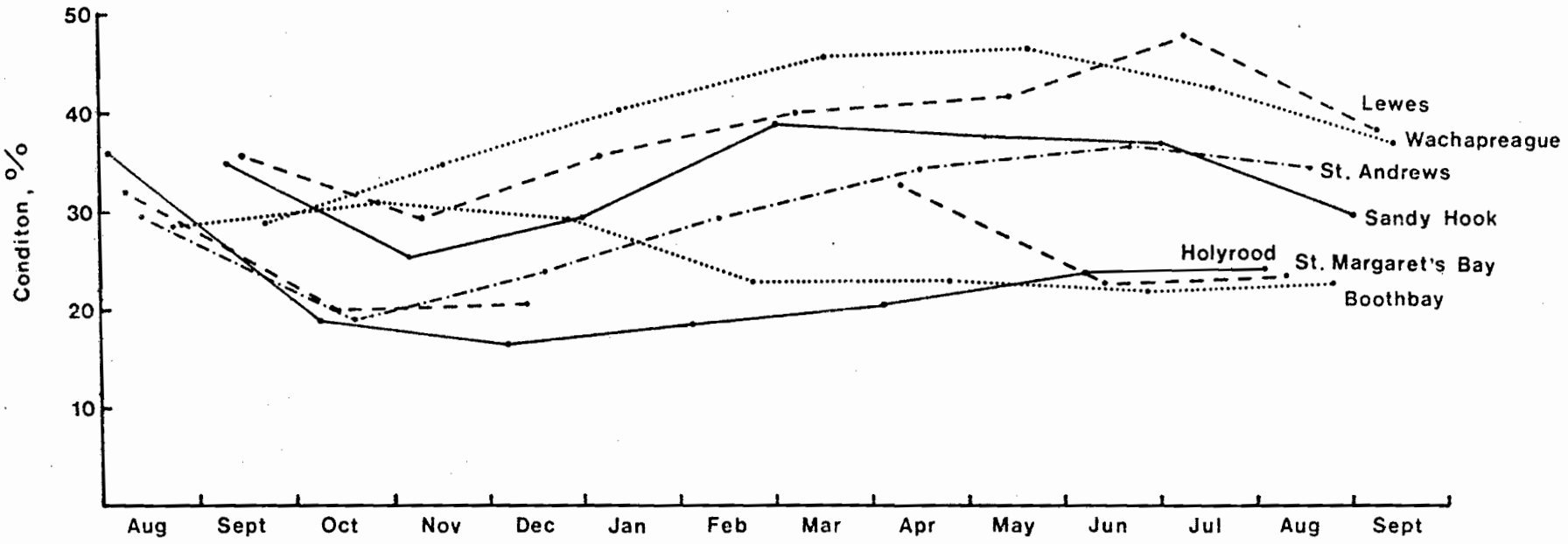
i) Oxygen consumption or growth may be affected by some extraneous factor, e.g. creosote at St. Margaret's Bay, or short term low ambient oxygen levels at Sandy Hook.

ii) There are no oxygen consumption data for Woods Hole, but growth rate at this station does not follow the seasonal variation in temperature over the entire year. Richards (1946) suggests that food may be limiting at Woods Hole in summer, but as yet this has not been ratified.

iii) At Sandy Hook, summer depression of oxygen consumption is accompanied by a disproportionate depression in growth rate. This indicates a breakdown or limitation of the processes of shell growth at a lower temperature level or within a shorter time interval than would be responsible for a similar reduction in total metabolic rate. That is, total metabolism still continues to be high but is not expressed as shell growth at high temperatures. This metabolism is probably not being directed into tissue growth, as condition is also on the downswing during the periods of highest temperatures. This phenomenon may signify the temperature-controlled balance between anabolism and katabolism discussed in the Introduction (see "Metabolic rate of M. edulis as related to latitude.") Figure 69 shows this effect at its most marked: mussels of 5 cm are at the local L_∞ and are extremely susceptible to any environmental changes.

Short term tissue growth is expressed as condition. This parameter is not related to temperature, except in the matter of thresholds. Condition at all stations bears relation to the gametogenic cycle, and this probably represents a complex balance between temperature, metabolic rate and food input, not explained by the present data. The existence of a

Fig. 72


Conditon, %
50
40
30
20
10
Aug
Sept
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sept
Lewes
Wachapreague
St. Andrews
Sandy Hook
Holyrood
St. Margaret's Bay
Boothbay

low temperature threshold for glycogen and gamete accumulation is suggested by the lack of condition over winter at the northern stations.

The low condition (low stored energy), together with low food availability from the Labrador Current waters during winter, would further ensure a low ("standard") metabolic rate. For northern mussels, with no resources to metabolize, lack of compensation for low temperature would be adaptive (cf. Dunbar, 1968; Holeton, 1973; see Introduction). The present study may be compared with the investigations of Widdows and Bayne (1971) on temperature and nutritive stress in Mytilus edulis, which were always applied to mussels with some stored reserves in the mantle. In this case, glycogen was mobilized to meet the metabolic demand. No data of this type are presently available for mussels without energy reserves. Holyrood mussels, which are capable of very meagre byssal thread production during mid-winter, were presumably using their own (non-storage) tissues as an energy source. The condition of these mussels was extremely low in winter (see Figure 72). Thus the biochemical/gametogenic cycles of Atlantic North American mussels are different to those of British mussels (cf. Dare and Edwards, 1975), and this may account for some of the observed differences in metabolic rate patterns.

II. THE EFFECT OF SIZE ON METABOLIC RATE.

(The comparability of the different stations with respect to size and L_∞.)

Some previously published studies suggest that Mytilids have equal oxygen consumption rates at different latitudes (see Introduction). That is, there exists acclimation, acclimatization or evolutionary adaptation of populations to a metabolic rate characteristic of the species, despite changes in environmental properties. Some of the early studies on several invertebrates did not report any latitudinal adaptation of metabolic rate (e.g. Fox and Wingfield, 1936-39) and these were criticized due to the fact that animals of equal size were not used in the experiments (Thorson, 1952; Berg, 1953). Since this time the problem of differential acclimation ability has largely been resolved as "some do, some don't", and the validity of latitudinal adaptation has switched arenas to a question of experimental technique (see Introduction). But the problem of size is not easily solved.

In the present study, an attempt was made to iron out the difficulties imposed by variations in mussel, and environmental characteristics, that is, hold all constant except for latitude. Mussels of approximately equal size were used in the oxygen consumption studies at each station. Too much labour would be involved for one person to get a good sample of oxygen consumption rates over a large size range of mussels at each station; and local populations only yielded certain size ranges of mussels. In fact, populations did not always yield mussels of identical size and those from the southern stations had, on average, smaller shell length and were younger than those from the northern stations, despite my efforts to the contrary. True to established metabolic rate/size theory (see Introduction), the smaller mussels from the south consumed oxygen at a greater rate per unit weight than the larger mussels from the north, that is, the size of the southern mussels may account for some of the difference in metabolic rate.

To adjust the Q_{O_2} lines (Figure 51) for the effect of size on metabolic rate an appropriate criterion of size must be found. This is

not a straightforward matter. Tissue weight is the traditional parameter used in oxygen consumption studies with Mytilus edulis. Metabolic rate/size theory implies that (tissue) weight ($m = kw^n$), and surface area of the gill epithelia and other surfaces related to metabolism, are the most appropriate size indices. But tissue weight is a poor index of size in the case of the Atlantic North American Mytilus used in this study. Due to the storage function of the mantle, the mussel's tissue weights vary enormously over short periods of time. The variations between the stations could be expected to even out over a year, but the data obtained show no correlation between oxygen consumption and tissue weight for the stations over a year's readings ($r = 0.33$). In fact, at all stations, particularly Boothbay, Sandy Hook and Lewes, mussels have similar meat weights but retain their latitudinal positions in the plot of meat weight on oxygen consumption. This is indicative of the lack of thermal acclimation shown in Figure 51.

Other parameters of mussel size were considered, and these showed better correlation with oxygen consumption than did tissue weight. These were shell length ($r = 0.88$), total weight ($r = 0.87$), shell weight ($r = 0.91$) and inner shell volume ($r = 0.82$). These parameters are all products of long term metabolism and indicate that oxygen consumption rate is more a result of the history of the mussel than of its instantaneous fleshy countenance. In other words, the life history of the mussel, which itself is a product of metabolic rate, determines the metabolic rate to a large extent.

Thus, a mussel of a certain size (any parameter of size may be used in this negative sense) at one station is not metabolically equivalent to a mussel of the same size at another station. This is most clearly shown in the growth curves in Figure 65. Points on these curves may be found that are somewhat metabolically equivalent, but this is doubtful in the case of widely separated stations where the shape of the growth curves are quite different (e.g. with respect to L_∞). The criterion of size used to compare the oxygen consumption rates at the various stations should therefore be related to the position on the growth curve. This is nothing more than employing the concept of "metabolic age."

For comparative purposes, "metabolic age" may be defined as length or age at time i, as a fraction of final length or final age. In the present case, the metabolic age of oxygen consumption study mussels is most easily expressed as length/L_∞. Four values may be estimated accurately: Holyrood (0.6), St. Margaret's Bay (0.4), Sandy Hook (1) and Lewes (0.9). The northern mussels used in this study are shown to be metabolically younger than the southern, and this finding serves to readjust the Q_{O_2} lines in Figure 51 for the size discrepancy between stations.

However, metabolic L_∞ is probably determined in (at least) 2 different ways in mussels from northern and southern stations. At the northern stations L_∞ is probably defined by the balance of growth attainable during the growing season (summer), and katabolism and shell abrasion which occur during the season of no growth (winter). The relative effects of these two processes would vary with latitude (length of growing season), food availability, and other local factors. At southern stations, the metabolic L_∞ may be defined by the summer balance of anabolism and katabolism, reaching its extreme in the summer mortality of mussels too large to be supported by their environment (e.g. at Sandy Hook).

SUMMARY AND CONCLUSIONS.

Mytilus edulis is a widely ranging species, occupying a eurythermal temperate biotope. It exhibits a variety of metabolic responses to environmental changes. These responses range from the subcellular level to that of the mussel community, and appear to indicate a metabolic rate which is flexible over the geographic range and over the seasons of the year. This apparent lability may be the reason the mussel is so successful in changing, unstable, or ecotone environments, particularly the thermal ecotone of the post-Miocene temperate and subpolar waters.

On the other hand, there is good evidence, from laboratory studies mostly carried out in Europe, that M. edulis can acclimate several metabolic rate functions for changes in environmental factors - including temperature. At which level then, is this flexibility of metabolic rate function, which is exhibited by natural populations, brought into play? It was hypothesized that this may be the level of the basic respiratory exchange with the environment, and an experiment was made in which the oxygen consumption of Mytilus edulis was measured over a range of latitude (Newfoundland to Virginia) over all seasons of the year (at 2-monthly intervals). Oxygen consumption rate was also compared with other possible metabolic rate functions - mussel parameters which are known to vary under different environmental conditions: shell growth rate, tissue condition and, to some extent, gametogenic cycle. The following results were obtained:

1. At all stations examined, oxygen consumption rate varied over the year, directly with temperature. There was no apparent seasonal acclimation to temperature; rates were maximal in summer and minimal in winter. Summer suppression of oxygen consumption rate was observed at southern stations at above-optimum temperatures.

2. Over the range of latitude, oxygen consumption was also directly related to temperature. Southern (warmer) stations had the highest rates, northern (cooler) stations had the lowest.

3. Shell growth rates, over the short term (seasonal), followed oxygen consumption rates (temperature) to a large extent, except at

southern stations - where high summer temperatures had an inhibitory effect, and at midlatitude stations (Boothbay? and Woods Hole) where non-thermal factors (food) may have been involved.

4. Latitudinal differences in shell growth parameters were observed. Growth at southern stations was initially rapid, but tapered off to a small L_∞ in 1-2 years. Life span here was short. At northern stations, growth was slow, the tendency to L_∞ depended on local factors, and life span was long.

5. The cycle of condition was related to the gametogenic cycle. This may have been important in determining the metabolic rate of the mussel. The most marked effect of the biochemical/gametogenic cycle was in northern latitudes, where the major spawning occurred in autumn. After the autumn spawning there was insufficient time (temperature or resources) to regain condition before the onset of winter, and the mussels had to face winter with no reserves (glycogen or gametes) in the mantle. This may have been the cause, or may have been the effect of the low activity (oxygen consumption) during the winter months.

6. The results of the present study do not reveal the acclimation ability that was predicted by the European laboratory studies. Two possible grounds for difference make themselves apparent:

i) Field conditions, especially in Atlantic North America, are always varying, and there is no possibility of complete acclimation in field populations.

ii) The biochemical/gametogenic cycle in North American M. edulis is different from that of European M. edulis. In the former, the major spawning period is the autumn, while in the latter it is spring. Other differences also exist. These include temperature range and rate of change, food availability, and the interaction of temperature and food in time. These probably determine the nature of the biochemical/gametogenic cycle, and in turn, the rate of metabolism of the mussels at any given season.

This reveals an additional level of flexibility in M. edulis metabolism - not just a simple variety of responses to temperature, but an ability to undergo changes in metabolism according to resource levels, the temperature

related changes in oxygen consumption rate being adapted to the low energy waters of Atlantic North America during the winter. The problem of temperature-or resource-limitation of metabolism could be resolved by examination of the energy budget of the mussel of Atlantic North American M. edulis, (cf. the current research in European laboratories - see Introduction).

ACKNOWLEDGEMENTS

I would like to blame M.J. Dunbar for providing financial support, through a grant from the National Research Council of Canada, over the long duration of this study. The work would not have been completed without his optimistic encouragement. D.C. Maclellan is also to be blamed for this latter activity.

Innocent parties who aided in the practical execution of the research include the Crosbie family of Holyrood, J. Beckett of FRB, S. Apollonio of State of Maine Fisheries, the Buchanan family of Meriden, J. Pearce of Sandy Hook Sport Fisheries Marine Laboratory, H. Seymour of University of Delaware Bayside Laboratory, and M. Castagna of VIMS Wachapreaque. R.A. Buchanan of Marine Sciences Centre was largely responsible for navigation through the hazards of Atlantic North American coastal fieldwork.

The following institutions provided experimental sites and laboratory space: Fisheries Research Board of Canada (Dartmouth), St. Margaret's Bay; Huntsman Marine Laboratory, St. Andrews; State of Maine Fisheries, Boothbay Harbor; Woods Hole Oceanographic Institute, Woods Hole; Sandy Hook Sport Fisheries Laboratory, Sandy Hook; University of Delaware Bayside Laboratory, Lewes; Virginia Institute of Marine Sciences, Wachapreaque.

Help with computations, diagrams and bibliography was given by A.P. Freeland. The photographs were prepared by T. Graham. Typing was done by K. Peterson and H. Hewitt. The manuscript was read critically by M.J. Dunbar, and parts by C. M. Lalli. D. C. Maclellan proof read the final manuscript.

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Appendix Table 1. Results of oxygen consumption study. Ambient conditions and mean oxygen consumption of over 10 Mytilus edulis per experiment (1 experiment = 1 horizontal row). All stations, August 1971 to September 1972. (For graphical representation see Figures 1-46.)

STATION	DATE	AMBIENT CONDITIONS			MYTILUS O_2 CONS.	
		t°C.	sal.‰	O_2 ml./l.	ml./g./hr.	S.D.
Bellevue	1 Aug. 71	16.5	29.36	6.94	0.18	0.07
		17.7		7.17	0.10	0.02
		18.4		7.17	0.12	0.03
		18.0		7.17	0.12	0.02
		16.2		6.70	0.11	0.03
		16.6		6.23	0.10	0.01
		16.4		5.76	0.11	0.01
		16.1		5.41	0.08	0.01
	Mean	17.0			0.12	
Holyrood	6 Oct. 71	10.1	30.11	6.41	0.14	0.04
		10.2	28.62	6.29	0.19	0.15
		10.9	26.69	6.29	0.14	0.01
		10.5	28.20	6.16	0.17	0.01
		10.3	27.54	6.16	0.09	0.01
		10.5	28.82	6.29	0.07	0.01
	Mean	10.4			0.13	
	6 Dec. 71	1.5	23.73	5.83	0.05	0.03
		1.5	24.98	7.95	0.06	0.03
		1.5	12.48	7.53	0.10	0.03
		0.5	12.45	7.62	0.05	0.01
		1.0	12.45	8.42	0.00	0.00
	Mean	1.2			0.05	

Appendix Table 1 Continued.

STATION	DATE	AMBIENT CONDITIONS			MYTILUS O_2 CONS.	
		t°C.	sal.‰	O_2 ml./l.	ml./g./hr.	S.D.
Holyrood	8 Feb. 72	-0.2	6.28	10.68	0.00	0.00
(Cont.)		-0.1	6.28	10.29	0.00	0.00
	Mean	-0.2			0.00	
	8 Apr. 72	0.8	28.06	9.22	0.05	0.03
		-0.2	19.92	9.81	0.01	0.01
		-0.5	33.66	9.18	0.04	0.02
		-0.5	31.16	8.93	0.02	0.03
	Mean	-0.1			0.03	
	7 Jun. 72	6.2	30.47	7.43	0.10	0.03
		6.0	31.47	7.57	0.06	0.03
		6.0	31.74	7.81	0.06	0.02
		5.2	31.59	8.00	0.05	0.03
		11.5	15.45	7.53	0.00	0.00
	Mean	5.8			0.05	
	2 Aug. 72	13.0	32.81	6.68	0.10	0.07
		13.8	32.81	7.08	0.12	0.07
		14.0	32.81	7.03	0.13	0.07
	Mean	13.6			0.12	

Appendix Table 1 Continued.

STATION	DATE	AMBIENT CONDITIONS			MYTILUS O_2 CONS.	
		t°C.	sal.°/oo	O_2 ml./l.	ml./g./hr.	S.D.
St. Margaret's Bay	7 Aug. 71	17.6	25.43	7.29	0.28	0.11
		17.4		7.29	0.23	0.08
		17.1		7.29	0.23	0.08
		17.4		7.06	0.23	0.08
		17.3		6.94	0.21	0.05
		16.4		7.88	0.17	0.06
		14.4		8.23	0.15	0.05
		14.8			0.18	
	Mean	16.6			0.21	
	14 Oct. 71	14.1		6.16	0.35	0.09
		14.2		5.77	0.17	0.04
		13.9	29.54	5.52	0.17	0.06
		14.1		6.16	0.12	0.02
	Mean	14.1			0.20	
	Mean without first experiment				0.15	
	12 Dec. 71	5.9	30.47	6.96	0.07	0.01
		5.5	29.19	6.77	0.06	0.01
		5.9	29.19	6.87	0.05	0.01
		6.1	29.19	6.82	0.05	0.02
	Mean	5.9			0.06	
	Feb. 72	NO DATA				
	15 Apr. 72	1.5	21.86	8.79	0.04	0.02
	*	3.0	30.10	7.63	0.09	0.02
	*	3.5	30.19	7.63	0.09	0.02

(* Done in lab. at St. Andrews)

Appendix Table 1 Continued.

STATION	DATE	AMBIENT CONDITIONS			MYTILUS O_2 CONS.	
		t°C.	sal.°/oo	O_2 ml./l.	ml./g./hr.	S.D.
St. Margaret's Bay (Cont.)	12 Jun. 72	10.0	25.14	6.82	0.18	0.05
		11.0	28.20	6.91	0.17	0.05
		11.5	27.75	6.82	0.17	0.05
	Mean	10.8			0.17	
	10 Aug. 72	18.2	30.70	5.84	0.16	0.05
		18.5	31.71	5.45	0.15	0.04
		19.0	27.75	6.03	0.17	0.05
		18.4	24.11	6.03	0.12	0.05
	Mean	18.5			0.15	
St. Andrews	12 Aug. 71	DATA OMITTED				
	18 Oct. 71	DATA OMITTED				
	15 Dec. 71	6.6	32.55	5.74	0.06	0.01
		6.2	32.39	5.83	0.06	0.00
		6.2	32.39	5.83	0.04	0.00
		6.1	31.74	5.74	0.05	0.01
		6.1	31.74	5.74	0.05	0.02
	Mean	6.2			0.05	
	15 Feb. 72	5.0	32.22	7.62	0.04	0.01
		2.8	32.22	8.01	0.02	0.01
		2.7	32.61	8.01	0.03	0.02
		3.4	31.98	7.77	0.02	0.01
		3.3	31.98	7.96	0.03	0.01
		3.2	31.98	8.11	0.04	0.01
	Mean	3.4			0.03	

Appendix Table 1 Continued.

STATION	DATE	AMBIENT CONDITION			MYTILUS O_2 CONS.	
		t°C.	sal.‰	O_2 ml./l.	ml./g./hr.	S.D.
	19 Apr. 72	4.2	28.95	7.54	0.05	0.01
		4.4	28.95	7.63	0.04	0.02
		4.3	28.95	7.63	0.05	0.01
		4.0	28.95	7.63	0.06	0.01
		4.2	28.95	7.63	0.05	0.02
	Mean	4.2			0.05	
	19 June. 72	12.8	31.26	6.59	0.18	0.03
		13.0	26.74	6.49	0.15	0.04
		13.0	27.36	6.40	0.29	0.04
		12.9	26.69	6.40	0.16	0.05
		12.9	28.67	6.49	0.17	0.05
	Mean	12.9			0.16	
	16 Aug.72	15.2	33.10	6.08	0.15	0.02
		15.4	31.79	6.03	0.15	0.02
		15.8	32.07	6.13	0.15	0.03
	Mean	15.5			0.15	
Boothbay	17 Aug. 71	15.4	26.51	7.64	0.26	0.06
		15.2		7.76	0.22	0.07
		15.5		7.64	0.21	0.06
		15.7		7.41	0.21	0.06
		15.6		7.17	0.19	0.04
	Mean	15.5			0.22	

Appendix Table 1 Continued.

STATION	DATE	AMBIENT CONDITION			MYTILUS O_2 CONS.	
		t°C.	Sal.‰	O_2 ml./l.	ml./g./hr.	S.D.
Boothbay (Cont.)	21 Oct. 71	12.0	32.00	5.39	0.21	0.05
		12.5		5.77	0.23	0.09
		12.5		5.77	0.18	0.09
	Mean	12.3			0.21	
	20 Dec. 71	5.6	31.10	7.06	0.10	0.02
		5.6	31.10	7.06	0.09	0.03
		6.0	31.10	7.01	0.10	0.03
		8.4	33.80	6.54	0.11	0.03
		8.7	33.54	6.59	0.09	0.04
	Mean	6.9			0.10	
	19 Feb. 72	2.3	31.89	7.72	0.06	0.03
		2.5	30.62	7.86	0.06	0.03
		2.7	31.36	7.67	0.05	
		2.7	31.86	7.72	0.06	0.02
		2.5	31.86	7.62	0.05	0.02
		2.0	31.36	8.11	0.05	
	Mean	2.5			0.06	
	23 Apr. 72	4.0	31.47	8.00	0.14	0.04
		4.0	30.19	8.14	0.13	0.04
		3.9	30.19	8.19	0.12	0.03
		4.0	30.19	8.19	0.13	0.03
	Mean	4.0			0.13	

Appendix Table 1 Continued.

STATION	DATE	AMBIENT CONDITIONS			MYTILUS O_2 CONS.	
		t°C.	sal.‰	O_2 ml./l.	ml./g./hr.	S.D.
Boothbay	20 June. 72	12.8	29.96	6.59	0.19	0.06
(Cont.)		12.8	29.96	6.59	0.17	0.06
		14.0	29.96	6.87	0.21	0.06
	Mean	13.2			0.19	
	20 Aug. 72	14.0	32.83	6.87	0.17	0.02
		14.4	32.83	6.97	0.14	0.01
		15.0	33.10	6.61	0.15	0.04
	Mean	14.5			0.15	
Sandy Hook	1 Sept. 71	22.1	30.72	2.71	0.12	0.06
		23.8		5.43	0.20	0.07
		23.3		8.01	0.27	0.10
		22.5		6.38	0.19	0.10
		20.7		4.75	0.12	0.07
	Mean	22.5			0.18	
	Mean without first and fifth experiments 23.2, 0.22.					
	2 Nov. 71	19.0	24.43	4.41	0.35	0.10
		18.0	24.11	4.28	0.36	0.17
		18.0	22.79	4.28	0.32	0.03
		17.5	24.11	4.41	0.28	0.09
	Mean	18.1			0.33	
	27 Dec. 71	6.0	24.75	7.34	0.13	0.02
		5.5	27.79	7.24	0.13	0.03
		8.0	27.30	6.59	0.30	0.04
	Mean	6.5			0.19	

Appendix Table 1 Continued.

STATION	DATA	AMBIENT CONDITIONS			MYTILUS O_2 CONS.	
		t°C.	sal.‰	O_2 ml./l.	ml./g./hr.	S.D.
Sandy Hook (Cont.)	1 Mar. 72	3.0	22.55	8.93	0.07	0.03
		4.5	23.37	8.84	0.11	0.04
		5.5	23.48	9.42	0.12	0.05
	Mean	4.3			0.10	
	4 May 72	13.6	23.03	8.65	0.20	0.07
		13.6	23.03	9.33	0.23	0.10
		14.3	21.73	9.10	0.24	0.07
	Mean	13.8			0.22	
	29 Jun. 72	19.0	16.50	4.63	0.17	0.05
		19.0	17.20	4.81	0.23	0.08
		19.0	15.25	5.18	0.23	0.05
	Mean	19.0			0.22	
	30 Aug. 72	24.5	27.25	5.70	0.26	0.10
Lewes	6 Sept. 71	22.9	29.76	4.59	0.27	0.06
		23.8	30.15	5.25	0.29	0.06
		25.4	25.21	4.07	0.25	0.10
		23.0	28.44	5.78	0.33	0.08
		22.5	30.72	4.99	0.29	0.06
		23.2	25.78	3.68	0.21	0.04
	Mean	23.5			0.27	

Appendix Table 1 Continued.

STATION	DATA	AMBIENT CONDITIONS			MYTILUS O_2 CONS.	
		t°C.	sal.‰	O_2 ml./l.	ml./g./hr.	S.D.
Lewes	5 Nov. 71	* 16.5	29.76	5.19	0.38	0.06
(Cont.)		15.5	28.26	5.19	0.28	0.08
		* 17.0	29.76	5.06	0.24	0.07
		* 16.5	29.06	5.26	0.34	0.12
	Mean	16.4			0.31	
* Silt deposition in respirometer bottles prior to experiment.						
	30 Dec. 71	6.8	25.52	7.34	0.12	0.02
		7.2	27.45	7.24	0.14	0.03
		9.2	27.79	7.20	0.17	0.02
		8.2	26.95	7.06	0.16	0.02
		8.0	23.78	6.96	0.14	0.02
	Mean	7.9			0.15	
	5 Mar. 72	5.0	26.53	7.38	0.12	0.03
		5.9	26.65	7.38	0.10	0.03
		6.0	26.65	7.38	0.11	0.03
	Mean	5.6			0.11	
	6 May 72	17.4	14.13	4.55	0.00	0.00
		14.8	24.59	7.28	0.22	0.05
		14.8	28.50	7.15	0.22	0.04
		15.0	28.50	7.15	0.25	0.06
		15.6	16.37	4.87	0.00	0.00
Mean at suitable salinity.		14.9			0.23	

Appendix Table 1 Continued.

STATION	DATE	AMBIENT CONDITIONS			MYTILUS O_2 CONS.	
		t°C.	sal.°/oo	O_2 ml./l.	ml./g./hr.	S.D.
Lewes	1 Jul. 72	23.2	23.83	5.74	0.33	0.09
(Cont.)		23.0	23.83	6.48	0.38	0.09
	Mean	23.1			0.36	
	3 Sept. 72	23.0	28.44	4.22	0.18	0.06
		23.2	23.12	4.17	0.19	0.06
		22.0	29.40	4.68	0.22	0.06
	Mean	22.7			0.20	
Wachapreague	9 Sept. 71	26.3	32.97	3.81	0.32	0.17
		25.6	31.65	4.73	0.28	0.08
		25.5	30.94	4.86	0.31	0.13
	Mean	25.8			0.31	
	9 Nov. 71	12.0		6.10	0.26	0.06
	4 Jan. 72	9.5	29.27	6.49	0.23	0.09
		9.2	29.07	6.63	0.16	0.06
		9.0	30.35	6.68	0.19	0.06
		11.2	31.40	6.30	0.18	0.06
		9.2	30.35	6.40	0.34	0.05
		9.1	28.42	6.40	0.23	0.06
	Mean	9.5			0.19	
	7 Mar. 72	9.2	24.56	6.70	0.15	0.04
		9.8	31.85	6.51	0.15	0.07
		9.8	30.55	6.51	0.15	0.03
	Mean	9.6			0.15	

Appendix Table 1 Continued.

STATION	DATA	AMBIENT CONDITIONS			MYTILUS O_2 CONS.	
		$t^oC.$	sal.$^o/_{oo}$	O_2 ml./l.	ml./g./hr.	S.D.
Wachapreague (Cont.)	10 May 72	13.6	32.14	5.40	0.19	0.04
		15.4	29.79	5.16	0.23	0.03
		15.0	29.79	4.76	0.19	0.03
		16.0	27.47	5.25	0.21	0.03
		17.0	24.50	5.11	0.19	0.04
		17.0	31.07	5.50	0.25	0.02
	Mean	15.7			0.21	
	6 Jul. 72	20.7	31.07	3.38	0.20	0.03
		21.1	29.04	3.42	0.19	0.03
		21.6	30.10	4.16	0.28	0.04
		23.0	31.79	4.72	0.31	0.04
		21.6	31.43	3.70	0.20	0.02
		22.6	29.76	3.75	0.21	0.03
	Mean	21.8			0.23	
	8 Sept. 72	22.1	30.72	3.81	0.22	0.03
		22.2	31.43	4.12	0.25	0.04
		24.5	31.16	4.78	0.30	0.04
		24.0	30.86	4.83	0.27	0.04
	Mean	23.2			0.26	

Appendix Table 2. Growth study data, 10 October 1971 to 14 October 1972. Holyrood.

Tag No.	Lengths (cm.)						
	10 Oct.	6 Dec.	31 Jan.	7 Apr.	7 Jun.	2 Aug.	14 Oct.
0	2.48	2.48	2.54	2.56	2.76	3.04	3.73
2	4.13	4.14					
4	5.55	5.55					
6	3.90	3.87	3.86	3.86	4.04	4.42	
11	3.81	3.80	3.82	3.81	3.90	4.00	4.92
12	1.42	1.42	1.43				
16	1.80		1.84				
18	3.07	3.18	3.25	3.25	3.41	3.62	4.19
21	2.79	2.81	2.79	2.82	2.83	3.06	3.30
25	2.30	2.32	2.32	2.32			
28	4.97	4.95	4.95	4.88	5.03	5.33	5.57
30	5.39	5.45					
31	2.32	2.37					
32	1.82	1.87	1.90	1.91	2.22	2.40	2.78
33	1.70	1.70	1.70	1.70	1.74	1.78	
34	1.71	1.71		1.74	1.97	2.17	2.52
35	6.73	6.75	6.73				
36	1.52	1.53					
37	2.08	2.09	2.10				
38	1.42	1.45					
39	4.19	4.22	4.25		4.40	4.47	4.64
40	5.60	5.62					
42	2.39	2.42					
43	1.62	1.82					
44	2.53	2.52	2.54	2.56	2.70	2.85	3.16
46	3.52	3.53	3.53	3.55	3.75	3.83	3.99
47	5.16	5.11					
49	4.17	4.19	4.19	4.20	4.28	4.52	5.22
50	4.34		4.32d				

Appendix Table 2 Continued.

Tag No.	Lengths (cm.)						
	10 Oct.	6 Dec.	31 Jan.	7 Apr.	7 Jun.	2 Aug.	14 Oct.
52	4.66	4.67					
53	2.18	2.21	2.26	2.29	2.45	2.82d	
56	5.46	5.51	5.50	5.47	5.54	5.76	6.26
58	4.18	4.18	4.20	4.16	4.27	4.39	4.94
59	2.50	2.50	2.49	2.49	2.75	2.83	
60	2.50	2.52					
61	2.87	2.90					
62	5.82	5.88	5.87	5.80	5.76	5.92	5.90
63	1.94	1.94	1.94	1.98	2.24	2.82	3.35
65	1.36	1.39	1.42	1.41	1.58	2.00	2.64
68	5.65	5.65	5.62	5.57	5.62	5.70	
71	1.94	1.97	2.01				
72	7.29	7.42					
74	2.97	3.01	3.03	3.06	3.19	3.38	3.64
77	1.21	1.22	1.23				
79	1.74	1.83					
80	1.88	1.88	1.89				
82	5.52	5.56					
83	2.11	2.16					
86	3.02	3.02	3.02	3.02	3.17	3.49	
87	2.17	2.20	2.22	2.27	2.43	2.63	3.37
88	4.00	3.97					
92	2.25(?)	2.80	2.82	2.72	2.94	3.12	3.54
93	5.02	5.03	5.04	5.03	5.02	5.07	5.13
97	2.56	2.57	2.58	2.59	2.57	2.90	3.40
98	6.89	7.03	7.00	6.92	7.06	7.02	7.18

Appendix Table 3. Holyrood. Additional growth data, not worked up in the present manuscript.

Tab No.	Lengths (cm.)				
	1 Feb.	7 Apr.	7 Jun.	2 Aug.	14 Oct.
900	2.90	2.90	2.92	3.05	3.43
904	4.16	4.17	4.39	4.41	4.63
906	7.31	7.43	7.44	7.44	7.46
908	2.51	2.50	2.65	2.93	3.24
912	3.97	3.96	3.95	4.28	4.72
928	1.84	1.83	2.08	2.41d	
930	5.52	5.54	5.60	6.06	6.92
939	3.71	3.70	3.73	3.76	3.80
943	1.67	1.69	1.88	2.26	3.60
953	5.60	5.63	5.62	5.78	6.10
956	2.99	2.99	3.20	3.35	3.80
960	1.63	1.74			
967	6.76	6.76	6.75		
968	5.60	5.59	5.66	5.73	6.00
975	5.42	5.45	5.49	5.65	5.92
977	4.68	4.68	4.74	4.97	
978	1.94	1.94	2.18		
980	5.12	5.16	5.21	5.20	5.31
986	2.89	2.89	3.01		
987	4.05	4.01	4.17	4.31	4.80
990	2.42	2.45	2.68	3.22	3.62

Appendix Table 4. Holyrood. Estimation of short term growth. From the Ford-Walford plot the following size ranges have been estimated as belonging to each year class.

Year n +	Range in Length (cm.)
1	0.07 - 1.99
2	2.00 - 3.09
3	3.10 - 3.99
4	4.00 - 4.64
5	4.65 - 5.23
6	5.25 - 5.69
7	5.70 - 6.09
8	6.10 - 6.39
9	6.40 - 6.69
10	6.70 - 6.89

Appendix Table 5. Holyrood. Estimation of short term growth continued. For each year class (see Appendix Table 4) short term growth is determined as follows for the year October 1971 to October 1972.

Year n+ (No.)	Length (cm.)						
	10 Oct.	6 Dec.	31 Jan.	7 Apr.	7 Jun.	2 Aug.	14 Oct.
1 (4)	1.70	1.72	1.74	1.76	2.00	2.34	2.82
2 (8)	2.60	2.69	2.72	2.74	2.85	3.07	3.54
3 (2)	3.66	3.66	3.67	3.68	3.81	3.91	4.45
4 (3)	4.18	4.19	4.21	4.20	4.31	4.46	4.93
5 (2)	4.99	4.99	4.99	4.95	5.02	5.20	5.35
6 (1)	5.46	5.51	5.50	5.47	5.54	5.76	6.26
7 (1)	5.82	5.88	5.87	5.80	5.76	5.92	5.90
8-9 (0)							
10 (1)	6.89	7.03	7.00	6.92	7.06	7.02	7.18

Appendix Table 6. St. Margaret's Bay. Growth study data, 9 August 1971 to 11 August 1972.

Tag No.	Lengths (cm.)						
	9 Aug.	14 Oct.	12 Dec.	12 Feb.	15 Apr.	12 Jun.	11 Aug.
800	2.62	2.64	2.96		2.98	3.01	3.10
801	4.36	4.46	4.56		4.77		
803	2.66	3.27	3.88		3.92d		
805	2.90	2.97	3.39		3.53	3.64g	3.70d
806		2.37	2.53		2.55d		
808	9.31	9.29	9.33		9.35	9.41	9.45
811	3.66	3.92	4.56		5.07		
812	1.17	1.25					
813	8.51	8.59	8.70		8.82	8.86	8.86
814	4.74	4.76	4.97		4.92	4.88	4.99
815	4.66	4.81	4.86		4.88		
816	6.53	6.70					
817	4.53	5.21	5.67		5.97	6.07	5.85
821	6.33	6.43	6.79		6.76	6.92	6.94
822	3.84	3.82	3.87		3.90d		
823	3.53	4.06	4.43		4.62	4.79g	4.88
824	6.77	6.99	7.15		7.22	7.28	7.35
825	6.37	6.42	6.66		6.77	6.62	6.74
826	1.66	1.94					
827	6.10	6.84	7.14		7.28	7.47	
831	3.99	4.05	4.10		4.18		4.14d
832	5.67	5.78	5.80		5.89		
834	3.65	3.65					
836	5.51	5.58	5.58		5.58	5.55	5.65
837	5.27	5.86	6.31		6.25	6.24	6.24d
838	5.12	5.20	5.63		5.79		
840	5.36	5.57	5.78		6.08		
841	8.21	8.25	8.23		8.27		
843	3.24	3.57	4.00		4.31		
845	5.50	5.66	5.73			6.08	6.08

Appendix Table 6 Continued.

Tag No.	Lengths (cm.)						
	9 Aug.	14 Oct.	12 Dec.	12 Feb.	15 Apr.	12 Jun.	11 Aug.
848	1.53	1.52	1.57		1.53d		
849	4.00	4.28	4.91		5.08	5.17	
850	2.93	3.59	3.75		3.90	3.96	3.99
855	8.25	8.27	8.26		8.31		
853	5.87	6.02	6.47		6.53	6.65	6.65
855	5.68	5.81	6.14		6.43		
857	6.19	6.79	6.89		6.86	6.95	6.98
858	2.64	3.15	3.22		3.28	3.30	3.29
859	3.83	3.96	4.19		4.22d		
860	10.21	10.73	10.69		10.16d		
861	6.09	6.12	6.06		6.16	6.15	6.05
862	7.78	7.90	7.93		7.92	7.93	7.99
863	8.65	8.64	8.67		8.74	8.82	8.74
865	3.64	4.16	4.70		4.64	4.67	
866	2.58		3.55		3.59		
867	5.31	5.55	5.64		5.68	5.81	
869	4.87	4.90					
870	1.52	1.61					
871	6.61	6.74					
873	2.25	2.33	2.35		2.35d		
874	5.86	5.90					
875	1.09	1.33					
877	2.34	2.41	2.42		2.44d		
878	6.13	6.35	6.53		6.53	6.60	6.65
880	3.31	3.37	3.55		3.75	4.03	4.24
882	4.15	4.89	5.48		5.75	5.86	5.92
883	1.83	2.40	2.64		2.67		
885	3.23	3.23	3.62		3.65	3.70	3.69
886	7.55	7.69	7.86		7.87	7.85	7.88

Appendix Table 6 Continued.

Tag No.	Lengths (cm.)						
	9 Aug.	14 Oct.	12 Dec.	12 Feb.	15 Apr.	12 Jun.	11 Aug.
887	2.86	2.91	3.03		3.06		
888	6.64	6.80					
889	6.52	6.51	6.65		6.80	6.69	6.83
891	4.99	4.90					
893	2.86	2.92	2.90jd				
895	4.88	5.57					
896	7.10	7.20	7.22		7.33		
898	7.04	7.22	7.26		7.12	7.29	7.17
901	8.08	8.07	8.09		8.17		
904	1.75	1.91	1.96		1.99	2.06	2.07d
905	2.19	2.33	2.38		2.39	2.42g	2.51
906	2.93	2.97	3.06		3.12		3.10
907	4.44	4.63	5.13		5.22		
908	5.94	6.14	6.23		6.16		
909	2.53	2.88	3.02		3.15		
910	2.39	2.69	3.20		3.48	3.71	3.81d
912	8.12	8.13	8.14		8.13		
913	7.70	7.69	7.71		7.70		
915	2.97	3.22	3.75		3.88	4.25	
916	4.82	4.96	5.36		5.47		
917	2.92	3.01	3.54		3.62	3.85	3.93
918	7.83	8.00	8.12		8.09		
919	6.81	6.94	6.96		6.97	6.88	6.93
920	3.82	3.77	3.92		3.95	4.22	4.17d
921	9.35	9.49	9.70		9.68	9.71	9.66
923	1.74	2.10					
925	5.41	5.49			6.24	6.23	6.38
926	1.93	2.27	2.44		2.53	2.62	
927	2.64	2.63	2.64		2.65d		
928	4.34	4.37					

Appendix Table 6 Continued.

Tag No.	Lengths (cm.)						
	9 Aug.	14 Oct.	12 Dec.	12 Feb.	15 Apr.	12 Jun.	11 Aug.
929	4.18	4.57	4.83		4.93		
931	2.48	2.89					
932	3.32	3.66	3.66		3.69	4.03	4.10
933	4.73	4.82	5.24		5.56	5.65	5.64
934	1.77	2.02					
936	2.05	2.12	2.56		2.88	2.99	2.94d
938	6.64	6.88	7.40		7.53	7.61	7.67
941	5.33	5.46	5.85		5.69	5.83	5.88
942	6.90	7.15	7.20		7.22	7.23	7.18
943	4.50	4.66					
945	2.46	2.48	2.48		2.49		
946	4.08	4.51	5.07		5.17	5.55	5.51
950	2.61	2.86	2.85		2.92	3.12	3.15
951	2.65	2.81	2.86		2.89d		
952	7.70		5.92				
956	5.85	6.38	6.69		6.71	6.79g	6.59
957	6.89	7.08	7.10		7.05	7.10	7.18
959	5.90	6.22	6.23				
960	2.33	2.55					
961	3.13	3.66	3.75		3.84	3.91	3.97
962	3.75	3.77	3.79		3.78	3.82	
965	4.30	4.36	4.45		4.37	4.43	
966	6.96	7.20	7.44		7.62	3.13	
968	4.42	4.40	4.49		4.89		
970	7.43	7.50	7.66		7.73		
971	4.79	5.17					
972	4.15	4.24	4.77		4.90	5.09	
973	2.14	2.23	2.82		2.91		
974	5.55	5.70	5.65		5.60		
976	6.83	7.02	7.19		7.26	7.45	

Appendix Table 6 Continued.

Tag No.	Lengths (cm.)						
	9 Aug.	14 Oct.	12 Dec.	12 Feb.	15 Apr.	12 Jun.	11 Aug.
977	4.06	4.10	4.40?		4.30	4.61	4.68
980	2.33	3.41	4.23		4.34	4.55	
982	8.02	8.12	8.27		8.23	8.25	8.32
984	9.25	9.25	9.24		9.26		
987	7.48	7.50					
989	2.84	3.23	3.38		3.40	3.76	
990	8.48	8.43	8.60		8.71		
991	2.86	3.32	3.41		3.47	3.76	3.78
992	3.58	3.62	3.63		3.59	3.57	3.64
994	4.13	4.35	4.82		4.96	5.25	5.54
996	6.10	6.18	6.23		6.25		
998	8.97	9.02	9.10		9.21	9.25	9.25
999	3.83	4.35	4.94		5.10	5.24	5.27

Appendix Table 7. St. Margaret's Bay. Estimation of short term growth. From the Ford-Walford plot the following size ranges have been estimated as belonging to each year class.

Year n +	Range in Length (cm.)
1	0.57 - 1.59
2	1.60 - 2.52
3	2.53 - 3.74
4	3.75 - 4.24
5	4.25 - 4.84
6	4.85 - 5.46
7	5.47 - 6.04
8	6.05 - 6.59
9	6.60 - 7.09
10	7.10 - 7.49
11	7.50 - 7.89
12	7.90 - 8.25
13	8.26 - 8.64
14	8.65 - 8.87
15	8.88 - 9.22
16	9.23 - 9.39
17-20	n/a
21	10.20 - 11.42

Appendix Table 8. St. Margaret's Bay. Estimation of short term growth, continued. For each year class (see Appendix Table 7) short term growth is determined as follows for the year August 1971 to August 1972.

Year n+ (No.)	Length (cm.)						
	9 Aug.	14 Oct.	12 Dec.	12 Feb.	15 Apr.	12 Jun.	11 Aug.
1 (0)							
2 (4)	2.09	2.26	2.52		2.68	2.79	2.83
3 (14)	3.02	3.29	3.48		3.56	3.69	3.75
4 (7)	4.00	4.28	4.67		4.77	4.98	5.03
5 (3)	4.66	4.93	5.32		5.48	5.53	5.49
6 (3)	5.33	5.60	6.02		6.06	6.10	6.16
7 (4)	5.67	5.91	6.11		6.14	6.26	6.24
8 (6)	6.27	6.43	6.59		6.64	6.65	6.69
9 (6)	6.84	7.04	7.17		7.18	7.23	7.24
10 (0)							
11 (2)	7.66	7.79	7.89		7.89	7.89	7.93
12 (1)	8.02	8.12	8.27		8.23	8.25	8.32
13 (1)	8.51	8.59	8.70		8.82	8.86	8.86

Appendix Table 8 Continued.

Year n+ (No.)	Length (cm.)						
	9 Aug.	14 Oct.	12 Dec.	12 Feb.	15 Apr.	12 Jun.	11 Aug.
14 (1)	8.65	8.64	8.67		8.74	8.82	8.74
15 (1)	8.97	9.02	9.10		9.21	9.25	9.25
16 (2)	9.33	9.39	9.51		9.51	9.56	9.55
17-20 (0)							
21 (1)	10.21	10.73	10.69		10.61d		

Appendix Table 9. Boothbay Harbor. Growth study data, 17 August 1971 to 19 December 1971.

Tag No.	Lengths (cm.)		
	17 Aug.	21 Oct.	19 Dec.
400	6.60	6.53	
403	4.67	4.30	4.72
411	3.85	4.08	4.26jd
429	4.23	4.33	4.75
434	4.11	4.13	4.14
435	7.08	7.08	7.15
438	4.00	4.00	3.95
443	6.10	6.34	
445	2.90	2.92	
458	3.38	3.32	4.10
462	4.07	4.16	
464	4.04	4.14	
466	4.48	4.49	
470	4.88	5.03	5.58
473	4.30	4.50	5.15
474	4.02	4.06	
481	6.18	6.32	6.63
482	4.28	4.51	4.62
489	4.77	4.94	5.34
492	3.81	3.94	
498	6.33	6.50	
501	4.23	4.30	4.23
502	3.95	4.06	
515	7.16	7.35	7.11
517	4.77	4.78	5.28
521	4.55	4.66	4.95
523	4.84	4.91	5.07
526	3.58	3.77	
528	4.16	4.27	4.56
530	3.43	3.76	4.30jd

Appendix Table 9 Continued.

Tag No.	Lengths (cm.)		
	17 Aug.	21 Oct.	19 Dec.
531	6.94	7.07	7.15
532	4.92	5.00	5.34
535	8.05	8.18	8.08
536	4.10	4.21	4.50
544	5.35	5.44	
545	3.92	3.91	4.13
549	5.59	5.58	5.99
554	6.80	6.84	7.09
559	7.80	7.78	7.87
561	3.95	4.04	
565	2.86	2.83	
566	4.62	4.77	4.98
575	3.25	3.20	
581	5.45	5.50	5.47
584	4.14	4.14	4.35
586	5.00	5.08	5.37
595	4.34	4.43	4.94
596	5.61	5.58	5.76
597	4.87	4.89	4.90
607	3.42	3.42	
632	7.27	7.43	7.76
646	2.92	2.92	3.44
651	2.11	2.09	
656	6.98	7.04	7.23
670	4.65	4.82	4.96
677	3.44	3.66	3.90
726	7.81	7.87	7.89
732	3.72	3.88	4.25
733	3.90	4.10	
735	6.98	7.02	

Appendix Table 9 Continued.

Tag No.	Lengths (cm.)		
	17 Aug.	21 Oct.	19 Dec.
737	4.68	4.88	5.98
757	7.01	7.02	7.07
758	5.57	5.56	5.56
789	4.45	4.64	
793	4.92	4.63	4.92
$\bar{X}$	5.11	5.18	5.44
Mean increment		0.07	0.26

Appendix Table 10. Woods Hole. Growth study data, 24 August 1971 to 25 August 1972.

Tag	Lengths (cm.)						
No.	28 Aug.	27 Oct.	27 Dec.	22 Feb.	26 Apr.	24 Jun.	25 Aug.
005	6.52	6.55					
123	4.68	4.70					
124	5.32	5.42					
126	4.79	4.83					
134	5.80	5.88		6.20	6.42		
137	5.37	4.92?					
138	4.49	4.53		4.89	5.22	6.04	6.32
143	5.52	5.55		5.95	6.10		
144	5.73	5.74		6.12	6.38	6.37	6.43
145	5.73	5.77					
150	6.63	6.68		6.71	6.90	7.16	7.19
154	6.98	7.00		7.09	7.23	7.32	7.49
155	4.77	4.80		5.03	5.03	5.54	5.72
158	4.75	4.73		4.88	5.20	5.42	5.48
178	5.55	5.67		6.08	6.45	6.57	6.55
185	6.01	6.00		6.26	6.16	6.22	6.35
186	6.06	6.09		6.37	6.56	6.73	6.75
193	5.02	5.04		5.30	5.52	6.01	6.17
195	6.19	6.43		7.20	7.33	7.80	7.90
199	4.60	4.61					

Appendix Table 11. Woods Hole. Estimation of short term growth. From the Ford-Walford plot the following size ranges have been estimated as belonging to each year class.

Year	Range in length (cm.)
1	1.60 - 3.40
2	3.41 - 4.94
3	4.95 - 6.05
4	6.06 - 6.85
5	6.86 - 7.43
6	7.44 - 7.84
7	7.85 - 8.14
8	8.15 - 8.36
9	8.37 - 8.51

Appendix Table 12. Woods Hole. Estimation of short term growth, continued. For each year class (see Appendix Table 11) short term growth is determined as follows for the year August 1971 to August 1972.

Year	Length (cm.)						
(No.)	28 Aug.	27 Oct.	27 Dec.	22 Feb.	26 Apr.	24 Jun.	25 Aug.
1 (0)							
2 (3)	4.67	4.68		4.93	5.15	5.66	5.84
3 (4)	5.57	5.61		5.94	6.12	6.29	6.37
4 (3)	6.29	6.40		6.76	6.93	7.23	7.28
5 (1)	6.98	7.00		7.09	7.23	7.32	7.49

Appendix Table 13. Sandy Hook. Growth study data, 31 August 1971 to 30 August 1972.

Tag	Lengths (cm.)						
No.	31 Aug.	2 Nov.	29 Dec.	3 Mar.	4 May	30 Jun.	30 Aug.
214	3.30	3.55	3.60	3.68	3.92		
215	4.66	4.75	4.80	4.84	4.84		
221	3.91	3.98	4.23	4.31	4.60		
222	1.62	2.14	3.43				
223	3.29	3.65	4.05	4.18	4.25		
224	4.17	4.38					
237	3.95	4.21	4.62	4.70	5.03		
245	4.13	4.25	4.33	4.53	4.64		
246	1.81	3.18	3.32	3.46	3.90		
248	4.47	4.61	4.62	4.76	4.80		
261	3.96	4.03	4.10	4.24	4.41	4.44	4.30*
265	1.30	1.47					
278	4.24	4.40	4.81	5.00	5.26		
283	3.21	3.65	4.18	4.36	4.42	4.67	
290	4.12	4.25	4.64	4.80	5.28		
294	4.91	5.16	5.42	5.64	5.55		
297	3.27	3.40	3.60	3.56	3.72		
303	3.00	3.02	3.17	3.35	3.78		
304	1.79	2.52	3.19	3.25	3.34jd		
306	3.98	4.42	4.90	4.96	5.34		
316	3.92	4.00d					
326	3.45	3.95					
328	1.20	2.25	3.24	3.34	3.62		
343	3.08	3.78	4.06	4.33	4.30	4.33	
353	4.09	4.29	4.64				
355	3.58	4.03	4.59	4.67		4.94	

*Saggy shell!

Appendix Table 13 Continued.

Tag No.	Lengths (cm.)						
	31 Aug.	2 Nov.	29 Dec.	3 Mar.	4 May	30 Jun.	30 Aug.
356	3.28	3.85	3.95	3.99			
362	3.60	3.65	3.64	3.60			
369	3.17	3.83	4.32	4.35	4.66	4.90	
375	4.31	4.43	4.45	4.43	4.70		
381	3.06	3.14	3.13	3.11	3.10		
384	1.42	2.76	3.21				
395	5.17	5.25	5.32	5.29	5.37	5.47	
399	4.28	4.66	4.93	5.06	5.36		
$\bar{X}$	3.69	4.01	4.27	4.37	4.55		
Mean increment (/2 months)		0.31	0.26	0.10	0.18		
n = 24							

Sandy Hook. Additional data on growth. From population samples taken on 30 August 1971 three spatfalls are indicated, the size ranges of which are:

(1) 1.5 - 2.0 cm.
(2) 3.0 - 4.5 cm.
(3) 4.5 - 5.5 cm.

Observed spatfalls over the year August 1971 to August 1972 had the following growth rates:

31 Aug.	
	spatfall
2 Nov.	1.5 - 2.0 cm.
29 Dec.	2.5 cm. (rocks)
	3.5 - 4.0 cm. (wharfpiles)
3 Mar.	
4 May	
	spatfall
30 Jun.	
30 Aug.	2.0 - 3.0 cm. (rocks)

For graphical representation see Figure 61.

Appendix Table 14. Sandy Hook. Division of growth study into year classes, on the basis of population sample data and growth study data for up to 10 months.

Spatfall	Length on 31 August 1971
(i) summer of 1971	less than 2.0 cm.
(ii) summer of 1970	3.0 - 4.5 cm.
(iii) summer of 1969	4.5 - 5.5 cm.

Appendix Table 15. Mean lengths of growth study mussels in these three year classes, August 1971 to June 1972.

Year (n)	Lengths (cm.)					
	31 Aug.	2 Nov.	29 Dec.	3 Mar.	4 May	30 Jun.
1 (3)	1.66	2.65	3.25	3.35	3.62	
2 (5) (21)	3.66	3.94	4.18	4.28	4.53	4.65
3 (3)	4.91	5.05	5.18	5.25	5.25	
X (11)	3.41	3.88	4.20	4.29	4.47	
Mean increment (/2 months)		0.47	0.32	0.09	0.17	